

Lincoln University Digital Thesis

Copyright Statement

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand).

This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- you will use the copy only for the purposes of research or private study
- you will recognise the author's right to be identified as the author of the thesis and due acknowledgement will be made to the author where appropriate
- you will obtain the author's permission before publishing any material from the thesis.

**Climatic Limitation of Alien
Weeds in New Zealand:
Enhancing Species Distribution
Models with Field Data**

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Doctor of Philosophy

at
Lincoln University
by
Jennifer L. Pannell

Lincoln University
2016

“...think of a blossom in a painting rendered photographic in detail and as beautiful as life. In our minds the macroscopic entity has truth because it matches real flowers sprung from the soil. From a distance we might easily confuse the image with the real thing. But the algorithms that created it are radically different. Its microscopic elements are flakes of paint instead of chromosomes and cells. Its developmental pathways exist in the brain of the artist, not in prescription by DNA of the unfolding of tissues. How do theoreticians know that their computer simulations are not just the paintings of flowers?”

– Edward O. Wilson, “Consilience”

Abstract

Correlative species distribution models (SDMs) are often used to quantify the potential ranges of alien species. Despite rising popularity, there is ongoing debate surrounding whether SDMs can predict non-equilibrium species, how well they capture underlying biological mechanisms versus drawing spurious correlations, and how realistic the ensuing projections are. There have been numerous calls to integrate SDMs with real-world performance data to validate and improve projections, but such studies remain rare. In this thesis, I investigated the potential distributions of three alien plant species, *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*, in their introduced ranges of New Zealand. I used a combination of SDMs, observational and experimental approaches. I firstly developed correlative SDMs for the three species. Secondly, I quantified the species' climatic limits in the study region of Banks Peninsula, New Zealand, using field transplant experiments and surveys. Finally, I combined the aforementioned plant performance data into a single climate-driven population model, which I used to test and enhance the original SDM projections. I found that the New Zealand distributions of all three species are climatically novel relative to their distributions elsewhere, and constitute shifts in their realized niches. Although SDMs indicated that much of New Zealand is climatically suitable, transplant experiments on Banks Peninsula confirmed that the climate of Banks Peninsula is limiting. In all three species, low growth rates, low germination, and high mortality at high elevations will limit spread. In contrast, surveys found little evidence of direct climatic limitation to fecundity within the species' current distributions on Banks Peninsula. The final step of validating SDM projections against the population model revealed that the SDM performed better than k-folds cross-validation against occurrence data would suggest. However, the SDMs over-predicted suitable climate in the region. I therefore adjusted SDM thresholds of modelled suitability to optimise parsimony with field data and provide more robust projections for Banks Peninsula. This is the first thorough study of climatic limitation of the target species. It is also one of few to experimentally test SDMs and use field performance data to enhance projections. Although I found support for the usefulness of SDMs, the results emphasise the need for scepticism and rigorous testing of outputs. Validating SDMs against field data was highly effective, and was a better test of model performance than conventional methods using occurrence data. Uptake of similar methods as outlined in this thesis would improve understanding of uncertainty in distribution modelling. I encourage the use of such techniques not only for improving confidence in model projections, but also in recognizing the relative impact of sources of error in our models. At a time when generating projections of species' potential distributions has never been easier, the need for considered judgements in SDM building and cautious interpretation of outputs is emphasised by my findings.

Keywords: climate, Crassulaceae, elevation, equilibrium, fecundity, germination, growth, invasions, IPMs, mortality, New Zealand, niche, performance, population model, SDMs, validation.

Acknowledgements

I am thankful for the guidance, support and patience of my supervisory team, Professor Phil Hulme, Professor Richard Duncan and Associate Professor Sue Worner. Their collective wisdom has been invaluable and I have been consistently pushed to develop my modelling, statistical and writing skills. I am also grateful for the chance to collaborate with Dr Darren Kriticos, whose advice transformed my distribution modelling work, and was extremely helpful in the development and writing of Chapter 2.

I would also like to thank the many people who gave technical and field assistance during my long field seasons. I could not have hoped to do such an extensive field project alone.

Field surveys: I thank, in no particular order, my field assistants Haylee Wen See Lim, Amy McCulla, Corrine Staley, Robyn Butters, Kelly Murray, Lynda Doherty, Kenny Perry, and Ruairé Murray. I particularly thank those who gave up their days off to help me measure plants, despite not being the slightest bit interested in ecology, and who asked for nothing in return except perhaps lunch and a cold beer afterwards.

Experiments and lab work: I thank my field assistants Jagoba Malumbres-Olarte, Kirsty McGregor, Aimee McCulla, Katie Villano, and Ruairé Murray. I am especially grateful for being able to rely on Robyn Butters throughout my field work, only through her hard work was it possible to get such a large experiment completed. I also thank the Lincoln University Field Services Centre and Nursery, in particular Dan Dash for giving up his time to help me dig holes on hillsides. I also benefitted greatly from the knowledge of Maria-Elena Duter and the facilities of the Lincoln University Seed Research Centre. Perhaps most of all, I thank Di Carter and the Port Hills Rangers for their interest in the project and their ongoing assistance, for allowing the use of council reserves, and for practical help with removal of plant material. The field experiment was carried out under permits granted by Christchurch City Council, Environment Canterbury (ECan) and the Ministry for Primary Industries (MPI).

I have been lucky to be surrounded by many fantastic colleagues during my time in Lincoln. I thank Elizabeth Wandrag, Kirsty McGregor, Federico Tomasetto, Tyler Brummer, Samuel Tourtellot, Andreas Makiola, Tasha Shelby, Kevin McGinn, Senait Senay and Audrey Lustig for their moral and technical support. I also thank Makihiko Ikegami and Will Godsoe for their constructive feedback, and Jennifer Bufford for the crash course in integral projection models. Lastly, I would like to thank the wonderful people who helped keep me sane and grounded during my PhD studies, especially Sinead Carragher, Bridget Rowe and Tara Welham for being extremely good at pretending to be interested in my science rants. I thank my parents Lesley and Nick Pannell, and sisters Liz Barrett and Claire Gray, for their unconditional support. Finally, thanks to my fiancé Ruairé Murray, for being my personal cheerleader, unofficial research assistant and sounding board over the past few years, and for helping me remember, every time, where I left that very important post-it note.

Table of contents

| | |
|---|------------|
| Abstract..... | iii |
| Acknowledgements..... | iv |
| Table of contents | v |
| List of tables..... | ix |
| List of figures | xii |
| Chapter 1 - Introduction..... | 1 |
| 1.1 Spatial ecology – the where and why of invasions | 1 |
| 1.2 Making models of reality | 2 |
| 1.2.1 Correlative SDMs | 3 |
| 1.2.2 When SDMs go awry | 5 |
| 1.2.3 Complementing SDMs with real-world data | 5 |
| 1.2.4 Structure of thesis..... | 6 |
| 1.3 Alien Crassulaceae of New Zealand | 7 |
| 1.3.1 Selecting three study species..... | 7 |
| 1.3.2 Banks Peninsula | 10 |
| 1.4 Thesis objectives | 12 |
| 1.5 Thesis style..... | 12 |
| Chapter 2 – Modelling the global and New Zealand niches of alien Crassulaceae indicates invasion of novel climates | 13 |
| 2.1 Abstract..... | 13 |
| 2.2 Introduction..... | 13 |
| 2.2.1 Aims | 16 |
| 2.3 Methods | 16 |
| 2.3.1 Study species..... | 16 |
| 2.3.2 Distribution data..... | 17 |
| 2.3.3 Environmental variables | 19 |
| 2.3.4 Niche analysis | 19 |
| 2.3.5 Model of climate suitability | 20 |
| 2.3.6 <i>A priori</i> non-climatic constraints | 21 |
| 2.3.7 Land use constraints for <i>C. orbiculata</i> | 22 |
| 2.3.8 Model verification..... | 24 |
| 2.4 Results..... | 25 |
| 2.4.1 Niche analyses..... | 25 |
| 2.4.2 Performance of BIOCLIM models..... | 27 |
| 2.4.3 New Zealand projections and habitat suitability | 29 |
| 2.5 Discussion | 33 |
| 2.5.1 What do the models reveal about the niche? | 33 |
| 2.5.2 The role of non-climatic factors..... | 34 |
| 2.5.3 Potential distributions in New Zealand | 35 |
| 2.5.4 Limitations | 36 |
| 2.5.5 Conclusions..... | 37 |

| | |
|---|---------------|
| Chapter 3 – Testing performance along an elevation gradient reveals the climatic limits of alien Crassulaceae in New Zealand | 38 |
| 3.1 Abstract..... | 38 |
| 3.2 Introduction..... | 38 |
| 3.2.1 Aims | 41 |
| 3.3 Methods | 41 |
| 3.3.1 Study species..... | 41 |
| 3.3.2 Study area..... | 42 |
| 3.3.3 Experimental design..... | 42 |
| 3.3.4 Growth and mortality experiment | 43 |
| 3.3.5 Germination and seedling survival experiment..... | 46 |
| 3.3.6 Risk mitigation and site monitoring..... | 47 |
| 3.3.7 Analysis and environmental variables | 47 |
| 3.3.8 Model fitting and performance..... | 48 |
| 3.3.9 Comparison with observed distribution | 49 |
| 3.3.10 Sources of uncertainty..... | 50 |
| 3.4 Results..... | 51 |
| 3.4.1 Seedling establishment..... | 51 |
| 3.4.2 Annual relative growth..... | 51 |
| 3.4.3 Mortality..... | 56 |
| 3.4.4 Elevation limits on Banks Peninsula..... | 57 |
| 3.5 Discussion | 61 |
| 3.5.1 Predicted limits | 61 |
| 3.5.2 Climatic drivers..... | 62 |
| 3.5.3 Implications for Banks Peninsula..... | 64 |
| 3.5.4 Limitations | 65 |
| 3.5.5 Conclusions..... | 65 |
| Chapter 4 – Exploring the link between fecundity and climate in naturalized populations of alien Crassulaceae | 66 |
| 4.1 Abstract..... | 66 |
| 4.2 Introduction..... | 66 |
| 4.2.1 Aims | 68 |
| 4.3 Methods | 68 |
| 4.3.1 Study species..... | 68 |
| 4.3.2 Study area..... | 69 |
| 4.3.3 Flowering surveys..... | 70 |
| 4.3.4 Seed counts | 72 |
| 4.3.5 Climate variables..... | 73 |
| 4.3.6 Model fitting | 74 |
| 4.3.7 Model predictions | 75 |
| 4.4 Results..... | 76 |
| 4.4.1 General patterns | 76 |
| 4.4.2 Flowering probability..... | 76 |
| 4.4.3 Inflorescences per plant | 79 |
| 4.4.4 Flowers per inflorescence | 79 |
| 4.4.5 Seed production..... | 81 |
| 4.4.6 Site differences in canopy volume | 83 |
| 4.4.7 Total per capita fecundity..... | 84 |
| 4.5 Discussion | 85 |
| 4.5.1 Direct climate limitation | 85 |
| 4.5.2 Plant size – indirect climate limitation? | 86 |
| 4.5.3 Implications for spread, and limitations..... | 87 |
| 4.5.4 Conclusions..... | 88 |

| | |
|---|----------------|
| Chapter 5 – Validating SDM projections against field data | 90 |
| 5.1 Abstract..... | 90 |
| 5.2 Introduction..... | 90 |
| 5.2.1 Aims | 94 |
| 5.3 Methods | 94 |
| 5.3.1 Study species..... | 94 |
| 5.3.2 Study area..... | 94 |
| 5.3.3 Integral projection models..... | 95 |
| 5.3.4 Climate variables..... | 96 |
| 5.3.5 IPM parameters | 97 |
| 5.3.6 IPM structure..... | 99 |
| 5.3.7 Verification of IPMs | 100 |
| 5.3.8 Validation of BIOCLIM projections | 101 |
| 5.3.9 Improving BIOCLIM projections | 102 |
| 5.4 Results..... | 102 |
| 5.4.1 IPM predictions..... | 102 |
| 5.4.2 Perturbation analyses | 105 |
| 5.4.3 Validation of BIOCLIM projections | 105 |
| 5.4.4 Can BIOCLIM distinguish fundamental presences from absences?..... | 106 |
| 5.4.5 Improving BIOCLIM projections for Banks Peninsula | 110 |
| 5.5 Discussion | 112 |
| 5.5.1 Accuracy of IPM and BIOCLIM projections..... | 112 |
| 5.5.2 Why did BIOCLIM over-predict suitable climate?..... | 113 |
| 5.5.3 Limitations | 115 |
| 5.5.4 Conclusions..... | 116 |
| Chapter 6 - General discussion | 117 |
| 6.1 Summary of findings..... | 117 |
| 6.2 Species distribution models vs. reality..... | 118 |
| 6.2.1 How well did SDMs predict plant performance?..... | 118 |
| 6.2.2 Improving SDM accuracy | 119 |
| 6.3 The future of non-native Crassulaceae on Banks Peninsula | 120 |
| 6.3.1 Climatic limitation | 120 |
| 6.3.2 Non-climatic limitation, implications for spread | 121 |
| 6.4 Avenues for future research | 123 |
| 6.4.1 Study species – some important unknowns | 123 |
| 6.4.2 Limitations, and lessons learned | 124 |
| 6.5 Conclusions..... | 125 |
| Appendix A – Supporting information for Chapter 2 | 126 |
| A.1 An example MaxEnt model | 126 |
| A.2 Supporting data for study species | 127 |
| Appendix B – Supporting information for Chapter 3..... | 137 |
| Appendix C - Supporting information for Chapter 4..... | 147 |
| C.1 Road survey methodology | 147 |
| C.2 Supporting data | 148 |
| Appendix D - Supporting information for Chapter 5..... | 155 |

| | |
|--|----------------|
| Appendix E - Herbicide trial results..... | 165 |
| E.1 Rationale | 165 |
| E.2 Methods | 165 |
| E.3 Results..... | 166 |
| E.4 Summary | 168 |
| Supplementary materials..... | 169 |
| S.1 - IPM coefficients | 169 |
| S.2 - R code for IPMs, adapted from Merow, Dahlgren, <i>et al.</i> (2014)..... | 170 |
| References | 172 |

List of tables

| | |
|--|----|
| Table 1.1 Broad categories of SDMs, with examples and brief description, advantages and disadvantages of each category, and suitable uses. | 4 |
| Table 1.2 Key traits of study species <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> . Data on introduced ranges taken from occurrence records (source list Table A.1). Other traits collated from Webb <i>et al.</i> (1988), additional sources cited in table. | 9 |
| Table 2.1 Niche equivalency and similarity of target species between global and New Zealand ranges, following the methods of Broennimann <i>et al.</i> (2012). Similarity indicates whether niches in the target ranges are more similar to each other than random simulations. Asterisks denote bootstrapped levels of statistical significance of D ($p \leq 0.05$), where they signify rejection of niche equivalency at the 95% confidence level. | 25 |
| Table 2.2 Sensitivity (Sens.) and projected suitable area (PSA) of global (excluding New Zealand) and total (global plus New Zealand) BIOCLIM models of <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> , tested against the world and New Zealand. Statistical significance of sensitivity, given projected suitable area, calculated using Fisher's one-tailed binomial statistic (* $p < 0.05$, ** $p < 0.01$). Global models independently validated against New Zealand, total models cross-validated 5-fold (mean value given). | 27 |
| Table 2.3 Projected suitable area (PSA) for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> , with and without constraint by habitat. Sensitivity of constrained models shown with significance calculated using Fisher's one-tailed binomial statistic (** $p < 0.01$). Percent reduction in projected suitable area, after habitat masks were applied, is given relative to climate-only models. | 29 |
| Table 3.1 Target species traits. Maximum size and time to maximum size from Vogan (2003) and Royal Horticultural Society (2014). Elevation, precipitation and annual mean temperature in native, New Zealand, and all other introduced ranges taken from occurrence data (Table A.1) and Worldclim Bioclim variables [(Hijmans <i>et al.</i> 2005), available at http://www.worldclim.org]. Minimum elevation for all species in all regions is 0 MASL. | 44 |
| Table 3.2 Number of sites on Banks Peninsula used for cuttings only, seed trays only, or both, in each bioclimate zone as defined by Wilson (1993). | 44 |
| Table 3.3 Modelled seedling establishment (SEst), relative growth (RG) and summer and winter mortality (SM and WM), at various elevations (MASL), for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> . No random effects included except for SEst max, predicted seed establishment at the most favourable site using the highest random site effect. Predictions given for the 95 th percentile of the observed distribution (+), the maximum observed elevation (*, bold), and up to 300 MASL above the observed limit. The 95% prediction intervals are denoted by \pm . Frost and GDD assumed to increase linearly with elevation, other variables set to constant values. | 60 |
| Table 4.1 Total numbers of <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> flowering in 2011 (Y1) or 2012 (Y2) only, or both years. Mortality shown as % of all individuals, broken down into number of plants confirmed dead vs. not re-located. Number of samples for each models also provided. | 77 |
| Table 4.2 Analysis of variance (ANOVA) source tables, showing differences in fecundity among years (if applicable), sites, and plants (if applicable) for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> . ANOVAs run for numbers of log-standardised <i>Inflorescences</i> <i>Plant</i> , <i>Flowers</i> <i>Inflorescence</i> , and <i>Seeds</i> <i>Pod</i> . For total numbers flowering, columns show degrees of freedom, deviance, and residual degrees of freedom and deviance from a Chi-squared ANOVA of a binomial GLM with year and site effects. Significant results highlighted in bold and level denoted by asterisks (*), where; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ | 77 |
| Table 4.3 Source tables for one-way ANOVAs on among-site differences in log-standardized canopy volume and internode length, for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> . Analyses were run on second year data, both across all plants, and flowering plants only. | 83 |

| | |
|---|-----|
| Table 4.4 Predicted mean inflorescences per plant, flowers per inflorescence and seeds per pods for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> , with 95% bootstrapped confidence intervals in brackets. Models use mean plant volume or internode length of all flowering plants, aspect set to east (<i>A. arboreum</i>) or none (<i>C. orbiculata</i>). Seeds per plant is the product of the three models. | 84 |
| Table 4.5 Parameter elasticity values for GLMMs of inflorescences per plant, flowers per inflorescence and seeds per pod, calculated against predicted seeds per plant for <i>Aeonium arboreum</i> and <i>Cotyledon orbiculata</i> . Highest elasticity value per species is highlighted in bold. | 84 |
| Table 5.1 Linear regressions of vital rates of <i>Aeonium arboreum</i> (AA), <i>A. haworthii</i> (AH) and <i>Cotyledon orbiculata</i> (CO), as used in IPMs. Parameters of each regression shown, and whether the regression was fitted to experimental (Chapter 3) or survey (Chapter 4) data. Model coefficients are available in Table S.1. Units are plant volume (L), elevation (MASL), precipitation (mm/year) Frost days, GDD and precipitation were 2-year annual means for each variable. | 98 |
| Table 5.2 Verification of integral projection models of <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> , run at 83 point locations on Banks Peninsula. Sites divided according to species' current presence or absence. Sites with predicted population growth (λ) >1 were classified as suitable, <1 were classified unsuitable. | 103 |
| Table 5.3 Elasticity values of IPM parameters. Perturbation analyses conducted for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> at favourable sites (upper 95 th percentile of λ) and unfavourable sites (lower 95 th percentile of λ), with the three highest elasticities highlighted for each species. | 104 |
| Table 5.4 Single factor ANOVA comparing BIOCLIM scores at fundamental presence and absence locations for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> . Fundamental presences and absences distinguished by the threshold of $\lambda = 1$ for IPM predictions. | 106 |
| Table 5.5 Sensitivity, specificity, under prediction rate (UPR) and over prediction rate (OPR), and projected suitable area (PSA, %), for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> . All metrics calculated for Banks Peninsula only. Original models (unrefined BIOCLIM projections) validated against IPM predictions. The same metrics are shown for refined BIOCLIM projections, calculated against IPM predictions and true presences. | 110 |
| | |
| Table A.1 Sources and number of occurrence records collected for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> , before data cleaning and resampling. | 127 |
| Table A.2 Regions and Köppen-Geiger (KG) classes sampled within for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> niche analyses, and number of samples taken. | 128 |
| Table A.3 Description of land cover classes (Ministry for the Environment & Landcare Research 2014) that spatially intersect <i>Cotyledon orbiculata</i> occurrence records in New Zealand. Class descriptions summarized from Thompson <i>et al.</i> (2003). | 135 |
| | |
| Table B.1 Source list for Banks Peninsula distribution data of <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> | 138 |
| Table B.2 Details of all numbered sites in Figure 3.1. "Use" distinguishes between weather stations used for precipitation data (P), and field sites used for cuttings only (C), seeds only (S), or both (CS). Longitude and latitude in decimal degrees (WGS 84), elevation in MASL. Aspect (cardinal direction) and % overhead canopy cover (CC) measured at field sites only. Asterisks (*) denote sites where CC is caused by trees (as opposed to low garden features at seed sites). "Precip.WS" indicates the weather station used for precipitation data at each field site. | 139 |
| Table B.3 Individual seed weight of <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> , and weight of seed and chaff estimated to contain 100 seeds, according to seed source site. Also given are results of tetrazolium tests, as percentages of seeds found to be fully stained (viable, high vigour) and pale stained (viable, low vigour). | 141 |

| | |
|--|-----|
| Table C.1 Details of <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> survey sites. Longitude and latitude given in decimal degrees (WGS 1984), elevation in MASL, aspect to the nearest cardinal point. Habitat and earthquake (EQ) damage are visual assessments, geological units from G.N.S. Science (2014). Categories of EQ damage are none, rock fall (RF) or landslides (LS), divided into small (S), moderate (M) and large (L). | 151 |
| Table C.2 Life stage categories used in surveys of <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> on Banks Peninsula. | 152 |
| Table D.1 List of all point locations for which IPMs were run. Type denotes whether site is a weather station (WS; data available at http://cliflo.niwa.co.nz/), or a field experiment (FE) or survey site (FS; see Chapter 3 and Chapter 4). Longitude and latitude in decimal degrees (WGS 1984), elevation in MASL. Precip.WS denotes the ID of the weather station used for precipitation values for each site, also available through CliFlo, * denotes weather stations used for precipitation data only not listed in table, full names given below table. Species present indicates which species (<i>Aeonium arboreum</i> , <i>A. haworthii</i> , <i>Cotyledon orbiculata</i>) are present within the same 30-arc-second grid cell as the site. | 155 |
| Table D.2 Paired t-test results for mean annual frost days, GDD5 and GDD10 at weather stations used as IPM locations. Results given for 2-year versus 5-year, 10-year and 20-year means, with degrees of freedom (DF), t and p-values. Significant results indicated in bold. | 157 |
| Table D.3 Minimum, mean and maximum correlations (r) between data logger sites and the nearest weather station over 2011-2012. Minimum and maximum temperature rescaled as residuals of the site sample mean before calculating correlation coefficient. | 158 |
| Table E.1 Scale used for visual assessment of damage to <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> six weeks after herbicide treatment. | 165 |
| Table S.1 Coefficients used in IPMs of <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> | 169 |

List of figures

| | |
|---|----|
| Figure 1.1 Photographs of study species a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> , showing individual plants (left) and naturalized populations (right). All photographs taken on Banks Peninsula, Canterbury, New Zealand. | 11 |
| Figure 2.1 Known global distributions of a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> , after resampling onto a 30 arc-second grid. Number of presence points per region labelled. Red points were used for model training; black points removed as suspected to be plants in cultivation. | 18 |
| Figure 2.2 a-c) Kernel-smoothed PCA biplots of climatic niches, in the global range (red) and New Zealand range (blue), for a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> . Plots generated using 5 bioclimatic variables [(Hijmans <i>et al.</i> 2005), available at http://www.worldclim.org]. Solid lines delimit total background climate, dashed lines delimit 50% of background climate. Shading indicates density of occurrences after kernel smoother applied. Correlation circles show correlation between bioclimatic variables (see legend, g), with principal component axes for d) <i>A. arboreum</i> , e) <i>A. haworthii</i> and f) <i>C. orbiculata</i> | 26 |
| Figure 2.3 BIOCLIM global projections of climate suitability, using all available data, for a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> . Model scores between 1 and 0 signify the position within the <i>n</i> -dimensional climate space. Scores approaching 1 indicate similarity to the species' 50 th percentile of the species' rectilinear climate envelope ("core" climate), while 0 signifies that the climate is outside the 5 th or 95 th percentiles of the envelope. | 28 |
| Figure 2.4 a) New Zealand projections of final BIOCLIM climate-only models for <i>Aeonium arboreum</i> , with points showing occurrence records. Model (a) was then constrained by (b), the mask of habitat suitability to give (c), the final projection of overall suitability. BIOCLIM scores are percentiles of the species' distributions in climate space. Scores approaching 1 indicate similarity to the species' 50 th percentile of the species' rectilinear climate envelope ("core" climate), while 0 signifies that the climate is outside the 5 th or 95 th percentiles of the envelope. | 30 |
| Figure 2.5 a) New Zealand projections of final BIOCLIM climate-only models for <i>Aeonium haworthii</i> , with points showing occurrence records. Model (a) was then constrained by (b), the mask of habitat suitability to give (c), the final projection of overall suitability. BIOCLIM scores are percentiles of the species' distributions in climate space. Scores approaching 1 indicate similarity to the species' 50 th percentile of the species' rectilinear climate envelope ("core" climate), while 0 signifies that the climate is outside the 5 th or 95 th percentiles of the envelope. | 31 |
| Figure 2.6 a) New Zealand projections of final BIOCLIM climate-only models for <i>Cotyledon orbiculata</i> , with points showing occurrence records. Model (a) was then constrained by (b), the mask of habitat suitability to give (c), the final projection of overall suitability. BIOCLIM scores are percentiles of the species' distributions in climate space. Scores approaching 1 indicate similarity to the species' 50 th percentile of the species' rectilinear climate envelope ("core" climate), while 0 signifies that the climate is outside the 5 th or 95 th percentiles of the envelope. | 32 |
| Figure 3.1 a) Field sites, and weather stations providing precipitation data, b) field site elevations, and c) location of Banks Peninsula. Field sites contained cuttings only, seeds only or both (see legend), site numbers correspond to Table B.2 (site details). Base map is total annual precipitation with shaded relief, where grey indicates no data. Precipitation was interpolated from the 30 arc-second Worldclim layer [(Hijmans <i>et al.</i> 2005), available at http://www.worldclim.org]. | 45 |
| Figure 3.2 Mean seedling count at measurement intervals with 95% confidence intervals, for a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> . Sites are divided into low (0 – 150 MASL), medium (150 – 400 MASL), and high (400 – 700 MASL) elevations. Seedling models are based on November 2012 counts. | 52 |
| Figure 3.3 Coefficients of GLMMs of probability of seedling establishment (P[SEst]) ± 95% confidence intervals, with fixed (solid) and random (hollow) effects, for a) | |

| | |
|---|----|
| <i>Aeonium arboreum</i> c) <i>A. haworthii</i> and e) <i>Cotyledon orbiculata</i> , and GLMM predictions (lines) and raw data (points) for b) <i>A. arboreum</i> , d) <i>A. haworthii</i> and f) <i>C. orbiculata</i> . Predictions use fixed only effects between 0 – 1000 MASL (b, d), and 400 – 1400 mm p.a. (f). For <i>A. arboreum</i> (b), constant precipitation of 733 mm p.a., and linear relationships of GDD5 and frost days to elevation are assumed (section 3.3.9). Thus, lines are not fitted to points. | 53 |
| Figure 3.4 Mean relative growth, as $\ln \text{Volumet} + 1 - \ln \text{Volumet}$, since November 2010 baseline volumes at low, medium, and high elevations for a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> , and c) <i>Cotyledon orbiculata</i> . Here, t is measured in units of half-years. Shaded area shows 95% confidence interval of the mean. | 54 |
| Figure 3.5 GLMM coefficients \pm 95% confidence intervals of annual relative growth (RG) models, calculated as $\ln \text{Volumet} + 1 - \ln \text{Volumet}$, with fixed (solid) and random (hollow) effects, for a) <i>Aeonium arboreum</i> , c) <i>A. haworthii</i> and e) <i>Cotyledon orbiculata</i> . GLMM predictions (lines) and site means with standard errors (points) in years one and two, shown for b) <i>A. arboreum</i> , d) <i>A. haworthii</i> and f) <i>C. orbiculata</i> . Predictions generated using only fixed effects between 0 – 1 000 MASL. A linear relationship of annual frost days with elevation is assumed (section 3.3.9). Canopy cover (CC) is set to zero for <i>C. orbiculata</i> . Thus, lines are not fitted to points..... | 55 |
| Figure 3.6 Coefficients of binomial GLMs of summer mortality with 95% confidence intervals, for a) <i>Aeonium arboreum</i> , c) <i>A. haworthii</i> and e) <i>Cotyledon orbiculata</i> , and percentage of surviving individuals at each measurement period, at low, medium, and high elevations for b) <i>A. arboreum</i> , d) <i>A. haworthii</i> and e) <i>C. orbiculata</i> . Percentages measured out of $n = 50$ individuals at low and high elevations, and $n = 100$ at medium elevations. | 58 |
| Figure 3.7 Logistic GLMM coefficients of winter mortality \pm 95% confidence intervals, with fixed (solid) and random (hollow) effects, for a) <i>Aeonium arboreum</i> , c) <i>A. haworthii</i> and e) <i>Cotyledon orbiculata</i> , and modelled probability of death ($P[\text{Die}]$, lines) and observed mortality per site (points) vs. elevation, for b) <i>A. arboreum</i> , d) <i>A. haworthii</i> and f) <i>C. orbiculata</i> . Predictions (lines) generated for small (0.125 L), medium (1 L), and large (8 L) plants, using only fixed effects between 0 – 1000 MASL. A linear relationship of annual frost days with elevation is assumed, derived from recorded data. Consequently, lines are not fitted to points. | 59 |
| Figure 4.1 Populations of a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> in Banks Peninsula and New Zealand (inset), and locations of survey sites (green points, general region labelled). Background layer shows annual precipitation, interpolated from Worldclim data, with shaded relief [(Hijmans <i>et al.</i> 2005), available at http://www.worldclim.org/bioclim]..... | 71 |
| Figure 4.2 Coefficients and predictions of $P[\text{Flower}]$ GLMMs for <i>Aeonium arboreum</i> (a, b), <i>A. haworthii</i> (c, d) and <i>Cotyledon orbiculata</i> (e, f). Fixed effect coefficients shown with 95% confidence intervals (solid points), random effects with maximum and minimum values (hollow points). Plots b, d and f show modelled probability of flowering vs. canopy volume (lines). Axis rescaled to $\sqrt[3]{(\text{Volume} \times 10^3)}$, \approx plant height, for aesthetics. Proportion of plants flowering at midpoints of volume bins shown (points) with number of plants in bin (numbers). | 78 |
| Figure 4.3 Outputs of <i>Inflorescences Plant</i> GLMMs for <i>Aeonium arboreum</i> (a, c) and <i>Cotyledon orbiculata</i> (b, d). Plots a & b show model coefficients, solid points for fixed effects \pm 95% confidence intervals, hollow for random effects with maximum and minimum values. Plots c & d show predicted inflorescences (lines) vs. previous internode length (mm) and canopy volume (L), for <i>A. arboreum</i> (c) and <i>C. orbiculata</i> (d). Canopy volume axis rescaled to $\sqrt[3]{\text{Volume} \times 10^3}$ (\approx plant height) for aesthetics. | 80 |
| Figure 4.4 Outputs of <i>Flowers Inflorescence</i> GLMMs for <i>Aeonium arboreum</i> (a, c) and <i>Cotyledon orbiculata</i> (b, d). Plots a & b show model coefficients, solid points for fixed effects with 95% confidence intervals, and hollow for random effects with maximum and minimum values. Plot c shows predicted number of <i>A. arboreum</i> flowers (triangular points) versus aspect, with observed values in boxplot. Plot d shows predicted number of <i>C. orbiculata</i> flowers (line) versus canopy volume (L). Axis rescaled to $\sqrt[3]{\text{Volume} \times 10^3}$, \approx plant height, for aesthetics, observed values shown as points..... | 81 |

| | | |
|--------------|--|-----|
| Figure 4.5 | Outputs of <i>Seeds Pod</i> GLMMs for <i>Aeonium arboreum</i> (a, c) and <i>Cotyledon orbiculata</i> (b, d) and legend for plots c & d (e). Plots a & b show GLMM coefficients, solid points for fixed effects with 95% confidence intervals, hollow points for random effects with maximum and minimum values. The reference category for aspect is north. Plots c & d show predicted number of seeds per pod, versus pods per inflorescence, in <i>A. arboreum</i> and <i>C. orbiculata</i> respectively. Lines show predictions for aspect category, points show observed data (see legend). | 82 |
| Figure 5.1 | Graphical representation of confusion matrices validating BIOCLIM against IPM predictions. Points show BIOCLIM score vs. λ at each location where IPMs were run, for a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> . Lines indicate where BIOCLIM > 0 (projected suitable by BIOCLIM) and $\lambda = 1$ (threshold for suitable/unsuitable in IPM). Because BIOCLIM scores all unsuitable sites as 0, lines are drawn at the lowest BIOCLIM score on Banks Peninsula..... | 106 |
| Figure 5.2a) | New Zealand and b) Banks Peninsula BIOCLIM projections for <i>Aeonium arboreum</i> . Grey cells are projected as unsuitable by BIOCLIM. Predicted λ (IPM) for each species shown as graduated red points at each IPM location, black points represent $\lambda < 1$ (unsuitable). Shaded relief shown on Banks Peninsula. | 107 |
| Figure 5.3a) | New Zealand and b) Banks Peninsula BIOCLIM projections for <i>Aeonium haworthii</i> . Grey cells are projected as unsuitable by BIOCLIM. Predicted λ (IPM) for each species shown as graduated red points at each IPM location, black points represent $\lambda < 1$ (unsuitable). Shaded relief shown on Banks Peninsula. | 108 |
| Figure 5.4a) | New Zealand and b) Banks Peninsula BIOCLIM projections for <i>Cotyledon orbiculata</i> . Grey cells are projected as unsuitable by BIOCLIM. Predicted λ (IPM) for each species shown as graduated red points at each IPM location, black points represent $\lambda < 1$ (unsuitable). Shaded relief shown on Banks Peninsula. | 109 |
| Figure 5.5 | Refined BIOCLIM projections for b) <i>Aeonium arboreum</i> , c) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> on Banks Peninsula, with shaded relief, and extent indicator (a). Categories are: predicted unsuitable by BIOCLIM (blue, unsuitable), predicted suitable by BIOCLIM but below IPM-based threshold (yellow, likely unsuitable), and predicted suitable by BIOCLIM and above the IPM-based threshold (red, likely suitable). | 111 |
| Figure A.1 | Distribution of species Y in relation to a climatic variable X. Response curves (red) generated by a MaxEnt model with linear and quadratic features only (a), and all “auto-features” (b). In region 1 (R1), the species is most prevalent and occupies a wide range of climates, but can tolerate conditions in region 2 (R2) although it is less prevalent. Values of X between R1 and R2 are assumed to be climatically suitable. In a), suitable habitat in R2 is under-predicted, while in b), climate space between R1 and R2 is under-predicted..... | 126 |
| Figure A.2 | Frequency histograms of the five bioclimatic variables used in niche analysis and models of target species, at all global occurrence points. Plots shown for i) <i>Aeonium arboreum</i> ; ii) <i>A. haworthii</i> and iii) <i>Cotyledon orbiculata</i> . Variables are: a) BIO10 (Mean temperature of the warmest quarter, °C × 10); b) BIO11 (mean temperature of the coldest quarter, °C × 10); c) BIO16 (Precipitation of the wettest quarter, mm); d) BIO17 (Precipitation of the driest quarter, mm); e) BIO19 (Precipitation of the coldest quarter, mm). | 129 |
| Figure A.3 | Frequency of land use classification (Nachtergaele & Petri 2008) in grid cells (5 arc-minutes) containing <i>Cotyledon orbiculata</i> in a) Southern Africa (South Africa, Lesotho, Swaziland, Namibia, Mozambique, Angola); b) Europe (Corsica, Spain); c) the U.S.A.; d) Australia and e) New Zealand. Asterisks denote significance of land use type given its proportional area, according to Fisher’s exact test (• = $p < 0.05$, ★ = $p < 0.01$). | 130 |
| Figure A.4 | Density of cattle, goats and sheep (heads per km ²) in grid cells (0.05 decimal degrees) containing <i>Cotyledon orbiculata</i> (grey) versus randomly-selected background points (white) in a) U.S.A., b) Europe (Corsica, Spain), c) Southern Africa (South Africa, Lesotho, Swaziland, Namibia, Mozambique, Angola), d) Australia and e) New | |

| | | |
|------------|---|-----|
| | Zealand. Maximum density shown where whiskers extend beyond axes. Data courtesy of GLW (Robinson <i>et al.</i> 2014). | 131 |
| Figure A.5 | Livestock density of cattle, goats and sheep expressed as heads per km ² in grid cells (0.05 decimal degrees) containing <i>Aeonium arboreum</i> (grey) versus randomly-selected background points (white) in a) U.S.A., b) Europe (Spain, Portugal, Balearic Islands, Malta), c) Macaronesia (Canary Islands, Morocco, Madeira), d) Australia and e) New Zealand. Maximum values shown where whiskers extend beyond plots. Data courtesy of GLW (Robinson <i>et al.</i> 2014). | 132 |
| Figure A.6 | Livestock density of cattle, goats and sheep expressed as heads per km ² in grid cells (0.05 decimal degrees) containing <i>Aeonium haworthii</i> (grey) versus randomly-selected background points (white) in a) U.S.A., b) Europe (Spain, France), c) Macaronesia (Canary Islands), d) Australia and e) New Zealand. Maximum values shown where whiskers extend beyond plots. Data courtesy of GLW (Robinson <i>et al.</i> 2014). | 133 |
| Figure A.7 | a) Frequency of <i>Cotyledon orbiculata</i> occurrence records in land cover classes (Ministry for the Environment & Landcare Research 2014) and b) farm types (excluding non-farmland) according to Agribase™ (AsureQuality 2006). Black bars indicate statistical significance ($p < 0.01$) of <i>C. orbiculata</i> frequency, given total occurrences and the proportional area of each class in New Zealand, according to a one-tailed binomial test. | 134 |
| Figure A.8 | Global a) and New Zealand b) projections of BIOCLIM models for <i>Cotyledon orbiculata</i> , trained on subset of all occurrence data, with 7 points removed from the most extreme high elevations in Lesotho. BIOCLIM scores are percentiles of the species' distributions in climate space. Scores approaching 1 signify similarity to the species' 50 th percentile in climate space ("core" climate), and 0 signifies that the cell is outside of the species' rectilinear hypervolume. | 136 |
| Figure B.1 | Map of current distributions, cutting collection sites and seed collection sites, for a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> on Banks Peninsula. Location of Banks Peninsula relative to New Zealand also shown (d). | 137 |
| Figure B.2 | Elevation (MASL) versus total annual precipitation (mm) on Banks Peninsula, taken from 30-arc-second Worldclim layers [(Hijmans <i>et al.</i> 2005), available at http://www.worldclim.org]. Grey points show values for entire Peninsula, black points show values at recorded presence locations of a) <i>Aeonium arboreum</i> b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> | 140 |
| Figure B.3 | <i>Cotyledon orbiculata</i> seeds under microscope at 100 × magnification. Seeds have been stained with TTC and seed coat removed. Top row show pale and partial staining and are non-viable due to necrosis of vital tissue. Middle row show full staining indicating viability and high vigour. Bottom row show no staining and are completely non-viable. | 142 |
| Figure B.4 | Scatterplots showing similar relationships between relative growth, calculated as $[\ln(\text{Volume}_{t+1}) - \ln(\text{Volume}_t)]$, and annual frost days and elevation, in both years of field experiment. Year one indicated by black points, year two by red points. Shown for <i>Aeonium arboreum</i> (a, b) <i>A. haworthii</i> (c, d) and <i>Cotyledon orbiculata</i> (e, f). | 143 |
| Figure B.5 | Correlations of elevation with five annual climatic variables (a-e) at field transplant sites, over both years. Seed tray only sites not used due to incomplete year one data. Only one year of data presented for solar radiation (e) due to negligible differences between years. Pearson's correlation coefficient (r) and statistical significance indicated in figures, by * ($p < 0.05$), ** ($p < 0.01$), or *** ($p < 0.001$). | 144 |
| Figure B.6 | Canopy volume (L) at previous measurement interval of a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> , grouped by survival. Relationship between mean canopy volume, cumulative frost days and % deaths per site, of d) <i>A. arboreum</i> , e) <i>A. haworthii</i> and f) <i>C. orbiculata</i> | 145 |
| Figure B.7 | Canopy volume required for 50% survival at a given elevation, in years 1 and 2, according to final models for a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> . Predictions generated along a hypothetical gradient where frost increases linearly with elevation, and shade is set to zero. | 146 |

| | |
|---|-----|
| Figure C.1 All 30 arc-second cells surveyed for <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> on Banks Peninsula, b) extent indicator. | 148 |
| Figure C.2 Maps of populations of a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> on Banks Peninsula. Inset maps show New Zealand presences of each species. Points on Banks Peninsula scaled by population size (Abundant = extensive, constant; Frequent = extensive, scattered; Occasional = few, scattered; Rare = one individual). Red points indicate accessible populations, black points inaccessible (e.g. cliffs). Road centrelines shown in dark grey. | 149 |
| Figure C.3 Elevation vs. annual precipitation gradient across Banks Peninsula (grey), and at known populations of a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> (black), and at sites chosen for surveys (red). Precipitation data taken from 30 arc-second Worldclim layer [(Hijmans <i>et al.</i> 2005), available at http://www.worldclim.org/bioclim]..... | 150 |
| Figure C.4 Map of weather stations on Banks Peninsula ($n = 8$, dark blue points) with precipitation data for 2010 - 2012, the time period of flowering surveys. Survey sites ($n = 24$) shown as green points, all points labelled by site or station name, roads indicated by grey lines. Weather station data available from CliFlo (National Institute of Water and Atmospheric Research 2014). | 152 |
| Figure C.5 Histograms of a) annual growing degree days base 5 (GDD5), b) annual precipitation (mm), and c) annual solar radiation (KWh/M ²), at survey sites of all three target species. Data shown for both years of surveys. Temperature data taken from site data loggers, precipitation from the nearest weather station, and solar radiation modelled in ArcMap 10.1. | 153 |
| Figure C.6 Mosaic plots (a-c) and boxplots (d-l) of measured reproductive traits at survey sites in 2012. Columns, from left to right: <i>Aeonium arboreum</i> , <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> . Rows, from top to bottom: proportion of all plants flowering (black) and not flowering (grey) with thickness of bars scaled to sample size; and on flowering plants, inflorescences per plant; flowers per inflorescence; seeds per pod. Survey sites ordered by increasing GDD10, shown for each site (m-o). | 154 |
| | |
| Figure D.1 Annual frost days, GDD10 and GDD5 from 1992-2012, at weather stations used as IPM locations (see Table D.1 for abbreviations)..... | 157 |
| Figure D.2 a) Daily minimum and b) daily maximum temperatures, between December 2010 and November 2011, at sites with data loggers (black) and at weather stations (red)..... | 158 |
| Figure D.3 Structure of a Lefkovitch Matrix Model (size-structured). Lefkovitch matrices are conceptually similar to IPMs. In this example, there are 5 size classes, 4 of which are reproductive, and individuals may grow, shrink or stay the same size in each time step. Graphical representations of the IPM results of these components are given in Figure D.4, Figure D.5 and Figure D.6 (the reader should note that the matrices are transposed in the IPM, but the same concepts apply). | 159 |
| Figure D.4 Growth matrices (left) and fecundity matrices (right) at climatically good sites (upper 95 th percentile of λ) for <i>Aeonium arboreum</i> (OB1; a, b), <i>A. haworthii</i> (LCP; c, d) and <i>Cotyledon orbiculata</i> (LB; e, f). Unit of plant size is cm (approximately equal to height). Colours show transition probabilities between size classes (growth matrices) and individual fecundity (fecundity matrices). | 160 |
| Figure D.5 Growth matrices (left) and fecundity matrices (right) at climatically poor sites (lower 95 th percentile of λ) for <i>Aeonium arboreum</i> (MP5; a, b), <i>A. haworthii</i> (TO8; c, d) and <i>Cotyledon orbiculata</i> (TO8; e, f). Unit of plant size is cm (approximately equal to height). Colours show transition probabilities between size classes (growth matrices) and individual fecundity (fecundity matrices). | 161 |
| Figure D.6 Stable size distributions (left) and probability of survival versus plant size (right) for IPMs of <i>Aeonium arboreum</i> (a, b), <i>A. haworthii</i> (c, d) and <i>Cotyledon orbiculata</i> (e, f), at climatically “good” and “poor” sites (upper and lower 95 th percentiles of λ). Site ID indicated in legend, size classes based on plant height (cm). | 162 |

| | |
|---|-----|
| Figure D.7 Elasticity plots of IPM matrices at climatically good sites (left, upper 95 th percentile of λ) and poor sites (right, lower 95 th percentile of λ) for <i>Aeonium arboreum</i> (a, b), <i>A. haworthii</i> (c, d) and <i>Cotyledon orbiculata</i> (e, f). Plant size units are cm (height). | 163 |
| Figure D.8 Bootstrapped distributions ($n=1000$) of mean BIOCLIM scores at IPM locations where $\lambda > 1$ (climate suitable) and < 1 (climate unsuitable), for a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and c) <i>Cotyledon orbiculata</i> | 164 |
| Figure D.9 True skill statistic (TSS), under prediction rate (UPR), sensitivity and specificity of BIOCLIM projections assessed against IPM predictions and true presences, after iterative raising of suitability threshold, for a) <i>Aeonium arboreum</i> , b) <i>A. haworthii</i> and <i>Cotyledon orbiculata</i> | 164 |
| Figure E.1 Damage to <i>Aeonium arboreum</i> plants (0 = no damage, 5 = complete mortality, see Table E.1) after spraying with Escort (E), Escort with Silmaxx (ES), Grazon (G), Grazon with Silmaxx (GS), Roundup (R), and Roundup with Pulse (RP). | 166 |
| Figure E.2 Damage to <i>Aeonium haworthii</i> plants (0 = no damage, 5 = complete mortality, see Table E.1) after spraying with Escort (E), Escort with Silmaxx (ES), Grazon (G), Grazon with Silmaxx (GS), Roundup (R), and Roundup with Pulse (RP). | 166 |
| Figure E.3 Damage to <i>Cotyledon orbiculata</i> plants (0 = no damage, 5 = complete mortality, see Table E.1) after spraying with Escort (E), Escort with Silmaxx (ES), Grazon (G), Grazon with Silmaxx (GS), Roundup (R), and Roundup with Pulse (RP). | 166 |
| Figure E.4 Examples of before and six weeks after herbicide treatment at selected field sites. Commercial name of herbicide given in table, site names correspond to Table B.2. | 168 |

Chapter 1 - Introduction

1.1 Spatial ecology – the where and why of invasions

All species are limited in their distributions to varying degrees. The question of where particular species occur, and why, has been integral to our understanding of the natural world since at least the 5th Century BCE (Woodward 1987) and underpins the field of spatial ecology. Despite the apparent simplicity of the underlying question, spatial ecology is a large field of research that has seen rapid development with the advent of powerful computers. Substantial research goes into projecting species' current or potential ranges, forecasting how distributions may change in future, and identifying the fundamental drivers governing species' limits. These tasks are not trivial, thanks to a multitude of underlying factors that shape species' distributions. At the fundamental level, species are limited by climate, and this is thought to be the most important factor for understanding distributions at the global scale (Woodward 1987). Plants adapted to tropical rainforests, for example, evolve mechanisms to maximise leaf runoff that are disadvantageous in drier environments (Givnish 1984), while insect development is closely related to temperature and varies among species (Briere *et al.* 1999). Nested within these broad-scale climatic tolerances, species are further limited by a hierarchy of non-climatic factors. Abiotic factors including soil type, land use or microclimate shape distributions within otherwise climatically-suitable regions, as well as dispersal or migration (Brown *et al.* 1996). At the local scale biotic interactions can exclude or facilitate species through antagonism or mutualism (Pearson & Dawson 2003; Townsend Peterson & Soberón 2012), though some argue that biotic interactions can also affect broader-scale distributions (Godsoe & Harmon 2012; Wisz *et al.* 2013). Thus, the questions that underpin spatial ecology differ depending on scale. Spatial ecology has practical uses in many disciplines including conservation [*e.g.* optimal reserve design (Gitay *et al.* 1991), or predicting population persistence under climate change (Keith *et al.* 2008)], paleogeography [*e.g.* recreating past species' distributions (Collevatti *et al.* 2012)], and is also a key tool for understanding invasive species.

Species' distributions are dynamic and colonization of novel environments frequently occur in nature [for an extreme example, see Le Roux *et al.* (2014)], but anthropogenic influence fuelled by increasing global connectivity has moved species beyond their native ranges at unprecedented rates (Hulme 2009). Most species introduced to novel environments do not establish, and of those that do, only a small subset become invasive pests *i.e.* spread and become problematic (Richardson *et al.* 2000). Despite this, invasive species are now a serious ecological problem worldwide. Spatial ecology has obvious application in managing and preventing invasions. Such applications may include predicting spread through a landscape (Merow *et al.* 2011), or for pre-border assessment of species for import [*e.g.* Weed Risk Assessments that quantify risk using species' traits and distributions (Pheloung *et al.* 1999)]. Hotspots or risk areas for invasion can be identified for management or to monitor for new

incursions (Pitt *et al.* 2009), and preventative measures explored for potential future pests (Guichard *et al.* 2014). The latter is particularly important for agriculture as novel pests and pathogens may have devastating effects on crop yields (Pimentel *et al.* 2005). Projections of invasions may derive from species' traits (Roberts *et al.* 2011), expert knowledge (Martin *et al.* 2012; Smith *et al.* 2012) or laboratory and field data (Ross *et al.* 2008; Takahara *et al.* 2013), but increasingly, spatial modelling is the tool of choice.

1.2 Making models of reality

As a side effect of its explosion in popularity, spatial modelling is inundated by semantic confusion. Identical models can be referred to as ecological or environmental niche models (ENMs), envelope models, predictive habitat models, and bioclimatic models, all of which imply different ecological interpretations (McInerny & Etienne 2012; Warren 2012, 2013). I therefore adopt the stance of Elith and Leathwick (2009), hereafter using the more neutral term of species distribution models (SDMs). Most SDM efforts aim to map environmental suitability for a target species, or may even simulate spread over time through a landscape. However, all SDMs are approximations of reality, and there exist numerous approaches each with distinct strengths and weaknesses (Table 1.1). At the simpler end of the spectrum are top-down models, which infer species' limits by fitting responses to any number of environmental variables *e.g.* climate, soil or land use, against known occurrence locations (*correlative* SDMs). Correlative approaches are well suited for inferring broad-scale distributions, are usually static, and are particularly useful when knowledge of the species' physiology is limited (Elith 2013). However, they make a number of assumptions that cast doubt upon their realism (explained in section 1.2.2). Bottom-up approaches are considerably more complex, building predictions of range limits using knowledge of underlying physiological traits such as metabolic rates (*mechanistic models*), or vital rates such as mortality (*population modelling*). Bottom-up approaches are potentially highly realistic and accurate if correctly parameterized, but may suffer from a lack of generality, are more costly and data-intensive to implement, and are sensitive to errors in parameterization (Buckley *et al.* 2010). Between the two lie *fitted process-based* models such as CLIMEX (Sutherst & Maywald 1985), which have higher ecological realism than correlative approaches, but the user is restricted to inbuilt environmental variables with coarse grain size. There also exist hybrid models which combine bottom-up and top-down techniques [*e.g.* Brown *et al.* (2008)], and ensemble models of that generate projections from the consensus of multiple SDMs [*e.g.* Poulos *et al.* (2012)]. The suite of SDMs to choose from can appear overwhelming, and it may be tempting to assume that more complex models are better. This is not necessarily the case; the method should instead be chosen based on the question at hand (*e.g.* modelling species' actual spread vs. potential distributions) and the underlying data (*i.e.* is there sufficient knowledge to build a mechanistic model?).

1.2.1 Correlative SDMs

By far the most common methods for modelling distributions are correlative (Dormann *et al.* 2012), and hereafter I use SDMs to refer to correlative models unless explicitly stated. Correlative SDMs are popular thanks to a wealth of user-friendly software and low data requirement, and data that are required (*i.e.* occurrence records and maps of environmental variables) are often freely available (Ahmed *et al.* 2015). Each SDM differs and some have numerous settings that can be tailored to different scenarios [*e.g.* MaxEnt (Phillips *et al.* 2006)], but the general principle is the same for all. Grid layers of relevant environmental variables are chosen, and their values extracted where the species are present (and often where they are not). These data are interpreted by the underlying algorithm, inferring the species' environmental tolerances from the environmental conditions at presence (and absence) points. The resulting function is transformed back onto maps of environmental layers to give a final projection of relative suitability, which may be thresholded to predict presence or absence of the species in the landscape of interest.

The first SDMs were developed for conservation and were simple presence-only methods that created envelopes in environmental space around occurrence records, classifying any environment outside the occupied environmental space as unsuitable [*e.g.* BIOCLIM (Nix 1986), DOMAIN (Carpenter *et al.* 1993)]. Despite being used successfully in a number of studies (Booth *et al.* 2014), presence-only methods have now fallen out of favour and been replaced by more complex algorithms, capable of predicting non-linear responses and incorporating interactions between environmental variables. Most modern SDMs contrast presences with either known or assumed absences (*true* vs. *pseudo* absences) to parameterize response functions to environmental variables. Algorithms to differentiate suitable from unsuitable locations range from relatively simple generalized linear models (GLMs), to simple decision-tree approaches (CART), to machine learning (*e.g.* MaxEnt, SVM, BRTs) and recently, Bayesian techniques (Dorazio 2014). A thorough description of all SDM methods is beyond the scope of this thesis, and a number of studies have contrasted the performance of various algorithms (Elith *et al.* 2006; Hernandez *et al.* 2006; Tsoar *et al.* 2007; Jeschke & Strayer 2008; Webber *et al.* 2011). Generally, statistical approaches *i.e.* where the parameters are prescribed by the user, tend to be outperformed by machine learning models. Here, good performance is defined by the ability of the SDM to differentiate presences from absences. While machine learning approaches have higher discriminatory power, it is important to recognize that there is no “best” method – instead, certain SDMs are better suited to different applications (Table 1.1). A modeller should take into account the amount and quality of input data, the robustness of absence data, and whether the consequences are worse for under-prediction (*e.g.* invasions) or over-prediction (*e.g.* conservation). Most importantly, the species and underlying ecological questions are paramount.

Table 1.1 Broad categories of SDMs, with examples and brief description, advantages and disadvantages of each category, and suitable uses.

| Type | Occurrence Data | Algorithms | Description | Advantages | Disadvantages | Suited to modelling... | Examples |
|------------------|--------------------------|---|--|--|--|---|--|
| Correlative | Presence only (PO) | BIOCLIM ¹ DOMAIN ² HABITAT ³ ENFA ⁴ | Simple envelopes/boxcar techniques/ habitat matching around presence locations | Very low data requirement User friendly Less affected by sampling bias | No variable interactions Prone to under-fitting All variables equal No extrapolation Static | Broad scale Environmental suitability Unreliable/ no absences Few variables | (Podger <i>et al.</i> 1990; Zaniewski <i>et al.</i> 2002) |
| | Presence background (PB) | MaxEnt ⁵ MaxLike ⁶ | Machine learning, creates polynomial functions from PO data and contrasted with background, then adjusted to maximise entropy | Low data requirement User friendly High performance Variables weighted to reduce collinearity | Prone to over-fitting Sensitive to settings/ inputs Unstable when extrapolating Static | Any scale Environmental suitability/distributions Unknown survey effort Multiple variables | (Pearson <i>et al.</i> 2006; Rodda <i>et al.</i> 2011) |
| | Presence absence (PA) | Logistic regression GLM ⁷ GAM ⁸ MARS ⁹ Neural nets (ANN) Decision trees CART ¹⁰ RF ¹¹ BRT SVM | Logistic regression: fit parametric or non-parametric functions to PA data. Neural nets: interconnected neurons of variables weighted as model learns from data. Decision trees: Recursive binary splits of data into groups based on variable responses | Flexible to many applications High performance Variables weighted Prevalence can be estimated | Absence data needed Prone to over-fitting Less user friendly Highest data requirement of correlative SDMs Sensitive to bias and settings Static | Any scale Environmental suitability or distributions Well-surveyed sp. Multiple variables | (Drake <i>et al.</i> 2006; Elith <i>et al.</i> 2008) |
| Semi-mechanistic | PO, PB, PA, or none | CLIMEX ¹² | Tolerances to pre-defined variables set by user. Converts tolerances to growth/stress indices, combined to ecoclimatic index denoting suitability | Ecological meaning Stable extrapolation Absences not required Potentially dynamic Lower risk of spurious results | Knowledge of physiology advantageous Not user friendly Restricted to large grain size Less choice of variables Black box | Broad scale Environmental suitability or distributions Sp. with known traits Extrapolation | (Lozier & Mills 2011; de Villiers <i>et al.</i> 2013) |
| Mechanistic | None | Niche Mapper ¹³ | Uses thermodynamics to model body temperature and behaviour from climate and physiological data | High ecological meaning Dynamic Most stable when extrapolating Prevalence estimated | High data requirement Compounding of error possible Time-consuming Highly sensitive to inputs Not user friendly | Fine scale Well-studied sp. Known physiology Few explanatory variables | (Fort <i>et al.</i> 2010; Kearney 2012) |

1 (Nix 1986); 2 (Carpenter *et al.* 1993); 3 (Walker & Cocks 1991); 4 (Hirzel *et al.* 2002); 5 (Elith & Graham 2009); 6 (Royle *et al.* 2012) 7 (McCullagh & Nelder 1989); 8 (Hastie & Tibshirani 1990); 9 (Friedman 1991); 10 (Breiman *et al.* 1984); 11 (Breiman 2001); 12 (Sutherst & Maywald 1985); 13 (Kearney & Porter 2009)

1.2.2 When SDMs go awry

Despite the popularity of SDMs, they have been criticised for relying on questionable assumptions and debate continues as to how useful their projections are (Pearson & Dawson 2003; Hampe 2004; Pearson & Dawson 2004; Sinclair *et al.* 2010). One common assumption is that the species' niche (*i.e.* the environmental conditions that the species is capable of occupying) is stable across both space and time. If niche shifts occur, *e.g.* release from natural enemies after invasion allows occupation of novel climatic conditions otherwise inaccessible to the species (Keane & Crawley 2002), SDMs may under-predict suitable conditions. Methods exist to test for niche stability (Broennimann *et al.* 2012; Guisan *et al.* 2014) and it is recommended that niche analyses be carried out prior to modelling. A second, similar assumption is that the species is at equilibrium (*i.e.* its distribution is representative of the entire range of its environmental tolerances), and that occurrence records convey the range of the species' tolerances. While complete equilibrium never exists in nature, this becomes problematic for SDMs when non-equilibrium is severe, as often occurs during invasions (Elith *et al.* 2010). Non-equilibrium can be exacerbated by biotic interactions such as competition, and unless these correlate with environmental variables the model may make erroneous predictions (Hampe 2004; Godsoe & Harmon 2012). Many SDMs also assume that all environmental variables used are limiting and relevant to the species. The majority of SDM studies use climate variables based on temperature and precipitation, such as the Worldclim layers [(Hijmans *et al.* 2005), available at <http://www.worldclim.org>], and while these may not be physiologically limiting (*e.g.* average annual precipitation does not directly drive photosynthesis), they are assumed to correlate with limiting variables (*e.g.* evapotranspiration). Furthermore, while some SDM algorithms weight variables by explanatory power, ideally minimizing the effect of redundant variables, it remains vitally important to remove highly correlated variables and select only those which are relevant to the species (Jiménez-Valverde *et al.* 2011). When ecological meaning is disregarded in modelling decisions, spurious predictions can appear otherwise convincing (Lozier *et al.* 2009). Because of these pitfalls, the difficulty in modelling species' distributions lies not in the running of the SDM but in providing sound reasoning for modelling choices. Sadly, SDM methodologies are sometimes poorly explained and as a result it is difficult to evaluate the reliability of projections, as well as SDMs in general.

1.2.3 Complementing SDMs with real-world data

Even using best practice, SDMs are difficult to validate, further obscuring our understanding of their realism. Usually, SDMs are validated against a subset of presences and (pseudo-) absences held back from model training, using cross-validation or bootstrapping techniques. However, without sub-setting data carefully to avoid spatial auto-correlation between training and test data, these practices inflate estimates of model accuracy (Araújo *et al.* 2005). Independent validation against data in a distinct geographic region to training data is considered the gold standard, but it is rarely implemented as independent data are rarely available and costly to produce [though some notable exceptions are

described by Araújo *et al.* (2005)]. But, even independent validation does not provide definitive answers when attempting to model the hypothetical *e.g.* species' potential distributions. Testing SDMs of potential distributions against current occurrences penalizes models that predict spread to unoccupied sites, even if the SDM is correct. Models could therefore be better assessed by comparing projections with real-world performance data, within and outside of the projected suitable range. Despite calls for experimental validation of SDM predictions, it is rare in practice due to the high associated cost and effort [but see Ebeling *et al.* (2008); Elith *et al.* (2010); Sheppard *et al.* (2014)].

Though the cost of testing SDMs against real-world data is undeniably high, it is encouraged because it provides information that cannot be gathered from either technique alone (Kearney & Porter 2009; Dormann *et al.* 2012). Species' performance data, *e.g.* plant growth along climatic gradients, can provide detailed and ecologically meaningful information on limiting variables and thresholds to establishment. However, such information is usually not spatially explicit and may be difficult to apply across a landscape. On the other hand, SDMs provide spatially explicit predictions but translating outputs into estimates of species' performance, or probability of establishment, is difficult. By combining SDMs with real-world data, model realism and accuracy can be improved, providing more practical projections for management and better understanding of the target species (Franklin 2010). More generally, such methods may highlight sources of error in SDMs, how much we should trust in their projections, and where models can be improved to increase realism and accuracy. Methods for combining real-world data and SDMs vary and are discussed in detail in later chapters. Most commonly, they include either testing SDM projected suitability performance [*e.g.* Ebeling *et al.* (2008); Sheppard *et al.* (2014)] or creating a hybrid model to create more detailed and dynamic predictions, but under the assumption that the underlying SDM is correct [*e.g.* Brown *et al.* (2008); Franklin *et al.* (2014)].

1.2.4 Structure of thesis

The purpose of this thesis was to combine correlative SDM approaches with field survey and experimental data in order to test and improve model projections. This was carried out in the context of a case study, modelling climatic suitability in New Zealand for three selected non-native plant species. The themes of this thesis can therefore be divided into two categories – firstly using field data to complement SDMs, and secondly to quantify climatic limitation and predict the potential distributions of the study species in their invaded range. The applied aspect of the thesis is described in subsequent sections. The question of whether SDM projections are validated by real-world plant performance, and how these two approaches can be combined to improve forecasts, is addressed in three steps over four chapters. I develop simple climate-only SDMs for the target species, and test whether the climatic niches are conserved between New Zealand and the global distributions. The two subsequent chapters analyse field plant performance data, which is integrated into a climate-driven population model in the final data chapter. Using a novel approach, I validate SDM projections of climate suitability against predicted population growth. Probable sources of prediction error are

discussed, and model projections refined to improve agreement with the population model. This thesis is one of few studies to experimentally test SDM outputs, and demonstrates the importance of going beyond conventional validation techniques when predicting in novel climates.

1.3 Alien Crassulaceae of New Zealand

As a study system, I use introduced naturalized Crassulaceae plants in New Zealand. The Crassulaceae is a large family containing 33 genera (T'Hart 1997) with a cosmopolitan distribution and notable centres of diversity in Mexico, South Africa, the Mediterranean and Himalayas (van Ham 1995). Predominantly adapted to arid habitats, Crassulaceae plants have succulent, waxy leaves and often display xerophytic morphology (*e.g.* rosulate, mounding or matted forms). All species in the family are obligate or facultative Crassulacean Acid Metabolism (CAM) plants, with two possible exceptions (Pilon-Smits *et al.* 1996). In the CAM cycle, evapotranspiration is minimized by the stomata remaining closed during the day. An adaptation to environmental stress, CAM is most commonly associated with water limitation but light, temperature, salinity and nutrients also modulate CAM, and available CO₂ is considered the central limiting factor (Luttge 2004). Generally, CAM facilitates survival in extreme environments at the expense of lower efficiency than C₄ photosynthesis (Black 1973). It is unsurprising then, that the key centres of diversity of the Crassulaceae are extremely arid. It is precisely because they are generally adapted to hot, dry environments that this family was chosen as a study system; it was anticipated that climatic limitation might be apparent under the cooler and wetter conditions in New Zealand. Although some Crassulaceae have traditional medicinal uses (Ming *et al.* 2005; Ojewole 2005), they are usually planted for ornamental purposes. Exotic Crassulaceae were introduced to New Zealand by early European settlers, and were popular with rock garden enthusiasts (Anon 1871, 1920, 1950). The earliest mention of exotic Crassulaceae species in New Zealand is a newspaper article describing a herbal remedy using fresh *Cotyledon orbiculata* leaves (Anon 1866). Discounting hybrids, 22 non-native Crassulaceae species are now considered naturalized. New Zealand also has 13 native Crassulaceae species (all in the *Crassula* L. genus), but unlike the xerophytic introduced Crassulaceae, most natives are adapted to riparian, saline, or submerged habitats (Webb *et al.* 1988).

1.3.1 Selecting three study species

Three Crassulaceae species were selected for study based on their traits and the extent of naturalization in the region of interest. I eliminated species that, according to Webb *et al.* (1988) only exhibit vegetative spread in New Zealand (*i.e.* mature seed not seen; all three *Crassula* species, *Echeveria secunda* Booth ex Lindl., *Sedum decumbens* R. T. Clausen and *Sedum praealtum* A. DC.). I also mapped occurrences of all exotic Crassulaceae in the region of interest using herbarium data and existing survey data (full source list Table B.1). Based on the above factors I identified the three species which gave most cause for concern: *Aeonium arboreum* (L.) Webb & Berthel., *Aeonium haworthii* (Salm-Dyck) Webb & Berthel., and *Cotyledon orbiculata* (L.).

Aeonium arboreum was first described as naturalized in New Zealand in the 1950's, recorded in Dunedin (Allan Herbarium 1954) and Banks Peninsula (Healy 1959), but the genus has been present in New Zealand since the late 1800's (Anon 1871). An upright branching perennial subshrub, *A. arboreum* originates from Morocco where it occurs primarily on cliffs along the Atlantic coast (Mohammed Ater, *pers. comm.* 2011). Other than New Zealand, it is naturalized in Australia, the Canary Islands, the U.S.A. (California), Madeira and the Mediterranean. In New Zealand it occurs as far north as Auckland and as far south as Dunedin, but predominantly in dry climates close to residential areas and coastlines. Like all *Aeonium* species, its fleshy leaves form terminal rosettes, and leaf scars along the woody stems (internodes) indicate seasonal growth (Jorgensen & Olesen 2000). Vegetative growth occurs in winter, and in early spring the plant produces multiple compound inflorescences. *Aeonium arboreum*, *A. haworthii* and *C. orbiculata* all produce small (< 1 mm) wind-dispersed seeds called dust diaspores (van Rheede van Oudtshoorn & van Rooyen 1999).

Aeonium haworthii was first recorded as naturalized in Auckland (Allan Herbarium 1977). Like *A. arboreum*, it is a woody branching subshrub with terminal rosettes and annual internodes, but has a mounding habit, smaller thicker leaves and smaller inflorescences. This xeromorphic growth form is indicative of *A. haworthii*'s habitat in its native range of Tenerife (Canary Islands), where it occurs on cliffs at relatively high elevations (Lems 1960). Because it has been introduced in mostly the same regions as *A. arboreum*, the two overlap substantially in both their global and New Zealand distributions (Table 1.2). Growth also occurs in winter, but *A. haworthii* flowers later in the year than other *Aeonium* species, in early to mid-summer (Webb *et al.* 1988).

The third species, *C. orbiculata*, was first described as naturalized on Banks Peninsula (Allan Herbarium 1967). However, there is anecdotal evidence of *C. orbiculata* spreading from gardens in the region as early as 1947 (Robin Waghorn, *pers. comm.* 2010). *Cotyledon orbiculata* is distinct from the two *Aeonium* species both in distribution and biology. Its evolutionary origins are South African (Mort *et al.* 2005) and it is widely distributed across the whole of Southern Africa as far north as Angola. Within South Africa there are five varietals with distinct biogeography and habitat preferences, and as such the taxonomy is highly disputed [specifically, whether each varietal should be a separate species (Van Jaarsveld & Koutnik 2004); Ernst Van Jaarsveld, *pers. comm.* 2014]]. According to herbarium records, only *C. o. var. orbiculata* (L.) and *C. o. var. oblonga* (Haw.) DC. are present in New Zealand. *Cotyledon orbiculata* has been introduced to the same global regions as both *Aeonium* species (albeit with fewer records in the Mediterranean and none in Macaronesia), but in the USA, Australia and New Zealand it is much more widespread. One likely reason for the wide distribution of *C. orbiculata* is that unlike *Aeonium* species, it is not limited to cliffs, outcrops and bare ground – it also occurs in sparse vegetation (Webb *et al.* 1988). It is the only species of the three to be recognized by the Ministry of Primary Industries (MPI) as an unwanted organism (UO), and propagation, sale and importation of the species is prohibited without a permit (Ministry for Primary Industries 2015).

Table 1.2 Key traits of study species *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. Data on introduced ranges taken from occurrence records (source list Table A.1). Other traits collated from Webb *et al.* (1988), additional sources cited in table.

| Species | Clade (Mort <i>et al.</i> 2001) | Native Range | Other introduced ranges | Status in NZ | First record in NZ | Growth form, height | Flowering time NZ | Seed size (mm) | Pollinators & reproduction | Habitat |
|----------------------|------------------------------------|---------------------|--|--------------------------------------|---|---------------------------------|----------------------|-------------------|--|--|
| <i>A. arboreum</i> | <i>Aeonium</i> | Morocco | Australia Balearic Is. Canary Is. Madeira Malta N.Z. Portugal Scilly Is. Spain U.S.A. | Naturalized No restrictions | Wellington - Newspaper; horticultural society notes (Anon 1871) | Upright subshrub 20-70 cm | Jul-Oct** | c. 0.5 | Generalist insects (Jorgensen & Olesen 2001) Wind, selfing (Alamo <i>et al.</i> 1996) Veg. spread | Coastal cliffs Volcanic rock Low scrub Sand Rocks Loess banks |
| <i>A. haworthii</i> | <i>Aeonium</i> | Tenerife | Australia France N.Z. Spain U.S.A. | Naturalized No restrictions | Wellington - Newspaper; horticultural society notes (Anon 1871) | Mounding subshrub < 60 cm | Oct-Dec (Feb)** | 0.6 – 0.7 | Generalist insects (Jorgensen & Olesen 2001) Wind, selfing (Alamo <i>et al.</i> 1996) Veg. spread | Coastal cliffs Steep banks Rocks Lava rubble Low open scrub Loess banks |
| <i>C. orbiculata</i> | <i>Kalanchoe</i> | Southern Africa* | Australia Corsica N.Z. Spain U.S.A. | Naturalized, Unwanted Organism | Nelson – Newspaper; herbal remedy (Anon 1871) | Upright subshrub < 50 cm | Dec-Jun** | 0.5 - 0.8 | Birds, selfing (Zietsman 1998) Veg. spread | Coastal cliffs Beaches Steep banks Rock outcrops Low scrub Dry depleted grassland |

* Known occurrences: South Africa, Lesotho, Namibia, Swaziland, Mozambique, Angola, Zimbabwe.

** According to Webb *et al.* (1988). In the study region of Banks Peninsula *A. arboreum* is said to begin flowering in midwinter, but personal observations (JP) indicate peak flowering occurs around November-December in the study populations, similarly *A. haworthii* was observed to flower from January-March, and *C. orbiculata* from January-April (peaking in February).

Prior knowledge and specific traits of the three study species are described in detail in the following chapters as they become relevant. However, little research has been carried out regarding the ecology of any of the three, and save for one Masters' thesis on *C. orbiculata* (Nghindinwa 2009), the species have not been studied in New Zealand. There have been occasional small-scale studies of the species' cold tolerances and fecundity in their native ranges (Lösch & Kappen 1981; Van Collier & Stock 1994; Alamo *et al.* 1996; Zietsman 1998), but it is clear that there is insufficient prior information on any of the three species to assess their climatic limits in New Zealand.

1.3.2 Banks Peninsula

The majority of this thesis focusses on Banks Peninsula, Canterbury, a coastal volcanic region of 1150 km² situated south-east of Christchurch. It is bounded by Kaitorete Spit in the west (- 43.856, 172.378 decimal degrees WGS 1984), Mount Pleasant in the North (- 43.555, 172.715), Le Bons Bay in the East (- 43.742, 173.102) and Waihuakina Bay in the South (- 43.898, 172.947). The region was selected because it is a hotspot for alien Crassulaceae; 15 of the 22 species in New Zealand are naturalized there, and the cliffs near Sumner and Lyttelton were among the first locations where many were described as naturalized (Healy 1959). The successful establishment of the Crassulaceae is likely due to a relatively warm and dry climate in the northern bays (where most populations are), combined with ample suitable habitat – specifically, coastal cliffs, rock outcrops, roadside cuttings and sparsely vegetated slopes (Webb *et al.* 1988). As the species are ornamental, garden escapes are the most likely invasion pathway, and although most species appear to have just a few small populations, local experts have expressed concern over continued spread and some species are unofficially controlled (Di Carter, Chris Challies, *pers. comm.*, 2010). On Banks Peninsula, dense populations of *A. arboreum* are visible on cliffs and roadside cuttings (Figure 1.1a) but are mainly limited to areas surrounding the towns of Sumner and Diamond Harbour, and it is the least widespread of the three species. *Aeonium haworthii* occurs in many of the same locations as *A. arboreum* but is more widespread, reaching further around the northern coastal cliffs than its congener. *Cotyledon orbiculata* is the most widespread of the three on Banks Peninsula. It has near-continuous populations on the coastal cliffs between the northern and eastern bays, and there are occasional large populations in grassland (Figure 1.1c).

Invasions are of particular concern on the Peninsula because it is known as Canterbury's biodiversity hotspot, boasting a number of locally endemic plants and invertebrates (Wilson 1986). Rock outcrops, prone to invasion by the non-native Crassulaceae, are refugia for 50% percent of the region's endemics (Wiser & Buxton 2009), and the coastal volcanic cliffs have been recently recognized as a naturally uncommon ecosystem (Holdaway *et al.* 2012). Despite the concern over future regional spread of alien Crassulaceae, their current and potential distribution limits are unknown and their climatic tolerances have been largely unexplored. Banks Peninsula's steep terrain provides a useful backdrop for studying the species' climatic tolerances, as the highest elevations are likely too cold and wet for these warmth-loving xerophytes. While the northern bays of the Peninsula are ostensibly suitable, the inland peaks reach some 919 metres above mean sea level (MASL) and average

precipitation varies from 600-2000 mm per year (Wiser & Buxton 2009). Banks Peninsula is therefore a practical and ecologically relevant choice for studying the climatic limitation of the study species in New Zealand.

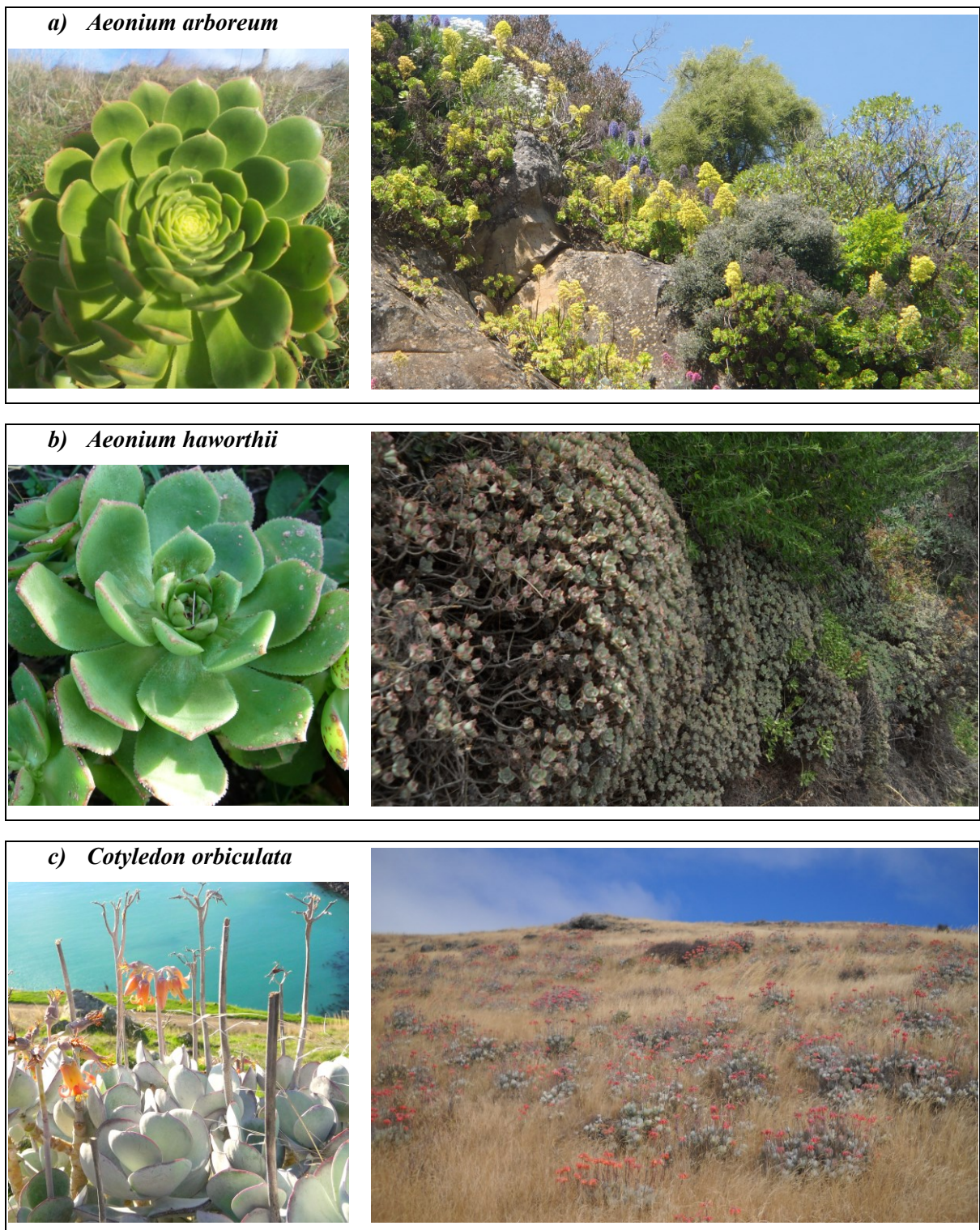


Figure 1.1 Photographs of study species a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata*, showing individual plants (left) and naturalized populations (right). All photographs taken on Banks Peninsula, Canterbury, New Zealand.

1.4 Thesis objectives

The specific objectives addressed in this thesis are:

1. Are the current distributions of *A. arboreum*, *A. haworthii* and *C. orbiculata* in New Zealand climatically distinct from their distributions elsewhere, and what are their potential distributions as estimated using SDMs? (Chapter 2)
2. Is there evidence that climate limits the distributions of these species on Banks Peninsula, and how do demographic processes correlate with climate within and beyond the species' current distributions? (Chapter 3)
3. Is variation in fecundity in naturalized populations on Banks Peninsula related to variation in local climate? (Chapter 4)
4. How well do SDMs predict the actual performance of the target species on Banks Peninsula, and can field data be used to improve SDM projections? (Chapter 5)

To answer my first objective, I use SDMs to estimate the potential distributions in New Zealand of the study species, firstly using climate alone, then constrained by non-climatic factors. I test whether the species' distributions in New Zealand are climatically novel compared with their distributions elsewhere, and explore the implications for ongoing spread. In the remaining chapters I focus on climatic limitation on Banks Peninsula, firstly using transplant experiments to test how germination, growth and survival of the species varies along an elevation gradient. The field experiment also investigates how close the three species are to their climatic limits in the region. In the fourth chapter, I test whether fecundity (flowering and seed production) varies among naturalized populations in the region. Finally, I synthesize the information in the previous chapters into a climate-driven population model, and test climate-only SDMs against predicted performance. I also refine regional projections of climatic suitability for the species and explore the relative risk each species poses to Banks Peninsula. To my knowledge, this is the first study of the target species across multiple stages of their life cycles, and the first to test their climatic limitation in New Zealand.

1.5 Thesis style

The thesis data chapters (Chapters 2-5) are written in the style of self-contained manuscripts, with the intention of publication at a later date. Each chapter addresses a separate objective, as described above. I have endeavoured to minimize any resulting repetition. The final chapter discusses the findings as a whole, with a focus on potential spread of the study species on Banks Peninsula.

Chapter 2 – Modelling the global and New Zealand niches of alien Crassulaceae indicates invasion of novel climates

2.1 Abstract

Correlative species distribution models (SDMs) are increasingly used to identify suitable environments where non-native species might establish. Typically, SDMs fit response functions to climatic variables using species' occurrence data. However, non-climatic factors often prevent establishment in otherwise suitable climates, thus restricting distributions in geographic and climatic space. Such discontinuities can lead to spurious model projections that seriously affect estimates of species' potential distributions. This chapter presents a case study modelling climatically suitable habitat for three non-native species naturalized in New Zealand, all of which have distributions that are strongly influenced by non-climatic factors. The study species, *Aeonium arboreum*, *Aeonium haworthii* and *Cotyledon orbiculata*, are succulent xerophytes with specific habitat requirements (predominantly bare rock) and native ranges that differ climatically to New Zealand (Morocco, Tenerife and South Africa, respectively). To provide national-scale assessments of suitable habitat in the introduced range, a three-step method is applied. First, climatic novelty is assessed in the New Zealand occupied ranges versus the global distributions, and discontinuities shown in the species' occupied climatic niches. Second, informed by the niche analyses climate envelope models are trained with data from outside of, and then including, New Zealand, to project suitability in the introduced range. Third, to refine projections of at-risk habitat, model outputs are constrained by non-climatic factors, using knowledge of the species' biology and inferential spatial analyses. Results show that *C. orbiculata* poses a larger threat to New Zealand than both *Aeonium* species, and that while models classify much of the country as climatically suitable, availability of suitable habitat for *Aeonium* species is low. New Zealand represents an expansion of the global occupied niche for all three species, suggesting that further expansion into novel climates cannot be discounted. This is the first study of the potential distributions of the three species in New Zealand, and demonstrates a method for modelling distributions of species that are strongly limited by non-climatic factors.

Keywords: Crassulaceae, invasions, New Zealand, niche, SDM, BIOCLIM

2.2 Introduction

Biological invasions are a pressing ecological issue worldwide (Sutherland *et al.* 2013). A vital component of prevention and control of invasions is estimating where non-native species may encounter suitable environmental conditions for establishment, and pest risk modelling is integral to this process (Venette *et al.* 2010). Species Distribution Models (SDMs) were originally developed for use in conservation biology (Booth *et al.* 2014), although they are now commonly used to estimate potential distributions of non-native species (Elith & Leathwick 2009) despite problems with

extrapolation into novel climates (Sutherland & Bourne 2009; Webber *et al.* 2012). Although most commonly used to infer climatic suitability for target species [e.g. Di Febbraro *et al.* (2013); Peña-Gómez *et al.* (2014)], SDMs correlate any number of environmental variables with species' occurrence data to infer suitable habitat [e.g. Randin *et al.* (2009); Vicente *et al.* (2011)]. However, SDMs rely on a number of assumptions that make their application to invasions problematic.

Two concepts central to SDMs, particularly when modelling invasions, are *niche* and *equilibrium*. The term *niche* encompasses many concepts (Grinnell 1917; Elton 1927; Hutchinson 1957), but commonly indicates the conceptual space in n dimensions along axes of limiting environmental variables that a species may potentially occupy as a result of its biological traits. This is similar to Hutchinson's *fundamental niche* (1957), which is constrained by biotic and other factors resulting in a *realized niche*. A species at equilibrium, meanwhile, occupies all suitable areas within the geographic region of interest, and while species are rarely present in all suitable locations, extreme non-equilibrium distributions can misrepresent species' climatic limits (Araújo & Pearson 2005). The niche and equilibrium of the species being modelled are important, as most SDMs assume that a species' geographic distribution reflects its niche, that the niche does not change over space or time (*niche stability*), and that the species is sufficiently close to equilibrium to infer climatic tolerances (Wiens *et al.* 2009). Unfortunately, assumptions of niche stability and equilibrium are often violated during invasions (Broennimann & Guisan 2008; Elith *et al.* 2010). During the early stages of invasion, spread may be ongoing and the species will be far from equilibrium (Sutherland & Bourne 2009; Václavík & Meentemeyer 2012). Furthermore, although some studies suggest that niche conservatism is the norm (Petitpierre *et al.* 2012; Strubbe *et al.* 2013), niche shifts, for example through release from natural enemies (Keane & Crawley 2002), have been posited in a number of systems (Broennimann *et al.* 2007; Gallagher *et al.* 2010; Langer *et al.* 2013). It is therefore a vital first step when modelling the distribution of a species to determine whether niche stability and equilibrium is a reasonable assumption. If not, model uncertainty is high, as extrapolation into novel climates is inherently risky (Webber *et al.* 2011; Mesgaran *et al.* 2014). If a species' climatic niche in the invaded range is otherwise unrepresented by its distribution elsewhere, it is difficult to infer whether continued expansion into novel climates will occur.

Even in the absence of niche shifts and extreme non-equilibrium, estimating climatic suitability using SDMs becomes difficult if a species is strongly limited by non-climatic factors (Sutherland *et al.* 2007). Factors such as natural enemies, dispersal limitation and land use affect distributional patterns, and are nested hierarchically within the climate envelope (Brown *et al.* 1996; Mackey & Lindenmayer 2001). Such constraints can cause fragmentation (*disjunct distributions*) over both geographic and climatic space, sometimes likened to "Swiss cheese" (Brown *et al.* 1996; Kriticos *et al.* 2015). Whilst all species experience some degree of non-climatic limitation (Brown *et al.* 1995), in extreme cases, SDMs may be unable to reconcile populations of the same species as having the same climatic requirements (Godsoe 2010). This is because most correlative SDMs fit climatic response curves to

frequency distributions of occurrence data, and these responses may be biased by discontinuities in the species' distributions, *e.g.* those caused by non-climatic limitation. Depending on the types of functions fitted to the occurrence data, many SDMs will under-predict the range of suitable climates in such situations (Webber *et al.* 2011). Under-predicting suitable habitat is undesirable when modelling invasions, as it under-estimates pest risk (Sutherst 2013). For an illustration of how non-climatic limitation may cause SDMs to under-predict, see Section A.1 and Figure A.1. Despite the problems of niche instability, non-equilibrium and disjunct distributions when using SDMs to model invasions, there are many available methods to minimize the associated biases. These might include sub-sampling data or correcting for sampling bias (Kramer-Schadt *et al.* 2013), modelling disjunct populations separately or comparing models fitted to different combinations of ranges (Wharton & Kriticos 2004; Fourcade *et al.* 2014), testing for novel conditions (Elith *et al.* 2011; Mesgaran *et al.* 2014), and selection of an appropriate model for the task (Elith & Graham 2009). There is no “one-size-fits-all” method, but it is clear that failure to investigate or account for a species' distribution in climate space can seriously compromise the reliability of model projections.

The goal of this study was to model potentially suitable habitat for three non-native succulent plants naturalized in New Zealand, informed by their known global distributions and climatic niches, at a scale suitable to national-scale pest management. All three species are in the Crassulaceae family: *Aeonium arboreum*, *A. haworthii*, and *Cotyledon orbiculata*. Their establishment in New Zealand is surprising due to the comparatively hot and dry conditions of the native ranges. They originate from Morocco, Tenerife and South Africa, respectively, and these origins are reflected in their utilization of Crassulacean Acid Metabolism (CAM) photosynthesis, commonly an adaptation to arid conditions (Luttge 2004). They are present in a number of localities in both the North and South Islands of New Zealand, and localized spread appears to be ongoing, partly facilitated by high output of viable seed (Webb *et al.* 1988). This is of concern to biosecurity managers as they form dense populations that potentially threaten native species, and *C. orbiculata* is poisonous to a number of animals (Botha & Penrith 2008).

In addition to hypothesized climatic limitations, non-climatic factors may strongly influence all three species' potential distributions in New Zealand. Literature suggests that they predominantly occur on bare surfaces such as cliffs, roadside cuttings and rock outcrops, exclusively so for both *Aeonium* species (Webb *et al.* 1988; Bramwell & Bramwell 1990). It is also thought that they are shade intolerant (Vogan 2003), especially *C. orbiculata*, which produces photoprotective leaf wax (Barker *et al.* 1997). Land use may also be important for *C. orbiculata*, which can occur in sparse vegetation (Webb *et al.* 1988; Van Jaarsveld & Koutnik 2004). Strong non-climatic limitation is ecologically plausible as CAM photosynthesis is an adaptation to multiple environmental stressors, *e.g.* water limitation, allowing plants to occupy stressful niches at the cost of lower maximum potential photosynthetic efficiency. Hence, CAM plants are less competitive than their C3 and C4 counterparts when environmental resources are relatively abundant (Black 1973; Grime 1979; Luttge 2004). The

target species might therefore be restricted to specific habitats by an inability to compete in other environments, considerably altering their potential distributions in New Zealand. To provide a useful estimate of environmental suitability for all three species, both climatic and non-climatic factors are therefore taken into account.

2.2.1 Aims

1. To investigate whether the global realized niches of *A. arboreum*, *A. haworthii* and *C. orbiculata* are conserved in New Zealand.
2. Based on the species' climatic niches, to use an appropriate SDM to infer suitable climatic conditions in New Zealand.
3. Using *a priori* knowledge of the target species and inferential spatial analysis, to characterize habitat suitability according to non-climatic factors in New Zealand, and constrain projected climatic suitability by habitat to estimate overall environmental suitability.

2.3 Methods

2.3.1 Study species

The study species are each native to a distinct region but all are adapted to hot, semi-arid climates; *A. arboreum* is native to Morocco, *A. haworthii* to Tenerife (Canary Islands), and *C. orbiculata* to South Africa (Webb *et al.* 1988). Other areas of documented naturalization for all three species include California (U.S.A.) and Australia (Fuller & McClintock 1988; Hussey *et al.* 2007). Climatic limitation is expected under the comparatively cool and wet conditions of New Zealand, but the full extents of the species' tolerances are unknown. While horticultural guides list all three as frost sensitive (Vogan 2003), studies report freezing avoidance and acclimation to around -10 °C in closely-related *Aeonium* species and *C. orbiculata* (Lösch & Kappen 1981; Van Coller & Stock 1994). The ecophysiology of the three species has been occasionally studied in their native ranges (Alamo *et al.* 1996; Barker *et al.* 1997), and there are no studies from their introduced ranges. Their potential distributions in New Zealand are therefore highly uncertain. All three species are present in both the North and South Islands, forming locally dense populations along coastlines. Their distributions in New Zealand appear to be influenced by human activity, as they commonly occur close to cities and residential areas. This perhaps reflects propagule pressure from gardens (Healy 1959), a common factor in plant invasions (Groves *et al.* 2005; Hulme 2007, 2011). There is potential for ongoing colonization due to the species' high fecundity (Alamo *et al.* 1996; Zietsman 1998), facultative vegetative reproduction and high population density, along with wind dispersal (van Rheede van Oudtshoorn & van Rooyen 1999). Regional spread is apparent along coastal cliffs and rock outcrops, leading to concern over the species' potential impacts in habitats that provide refugia for endemic and threatened species (Wiser & Buxton 2009). *Cotyledon orbiculata* is now an unwanted organism under

the Biosecurity Act (Ministry for Primary Industries 1993), meaning that sale and propagation of the plant is prohibited, and it was under official surveillance in Auckland until 2012 (Auckland Regional Council 2007).

2.3.2 Distribution data

Global species' occurrence data was collated from online data portals, herbarium records, botanical journals, vegetation surveys and personal communication with local residents and experts (for full source list, see Table A.1). Where occurrence locations were unclear, the surrounding area was searched using Google Street View (<https://maps.google.com>). This also resulted in 19 additional presences across the three species where they had previously not been recorded. Harvesting occurrence data using Google Street View was tested by Rousselet *et al.* (2013) and found to be robust. Some varieties of *C. orbiculata* were excluded from the dataset because they are not currently present in New Zealand and have distinct biogeographic patterns, namely, *C. o. var. flanganii* (Schönl. & Baker f.) Töelken, *C. o. var. dactyloopsis* (L.) Töelken and *C. o. var. spuria* (L.) Töelken. The variety *C. o. var. dactyloopsis* occurs at high elevations (Scott & Springfield 2004) and *C. o. var. spuria* inhabits depressions in riverbanks (Mort *et al.* 2005). Records where variety was unknown were included. From Morocco, nine out of the ten *A. arboreum* records were obtained through personal communication with local experts. Canary Island data for *A. haworthii* were obtained primarily through a biodiversity survey of habitat types (Ministerio de Agricultura Alimentación y Medio Ambiente 2005) and a floristic guide to the Canary Islands (Bramwell & Bramwell 1990), which broadly describes the regions in which *A. haworthii* is found. The survey data are polygon maps showing *Aeonium* dominated habitat, including *A. haworthii*. Polygons were converted to a 30 arc-second raster and the centroid of each cell containing *Aeonium* converted to point locations, constrained within regions that Bramwell and Bramwell (1990) describe as containing *A. haworthii*.

The resulting global occurrence datasets were cleaned and resampled, to partly reduce the effects of biased and auto-correlated data in the calculation of the goodness of fit statistics. Occurrence data were cleaned by removing records where their associated description and location data indicated that the plants were likely to be indoor cultivars. The cleaned point location records were then converted to WGS 1984 latitude/longitude coordinates, then resampled to centroids of 30 arc-second grid cells containing presences, to match the grain size of environmental layers. The resulting occurrence datasets contained 198 records for *A. arboreum*, 171 for *A. haworthii* and 725 for *C. orbiculata* (Figure 2.1). Despite resampling, there is notably a strong bias towards Southern Africa for *C. orbiculata*. In New Zealand there is a bias towards the region of Banks Peninsula for all three species, which contained 52% of all New Zealand *Aeonium* records, and 75% of all New Zealand *C. orbiculata* records. While Banks Peninsula contributes only 9, 12 and 8% of global occurrences of *A. arboreum*, *A. haworthii* and *C. orbiculata* respectively, the potential bias is an important consideration in model selection and interpretation of outputs.

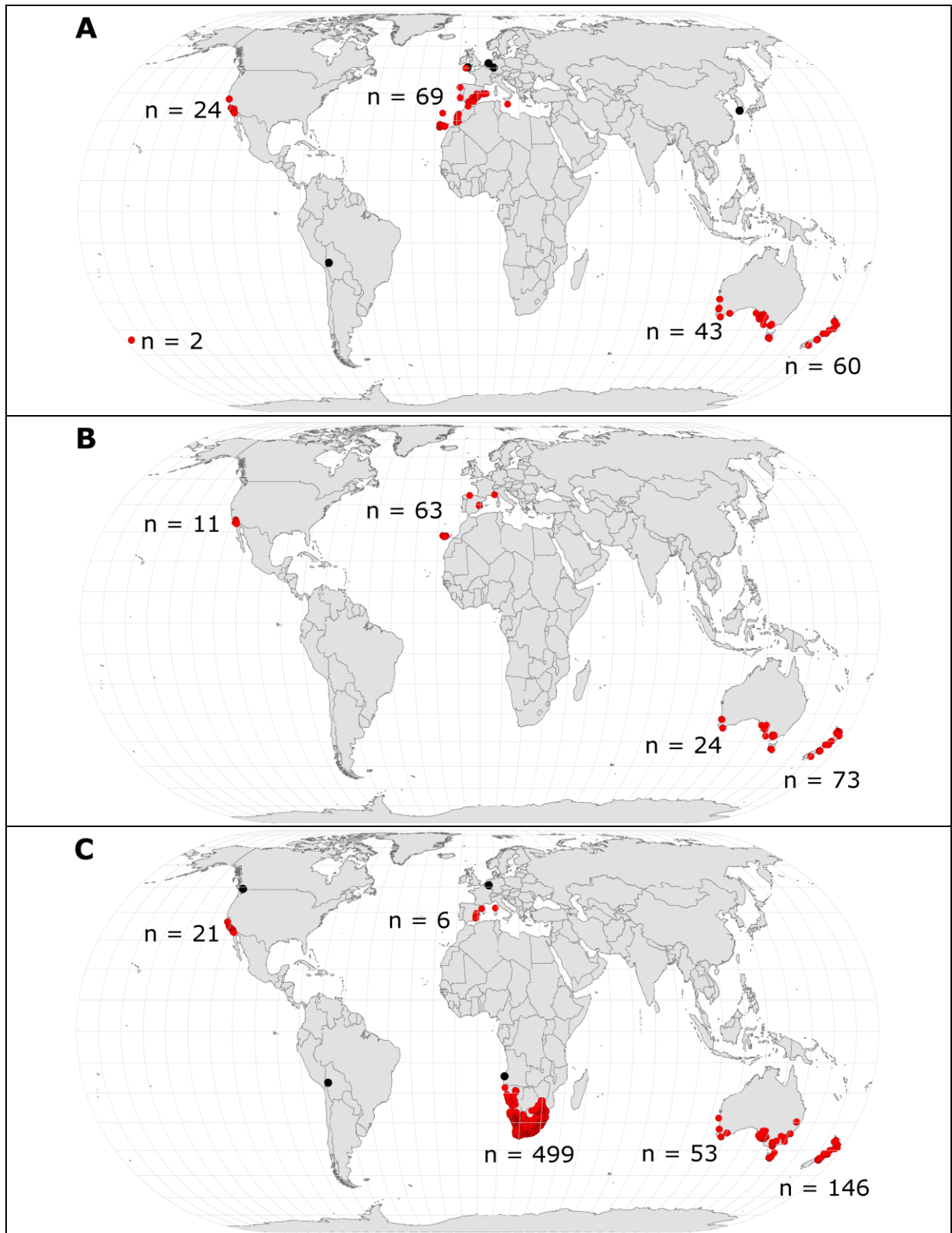


Figure 2.1 Known global distributions of a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata*, after resampling onto a 30 arc-second grid. Number of presence points per region labelled. Red points were used for model training; black points removed as suspected to be plants in cultivation.

2.3.3 Environmental variables

Nineteen 30 arc-second bioclimatic variables [(Hijmans *et al.* 2005), hosted at www.worldclim.org], were available for niche analyses and SDMs. Because all variables contribute equally in the niche analyses and the chosen SDM, it was particularly important to choose a subset based on the species' known requirements and the correlation between variables. Pearson's correlation coefficient was calculated for all 19 variables within all countries containing presences, and highly correlated variables ($r > 0.8$) were removed. In addition, histograms of the frequency distributions of the 19 variables across all presence locations were compared with histograms across the global background. Variables that poorly distinguished the occupied range from the global background were discarded (see Figure A.2 for histograms of the final variables).

Five common climate variables were selected for all three species, since they have similar geographic distributions and ecophysiology: mean temperature of the warmest quarter (BIO10), mean temperature of the coldest quarter (BIO11), precipitation of the wettest quarter (BIO16), precipitation of the driest quarter (BIO17), and precipitation of the coldest quarter (BIO19). The variables BIO10 and BIO11 were chosen as the species are adapted to hot environments and are believed to be frost-sensitive (Médail & Quézel 1999; Vogan 2003; Royal Horticultural Society 2014). The variable BIO16 was chosen as desert succulents often depend on seasonal pulses of rainfall (Ogle & Reynolds 2004), and BIO17 as it is thought that for at least one of the species flowering time aligns with the dry season (Harris & Reynolds 2004). Furthermore, their inflorescences are large and fleshy (Zietsman 1998), and personal observations in New Zealand revealed that in wet environments, flowers of *C. orbiculata* may rot. Hence, they may require a distinct dry period to facilitate dehiscence. Finally, BIO19 was included as succulent species are expected to be sensitive to high rainfall under cooler temperatures, when potential evapotranspiration is lower and plants may become waterlogged. This is especially likely for *C. orbiculata*, which commonly experiences hot, dry winds immediately after high rainfall in the native range (Eller & Ferrari 1997).

2.3.4 Niche analysis

Prior to calibrating an SDM, it is good practice to perform a niche analysis to highlight issues of niche shifts, non-analog climates and occupancy patterns that may affect model performance. Niche analyses were used to assess whether New Zealand is climatically novel compared with the species' global distributions, following the methodology of Broennimann *et al.* (2012). This technique plots the two realized niches of interest in climate space against user-defined background areas, where niches are smoothed to minimize occurrence density bias. In addition, it calculates the proportion of niche equivalency, or overlap [D; (Schoener 1970)], and similarity between the niches. Statistical significance of equivalency is tested by pooling and randomly splitting all occurrences 100 times and D calculated for each split. If the observed D is outside 95% of simulated values, the niches are considered significantly non-equivalent. Similarity is measured by randomly sampling within the

climate space of one region, and calculating D against the observed niche in the other. This process is repeated 100 times for each region, and if observed D is greater than 95% of simulated values the niches are considered more similar than by chance.

Regions of interest were defined as the global range (the world excluding New Zealand) and New Zealand. The background area should represent the climate where the species could reasonably be able to colonize, because including climate extremely different to the niche, or not available to the species because of geographic barriers, can exaggerate niche divergence (Barve *et al.* 2011). Background area is often defined using known dispersal distances and barriers to dispersal, but because all three species' dispersal abilities are unknown and their propagation is not restricted outside of New Zealand, it was not practical to use such an approach. Instead, within New Zealand the five bioclimatic variables were randomly sampled at 10 000 points, no less than 1 km apart within all islands containing occurrence records for at least one species (the North, South, Stewart and Chatham Islands), assuming they are likely to have been planted in gardens throughout the country. The global background was delimited to include only countries in which we had occurrence records. Sampling was further restricted to within the same Köppen - Geiger classification as each species is found (see Table A.2) to avoid including extremely different climates to the species' niches in large countries *e.g.* Alaska (USA). Within these regions, up to 50 000 points no less than 10 km apart were randomly generated for sampling background climate.

2.3.5 Model of climate suitability

Due to the patchy global distributions of the target species and distinct climatic conditions in New Zealand compared with the native ranges, SDMs that generate climatic response curves based on occurrence records were likely to under-predict suitable habitat (as illustrated in Figure A.1). Consequently a simpler SDM was chosen, BIOCLIM (Nix 1986), as it does not derive response curves and it is largely unaffected by clustering or sampling biases within the occupied climate space.

BIOCLIM was the first SDM to be widely used, and was a popular modelling tool for over 20 years (Booth *et al.* 2014). It is a presence-only model, based on Hutchinson's *n*-dimensional niche concept (Hutchinson 1957) and loosely on Shelford's Law of Tolerance (Shelford 1931). BIOCLIM defines a rectilinear hypervolume around all known presences with each climatic variable as a distinct dimension, and the outer limits are defined by the climatic extremes associated with species occurrence records. Within this hypervolume, it calculates a percentile distribution of occurrences for each variable, and a BIOCLIM score between 0 and 1 is derived from the distance to the 50th percentile or median, *i.e.* the centre of the rectilinear envelope. Low scores indicate greater distance, and the minimum BIOCLIM score of all variables is used as the final score for each grid cell. Scores of 1 are rarely observed, as it signifies that all environmental variables are equivalent to the 50th percentile of the species' distribution, while the commonly observed zero score indicates that one or more variables is outside of the 5th - 95th percentile range (Hijmans *et al.* 2014).

In recent years BIOCLIM has declined in use, overtaken by more complex tools such as MaxEnt (Phillips *et al.* 2006). It has been criticized for low specificity and a tendency to over-predict, a product of the rectilinear definition of the niche (Townsend Peterson 2011). In addition, BIOCLIM cannot model interaction effects between variables, and a number of studies have reported low AUC (Fielding & Bell 1997) and Kappa (Cohen 1960) relative to other models (Elith *et al.* 2006; Drake 2014; Tassarolo *et al.* 2014). While BIOCLIM is clearly unsuited to many SDM studies, the degree of model complexity should be grounded in the ecological question and characteristics of the underlying data (Merow, Smith, *et al.* 2014). BIOCLIM's coarse envelope, defined by the species' extremes, is better suited to modelling the study species' potential distributions than complex models with functions likely to over-fit and under-predict suitable habitat.

Three BIOCLIM models were run for each species in the R package *dismo* (Hijmans *et al.* 2014; R Core Team 2014), using the same five bioclimatic variables as for the niche analyses. BIOCLIM's two-tailed settings were chosen (*i.e.* cells are marked unsuitable where climate variables fall above the maximum where the species occurs, and below the minimum). The first models were trained on global data (world occurrence data excluding New Zealand), to determine whether distributions in New Zealand were predictable based on the global range alone. The second models were trained on five random subsets of total data (global data plus New Zealand), each comprising 80% of all available data, setting the remaining 20% aside for cross-validation. The mean predicted value of all five projections was then calculated. The third, final models were trained on one run with total data, which were compared with the cross-validated models before being refined by non-climatic constraints.

2.3.6 *A priori* non-climatic constraints

The study species' biology suggests that non-climatic factors contribute strongly to environmental suitability, and non-climatic range limitation was evidenced by the species' clustered distributions in geographical and climatic space. Although over-prediction is preferable to under-prediction when modelling invasions, over-prediction risks unnecessary spending on management of low-risk species (Guisan *et al.* 2013). The final New Zealand BIOCLIM projections were therefore constrained by non-climatic factors to provide more realistic projections of environmental suitability for the target species than those with climate alone. Two separate masks mapping non-climatic limiting factors, hereafter referred to as "habitat suitability" masks, were created for New Zealand. One mask was created for the two *Aeonium* species and one for *C. orbiculata*, as the specific non-climatic limitations appear to differ between the two. Although all three species grow on bare surfaces such as cliffs, outcrops and roadside cuttings (Webb *et al.* 1988), *Aeonium* species are exclusively found in these habitats whereas *C. orbiculata* may grow in sparse vegetation such as grasslands (Van Jaarsveld & Koutnik 2004).

Suitable habitat for *Aeonium* species was defined *a priori* according to knowledge of the species and its distribution, taken from floras (Webb *et al.* 1988; Bramwell & Bramwell 1990), local experts (Mohammed Ater, *pers. comm.* 2011) and habitat descriptions associated with herbarium records.

Suitable habitat included cliffs (sea and inland), bare rock (including coastal rocks and outcrops), quarries, embankments and road cuttings, as these are where the species are most commonly described. In addition, urban and residential areas were included as *Aeonium* species are grown and sold as ornamental plants, and are therefore likely sources for naturalization. All aforementioned features were selected from the NZ Mainland Topo50 topographic shape files (CC-BY Land Information New Zealand, <http://creativecommons.org/licenses/by/3.0/nz/>), then converted to a 30 arc-second raster layer with a buffer of 1 km. This allowed for unmapped small cliffs and outcrops, under the assumption that large rocky habitats are likely to have similar microhabitats in the surroundings, and gave flexibility to allow for geo-referencing errors in occurrence records.

2.3.7 Land use constraints for *C. orbiculata*

Land use was hypothesized to be an important additional habitat factor for *C. orbiculata*, as it is known to grow in sparse vegetation (Webb *et al.* 1988), and, in the native range at least, likely co-occurs with livestock as it regularly causes stock poisonings (Botha & Penrith 2008; Botha 2013). The importance of land use was tested using a similar method to that used by Kriticos *et al.* (2015), first subdividing known presence locations into five major regions: Southern Africa (S. Africa, Lesotho, Swaziland, Namibia, Angola and Mozambique); Europe (Spain and Corsica); the U.S.A.; Australia; and New Zealand. Presence points were spatially intersected with the FAO Land Use Systems of the World (LUS) dataset (Nachtergaele & Petri 2008), with presence data resampled to 5 arc-minutes to correspond with the layer. The LUS divides land use into 37 categories describing dominant vegetation (forest, grassland, shrub, *etc.*), livestock density (low, moderate or high), agricultural activities and irrigation, in addition to urban areas and water bodies.

Because of the possible association of *C. orbiculata* with livestock, the importance of grazing activities was investigated by spatially intersecting occurrence points with density of sheep, goats and cattle provided by the FAO's Gridded Livestock of the World v1.0 (Robinson *et al.* 2014). This dataset gives projected estimates of heads per km² based on census data from 2005, at a 3 arc-minute resolution. Densities at occurrence points were compared with a randomly sampled background of up to 500 000 points no less than 10 km apart, in each of the five major regions. I also attempted to investigate whether soil type or underlying geology was important, but due to limited data in some global regions and the wide range of soil and rock types *C. orbiculata* is found on, there was no discernible pattern. These covariates may be better suited to an *a priori* analysis as used for *Aeonium* species, but would require initial knowledge of the species' preferences.

To minimize the likelihood of geo-referencing error and microhabitat affecting land use constraints for *C. orbiculata*, results of the spatial analysis were tested for statistical significance. The one-tailed binomial statistic (Webber *et al.* 2011) was calculated for land use classes in each of the five regions. The statistic estimates the probability of the observed patterns arising by chance using the proportion of occurrences in the region falling within a given land use class, and the proportional area between

0 and 1 of each land use class in the region. Because of the high number of occurrences and large areas involved, a threshold p-value of 0.01 was chosen for significance.

The analyses revealed that *C. orbiculata* was significantly more likely than chance to occur in a range of land use classes in both the native and invaded ranges, but predominantly those with moderate to high livestock density (Figure A.3). Urban land use classes were also statistically significant in all areas. In New Zealand, Australia and the native range, the upper quartile of livestock density was higher at *C. orbiculata* occurrence points than the overall background, especially noticeable for sheep (Figure A.4). As this could be a sampling artefact due to higher overall sheep density in New Zealand, the same analysis was run at *Aeonium* occurrence locations, and the same patterns did not occur (see Figure A.5 and Figure A.6). In Australia the observed patterns may be biased by the large expanse of desert, so no inferences should be made in this region. It is important to note that the FAO data are coarse-scale, and that *C. orbiculata* also occurs on coastal cliffs and urban areas where livestock density is zero, adding noise to the data.

To provide finer-scale analysis for New Zealand, the spatial intersection was redone using the New Zealand Land Cover Database (LCDB) v4.0 (Ministry for the Environment & Landcare Research 2014) and farm type [Agribase Enhanced LCDB2™ 2006. (ASUREQuality 2006)]. The LCDB classifies land into 43 hierarchical classes based on broad characteristics (e.g. grassland, urban), with finer scale sub-classifications (e.g. evergreen, urban parks), and is derived from satellite images taken between 2011 and 2013. Agribase, meanwhile, classifies farmland into categories (e.g. sheep grazing, dairy) based on census data. These polygon layers were converted to 30 arc-second rasters to correspond with occurrence data, using maximum combined area. The frequency of occurrences in each class were tested for significance using the one-tailed binomial statistic with a $p < 0.01$ threshold. The results were similar to the global analysis, although the class descriptions themselves are different. In New Zealand, *C. orbiculata* was significantly likely to occur in both high-production grassland and low production grassland, mixed exotic shrubland and built-up areas (Figure A.7a, Table A.3 for class descriptions). The Agribase analysis showed that within agricultural land, *C. orbiculata* was significantly likely to occur only in pasture grazed by sheep or mixed sheep and beef (Figure A.7b).

To create the habitat mask for *C. orbiculata* the statistically significant LCDBv4 classes were selected, also including any classes that were directly comparable to statistically significant LUS global classes (i.e. urban classes and bare ground, excluding snow and ice). Selected grid cells that fell within farmland covered by Agribase were further constrained to include only sheep, or mixed sheep and beef pasture. The resulting layer defined suitable land use classes. Because *C. orbiculata* occurs on cliffs and outcrops as well as in vegetation (Webb *et al.* 1988), the suitable land use was merged with the *a priori* layer used for *Aeonium* species, to create the final habitat suitability layer.

2.3.8 Model verification

Model goodness-of-fit was assessed by calculating sensitivity (the proportion of occurrence records falling within cells modelled as suitable), both in New Zealand and globally. Sensitivity assesses whether the modelled envelope is too conservative. BIOCLIM, by definition, will have high sensitivity, perhaps at the cost of specificity (*i.e.* detection of true absences). A common problem in modelling invasions is that the most commonly used statistics (*e.g.* AUC, Kappa) require generation of pseudo-absence data and penalize models for predicting suitability where the species is currently absent, despite the fact that not all absences are informative when modelling the potential distributions of range-extending species (Soberón & Nakamura 2009).

To assess whether BIOCLIM was over-estimating climatic suitability, while avoiding generation of pseudo-absence data and the attendant self-reinforcing consequences (Stokland *et al.* 2011; Golicher *et al.* 2012), the same one-tailed binomial statistic as used in the land use analysis was calculated. This statistic tests the statistical significance of sensitivity scores given the proportion of the model universe projected as suitable (between 0 and 1), and estimates the probability of obtaining the observed sensitivity or greater under a random model with the same projected suitable area. Statistics were calculated for BIOCLIM models trained on both non-New Zealand data and all data. This compared the effect of including New Zealand in the training data, where little difference in the projections with and without the New Zealand data would indicate more stability in projections. High sensitivity to the inclusion of New Zealand data should warrant caution when interpreting the results, given that the species may not be at equilibrium in the invaded range.

Models trained on global (non-New Zealand) data were validated against New Zealand data. For the total models (world including New Zealand) training data had previously been split 80:20 for 5-fold cross-validation, setting aside 20% of occurrences from each run for verification. The mean sensitivity and p-values were calculated across all five runs. The final model (*i.e.* one run, trained on all available data with no splitting), was compared with the total model for overlap. Statistics were also recalculated for the final model, after constraint by habitat suitability, against all New Zealand occurrences. This was to quantify the difference in projected suitable area and whether habitat constraint adversely affected model sensitivity.

2.4 Results

2.4.1 Niche analyses

In the niche analyses, principal components 1 and 2 accounted for 94%, 89% and 92% of variation in the five bioclimatic variables for *A. arboreum*, *A. haworthii* and *C. orbiculata*, respectively. Principal component 1 correlated positively with precipitation (primarily BIO17 and BIO19), except for *C. orbiculata* where it was negatively correlated. Principal component 2 largely correlated negatively with temperature (BIO10 and BIO11). Niche plots for all three species demonstrated clustered, disjunct distributions in climatic space (Figure 2.2). The global occupied niche of *C. orbiculata* represented a wider climatic range than either *Aeonium* species, while all three species' occupied New Zealand niches were similar and overlapped with the edges of the global niches to varying degrees. All species' New Zealand centroids were close to the climate most similar to that of the global distribution (dry, mild climates), but generally, New Zealand represented an expansion of the occupied niche into wetter conditions. None of the species occupy equivalent climates to the centroids of the New Zealand niches elsewhere in the world, despite such environments being available.

All three species' New Zealand niches were significantly different to the global distributions at the 95% confidence level (Table 2.1), in other words niche overlap (D) was lower than 95% of pooled and randomly split occurrences. Furthermore, similarity p-values for *A. haworthii* between the global and New Zealand niches were approaching 1, meaning that observed D was close to the mean of randomly simulated niches. Only for *A. arboreum* was the observed global niche significantly more similar to the New Zealand niche than random simulations.

Table 2.1 Niche equivalency and similarity of target species between global and New Zealand ranges, following the methods of Broennimann *et al.* (2012). Similarity indicates whether niches in the target ranges are more similar to each other than random simulations. Asterisks denote bootstrapped levels of statistical significance of D ($p \leq 0.05$), where they signify rejection of niche equivalency at the 95% confidence level.

| Species | Equivalency (D) | Similarity of world niche to NZ (p-value) | Similarity of NZ niche to world (p-value) |
|----------------------|-----------------|---|---|
| <i>A. arboreum</i> | 0.38 * | 0.06 | 0.02 |
| <i>A. haworthii</i> | 0.13 * | 0.81 | 0.77 |
| <i>C. orbiculata</i> | 0.19 * | 0.08 | 0.08 |

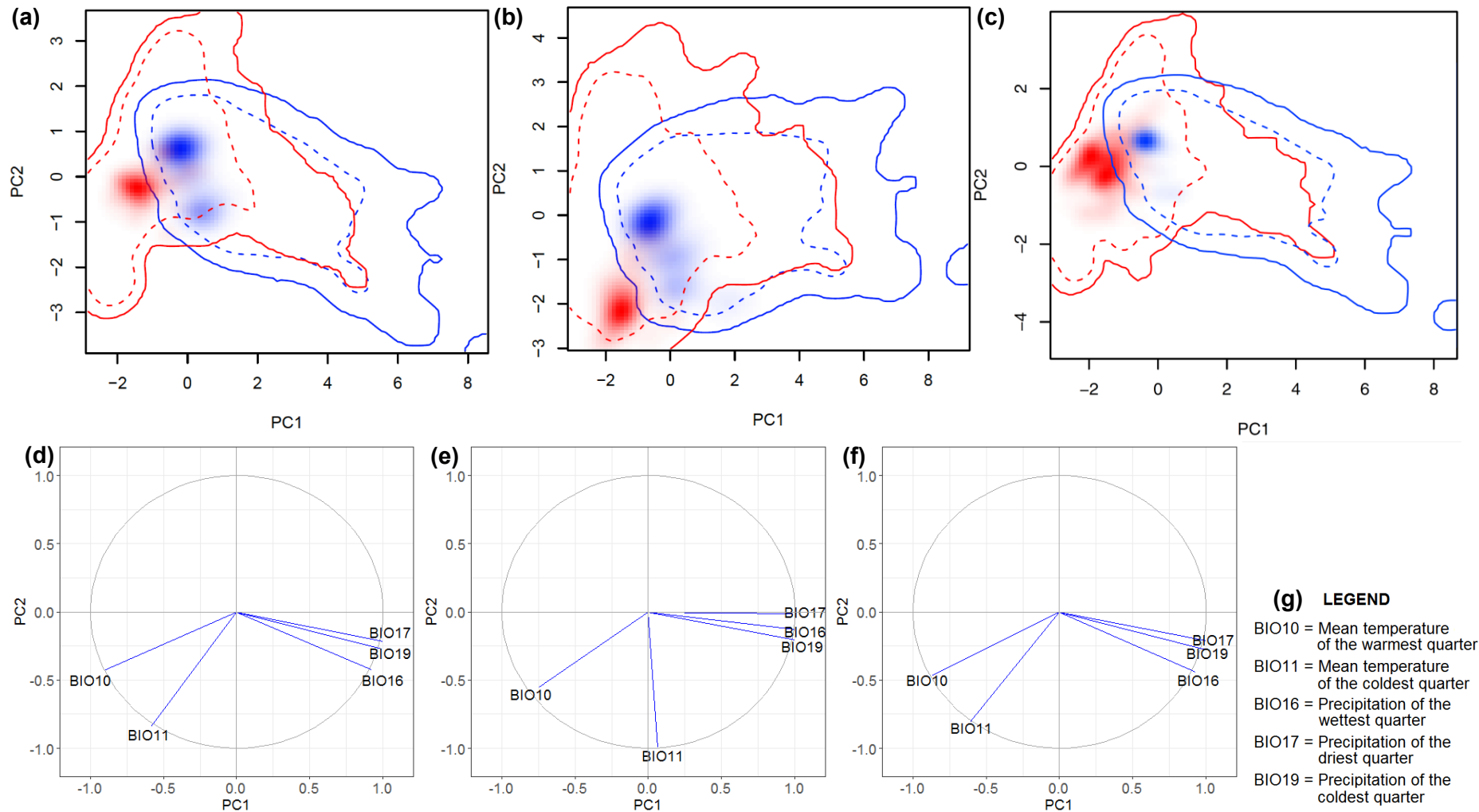


Figure 2.2 a-c) Kernel-smoothed PCA biplots of climatic niches, in the global range (red) and New Zealand range (blue), for a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata*. Plots generated using 5 bioclimatic variables [(Hijmans *et al.* 2005), available at <http://www.worldclim.org>]. Solid lines delimit total background climate, dashed lines delimit 50% of background climate. Shading indicates density of occurrences after kernel smoother applied. Correlation circles show correlation between bioclimatic variables (see legend, g), with principal component axes for d) *A. arboreum*, e) *A. haworthii* and f) *C. orbiculata*.

2.4.2 Performance of BIOCLIM models

In all cases, the sensitivity of BIOCLIM models trained on global data was lower than models trained on 80% of total data (Table 2.2). Models trained on global data under-predicted suitable climate in New Zealand, with only 5%, 2% and 29% of the country projected as climatically suitable for *A. arboreum*, *A. haworthii* and *C. orbiculata*, respectively. While global models for both *Aeonium* species correctly identified parts of the east coasts as suitable, notable areas where the species have naturalized including Dunedin, Wellington and Auckland, were classified as unsuitable. The global model for *C. orbiculata* performed better than for *Aeonium* species, but under-predicted in the North Island, particularly the Bay of Plenty and Auckland. As expected, inclusion of New Zealand data improved sensitivity and the cross-validated models performed significantly better than chance. Models trained with New Zealand data had higher proportional projected suitable area both globally and in New Zealand, a result of the New Zealand distributions representing an expansion of the realized climatic envelope. The proportional projected suitable area of the final models (using total data) was identical to the cross-validated models, and the two projections overlapped by 100% for all three species. Global projections of final models (Figure 2.3) demonstrated narrow ranges of climatically suitable conditions for both *Aeonium* species, with a high degree of overlap in Mediterranean-type climates [*i.e.* warm temperate with dry summers (Peel *et al.* 2007)]. The global projection for *C. orbiculata* shared similarities with both *Aeonium* species, but projected suitable area was substantially higher, indicating broader climatic tolerances.

Table 2.2 Sensitivity (Sens.) and projected suitable area (PSA) of global (excluding New Zealand) and total (global plus New Zealand) BIOCLIM models of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*, tested against the world and New Zealand. Statistical significance of sensitivity, given projected suitable area, calculated using Fisher's one-tailed binomial statistic (* $p < 0.05$, ** $p < 0.01$). Global models independently validated against New Zealand, total models cross-validated 5-fold (mean value given).

| Species | Model | World | | New Zealand | |
|----------------------|--------|--------|------|-------------|------|
| | | Sens. | PSA | Sens. | PSA |
| <i>A. arboreum</i> | Global | | 0.02 | 0.57** | 0.05 |
| | Total | 0.96** | 0.03 | 0.93** | 0.30 |
| <i>A. haworthii</i> | Global | | 0.01 | 0.16** | 0.02 |
| | Total | 0.98** | 0.02 | 0.99** | 0.45 |
| <i>C. orbiculata</i> | Global | | 0.13 | 0.91** | 0.29 |
| | Total | 0.99** | 0.14 | 0.99** | 0.60 |

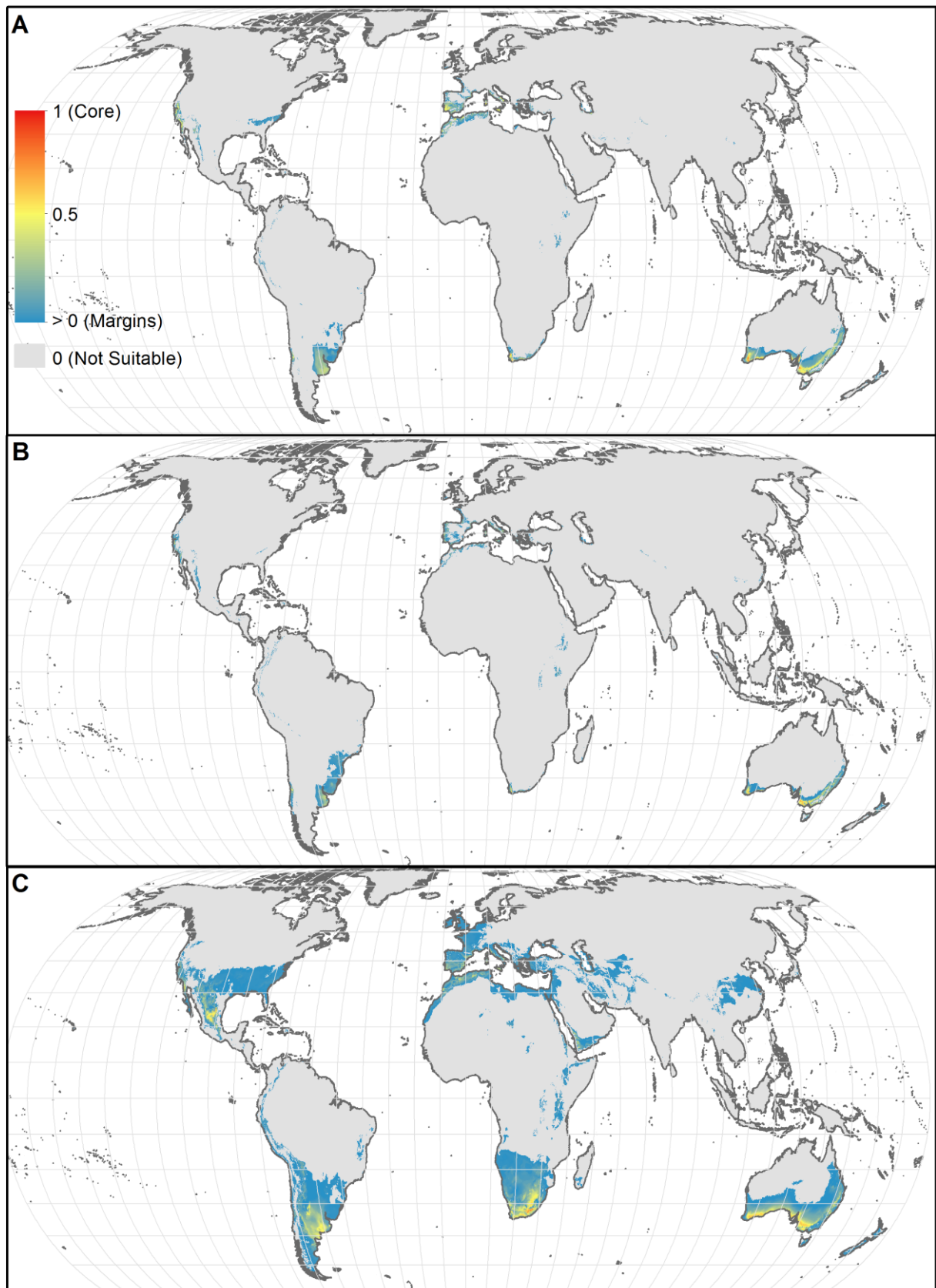


Figure 2.3 BIOCLIM global projections of climate suitability, using all available data, for a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata*. Model scores between 1 and 0 signify the position within the n -dimensional climate space. Scores approaching 1 indicate similarity to the species' 50th percentile of the species' rectilinear climate envelope ("core" climate), while 0 signifies that the climate is outside the 5th or 95th percentiles of the envelope.

2.4.3 New Zealand projections and habitat suitability

Projected suitable climate was concentrated primarily around the coastlines, but more prevalent in the North Island than the comparatively colder South Island. In the South Island, projected suitable climate was exclusively coastal for both *Aeonium* species, and restricted to the drier eastern side of the Island for all three. BIOCLIM scores reflect distance to the 50th percentile in climate space, and should not be interpreted as relative suitability because they are sensitive to biases in the training data. However, the comparatively low New Zealand scores for *C. orbiculata* indicated that although the projected suitable area was large, most of it is climatically similar to the outer extremes of the species' distribution.

Masks of habitat suitability demonstrated lower availability of suitable habitat for *Aeonium* species than for *C. orbiculata*, because *C. orbiculata* occupies a broader range (e.g. sheep pasture). The masks demonstrated that there is suitable *Aeonium* habitat (e.g. cliffs) across much of New Zealand, albeit patchily distributed. Suitable *C. orbiculata* habitat was not only less restricted than for *Aeonium* species, but had higher connectivity in certain areas, particularly along the east coast. Constraining BIOCLIM projections of climate suitability by habitat masks reduced the proportion of projected suitable area in New Zealand for both *Aeonium* species by over 60% (Table 2.3). Projected suitability for *C. orbiculata* was reduced by only 44% by habitat masks, with 34% of New Zealand still classified as suitable. Sensitivity for the constrained models were slightly lower than climate-only projections due to a small number of presences excluded by the masks ($n = 7$ for both *Aeonium* species, $n = 2$ for *C. orbiculata*). This may have been due to incorrect geocoding, presence of unmapped microhabitats, land use mosaics within grid cells or, potentially, exclusion of a suitable land use type.

Table 2.3 Projected suitable area (PSA) for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*, with and without constraint by habitat. Sensitivity of constrained models shown with significance calculated using Fisher's one-tailed binomial statistic (** $p < 0.01$). Percent reduction in projected suitable area, after habitat masks were applied, is given relative to climate-only models.

| Species | PSA (unconstrained) | PSA (constrained) | Sensitivity (constrained) | % Reduction in Suitable Area |
|----------------------|------------------------|----------------------|------------------------------|---------------------------------|
| <i>A. arboreum</i> | 0.30 | 0.11 | 0.88** | 62% |
| <i>A. haworthii</i> | 0.45 | 0.15 | 0.90** | 67% |
| <i>C. orbiculata</i> | 0.60 | 0.34 | 0.99** | 44% |

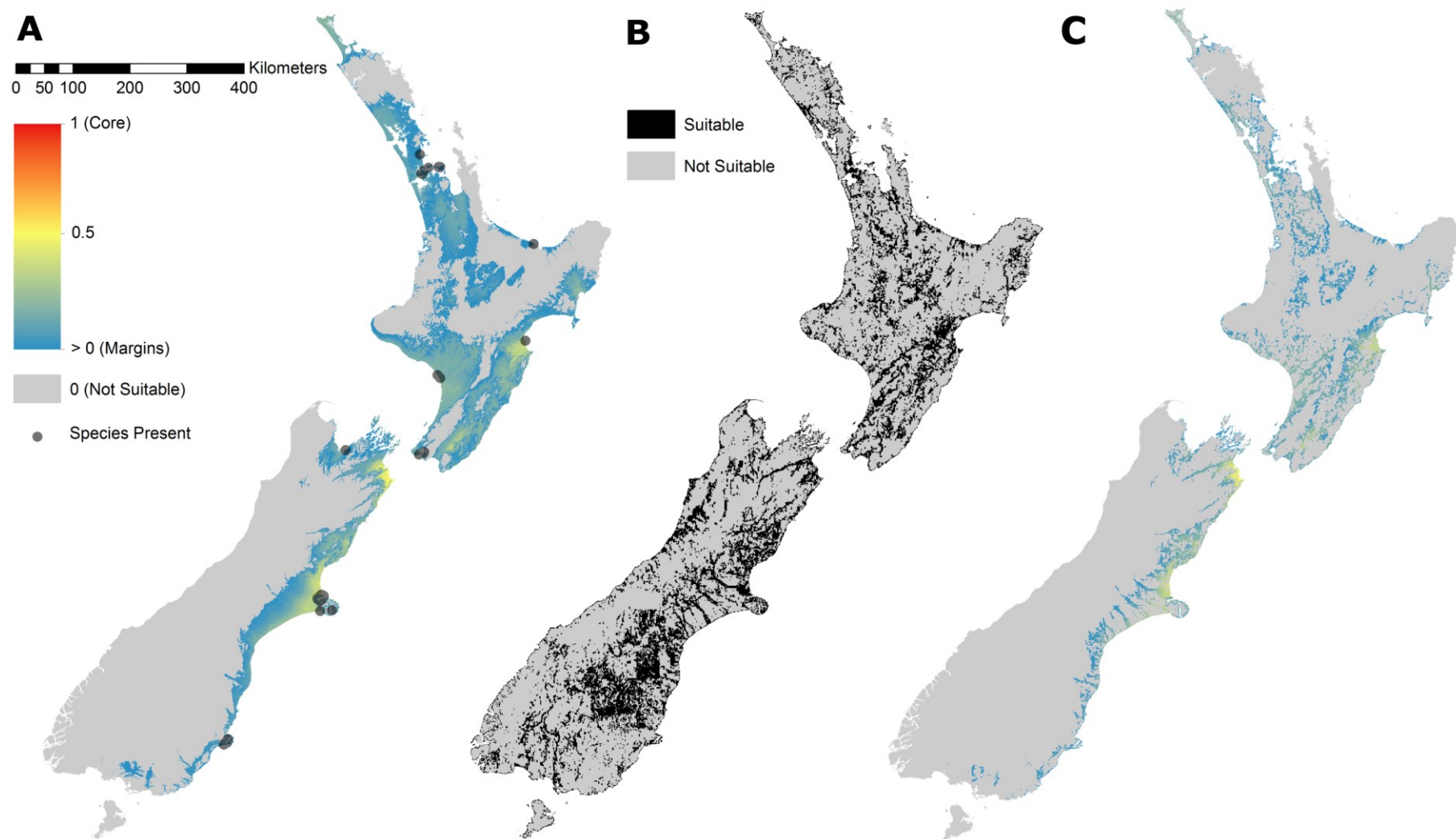


Figure 2.4 a) New Zealand projections of final BIOCLIM climate-only models for *Aeonium arboreum*, with points showing occurrence records. Model (a) was then constrained by (b), the mask of habitat suitability to give (c), the final projection of overall suitability. BIOCLIM scores are percentiles of the species' distributions in climate space. Scores approaching 1 indicate similarity to the species' 50th percentile of the species' rectilinear climate envelope ("core" climate), while 0 signifies that the climate is outside the 5th or 95th percentiles of the envelope.

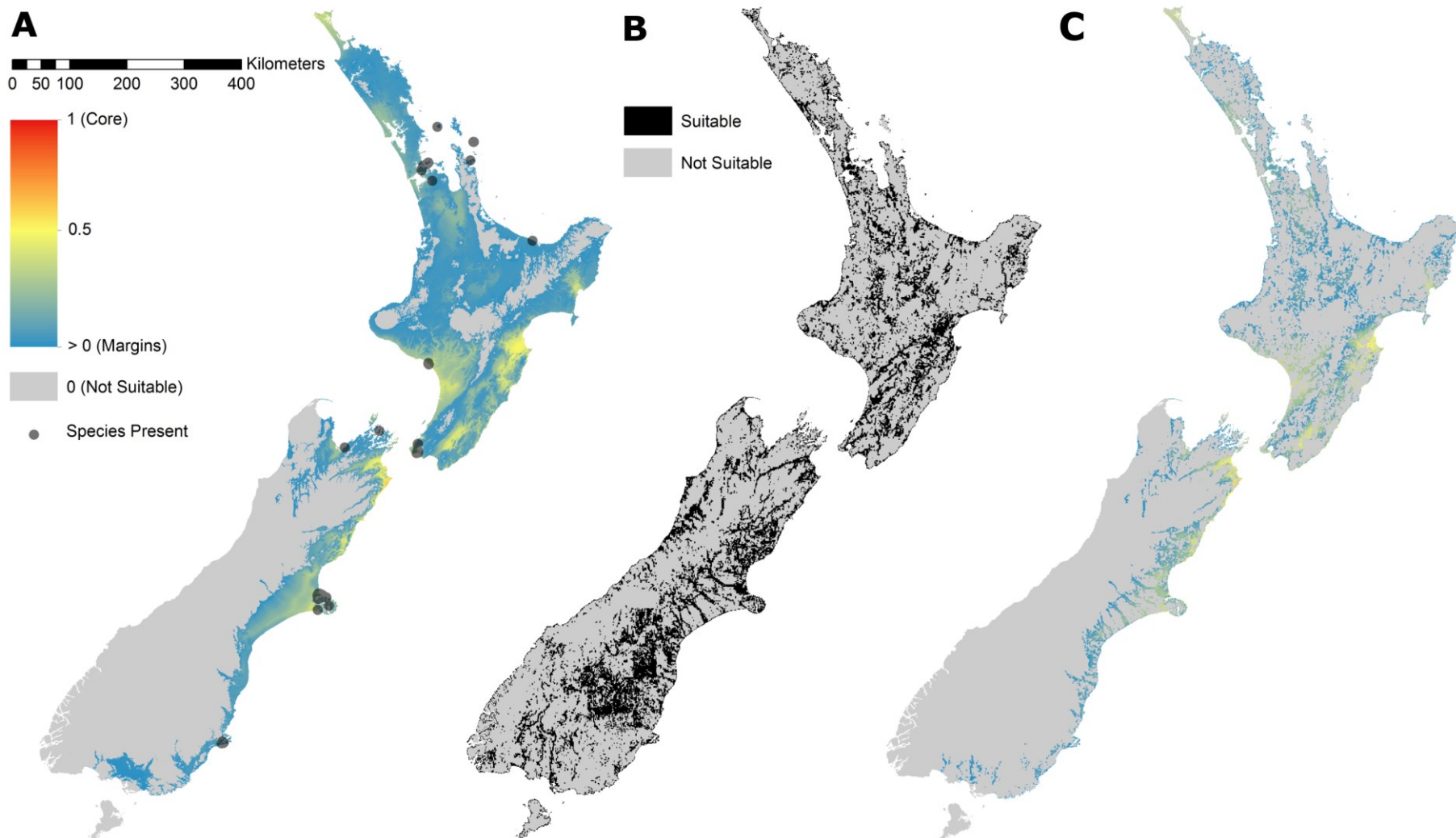


Figure 2.5 a) New Zealand projections of final BIOCLIM climate-only models for *Aeonium haworthii*, with points showing occurrence records. Model (a) was then constrained by (b), the mask of habitat suitability to give (c), the final projection of overall suitability. BIOCLIM scores are percentiles of the species' distributions in climate space. Scores approaching 1 indicate similarity to the species' 50th percentile of the species' rectilinear climate envelope ("core" climate), while 0 signifies that the climate is outside the 5th or 95th percentiles of the envelope.

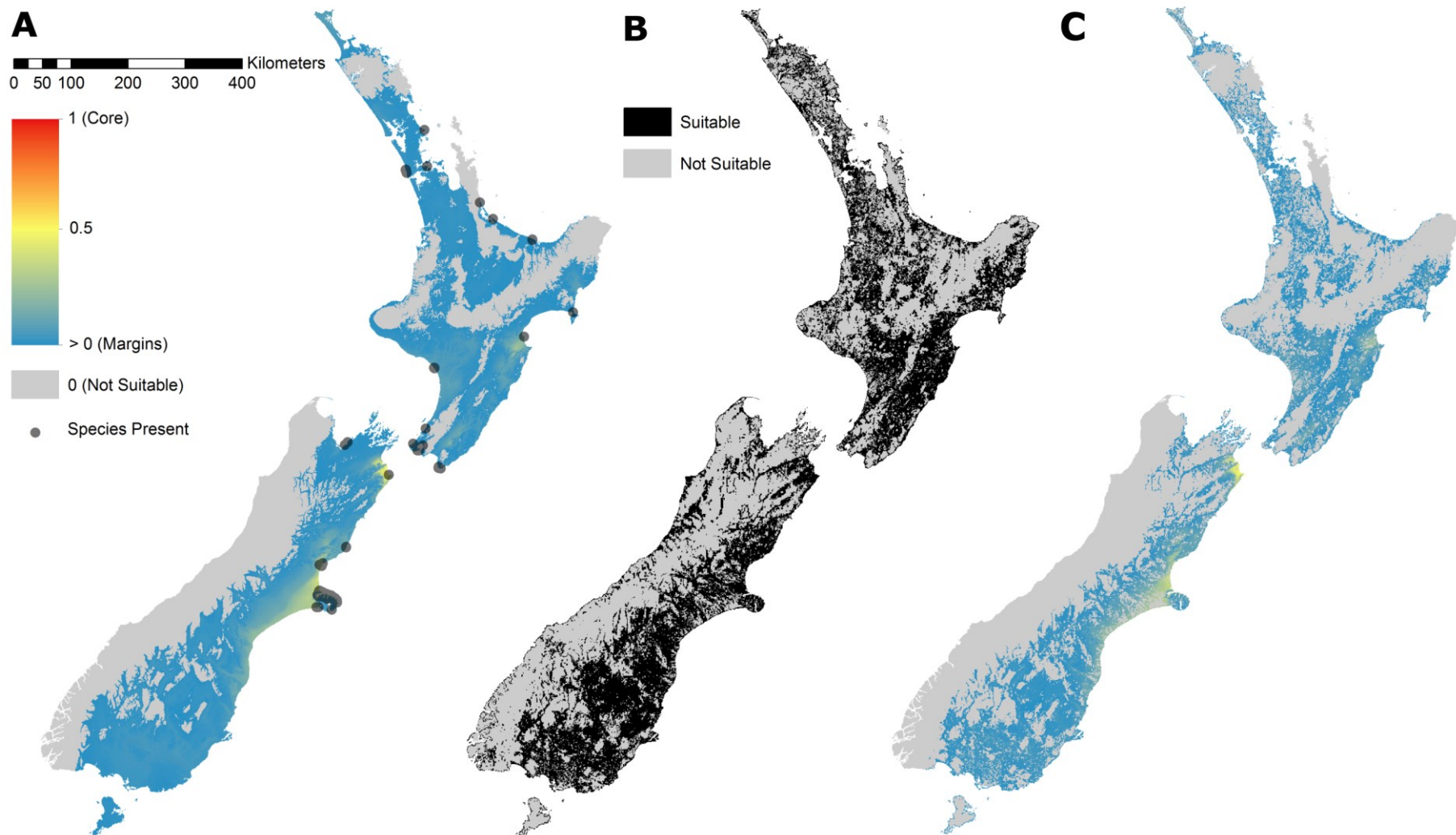


Figure 2.6 a) New Zealand projections of final BIOCLIM climate-only models for *Cotyledon orbiculata*, with points showing occurrence records. Model (a) was then constrained by (b), the mask of habitat suitability to give (c), the final projection of overall suitability. BIOCLIM scores are percentiles of the species' distributions in climate space. Scores approaching 1 indicate similarity to the species' 50th percentile of the species' rectilinear climate envelope ("core" climate), while 0 signifies that the climate is outside the 5th or 95th percentiles of the envelope.

2.5 Discussion

Niche analyses confirmed disjunct distributions in climate space for all three species. The observed “gaps” in climate space may be partially due to non-climatic limitation as a result of specific habitat requirements of the species. Despite a small degree of niche overlap all three species occupy significantly different climatic niches in New Zealand compared with the rest of the world, where New Zealand represents an expansion into wetter conditions. The results of the niche analysis were mirrored in the BIOCLIM projections where only models incorporating all global data performed adequately in New Zealand, for any species. While some over-prediction in final models is to be expected because of the nature of BIOCLIM and the use of few climate variables, projections indicate that a large proportion of New Zealand is climatically matched to the species’ current ranges. Constraining BIOCLIM projections by suitable habitat did not adversely affect model sensitivity, and provided a more conservative projection of areas at risk of invasion by the three species. Although final models are not a prediction of spread, they do provide valuable information for national weed management, particularly regions where new incursions should be controlled, potential risk areas for surveillance and the comparative threat posed by the different species.

2.5.1 What do the models reveal about the niche?

When including New Zealand in model training, projected suitable area increased dramatically for all three species. This was especially true of *A. haworthii*, where the projected climatic niche expanded from 2% to 45% of New Zealand when trained on all available data. The niche analyses demonstrated the underlying cause. All three species’ occupied New Zealand niches are in considerably wetter climates than elsewhere. In conjunction with the fact that similar climate is available in the global background but unoccupied, a niche expansion in New Zealand is implied for all three species. It is, however, impossible to determine through correlative methods alone whether it is an expansion of the fundamental or the realized niche (Hulme & Barrett 2013; Guisan *et al.* 2014). Possible causes for shifts in the fundamental niche include pre-adaptation to climates similar to the novel range in the species’ evolutionary history (Petitpierre *et al.* 2012), exaptation (Gould & Vrba 1982), and evolutionary change in the invaded range as a response to novel pressures or founder effects (Sax *et al.* 2007). Changes in the realized niche could arise from natural enemies (Keane & Crawley 2002) or other non-climatic effects (González-Moreno *et al.* 2015), or phenotypic plasticity facilitating invasion of novel climates (Price *et al.* 2003). Realized niche shifts might take the form of expansion in the invaded range or un-filling in the native range [*i.e.* the species does not occupy all suitable climates due to non-climatic factors, for example dispersal limitation; (Petitpierre *et al.* 2012)].

Regardless of the processes leading to the observed niche differences, an important consideration is that the species’ current distributions in New Zealand could not have been adequately predicted prior to their introduction. Global models performed better than chance and correctly identified some of the invasion hotspots for the three species (*Aeonium* models correctly identified Banks Peninsula and

Napier as suitable, and the *C. orbiculata* model correctly identified most hotspots except those in the wetter parts of the North Island *e.g.* Auckland). However, all three global models would have underestimated species' distributions. Given the sensitivity of the models to the inclusion of the New Zealand data, and the consequent increase in the potential distribution globally and nationally, the final projections must be interpreted with caution. Despite the apparently wide potential distributions, projections could be conservative if the species are not at equilibrium in New Zealand, and continued spread further into novel climates cannot be discounted.

In contrast to *Aeonium* species, *C. orbiculata* had a noticeably wider projected suitable area, both with and without the inclusion of New Zealand data. *Cotyledon orbiculata* occupies a diverse range of climates in Southern Africa, which is a key factor in the projected climatic suitability of New Zealand. Final models project suitable climate throughout the southern South Island and Central Otago [the region closest to a continental climate in New Zealand, where some of the coldest temperatures in the country have been recorded (MetService 2010)]. These surprising results are caused by a small number of recorded presences in Lesotho at up to 3173 MASL, where minimum daily temperatures are frequently sub-zero and seasonal and diurnal fluctuations can be extreme (Lesotho Meteorological Services 2013). Although a high-elevation variety of *C. orbiculata* exists, it is not present in New Zealand, and a local botanical expert in South Africa has confirmed that *C. o. var. orbiculata* (the most widespread variety in New Zealand) is common at high elevation sites in Lesotho (Ernst Van Jaarsveld, *pers. comm.*, 2014). Freezing tolerance in *C. orbiculata* reportedly differs between coastal and high-elevation populations, where plants from Lesotho can avoid freezing damage to -9.3 °C. Crucially, this freezing avoidance may have a genetic basis as this trait persists after de-hardening (Van Coller & Stock 1994). The cold tolerance limits of *C. orbiculata* in New Zealand may therefore depend on the original source population of introduced plants. Removal of just 7 of the highest elevation points in Lesotho resulted in a 23% reduction in projected suitable area in New Zealand (Figure A.8). The climatic limits of *C. orbiculata* in New Zealand will therefore depend on whether frost hardiness is an evolved genetic trait specific to Lesotho populations, or a result of pre-adaptation or phenotypic plasticity, and the origins of New Zealand populations.

2.5.2 The role of non-climatic factors

The target species' distributions are hypothesized to be restricted due to the effects of competition avoidance, based on their highly specific habitat requirements and the low efficiency of CAM photosynthesis relative to C3 and C4 plants. The two *Aeonium* species may achieve this primarily through occupation of crevices in bare rock and other sparsely-vegetated habitats, based on the species' descriptions (Webb *et al.* 1988; Bramwell & Bramwell 1990). However, reports of stock poisoning in the native range (Botha & Penrith 2008) and the U.S.A. (Fuller & McClintock 1988) imply that *C. orbiculata* is also regularly found in pasture, a pattern which was confirmed by the land use analysis (although occurrence records in the U.S.A. were in urban areas only). The tendency to appear in grazed land was especially obvious in New Zealand data, and analyses indicated that this

was not a statistical artefact of higher overall grazing. Although grassland may seem at odds with other *C. orbiculata* habitat (*i.e.* bare rock), this may also be a result of competition avoidance. *Cotyledon orbiculata* produces bufadienolide cardiac glycosides, the toxic compound which results in either immediate death, or the chronic disease known as “krimpsiekte”, in a number of animals including sheep and cattle (Botha *et al.* 2007). The production of bufadienolide toxins is thought to be a defence against ungulate herbivory (Van Jaarsveld & Koutnik 2004), thereby allowing populations to establish in pasture while other would-be-competitors are grazed.

There are examples of other Crassulaceae benefitting indirectly from the presence of herbivores via consumption avoidance. Experimental manipulation of vertebrate grazing pressure on *Crassula helmsii* (Kirk) Cockayne in the U.K. found that cover increased in the presence of sheep and buffalo due to the removal of competitors (Dean *et al.* 2015). *Bryophyllum delagoense* (Ecklon & Zeyher) Schinz contains the same toxic compounds as *C. orbiculata* and is a serious pest of grazing land in Australia (Witt 2004), although low frequency and intensity of fires in grazed land may also contribute to spread (Witt & Nongogo 2011). It is unclear whether fire is also important for *C. orbiculata*, and this cannot be discounted as a potential contributing factor to spread. Roadside spread of *B. delagoense* in Australia has been exacerbated by the use of mechanical slashers that simultaneously spread its seeds and plantlets and reduce competition from other species (Department of Agriculture and Fisheries 2013). The functional similarity of slashing to ungulate herbivory suggests that *B. delagoense* could be exapted to disturbance by herbivores. Meanwhile, many other species in the Cotyledonoideae clade produce the same toxic compounds as *C. orbiculata* (van Ham 1995; Mort *et al.* 2005), all of which evolved in South Africa. The region’s dry climate and many large native herbivores may elicit strong selective pressure, and evolved grazing avoidance or tolerance could explain why some South African Crassulaceae species have been shown to increase cover in the presence of elephants (Moolman & Cowling 1994). *Aeonium* species, in contrast, evolved in the Canary Islands where the only large native herbivore is the giant tortoise, therefore they have not evolved herbivore defences (Jorgensen & Olesen 2001). It is possible, then, that similar processes have been conducive to the spread of *C. orbiculata* in New Zealand sheep pasture, specifically grazing avoidance and re-rooting from broken material, easily caused by vertebrate trampling (JP, *personal observation*). What the analyses were not able to determine is whether grazing intensity is important in determining *C. orbiculata* distributions, a question better addressed with experimental techniques.

2.5.3 Potential distributions in New Zealand

Model projections indicated that a large proportion of the North Island and east coast of the South Island is climatically favourable for all three species. However, constraint by suitable habitat strongly reduced projected suitable area. This was especially the case for *Aeonium* species, where over 60% of climatically suitable area was excluded based on non-climatic factors. The reduction in climatically suitable area for *C. orbiculata* was only 44%, but indicates that land use may still constrain potential distributions considerably.

The strong reduction of suitable habitat for *Aeonium* species does not exclude the possibility of suitable microhabitats in other grid cells, or the fact that the realized distribution may be further constrained by other factors *e.g.* geology. For example, in Canterbury in the South Island riparian cliffs were classified as potential habitat, but it is unknown whether the alluvial sediment of the region (G.N.S. Science 2014) might be suitable for *Aeonium* species. Assuming, then, that final models most likely over-predict in New Zealand, the availability of suitable *Aeonium* habitat can be assumed to be low unless the species are able invade habitats other than where they have been previously described. It is unlikely that *Aeonium* species would be capable of invading pasture as *C. orbiculata* has, as they do not have herbivore defences and succulents are otherwise high-quality forage in dry environments (Moolman & Cowling 1994). *Aeonium* species are thus likely to be more restricted by availability of suitable land forms (*e.g.* cliffs) than by climate in New Zealand, but if the climatic niche continues to expand other rocky habitats could become vulnerable, potentially threatening native species that also use rock outcrops as refugia (Wiser & Buxton 2009).

Cotyledon orbiculata, conversely, has little shortage projected suitable habitat. Further expansion of the climate envelope in New Zealand would thus likely have a greater effect on the potential distribution of *C. orbiculata* than *Aeonium* species. However, as with the *Aeonium* species, projections could be further refined by additional non-climatic factors, *e.g.* soil type. Attempts to use spatial intersection techniques for soil type with *C. orbiculata* were unsuccessful, presumably because the species is found on a wide range of soils (Van Jaarsveld & Koutnik 2004), and where the species occurs on bare rock the surrounding soil type is irrelevant. To understand the importance of other non-climatic factors, experimental techniques could be informative. Nonetheless, the risk posed by *C. orbiculata* to New Zealand is highly dependent on climatic suitability, which as discussed, is uncertain depending on the source of introduction and degree of non-equilibrium in New Zealand.

2.5.4 Limitations

An SDM is, at best, an approximation of reality. I aimed to estimate the extent of climatically suitable habitat in New Zealand for the three species, and the limitation of their potential distributions by non-climatic factors. In reality, the species' distributions will be constrained further by additional factors not included in final projections, for example topology, geology, soil, biotic interactions and dispersal. As discussed, teasing apart the influences of these factors on the species' distributions may be more suited to experimental techniques at a finer scale and is a worthwhile avenue for further study. Additionally, testing all three species' climatic limits in the invaded range would provide valuable insight into their potential to continue spreading into novel climates.

It is important to consider model uncertainty arising from spatial scale (grain size), model type and the quality of input data. Potential habitat was modelled at a 30 arc-second scale (approximately 1 km²), so variation in climate and land use within "unsuitable" grid cells may give rise to suitable microhabitats. The model BIOCLIM, while useful for this study, is particularly prone to over-

prediction relative to other SDMs (Tessarolo *et al.* 2014). Furthermore, the Worldclim bioclimatic layers used are interpolated and averaged from weather station data over a 30 or 50-year period depending on location (Hijmans *et al.* 2005). The variables therefore mask inter-annual variation and climatic extremes that may be limiting. Other climate variables only indirectly represented by the Worldclim data may be more biologically meaningful for the species, *e.g.* frost or growing degree days. Finally, while use of pseudo-absence data in model validation was avoided, there remains no way to fully validate SDM outputs without independent data including true absences (*i.e.* where it is certain that the species does not occur). The final models therefore are likely to over-predict habitat suitability, and represent a “worst-case” scenario of potential distributions. This list of assumptions is not exhaustive, and I emphasize that model projections, as with any SDM, should be interpreted with these caveats in mind.

2.5.5 Conclusions

I show that *A. arboreum*, *A. haworthii* and *C. orbiculata* occupy novel climate space in their invaded ranges in New Zealand, constituting a shift in the occupied niche towards wetter climates. BIOCLIM projections trained on all known occurrences project a high proportion of New Zealand as climatically suitable for all three species, and therefore spread can be expected to continue. Accounting for non-climatic limitation dramatically reduces all three species’ potential distributions in New Zealand, especially *Aeonium* species. Relative to the *Aeonium* species, it is clear that *C. orbiculata* poses a greater threat to biodiversity and productive ecosystems in New Zealand.

Chapter 3 – Testing performance along an elevation gradient reveals the climatic limits of alien Crassulaceae in New Zealand

3.1 Abstract

Predicting climatic limits and potential distributions of non-native plants is a rapidly growing discipline. Correlative or observational approaches are commonly employed to predict limits but they usually assume that species are at climatic equilibrium, and this condition is rarely fulfilled. To confidently project climatic limitation an understanding of how far the species is from equilibrium is necessary, especially in the introduced range where non-equilibrium may be exaggerated. Yet, few studies experimentally test climatic limits in the introduced range. Fewer still go on to predict plant performance beyond current range limits. In this study I experimentally test vital rates, in response to climate, of three non-native plant species in New Zealand. By transplanting cuttings and seeds of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* over a gradient of 0 - 700 MASL in the Banks Peninsula region, seedling establishment, growth and mortality are quantified in response to climate, within and beyond species' range limits. Performance was measured over two years and observed vital rates modelled against climatic variables, using the resulting functions to predict performance up to 300 m above current range limits. Results are used to infer whether the species have reached their climatic limits, and whether spread to higher elevations is likely. There is evidence that all three species are strongly climate-limited on Banks Peninsula, and that high elevations are detrimental to plant performance. All species appear close to their climatic limits in the region, particularly *Aeonium* species, which are likely to be confined to around 300 - 400 MASL. *Aeonium* species are limited at high elevations by reduced growth and seedling establishment, and higher mortality. *Cotyledon orbiculata* poses a greater risk to the region than *Aeonium* species as it is already present at higher elevations, and there is less consensus between predicted vital rates at higher elevations. *Cotyledon orbiculata* appears to be primarily limited by relative growth and upward spread cannot be discounted, although such populations would likely be marginal. This is the first study of climatic limitation of the three species in any introduced range, and provides key information for assessing their potential distributions in New Zealand.

Keywords: climate, elevation, transplant, invasion, Crassulaceae

3.2 Introduction

Untangling drivers of invasive species' distributions and predicting potential spread is a prominent area of ecological research (Guisan & Thuiller 2005). Once a species has established in an introduced range, determining the extent to which it may spread is a complex and often uncertain process (Wilson *et al.* 2007; Bradley *et al.* 2010) that relies on knowledge of the species' climatic limits. It is generally accepted that species' distributions are limited by numerous factors that are scaled hierarchically

(Mackey & Lindenmayer 2001); ultimately, climate is thought to limit ranges at the coarsest grain and largest extent (Woodward 1987), with other factors, *e.g.* biotic interactions, limiting distributions at finer grains and in smaller regions (Collingham *et al.* 2000; Guisan & Thuiller 2005). Therefore, to assess potential spread of a non-native plant in its introduced range its climatic tolerances must first be determined, as this will define its coarsest distribution limits.

Measuring species' responses along elevation gradients is a useful proxy for investigating climatic limitation. Elevation is a strong determinant of plant distributions (DeFerrari & Naiman 1994) and many species have well-defined limits. Species richness generally declines as elevation increases (Marini *et al.* 2009). Furthermore, elevation limits are often stable between species' native and introduced ranges, and correspond well with their climatic tolerances (Alexander, Naylor, *et al.* 2009). Studies along elevation gradients are also practical as they allow us to measure responses to a wide range of climates over a small study area (Haider *et al.* 2011). Climatically, high elevations exhibit cooler temperatures, more frequent frosts and shorter growing seasons, and are overall less conducive to plant performance (Körner 2007). It is difficult, however, to determine which causal effects shape distributions along elevation gradients without experimental approaches. While high elevations are generally less favourable for plant growth and performance, there are multiple contributing factors not necessarily related to physiological limits that may be confounded by observational methods. Numerous non-climatic factors affect performance at high elevations: soil quality is often poorer, disturbance regimes altered, physical area reduced, and land use may change (Körner 2007; Pauchard *et al.* 2009). Further, propagule pressure may diminish due to the gravitational difficulty of dispersing uphill and reduced anthropogenic activity (Marini *et al.* 2009; Alexander *et al.* 2011), and biotic interactions may change (Badano *et al.* 2007). Therefore, while purely observational or correlative studies often identify that elevation is a determinant of non-native species richness (Pauchard & Alaback 2004), the underlying mechanisms may be clouded as they cannot standardize for non-climatic effects. In contrast, experiments testing performance along elevation gradients provide opportunities to identify the extent of climatic limitation and the relative importance of individual variables (Paiaro *et al.* 2007; Leger *et al.* 2009).

Studies of species' climatic limits also benefit from looking beyond just presence-absence data into the underlying demographic processes driving limitation (Hastings *et al.* 2005). Demographic processes (*i.e.* population mortality, fecundity) determine whether plants can colonize and form self-sustaining populations, and each individual vital rate (*e.g.* germination, survival) may be differentially influenced by a multitude of climatic and non-climatic drivers [*e.g.* Baret *et al.* (2004)]. Vital rates may vary within populations due to genetic effects, microhabitat factors and biotic interactions (Sexton *et al.* 2009), and between populations due to larger scale climatic, environmental or biotic effects (Kollmann & Bañuelos 2004; Leger *et al.* 2009). They may also vary within individuals because of time-dependent effects, such as ontogenetic drift (McConnaughay & Coleman 1999). Classifying habitat suitability without knowledge of underlying processes may be misleading (Haider *et al.* 2011). If the

climate is sufficient for survival but not germination, populations may be inexplicably absent. Similarly, sink populations may exist where conditions are sufficient for germination and survival, but not reproduction (Willis & Hulme 2002; Baret *et al.* 2004).

A further reason to experimentally investigate non-native species' climatic limits is that invasions are sometimes characterized by non-equilibrium. While a species at geographic equilibrium occupies all potentially suitable habitat (Hutchinson 1957), this condition is rarely fulfilled due to non-climatic factors that limit dispersal (Brown *et al.* 1996). More importantly, non-equilibrium may be particularly extreme during invasions (Thuiller *et al.* 2006; Wilson *et al.* 2007), where the species' range of occupied habitats may not be indicative of its full tolerances. This can be caused by invasion lags, where the invader remains at low prevalence for a number of years following introduction (Aikio *et al.* 2010), and anthropogenic effects such as human population density (Pyšek *et al.* 2010), among other factors. Yet, the most popular methods for predicting non-native species' climatic limits are correlative (Guisan & Thuiller 2005; Araújo & Peterson 2012; Ahmed *et al.* 2015), and most assume equilibrium in the training range (Elith *et al.* 2010). Correlative approaches may produce unreliable predictions in non-equilibrium situations and over or under-estimate the risk of spread (Varela *et al.* 2009; Václavík & Meentemeyer 2012), and only experimental approaches can test whether the assumption of equilibrium holds true. Despite these problems, studies that measure non-native species' vital rates across climate gradients (Alexander, Edwards, *et al.* 2009; Seipel *et al.* 2015; Walter *et al.* 2015), or use experimental methods to test climatic limits (Willis & Hulme 2002; Angert & Schemske 2005; Griffith & Watson 2006; Leger *et al.* 2009), are relatively rare. Even fewer go on to make explicit predictions (Ross *et al.* 2008), and many lack the experimental design necessary to strongly infer species' range limits (Hargreaves *et al.* 2014).

In this chapter, I investigate the climatic responses of three succulent plants over part of their introduced ranges in New Zealand. Cuttings and seeds of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* were transplanted within and beyond their current elevation limits on Banks Peninsula, an invasion hotspot for all three species south of Christchurch. The topography provided a steep elevation gradient, ranging from evidently climatically suitable along the coastline, to beyond their hypothesized climatic tolerances at the inland peaks. All three species occur predominantly at low elevations near coastlines, and since naturalization in the late 19th century, they have spread along coasts and upwards to around 400 MASL. The three species are strongly limited by non-climatic factors; they prefer bare substrate (*e.g.* cliffs), and *C. orbiculata* can colonize sparse grasslands (Webb *et al.* 1988). It is particularly difficult to infer climatic requirements using observational data when suitable habitat is restricted (Brown *et al.* 1996), therefore it was necessary to experimentally test the species' climate limits to assess potential spread. Climatic factors influencing growth, mortality and germination are modelled, and used to infer the likelihood of spread to higher elevations. This study is the first to quantify the climatic responses of these species and link it to their invasive potential.

3.2.1 Aims

1. Using a field experiment along an elevation gradient, to test whether current distribution limits on Banks Peninsula of *A. arboreum*, *A. haworthii*, and *C. orbiculata* represent the climatic limits of the species.
2. To identify which vital rates (mortality, growth and seedling establishment) are most limiting to continued upward spread in the region, by quantifying their responses to climate.
3. To examine the potential for the species to continue spreading in the region by comparing predicted vital rates at high elevations on Banks Peninsula to predictions at their current elevation limits.

3.3 Methods

3.3.1 Study species

Aeonium arboreum, *A. haworthii* and *C. orbiculata* are succulent long-lived perennials in the family Crassulaceae. These species were chosen because they are thought to be strongly restricted by habitat and climate in New Zealand, are potential environmental weeds, and there is evidence that they may not have reached equilibrium (Chapter 2). In their native ranges, all three species occupy relatively warm, dry environments (Table 3.1), but how their reproduction, growth and survival respond to climate is uncertain. All three are polycarpic, producing multiple compound inflorescences in summer, with the resulting wind-dispersed seeds germinating the following spring (Alamo *et al.* 1996; Zietsman 1998). Little is known about their germination capabilities or optimal conditions, though there are reports of between 0 and 84% germination, and optimal temperatures between 16 and 24 °C, in closely related species (Alamo *et al.* 1996; Daws *et al.* 2007; Royal Horticultural Society 2014). Although all three species currently occur at lower elevations in New Zealand than in their native ranges, the climates of the New Zealand distributions are wetter and cooler (Table 3.1). Their climatic limits are particularly unclear as CAM photosynthesis is often associated with phenotypic plasticity and flexible niche occupation (Luttge 2004). In general, all three species are drought tolerant and *C. orbiculata* can withstand fluctuating periods of drought and high rainfall (Eller & Ferrari 1997). They require free-draining soil and dry climates (Vogan 2003), with some precipitation during the growing season (Jorgensen & Olesen 2000; Royal Horticultural Society 2014), prefer sunny aspects with minimal shade (Vogan 2003), and *C. orbiculata* may be somewhat adaptable to solar radiation intensity as it can regulate its photoprotective epicuticular wax in response to light levels (Barker *et al.* 1997). The high water content of these species, up to 95% for *C. orbiculata* (Eller & Ferrari 1997), may result in frost sensitivity. However, there is conflicting evidence of freezing avoidance, with sources reporting minimum temperatures ranging between 5 °C and - 9.8 °C (Lösch & Kappen 1981; Van Coller & Stock 1994; Vogan 2003; Royal Horticultural Society 2014). In addition, high levels of flavonoid aglycones in *Aeonium* species may aid robustness to climatic stress (Stevens 1995).

3.3.2 Study area

This chapter focusses on Banks Peninsula, a volcanic region of 1150 km² directly south of Christchurch, New Zealand between latitudes -43.56 and -43.90 decimal degrees, and longitudes 172.38 and 173.13 (WGS 1984). The terrain of Banks Peninsula results in a steep climatic gradient (Boffa Miskell 2007), with four distinct bioclimatic zones based on distance to the coast and elevation (Wilson 1993). Annual rainfall varies between 600 mm per annum (p.a.) in the drier northern bays, to 2000 mm p.a. in the southern valleys (Figure 3.1). Mount Herbert is the highest peak at 919 MASL, and while temperatures are mild at low elevations, the hilltops are temporarily snow-covered during most winters (Soons et al. 2002). I expected the elevation gradient on Banks Peninsula to encompass climatic conditions ranging from suitable to unsuitable for the study species. Climate is likely to be the primary limiting factor on Banks Peninsula, as suitable habitat is abundant; the volcanic landscape forms abundant cliffs and outcrops, preferred habitat for all three species, and the primary land use in the region is sheep pasture (Boffa Miskell 2007), suitable for *C. orbiculata*. Current occurrence records of all three species are concentrated in the northern bays at low elevations (Figure B.1), confined to the warmest, driest parts of the region, though *C. orbiculata* occupies a wider climatic range than the two *Aeonium* species (Figure B.2)

3.3.3 Experimental design

Growth, survival and germination of the three species were tested by transplanting cuttings and seeds at 40 field sites on Banks Peninsula. Sites were placed between 7 and 681 MASL at varying distances to the coast, within and beyond the species' current limits. A preliminary power analysis was conducted to estimate the necessary degree of replication, and based on the results each site contained five cuttings and 300 seeds of each species (a total of 15 plants and 900 seeds). Raster maps of climate [500 m, (Tait 2007)] were then used to classify grid cells on Banks Peninsula according to annual average air temperature (*Temp*) and average summer precipitation (*Rain*). Averages were calculated over 1971–2009. Each cell was assigned into one of five categories using equation 1, where μ = mean for Banks Peninsula, and σ = standard deviation. Grid cells were divided into five categories, from cold and wet, to hot and dry, by ranking the climate index.

$$\text{Climate index} = [(Temp - \mu Temp) - \sigma Temp] - [(Rain - \mu Rain) - \sigma Rain] \quad (1)$$

Field sites were located within Christchurch City Council reserves because public land was more easily accessible, it was more straightforward to gain the necessary permissions, and the Council were highly supportive of the work. Sites were selected by dividing available council reserves into the range of climate index categories within, and selecting individual sites no less than 50 m apart, attempting to evenly represent both the climate indices and elevation (between the lowest and highest points in each reserve, and overall between sea level and the maximum elevation possible). Three of the four bioclimate zones on Banks Peninsula (Wilson 1993) were represented in the design (Table 3.2). I also

attempted to represent aspect evenly (cardinal directions N, E, S, W), but because accessibility was limiting neither elevation nor aspect are perfectly balanced. Following the Christchurch earthquake in February 2011, it was necessary to select an additional seven sites for germination trials (see section 3.3.5 for details). Full site details are provided in Table B.2.

3.3.4 Growth and mortality experiment

The second aim of this chapter was to identify which vital rates are most likely to limit upward spread. Growth and mortality were tested by transplanting cuttings to sites, and seeds were transplanted to measure germination (section 3.3.5). In October 2010, I sourced 220 cuttings from 11 naturalized Banks Peninsula populations per species (total = 660 cuttings), attempting to sample as wide a range of occupied climates as possible (Figure B.1). This allowed investigation of potential source effects on performance (after de-hardening), where differential responses could suggest local adaptation. When collecting cuttings I took at least one apical leaf pair for *C. orbiculata* and at least one terminal rosette with 5 cm of stem for *Aeonium* species. Cuttings were planted in trays of sterilized pumice within 12 hours of collection, dipping stems into Seradix™ rooting powder (active ingredient 0.1% 4-indole-3-butyric acid) beforehand. After two weeks' cultivation in glasshouse conditions, cuttings were planted into individual 0.9 L pots containing seedling potting mix; a 3:2 mix of peat and pumice, with 200 g dolomite, 50 g soil wetting agent (Hydraflo L®), and 100 g slow-release fertilizer (Osmocote® Exact Mini 3-4M) per 50 L. During planting, root length was measured. Cuttings were cultivated in glasshouse conditions for a further four weeks before transferring outside for two weeks to minimise shock before transplantation. Before transferring plants to the field, their heights and widths (mm) were measured as a baseline.

In November 2010, the beginning of the three species' flowering seasons, plants were transferred to the field sites. Cuttings were individually and randomly assigned to sites, first excluding the 20 with shortest root lengths. On transplanting, individuals were placed approximately 15 cm apart, in pots, into holes of 10 cm depth. Pots were arranged in a grid of 5 rows by 3 columns, each column comprising a single species, rotating the order of species' columns at each new site. To record air temperature, one Thermochron® iButton data logger was placed facing south in the central pot of each site, 5 cm above ground level with a cover of aluminium foil to protect from precipitation and solar radiation. Data loggers were programmed to record temperature every four hours to the nearest 0.5 °C. I measured aspect at each site to the nearest cardinal direction (N, E, S, W or NA on flat terrain), and vegetation canopy cover using a convex spherical densiometer (Forestry Suppliers Inc., model 43887), according to the methods of Lemmon (1956). Canopy measurements were taken from 50 cm above ground at four cardinal directions (N, E, S, and W), and averaged to give percentage overhead density. To protect from livestock, a steel cage measuring 1 × 1.5 × 0.8 m was secured over the cuttings.

Table 3.1 Target species traits. Maximum size and time to maximum size from Vogan (2003) and Royal Horticultural Society (2014). Elevation, precipitation and annual mean temperature in native, New Zealand, and all other introduced ranges taken from occurrence data (Table A.1) and Worldclim Bioclim variables [(Hijmans *et al.* 2005), available at <http://www.worldclim.org>]. Minimum elevation for all species in all regions is 0 MASL.

| Species | Native range | Growth form | Max size (cm) | Time to max size (years) | Max elevation (MASL.) | | | Annual precip. (mm) | | | Annual mean temp. (°C) | | |
|----------------------|-----------------|-------------|-----------------|--------------------------|-----------------------|-----|-------|---------------------|----------|----------|------------------------|-------|-------|
| | | | | | Native | NZ | Other | Native | NZ | Other | Native | NZ | Other |
| <i>A. arboreum</i> | Morocco | Upright | 180 tall | 5-10 | 1600 | 200 | 1000 | 100-600 | 600-1500 | 300-1200 | 12-20 | 10-15 | 11-20 |
| <i>A. haworthii</i> | Canary Islands | Mounding | 60 tall 80 wide | 10-20 | 900 | 400 | 500 | 300-500 | 600-2200 | 300-1000 | 15-21 | 10-16 | 12-19 |
| <i>C. orbiculata</i> | Southern Africa | Upright | 150 tall | Unknown | 2700 | 400 | 700 | 0-1100 | 600-1800 | 300-900 | 8-23 | 10-15 | 11-20 |

Table 3.2 Number of sites on Banks Peninsula used for cuttings only, seed trays only, or both, in each bioclimate zone as defined by Wilson (1993).

| Elevation (MASL) | Wilson (1993) bioclimate zone | Number of sites | | |
|------------------|-----------------------------------|-----------------|------------|------|
| | | Cuttings only | Seeds only | Both |
| 0 - 150 | Maritime cool temperate (coastal) | 4 | 6 | 8 |
| 150 - 500 | Lower cool temperate * | 3 | 1 | 16 |
| 500 - 750 | Upper cool temperate | 0 | 0 | 9 |
| 750 - 900 | Subalpine | 0 | 0 | 0 |

* 0-100 MASL inland

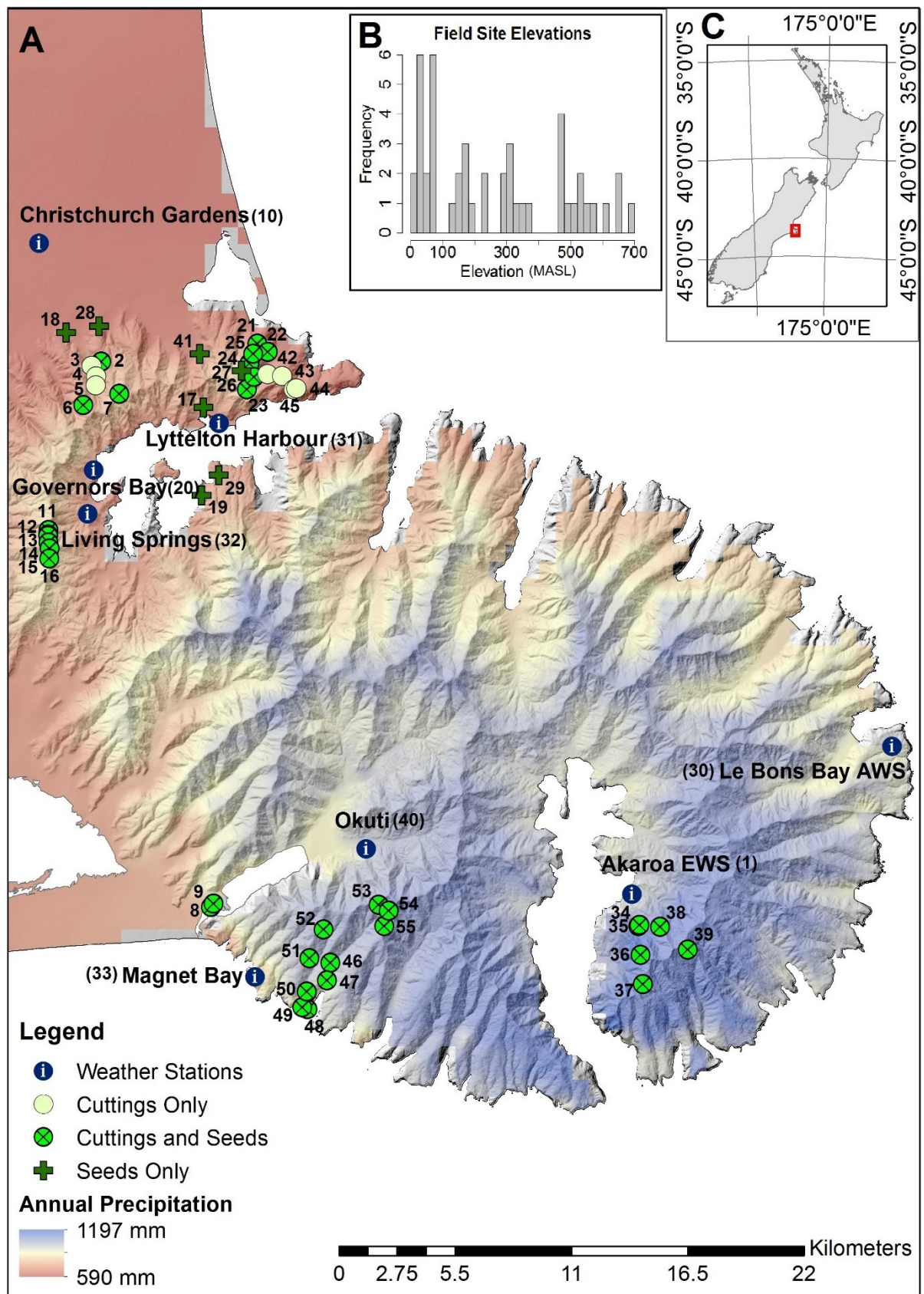


Figure 3.1 a) Field sites, and weather stations providing precipitation data, b) field site elevations, and c) location of Banks Peninsula. Field sites contained cuttings only, seeds only or both (see legend), site numbers correspond to Table B.2 (site details). Base map is total annual precipitation with shaded relief, where grey indicates no data. Precipitation was interpolated from the 30 arc-second Worldclim layer [(Hijmans *et al.* 2005), available at <http://www.worldclim.org>].

3.3.5 Germination and seedling survival experiment

Germination and seedling survival was assessed by transplanting seed trays to experimental sites and monitoring for one year. Seed was sourced in 2011 from wild inflorescences, harvested from eight distinct populations per species (Figure B.1) from a range of climates to test for possible source effects. Pods were emptied and the contents homogenised into one mixed sample per source population. Differences in seed size between *Aeonium* species and *C. orbiculata* required that *Aeonium* seeds were sown by weight, while *C. orbiculata* seeds were visible to the naked eye and were sown by hand. Due to the small size of *Aeonium* seeds, a 0.1 g sample of mixed seed and chaff from each source population was weighed (to the nearest 100 µg), sorted under a dissection microscope at 10 × magnification, and all seed counted to estimate the weight (g) of 100 seeds. This amount was weighed and subdivided equally into ten samples, assumed to contain approximately ten seeds (Table B.3). I tested baseline seed viability in order to account for any effect of seed source on germination. Samples of 100 seeds were drawn from each of the mixed samples used for sowing, and suspended in 5 ml of triphenyl tetrazolium chloride (TTC) solution inside a sealed test tube. The TTC was dissolved in deionized water at 1%. Test tubes were kept in the dark at 21 °C for 36 hours, after which point seeds were individually examined under the microscope at 40 × magnification. Seed coats were removed with a needle. The TTC is a redox indicator that reacts with tissue exhibiting cellular respiration, and is used to assess viability, vigour and malformed embryos (Leist & Krämer 2003). Darker staining indicates more vigour, while partially stained seeds indicate non-viability of the cotyledon or radicle and therefore malformation, while absence of staining indicates non-viability. Each seed was categorized as high vigour, low vigour, malformed or non-viable (Figure B.3), and summed over each site to give a percentage for each category.

Seeds were sown into germination trays and transported to the field in July 2011 (the austral winter), to allow dormancy to be broken naturally prior to germination in spring. Seeds were planted into cell trays of 9 columns by 10 rows, where each cell had a 10 ml capacity. Trays were subdivided into 3 blocks of 3 columns (one block per species), and the order of blocks was rotated at each site. Each column corresponded to one source population, assigned with a stratified design evenly representing sources across elevations. A total of 900 seeds were sown in each tray, with approximately 10 seeds in each cell. The same standard seedling potting mix was used as for plant cuttings. To minimise risk of seed escape, trays were covered with a fine-gauge mesh, white to prevent artificial warming via solar absorption. Because of an earthquake on February 22nd 2011, seven sites were inaccessible for over one year and so could not receive seed trays. Instead, six volunteers offered the use of private residential gardens on Banks Peninsula and these were used as replacement sites, as well as one additional site provided by the Christchurch City Council. These seven sites were used for germination trials only (Figure 3.1).

3.3.6 Risk mitigation and site monitoring

Cotyledon orbiculata is an Unwanted Organism in New Zealand, therefore propagating the organism requires an exemption from the Ministry for Primary Industries (MPI). Permission was granted under the condition that all plant material was transported securely, had minimal chance of escape or reproduction, and was destroyed in November 2012. Cuttings remained in place for two years and were monitored every four to six weeks over spring and summer, and every three months during autumn and winter. Visits were to check for inflorescences, to ensure that data loggers were functioning, and to record mortality. I allowed inflorescences to develop and counted emerging flowers, but removed them before seeding. Plants were measured every 6 months at the end of November and beginning of June, recording aboveground canopy volume (height, width and length) in millimetres. Seedlings were counted at each visit for the first three months after planting to capture emergence and mortality, then afterwards at the normal 6 - monthly measurement intervals. When the experiment ended in November 2012, plants and seed trays were sprayed with one of six herbicides: glyphosate, picloram, or metsulfuron, each with or without additional penetrant. One month later, all roots and plant material were removed and destroyed, and the soil was re-sprayed with the most effective of the herbicides (see Appendix E). Annual site monitoring continued until November 2015.

3.3.7 Analysis and environmental variables

Seedling establishment, and plant growth and mortality were modelled using generalized linear mixed models (GLMMs) in the R package *lme4* (Bates *et al.* 2014; R Core Team 2014), as a function of environmental variables. To account for pseudo-replication, the variables *Site* (field site) and *Source* (plant/seed source population) were included as crossed random effects in all models. Eight environmental variables were used, calculated as annual or six-monthly means depending on the response variable. Variables were added as linear fixed effects except where otherwise stated, first testing for significant effects of variables individually, then fitting a model with all significant effects and removing non-significant redundant variables in a stepwise fashion, testing for improvement in AIC at each step using a Chi-squared test using the *anova* function in R's base package. I also tested for potential interaction effects between significant variables. Models were tested against a null model with random effects only, also with a Chi-squared test. All model coefficients are reported with 95% confidence intervals, calculated with the *confint.merMod* function using 500 bootstrapped replicates.

Eight environmental variables were used to explain variation in plant performance. Solar radiation (KWh/m²) was included on the basis that sunlight is fundamental to photosynthesis and plant growth (Monteith 1972), and was modelled using the Solar Radiation Spatial Analyst tool in ArcMap 10.1 (Fu & Rich 1999; Environmental Systems Research Institute 2011) with a 15 m DEM base layer. Growing degree days (GDD) and frost days (minimum temperature below 0 °C) were included as plants generally respond to heat sums (Bonhomme 2000) and because the species are believed to be frost sensitive (Vogan 2003). I calculated GDD at bases 5 and 10 °C using the raw four-hourly temperature

data from the site data loggers (see section 3.3.4). Bases 5 and 10 were chosen despite being correlated ($r = 0.88$), because it was unknown which temperature would be most biologically relevant to the species. Total precipitation (mm) was included because high rainfall is likely to be limiting to xerophytes. Data were obtained from the nearest weather station in the CliFlo database [$n = 7$, Figure 3.1, (National Institute of Water and Atmospheric Research 2014)]. Limitations are discussed in section 3.3.10. Aspect was included as a categorical variable of the nearest cardinal direction (NA on flat terrain), because occurrence data indicate that most populations are on north-facing slopes, and, in the event that modelled solar radiation did not accurately reflect site conditions aspect would be a crude proxy. Elevation (MASL) was included to capture any unexplained variation along the experimental gradient, and overhead canopy cover (%) was included as the species are thought to be shade-intolerant (Vogan 2003). Canopy cover (CC) was calculated from spherical densiometer readings (see section 3.3.4). All climatic variables were standardized to a mean of zero and standard deviation of one to allow comparison of effect sizes where data are measured on different scales.

3.3.8 Model fitting and performance

Models of germination, mortality and growth were each fitted separately with varying time steps for environmental variables. Germination was modelled as the total number of seedlings in November 2012 out of 100 seeds originally sown, fitted with a logistic GLMM. This model accounted for germination and subsequent survival, over approximately the same annual time step as other models, and is hereafter referred to as “seedling establishment”. While a survival analysis would also be appropriate for these data, it was decided to maximize simplicity to facilitate later extrapolation. Although some emergence occurred in September (Figure 3.2), climate variables were summed over an annual time step (November - November) rather than, for example, July 2011 - November 2012, to allow comparison of predictions with other vital rates. Climate variables were highly correlated between 12 and 17-month sums, thus choice of time step did not affect model performance.

Relative growth between each measurement interval was calculated from estimates of aboveground canopy volume (height \times width \times length, reported hereafter in litres). Relative growth standardises for differences in raw volumes, and was calculated according to equation 2.

$$\text{Relative Growth} = [\ln(\text{Volume}_{t+1}) - \ln(\text{Volume}_t)] \quad (2)$$

Annual relative growth in years one and two was modelled as a Gaussian GLMM over a November - November time step. Although growth varied throughout the year, net annual growth was modelled rather than seasonal growth, because it is likely to be more relevant to the species' climatic limits. Additionally, predictions were considerably easier to interpret, and simplicity was preferable for extrapolating model predictions. In addition to all aforementioned climate variables, a quadratic elevation term was included in the growth models because scatterplots indicated a clear quadratic relationship between relative growth and elevation. Year was included as a fixed factor effect due to

lower relative growth over time at all sites. This assumes the same slope in the relationship between growth and climate, but fits a different intercept for each year. To test the validity of this assumption I ran single-year models of annual relative growth, and found similar effect sizes for the same climate variables as in the two-year model. Plotting relative growth against significant variables revealed similar gradients over both years, but with different intercepts (Figure B.4).

Mortality was modelled using two distinct 6 - monthly models, as survival patterns were highly seasonal. Logistic models were run using the binomial response variable, dead/alive, for individual plants. One model was run for “summer” (December 1st - May 31st) and one for “winter” (June 1st - November 31st). There were two years of observations for the winter models, but only one for summer due to zero deaths in the first 6 months. Summer mortality therefore had insufficient replication to be modelled using a GLMM, and was instead modelled using a binomial GLM without random effects. The additional variable, canopy volume at the time of last measurement (six months previously), was included for all mortality models under the hypothesis that small plants had higher risk of mortality. Canopy volume (v) was log-standardized according to equation 3 (\bar{x} = mean, s = standard deviation).

$$\text{Log Standardized Canopy Volume} = \{\ln [v_i] - \bar{x} [\ln (v)]\} / \{2s [\ln (v)]\} \quad (3)$$

To test degree of fit in final models, marginal and conditional R^2 were calculated using a function based on the methods of Johnson (2014), which estimates a pseudo- R^2 using fixed effects only and all effects, respectively. I calculated McFadden’s pseudo- R^2 (McFadden 1973) for the simple binomial models of summer mortality. In addition, prediction of binary outcomes for seedling and mortality models was assessed using area under the receiver operating curve (AUC). The AUC is a threshold-independent measure that tests whether models are more likely than chance to assign higher scores to positive outcomes, where $\text{AUC} > 0.5$ indicates better predictive ability than chance (Fielding & Bell 1997). I calculated AUC and corresponding 95% confidence intervals using the *ci.auc* function in R’s *pROC* package (Robin *et al.* 2011).

3.3.9 Comparison with observed distribution

The third aim of this chapter was to infer potential upward spread on Banks Peninsula for the target species. Seedling establishment, growth and mortality models were extrapolated to various elevations and compared with predictions at current distribution limits. This was only possible where elevation, or a highly correlated variable (*e.g.* frost days) was a significant predictor, and assumptions are detailed in the following paragraph. Species distribution data were collected for Banks Peninsula through online databases, herbaria, publications and surveys (Table B.1, Figure B.1 and Figure B.2). Where possible, relative growth, mortality and seedling establishment were predicted at the following elevations: the 95th percentile of the observed distribution on Banks Peninsula, the maximum observed elevation on Banks Peninsula, and at 100, 200 and 300 metres above the maximum elevation. This allowed comparison of predicted values between ostensibly suitable elevations and beyond current

limits. Results were used to infer the likelihood that the species are near their elevation limits on Banks Peninsula, or whether upward spread might occur. Comparisons between vital rates suggest whether seedling establishment, mortality or growth will most likely determine upward spread. I calculated 95% confidence intervals around GLMM predictions using the *bootMer* function in *lme4*, and for GLMs of summer mortality with the *predict* function in base R. Some assumptions were necessary to extrapolate models containing variables other than elevation. I assumed that observed linear relationships between site elevation, frost and GDD variables would hold when generalizing across the Peninsula. Post-hoc examination revealed strong linear correlations between elevation and temperature variables, weakly positive linear correlations solar radiation, and no significant correlation with annual precipitation (Figure B.5). Canopy cover was set to zero for extrapolations, representing unshaded sites. Where canopy volume was a driving variable, it was set to 1 L to represent vital rates for a small but established plant. Precipitation was set to a constant 733 mm p.a., the lower quartile of site values (*i.e.* models predict elevation limits under dry, favourable site conditions). Random effects were set to zero to give generalized predictions under mean site and source effects. The exception was seedling establishment as it was strongly influenced by random site effects, so predictions were generated with site effects at zero, and also with the maximum site value representing favourable sites. Relative growth models were run for both the first year (“rapid” growth phase) and without a year effect (“steady” growth applicable to mature plants).

3.3.10 Sources of uncertainty

While the experimental design had high power and care was taken to minimize bias, there are some key uncertainties to note. Firstly, seedling establishment was measured out of a possible 100 seeds sown, but seeds were planted by weight and error around this estimate is likely. In addition, seeds may have been lost from germination trays throughout the course of the experiment, despite efforts to prevent this. Standard potting mix eliminated site soil effects, but results may translate poorly to responses on bare substrate. Model predictions are particularly uncertain, as in addition to the assumptions described previously they do not account for microclimates. All models are based on two years of data, assuming that these years are representative of longer-term climatic trends at sites, and extreme weather events can also affect species’ range limits (Parmesan *et al.* 2000). Rainfall data is particularly uncertain due to the low number of available stations and large elevation differences between some stations and field sites (Table D.1). Orographic effects on rainfall are possible, though elevation and precipitation were not highly correlated (Figure B.5). It is also debateable whether two years is sufficient to understand processes in perennial plants (Van Der Veken *et al.* 2007). Despite these uncertainties, the models provide a necessary guideline on the species’ potential to spread beyond their current limits.

3.4 Results

3.4.1 Seedling establishment

Seedling emergence began between September and November 2011, and seedling counts declined over time due to mortality and decreasing emergence. Emergence and survival was highest at low to medium elevations, below 400 MASL (Figure 3.2a-c). Emergence was low overall; the maximum rate observed was 35% for *A. arboreum*, 25% for *A. haworthii* and 15% for *C. orbiculata*. Mean viability across all sites, however, was high (83%, 66% and 80% for *A. arboreum*, *A. haworthii* and *C. orbiculata* respectively) with over half of all seeds classed as “high vigour” (Table B.3). Viability between source sites varied by 17% for *A. arboreum*, 53% for *A. haworthii* and 44% for *C. orbiculata*. Seed source random effects had a minimal impact on models (Figure 3.3a-c), with variances of 0.14 for *A. arboreum*, 0.38 for *A. haworthii* and 0.02 for *C. orbiculata*.

Establishment of *A. haworthii* correlated negatively with elevation (Figure 3.3b), and with the exception of a single site, no seedlings survived above 319 MASL (Figure 3.3e). *Aeonium arboreum* establishment was correlated negatively with annual frost days, with lesser effects of annual precipitation (-) and GDD5 (+), resulting in a similar response to elevation as *A. haworthii* (Figure 3.3d). No *A. arboreum* seedlings established above 358 MASL; while up to 17% emerged at higher sites, none survived. *Cotyledon orbiculata* differed from *Aeonium* species as neither elevation nor temperature correlated with establishment. Annual precipitation was the only significant variable, with higher establishment at dry sites (Figure 3.3f). However, no seedlings survived above 370 MASL. Final models of seedling establishment were significantly better than null models according to Chi-squared tests ($p < 0.001$). Marginal R^2 values were higher for *Aeonium* species (*A. arboreum* 0.76, *A. haworthii* 0.47) than *C. orbiculata* (R^2 of 0.35), and conditional R^2 show additional unexplained variation within random effects (*A. arboreum* 0.85, *A. haworthii* 0.76 and *C. orbiculata* 0.80). Models of all three species predicted binary outcomes well (seedlings establish yes/no), as AUC values were high (0.95 ± 0.01 for both *Aeonium* species, 0.91 ± 0.01 for *C. orbiculata*).

3.4.2 Annual relative growth

Annual relative growth differed markedly between years. Rapid initial growth was followed by levelling off, or some die back, over the remainder of the experiment (Figure 3.4). *Aeonium* species grew larger than *C. orbiculata*; in November 2012, the mean *A. arboreum* was $13.5 \text{ L} \pm 1.1$ (SE) in volume, *A. haworthii* was $7.5 \pm 0.9 \text{ L}$, and *C. orbiculata* $3.2 \pm 0.3 \text{ L}$. This is despite *Aeonium* plants having a lower mean initial volume than *C. orbiculata* ($0.1 \pm 0.006 \text{ L}$, $0.05 \pm 0.002 \text{ L}$, and $0.2 \pm 0.01 \text{ L}$ for *A. arboreum*, *A. haworthii*, and *C. orbiculata*). Relative growth also varied with elevation. When divided into bins of low (0 - 150 MASL), medium (150 - 400 MASL), and high (400 - 700 MASL) elevations, plants at high elevations exhibited fluctuating periods of dieback and recovery, and the lowest net relative growth at the end of the experiment (Figure 3.4).

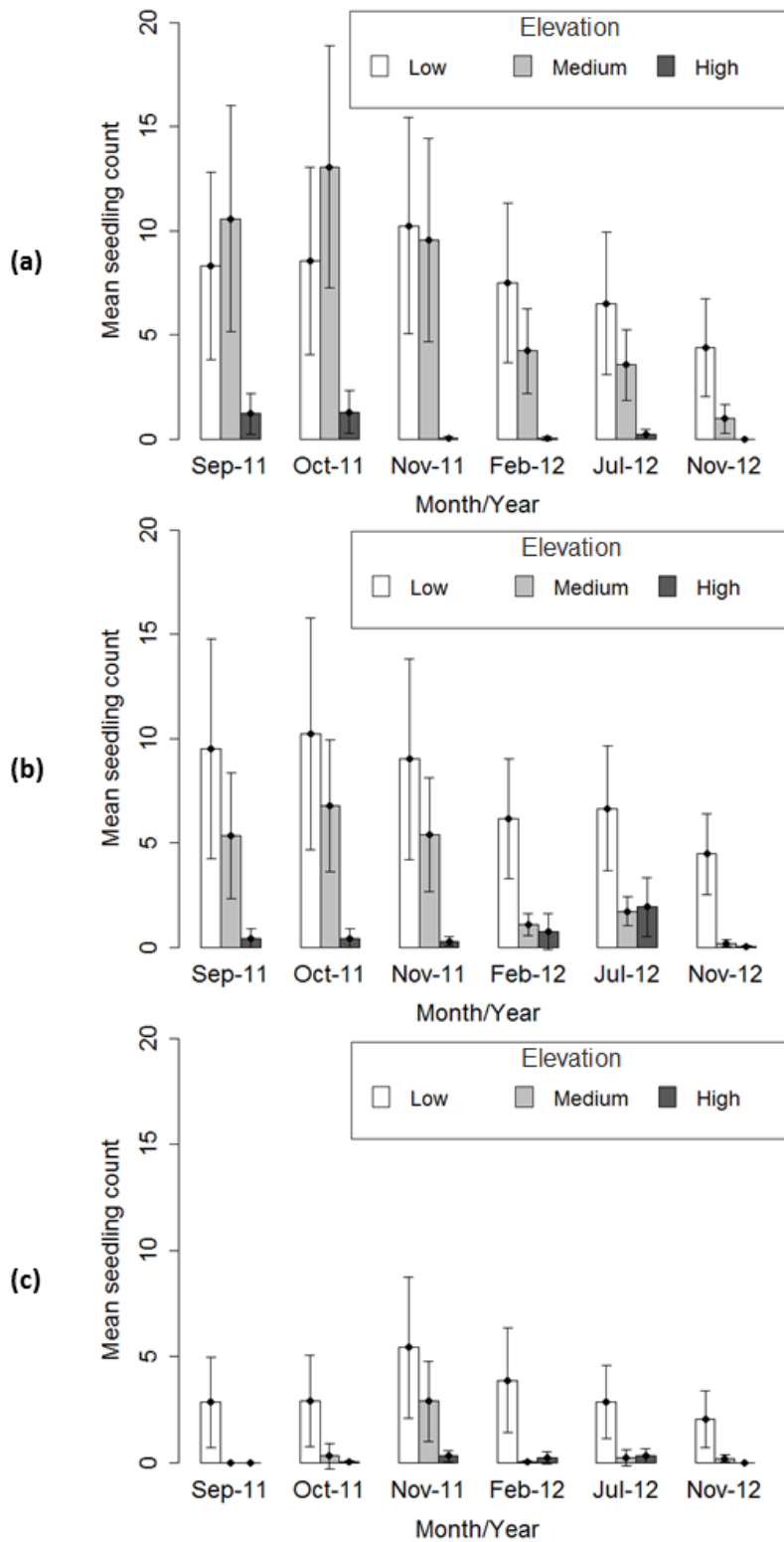


Figure 3.2 Mean seedling count at measurement intervals with 95% confidence intervals, for a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata*. Sites are divided into low (0 – 150 MASL), medium (150 – 400 MASL), and high (400 – 700 MASL) elevations. Seedling models are based on November 2012 counts.

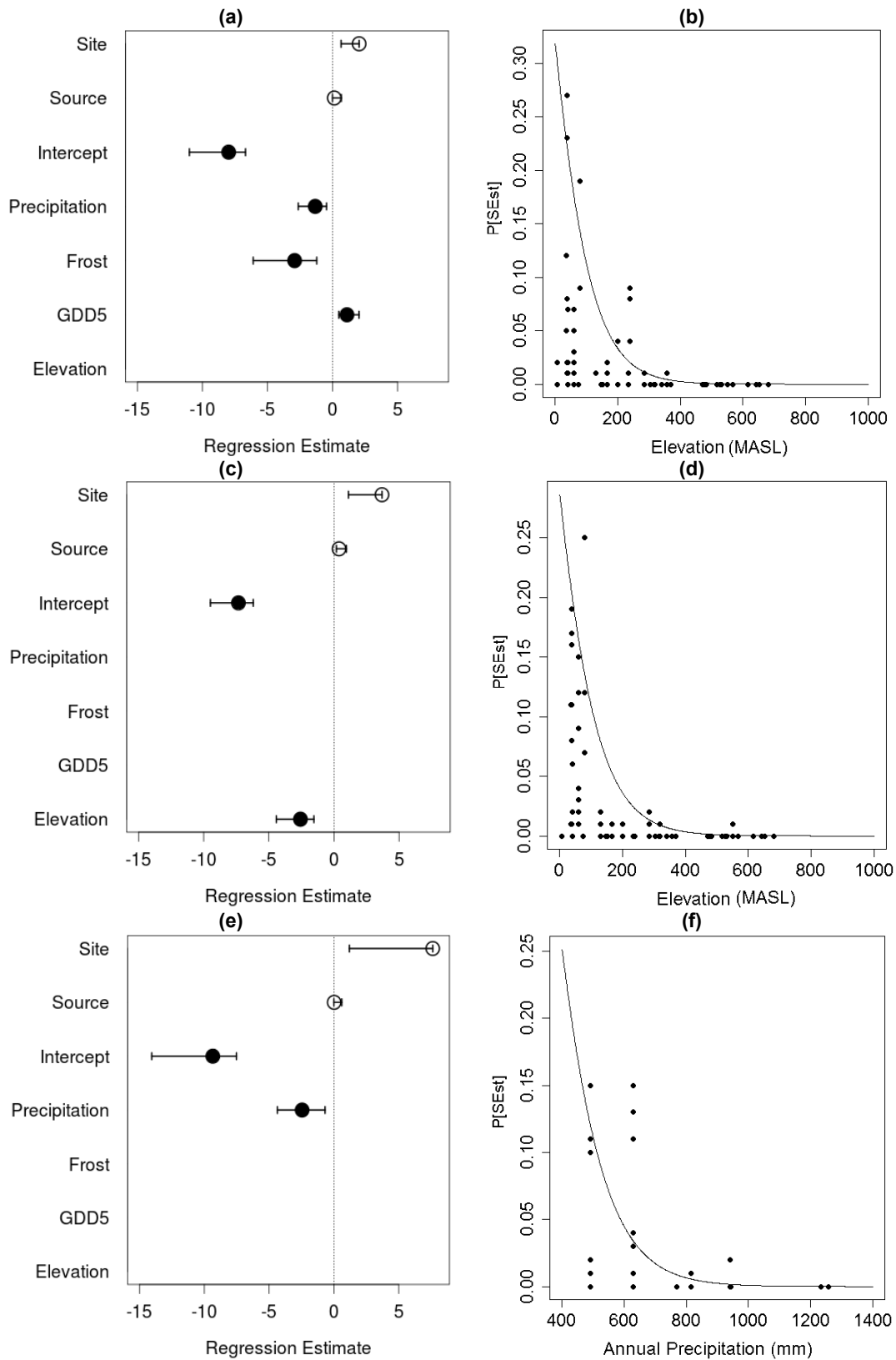


Figure 3.3 Coefficients of GLMMs of probability of seedling establishment ($P[SEst]$) \pm 95% confidence intervals, with fixed (solid) and random (hollow) effects, for a) *Aeonium arboreum* c) *A. haworthii* and e) *Cotyledon orbiculata*, and GLMM predictions (lines) and raw data (points) for b) *A. arboreum*, d) *A. haworthii* and f) *C. orbiculata*. Predictions use fixed only effects between 0 – 1000 MASL (b, d), and 400 – 1400 mm p.a. (f). For *A. arboreum* (b), constant precipitation of 733 mm p.a., and linear relationships of GDD5 and frost days to elevation are assumed (section 3.3.9). Thus, lines are not fitted to points.

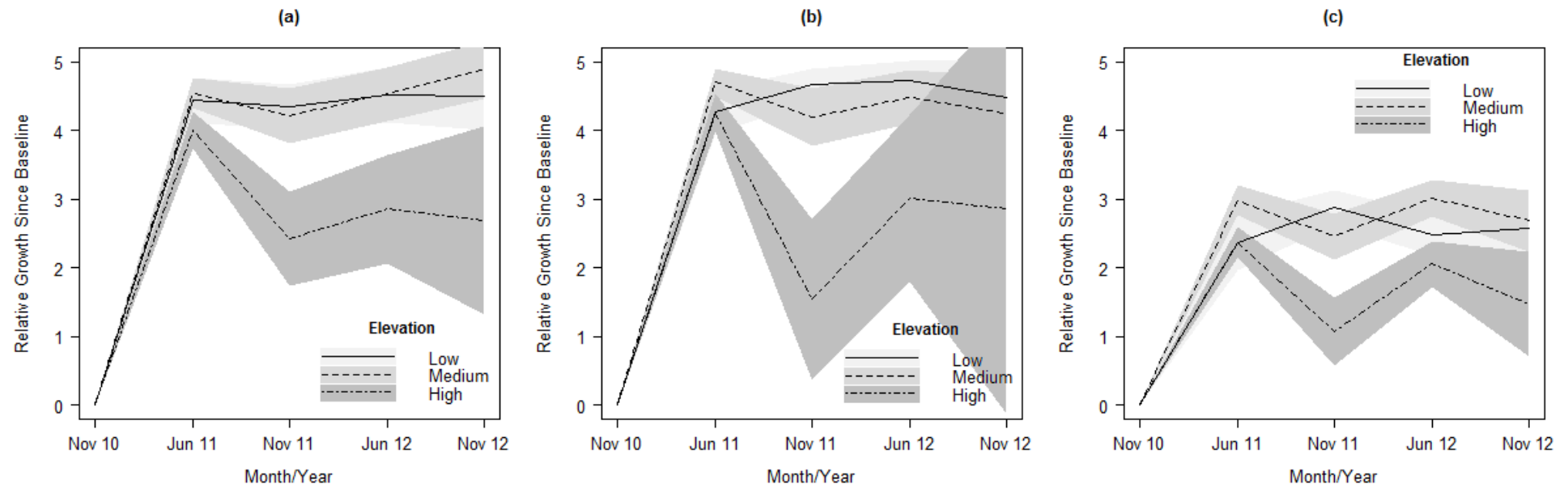


Figure 3.4 Mean relative growth, as $[\ln(\text{Volume}_{t+1}) - \ln(\text{Volume}_t)]$, since November 2010 baseline volumes at low, medium, and high elevations for a) *Aeonium arboreum*, b) *A. haworthii*, and c) *Cotyledon orbiculata*. Here, t is measured in units of half-years. Shaded area shows 95% confidence interval of the mean.

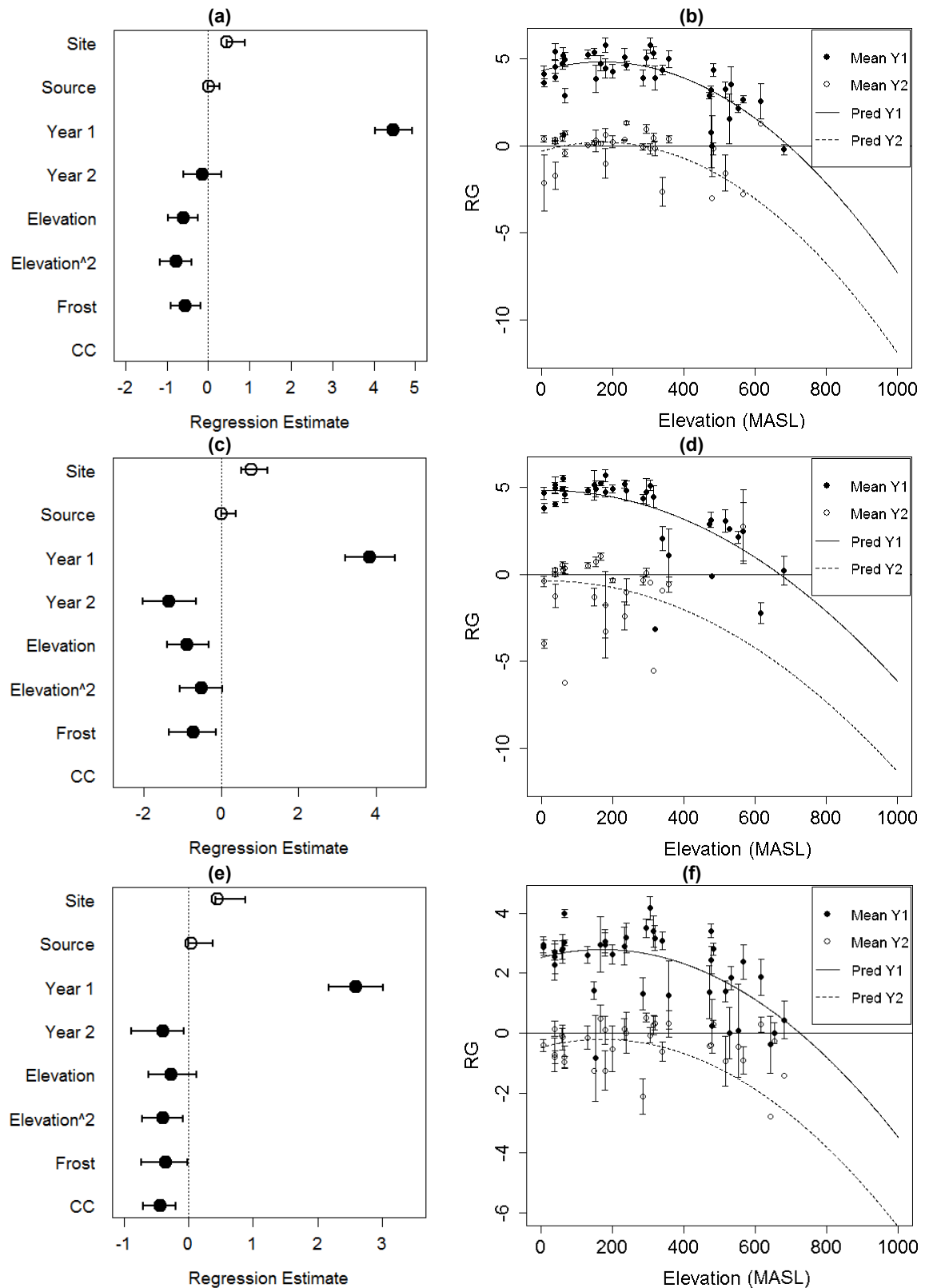


Figure 3.5 GLMM coefficients \pm 95% confidence intervals of annual relative growth (RG) models, calculated as $[\ln(\text{Volume}_{t+1}) - \ln(\text{Volume}_t)]$, with fixed (solid) and random (hollow) effects, for a) *Aeonium arboreum*, c) *A. haworthii* and e) *Cotyledon orbiculata*. GLMM predictions (lines) and site means with standard errors (points) in years one and two, shown for b) *A. arboreum*, d) *A. haworthii* and f) *C. orbiculata*. Predictions generated using only fixed effects between 0 – 1 000 MASL. A linear relationship of annual frost days with elevation is assumed (section 3.3.9). Canopy cover (CC) is set to zero for *C. orbiculata*. Thus, lines are not fitted to points.

The key variables in growth models of all three species were elevation (as a quadratic term) and annual frost days, with both of which growth was negatively correlated (Figure 3.5a-c). Relative growth was highest at around 200 MASL for *A. arboreum* and *C. orbiculata*, and sea level for *A. haworthii* (Figure 3.5d-f). Canopy cover was also a good predictor for *C. orbiculata*, where open plots were more favourable. Fixed year effects show that for all three species, growth in year one was considerably higher than in year two. Site remained an important source of variation in all three models (variance 0.45, 0.79, and 0.45, for *A. arboreum*, *A. haworthii*, and *C. orbiculata*) relative to plant source (variance 0.01, 0.00, and 0.04 respectively). Final models of relative growth performed significantly better than null models for all species ($p < 0.001$). Marginal and conditional R^2 values indicated high levels of explanatory power from fixed effects relative to random effects: 0.71 vs. 0.78 for *A. arboreum* respectively, 0.65 vs. 0.74 for *A. haworthii*, and 0.54 vs. 0.66 for *C. orbiculata*.

3.4.3 Mortality

Mortality was highly seasonal and showed a clear positive relationship with elevation. There were fewer deaths over the December - May “summer” period than the June-November “winter” period (final mortality in summer vs. winter: 2% vs. 17% for *A. arboreum*, 5% vs. 27% for *A. haworthii*, and 3% vs. 16% for *C. orbiculata*). In general, mortality increased with elevation regardless of season (Figure 3.6a-c). Above 400 MASL, 87% of *A. arboreum* individuals were dead after 2 years, 97% of *A. haworthii*, and 69% of *C. orbiculata*. Mortality also increased over time. There were more deaths in year two than year one, where mortality rose by 17% for *A. arboreum* in the second year, 13% for *A. haworthii* and 27% for *C. orbiculata*. This appeared to be due to increasing plant damage over time.

Plants that died over summer tended to be smaller than survivors (Figure B.6a-c). There was a negative relationship between canopy volume and summer mortality in all three species (Figure 3.6), and canopy volume was the strongest explanatory variable in the models. Elevation significantly improved models of summer mortality for *Aeonium* species. Intercept terms were negative indicating low probability of death for plants with a mean canopy volume. Final models of mortality performed better for *A. arboreum* and *A. haworthii* than for *C. orbiculata* (Pseudo- $R^2 = 0.41, 0.55$ and 0.19 respectively), but all constitute excellent fit (McFadden 1973). Model AUCs indicate excellent prediction for both *Aeonium* species (0.95 ± 0.04 for *A. arboreum* and 0.96 ± 0.04 for *A. haworthii*), and good prediction for *C. orbiculata* (0.73 ± 0.18).

Canopy volume, time, and frost days explained variation in winter mortality for all three species. Individuals that died were smaller on average than survivors (Figure B.6a-c), meanwhile mortality increased in the second winter and with increasing number of frost days. To reflect repeated cold stress over time, cumulative frost days were used in GLMMs instead of a fixed year effect, as it was more biologically meaningful and significantly improved model fit. Because of the non-normal distribution of cumulative frost days, this variable also needed to be log-standardized in the same way as canopy volume (equation 3). Cumulative frost was used in winter mortality models only, as

mortality was the only vital rate that showed such change over time (although relative growth also changed over time, this is explicable with ontogenetic drift). Models show that large plants withstood fluctuating dieback and recovery, but small plants were only able to survive given favourable conditions (Figure B.6d-f). Frost was the most important predictor of winter mortality regardless of plant size (Figure 3.7a-c.), but only large plants are predicted to survive harsh conditions (Figure B.7a-c). Fixed effects explained most of the among site variation in winter mortality, with the exception of *C. orbiculata* (marginal vs. conditional R^2 of final models were 0.84 vs. 0.86 for *A. arboreum*, 0.74 vs. 0.85 for *A. haworthii*, and 0.53 vs. 0.95 for *C. orbiculata*). Model AUCs showed good prediction of binary outcomes (*A. arboreum* and *A. haworthii* 0.96 ± 0.02 , *C. orbiculata* 0.97 ± 0.02).

3.4.4 Elevation limits on Banks Peninsula

Currently, *A. arboreum* has the lowest distribution limit on the Peninsula (maximum 177 MASL), and *C. orbiculata* the highest (maximum 381 MASL). For both *Aeonium* species, the greatest difference between predictions at current elevation limits and 100 m higher was in winter mortality (Table 3.3). Even at *A. haworthii*'s current limits, predicted winter mortality is high and seedling establishment is low. Just 100 m higher, and winter mortality is predicted to be 88%, and seedling establishment $< 1\%$. Predictions for *A. arboreum*, meanwhile, are more favourable at its current limits, but a 100 – 200 m rise leads to similar predictions of growth, mortality and seedling establishment to *A. haworthii* at its distribution limit. Only two of the four vital rates modelled were correlated with elevation or temperature for *C. orbiculata*. Of those, relative growth declined most sharply as elevation increased, with net growth (the sum of both predicted RGs) becoming negative 200 m above its current distribution. However, winter mortality, based on a 1 L canopy volume, does not reach 75% (predicted mortality at *A. haworthii*'s current maximum elevation) until 681 MASL. It is unclear whether relative growth will be sufficiently limiting to *C. orbiculata* to prevent establishment of plants 1 L or more in volume that could survive multiple winters.

Prediction intervals were generally narrow, with the notable exception of winter mortality for *A. haworthii* and *C. orbiculata*. This indicates a high degree of confidence overall, but that winter mortality models should be interpreted with some caution. Random effects were not included in model predictions with the exception of seedling establishment, where predictions were also generated using the maximum site values. This was because site remained an important source of variation in seedling models, and heavily influenced model predictions. Under the assumption that site represented unknown environmental conditions, the maximum site intercept was used to predict seedling establishment at high elevations with all other environmental factors being favourable.

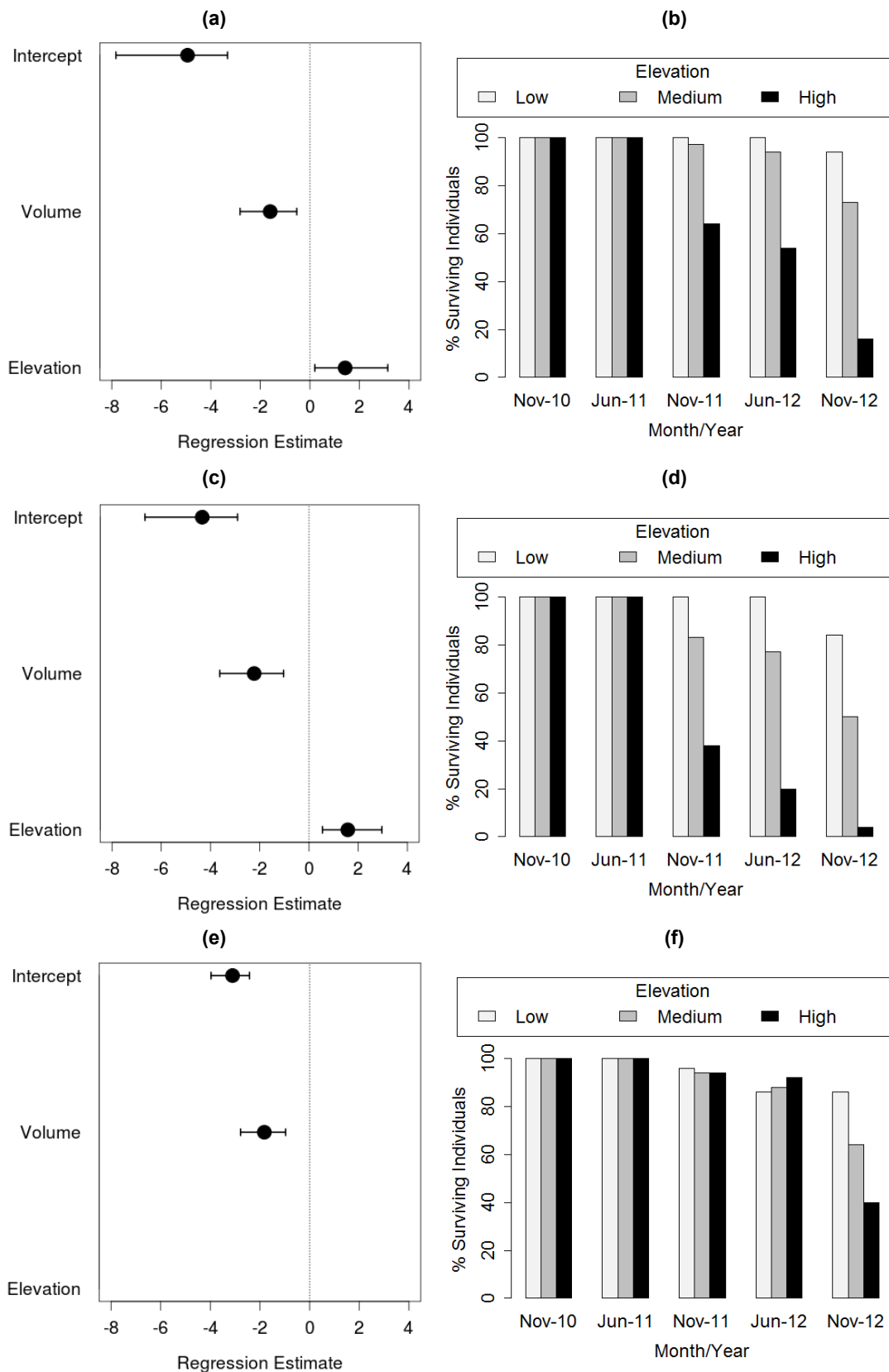


Figure 3.6 Coefficients of binomial GLMs of summer mortality with 95% confidence intervals, for a) *Aeonium arboreum*, c) *A. haworthii* and e) *Cotyledon orbiculata*, and percentage of surviving individuals at each measurement period, at low, medium, and high elevations for b) *A. arboreum*, d) *A. haworthii* and e) *C. orbiculata*. Percentages measured out of $n = 50$ individuals at low and high elevations, and $n = 100$ at medium elevations.

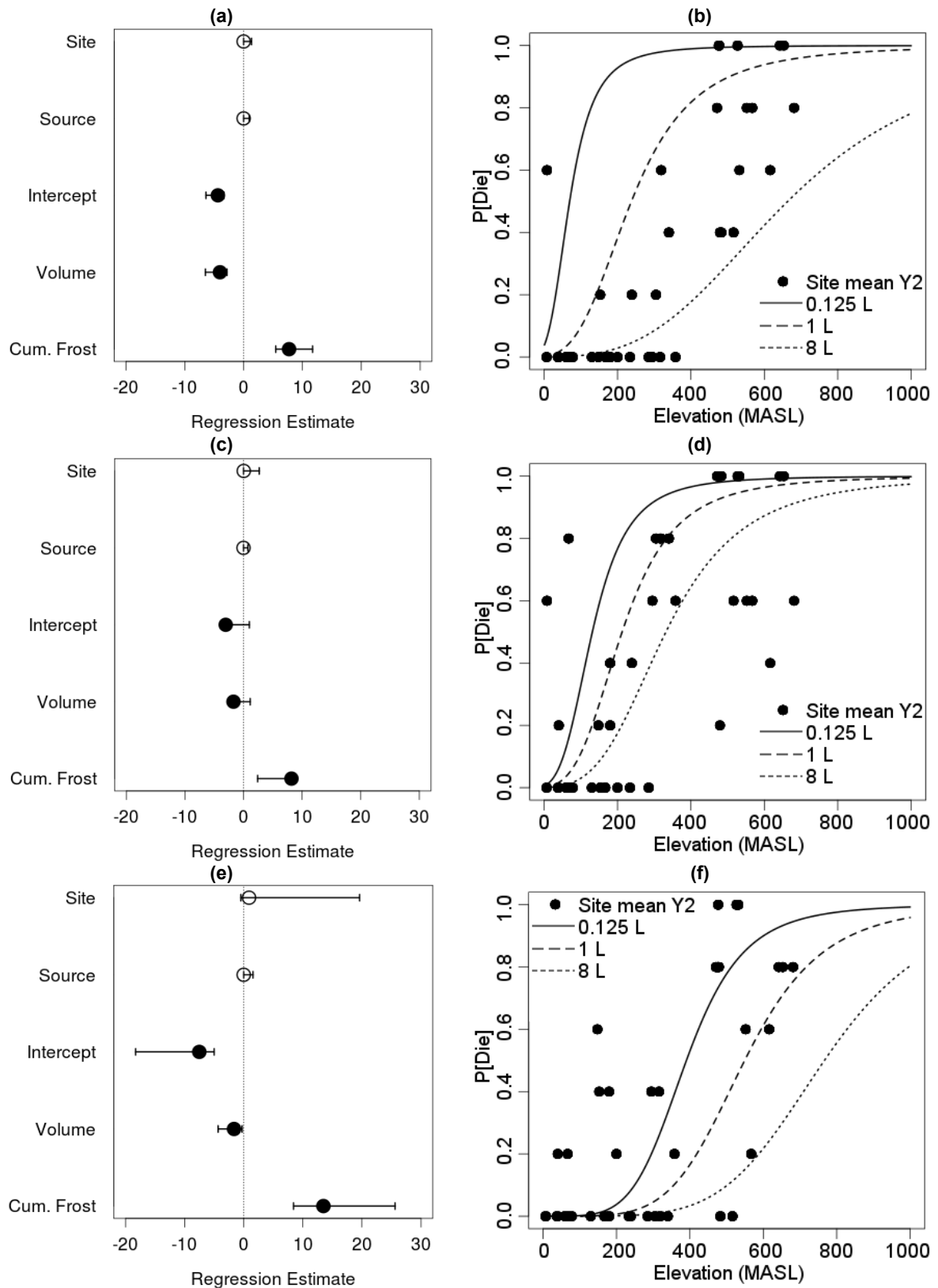


Figure 3.7 Logistic GLMM coefficients of winter mortality \pm 95% confidence intervals, with fixed (solid) and random (hollow) effects, for a) *Aeonium arboreum*, c) *A. haworthii* and e) *Cotyledon orbiculata*, and modelled probability of death (P[Die], lines) and observed mortality per site (points) vs. elevation, for b) *A. arboreum*, d) *A. haworthii* and f) *C. orbiculata*. Predictions (lines) generated for small (0.125 L), medium (1 L), and large (8 L) plants, using only fixed effects between 0 – 1000 MASL. A linear relationship of annual frost days with elevation is assumed, derived from recorded data. Consequently, lines are not fitted to points.

Table 3.3 Modelled seedling establishment (SEst), relative growth (RG) and summer and winter mortality (SM and WM), at various elevations (MASL), for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. No random effects included except for SEst max, predicted seed establishment at the most favourable site using the highest random site effect. Predictions given for the 95th percentile of the observed distribution (+), the maximum observed elevation (*, bold), and up to 300 MASL above the observed limit. The 95% prediction intervals are denoted by \pm . Frost and GDD assumed to increase linearly with elevation, other variables set to constant values.

| <i>A. arboreum</i> | | | | | | | <i>A. haworthii</i> | | | | | | | <i>C. orbiculata</i> | | | |
|--------------------|------------------------|------------------------|-------------|-------------|-------------|-------------|---------------------|--------------------------------------|------------------------|-------------|-------------|-------------|-------------|----------------------|-------------|--------------|-------------|
| MASL | SEst | SEst max | RG Y1 | RG | SM | WM | MASL | SEst | SEst max | RG Y1 | RG | SM | WM | MASL | RG Y1 | RG | WM |
| +152 | 0.004 | 0.06 | 4.79 | 0.34 | 0.01 | 0.23 | | | | | | | | | | | |
| | ± 0.004 | ± 0.004 | ± 0.35 | ± 0.36 | ± 0.04 | ± 0.17 | | | | | | | | | | | |
| *177 | 0.003 | 0.04 | 4.80 | 0.35 | 0.01 | 0.31 | +160 | 0.003 | 0.06 | 4.58 | 0.74 | 0.01 | 0.30 | | | | |
| | ± 0.003 | ± 0.003 | ± 0.37 | ± 0.39 | ± 0.04 | ± 0.19 | | ± 0.004 | ± 0.004 | ± 0.51 | ± 0.53 | ± 0.03 | ± 0.23 | | | | |
| 277 | 0.001 | 0.01 | 4.61 | 0.15 | 0.01 | 0.61 | *303 | 6×10^{-4} | 0.01 | 3.89 | 0.05 | 0.03 | 0.75 | +252 | 2.75 | 0.15 | 0.01 |
| | ± 0.001 | ± 0.001 | ± 0.46 | ± 0.45 | ± 0.05 | ± 0.14 | | $\pm 9 \times 10^{-4}$ | $\pm 9 \times 10^{-4}$ | ± 0.64 | ± 0.67 | ± 0.05 | ± 0.23 | | ± 0.41 | ± 0.42 | ± 0.44 |
| 377 | 2×10^{-4} | 0.003 | 4.06 | -0.39 | 0.03 | 0.79 | 403 | 2×10^{-4} | 0.003 | 3.13 | -0.70 | 0.06 | 0.88 | *381 | 2.39 | -0.21 | 0.13 |
| | $\pm 5 \times 10^{-4}$ | $\pm 5 \times 10^{-4}$ | ± 0.45 | ± 0.45 | ± 0.05 | ± 0.10 | | $\pm 4 \times 10^{-4}$ | $\pm 4 \times 10^{-4}$ | ± 0.66 | ± 0.71 | ± 0.07 | ± 0.29 | | ± 0.42 | ± 0.45 | ± 0.46 |
| 477 | 6×10^{-5} | 0.001 | 3.16 | -1.30 | 0.05 | 0.88 | 503 | 5×10^{-5} | 0.001 | 2.14 | -1.69 | 0.13 | 0.94 | 481 | 1.92 | -0.69 | 0.34 |
| | $\pm 3 \times 10^{-4}$ | $\pm 3 \times 10^{-4}$ | ± 0.42 | ± 0.45 | ± 0.06 | ± 0.07 | | $\pm 2 \times 10^{-4}$ | $\pm 2 \times 10^{-4}$ | ± 0.73 | ± 0.77 | ± 0.13 | ± 0.33 | | ± 0.39 | ± 0.40 | ± 0.47 |
| | | | | | | | 603 | 2×10^{-5} | 3×10^{-4} | 0.93 | -2.90 | 0.27 | 0.96 | 581 | 1.26 | -1.34 | 0.57 |
| | | | | | | | | $\pm 7 \times 10^{-5}$ | $\pm 7 \times 10^{-5}$ | ± 1.02 | ± 1.11 | ± 0.25 | ± 0.35 | | ± 0.48 | ± 0.54 | ± 0.49 |
| | | | | | | | | | | | | | | 681 | 0.42 | -2.18 | 0.75 |
| | | | | | | | | | | | | | | | ± 0.85 | ± 0.91 | ± 0.49 |

3.5 Discussion

There is strong evidence that the distributions of *A. arboreum*, *A. haworthii* and *C. orbiculata* on Banks Peninsula are limited by climate, with a plant performance declining with increasing elevation. This is consistent with the fact that New Zealand marks the coldest and wettest extremes of the species' realized niches and therefore, they are likely to be close to their limits of cold tolerance (see Chapter 2). In the *Aeonium* species, performance declined with increasing elevation and its covariates across all vital rates measured (seedling establishment, relative growth, summer and winter mortality). In *C. orbiculata*, only relative growth and winter mortality were associated with elevation or its correlates. The provenance of cuttings and seeds had a negligible effect on plant performance and germination, as demonstrated by the consistently negligible effect of the random source effect in GLMMs, and there is consequently no evidence for an adapted fitness gradient across Banks Peninsula [e.g. Holt and Keitt (2005)].

3.5.1 Predicted limits

Model extrapolations within and above the species' current distributions on the Peninsula suggest that all three are close to their elevation limits in the region. *Aeonium haworthii* appears to be closest to its limits, with 75% winter mortality and less than 1% seedling establishment predicted at its current maximum elevation. It appears unlikely that survival and seedling establishment of *A. haworthii* would be sufficient to facilitate colonization at much higher elevations. Models predict that *A. arboreum* would reach similar seedling establishment, growth and mortality rates at around 100 – 200 m above its current range. Assuming that *A. haworthii*'s vital rates are close to limiting at its current range edge, both *Aeonium* species are likely to have similar maximum elevations (around 300 MASL). *Cotyledon orbiculata*, meanwhile, is currently found at elevations where steady relative growth is predicted to be negative (381 MASL). However, at these elevations the rapid growth phase (year one) is strongly positive, so although plants at these elevations should be smaller than their low-elevation counterparts, they might still persist over a number of years. It is possible that similar populations of small plants could establish and survive well beyond the current limits, subject to relative growth. Again taking *A. haworthii*'s predicted rates at current limits as a reference, a 1 L *C. orbiculata* plant is not predicted to experience comparable winter mortality until 300 m above its current maximum (681 MASL).

All three species appear to be restricted to lower elevations in New Zealand than in their native ranges. In the case of the two *Aeonium* species this may be primarily explained by the difference in latitude between the native and New Zealand ranges. Using Hopkins' Bioclimatic Law (1920) as a rough estimate, the equivalent elevation of 400 MASL in New Zealand (slightly above the maximum elevation of *A. haworthii* in New Zealand, according to distribution data), would be approximately 2300 MASL in Tenerife when adjusted for latitude. Similarly, the maximum elevation of *A. arboreum* in Morocco of 1600 MASL would equate to roughly sea level in New Zealand. While these are not

highly accurate calculations, they illustrate that elevation is not necessarily comparable between the ranges. However, the dramatic differences in limits of *C. orbiculata* between ranges cannot be explained by latitude alone, as the highest elevation occurrences in the native range, Lesotho, are climatically very similar to Central Otago in New Zealand (according to the “match climates” function in CLIMEX™), where the minimum temperatures are much lower than anywhere on Banks Peninsula. A possible explanation for this is that frost tolerance in regional populations of *C. orbiculata* differ strongly across the native range, and these traits are heritable (Van Coller & Stock 1994). The cold limitation documented in this study suggests that the *C. orbiculata* in New Zealand are more likely to have originated from less-hardy, low-elevation populations in South Africa than hardy high-elevation populations, *e.g.* in Lesotho.

Results also indicate that the three species’ vital rates are not equally limiting to upward spread. There is considerable similarity in predictions of seedling establishment, relative growth and mortality between both *Aeonium* species. Of these, winter mortality appears to be the key limiting factor for upward spread, followed by seedling establishment, while summer mortality and relative growth in the rapid phase do not appear to be limiting. Conversely, *C. orbiculata* appears to be restricted primarily by relative growth. Elevation is a poor predictor of seedling establishment for *C. orbiculata* on Banks Peninsula, and while winter mortality increases with elevation, summer mortality is only indirectly linked to climate through canopy volume.

3.5.2 Climatic drivers

Although climatic predictors differed between models of vital rates, there was similarity between species in key driving variables and responses. This is consistent with the fact that, while the species’ native ranges differ, they have adopted similar life strategies. These include CAM photosynthesis, drought tolerance and occupancy of bare habitats (Webb *et al.* 1988; Vogan 2003). Surprisingly, precipitation was rarely a good predictor of plant performance, most probably because there were few weather stations available, but potentially the precipitation gradient across Banks Peninsula might not be sufficiently limiting.

Climatic predictors were markedly different between vital rates, indicating a variety of pressures acting across life stages. Comparable patterns have been found in a number of other species, *e.g.* *Lacuta serriola* L. (Prince & Carter 1985) and *Impatiens glandulifera* Royle. and *Heracleum mantegazzianum* Sommier & Levier. (Willis & Hulme 2002), and is to be expected. The key correlate of relative growth in all species was a quadratic relationship with elevation, where growth peaked between sea level and 200 MASL. This could perhaps be a result of higher light competition at low sites and harsher climatic conditions at high elevations, but it is difficult to infer whether it is limiting as reduced growth under stress may be beneficial for energy conservation (Grime & Hunt 1975). Mortality was partially dependent on canopy volume in all species, whereby smaller plants had a lower probability of survival in both winter and summer. This could simply be an effect of age-

specific mortality (Michod 1979), and given more years of observations mortality in large plants might rise as they approach their life expectancy. Alternatively, it may reflect that smaller plants are less tolerant of die back associated with harsh climatic conditions. The cumulative frost term in winter mortality models means that as individuals accumulate frost damage over time, they must recover and grow in order to avoid increasingly severe damage and eventually, death. The only models which differed strongly between species were seedling establishment. Seedling establishment in *A. arboreum* was largely correlated with frost (-) and GDD5 (+), which overall leads to similar responses as the elevation-based model for *A. haworthii*, although precipitation (-) was also significant for *A. arboreum* and does not correlate well with elevation. Generally, temperature appears to be important for the germination and seedling survival of *Aeonium* species across the Banks Peninsula, and *A. arboreum* additionally requires relatively dry conditions. In contrast, the only predictor of *C. orbiculata* seedling establishment was precipitation, as a negative effect.

The most common climatic predictors across all models were frost days and elevation. Frost often limits species' distributions (Larcher 2005) and this is consistent with the species' traits; succulents have a high water content and should therefore be sensitive to freezing damage (Nobel 1981; Luttge 2004). Yet, freezing avoidance has been documented in some succulents (Stuckey & Curtis 1938; Loik & Nobel 1993) and reported fatal temperatures of the study species in their native ranges are much lower than those encountered during this field experiment (Löscher & Kappen 1981; Van Coller & Stock 1994). This apparent contradiction potentially highlights the difficulties in reconciling laboratory results with responses in the field. The effect of elevation, meanwhile, is less easy to interpret biologically, as climatic and non-climatic factors correlate with this variable (Körner 2007; Pauchard *et al.* 2009). Many of these confounding effects were accounted for in the experimental design: for example, soil was a standard mix, and sites were secured to ensure minimal disturbance or grazing, and plots were weeded to minimize competition. It follows, then, that the response to elevation is likely due to climatic effects. Aside from temperature, other variables which often change with elevation include decreasing pressure with increased elevation, and higher solar and UVB radiation under clear skies (Körner 2007). However, modelled solar radiation was a poor predictor in all cases, and there is arguably not an extreme enough elevation gradient for atmospheric conditions to be limiting. Seasonality has a complex relationship with elevation (Körner 2007) and while seasonal effects are possible, high elevation negatively affected all species despite differences in their growing seasons (*Aeonium* species in winter, *C. orbiculata* in summer). It is most plausible that the relationship with elevation is a proxy for increased snow cover, as severe damage and mortality were commonly observed at sites immediately following heavy snowfall. Although snow can have protective properties as a thermal insulator, prolonged snow cover can limit respiration, cause anoxia, impair root activity through ground ice, encourage mould and stunt growth (Körner 2003). Unfortunately there are no regional snow data, although testing plant responses against modelled data might assist in disentangling the importance of elevation for the species.

Cotyledon orbiculata was the only species that responded to canopy cover, exhibiting low relative growth and winter survival under increasing cover. A likely mechanism is the photoprotective epicuticular wax of *C. orbiculata*, which both *Aeonium* species lack. While the thickness of the wax varies in response to light conditions, it is detrimental to performance in low light (Barker *et al.* 1997). It is likely that invasion of *C. orbiculata* will be limited to more open environments and largely absent from areas under dense canopy.

3.5.3 Implications for Banks Peninsula

Results indicate that *A. arboreum* and *A. haworthii* are currently near or at their climatic limits on Banks Peninsula. While upward spread is likely to be minimal, continued colonization of coastal headlands and bays (infilling) in the region appears likely, subject to habitat availability and dispersal patterns. As such, the threat from the two *Aeonium* species to high elevation rock outcrops, where the majority of the regions' endemic species are found (Wiser & Buxton 2009), is low. The interpretation for *C. orbiculata* is more nuanced, as persistence at high elevations will depend on whether plants are able to reach sufficient size to survive and recover from winter frosts. It is unknown whether *C. orbiculata* would be able to complete its life cycle above its current maximum elevation, and although arguably unlikely, marginal populations cannot be discounted. This, in conjunction with the wider range of habitats it is capable of colonizing (Figure A.3, Figure A.7), suggests that *C. orbiculata* poses a greater threat to the region than either *Aeonium* species.

Non-climatic factors that vary with increasing elevation were not accounted for in model predictions. Dispersal barriers and pollinator availability are presumed not to be limiting at the scale of Banks Peninsula as the species produce “dust-like” seeds (van Rheede van Oudtshoorn & van Rooyen 1999) and can self-pollinate (Zietsman 1998). Slope and disturbance increase with elevation but this is unlikely to limit species that preferentially occupy vertical, disturbed habitats *e.g.* cliffs and outcrops. Factors expected to be relevant to the species on Banks Peninsula include soil, land use, and anthropogenic activity. As elevation increases in the region, soil pH tends to become less acidic. Soils at low elevations are predominantly Fragic Pallic and Fluvial Recent, characterized by poor structure, high nutrient content, low organic matter and high erosion, often with loess deposits. At higher elevations these give way to Brown soils (Firm and Mafic) which are stable, with higher clay content and firmer structures and topsoil (Landcare Research 2015). The species generally prefer free-draining soil (Vogan 2003), therefore Brown soils are likely to be less suitable. However, there is no shortage of exposed rock outcrops at high elevations in the region. There is very little difference in land use with increasing elevation; high-production exotic grassland dominates Banks Peninsula, with a slight increase in forested areas and scrubland at higher sites, although anthropogenic disturbance is lower due to fewer roads and homesteads (Boffa Miskell 2007; Ministry for the Environment & Landcare Research 2014). Fire regimes might also vary with elevation as a result of vegetation and soil drainage changes, and though the related *Bryophyllum delagoense* (Ecklon & Zeyher) is likely facilitated by fire in Australia (Witt & Nongogo 2011), the target species' responses to fire are unknown and there

are no fine-scale fire data for Banks Peninsula. It seems probable that the non-climatic covariates of elevation will have minimal effects on the upward spread of *A. arboreum*, *A. haworthii* or *C. orbiculata* on Banks Peninsula, and that their eventual distributions will be largely determined by climate and propagule pressure.

3.5.4 Limitations

This study goes into greater detail than many transplant studies, which often investigate a single vital rate [e.g. Paiaro *et al.* (2007)], do not extrapolate beyond the current distribution [e.g. Kollmann and Bañuelos (2004)], or do not standardize for effects of source population (Hargreaves *et al.* 2014). Nevertheless, there are limitations to be considered when interpreting the results. The implications of model uncertainty are most severe for seedling establishment, as the three species produce vast numbers of seeds; varieties of *C. orbiculata* are reported to produce over 1000 viable seeds per flower in the native range, and flowers are numerous (Zietsman 1998). Even if a small percentage of seeds germinate and survive, it is still plausible that populations could establish, and variation in germination could have a large effect on population growth rate. Additionally, predictions assume linear correlations with frost and GDD5, while other factors were set to constant values (e.g. precipitation and canopy cover). Running *A. arboreum* seedling models under high precipitation (1100 mm p.a.) reduced predicted establishment at 177 MASL by 83%. A similar effect occurs with canopy cover for *C. orbiculata* models. It is therefore impossible to define absolute elevation limits, and estimates reflect cautious predictions assuming otherwise optimal (*i.e.* dry, open) conditions. Furthermore, as plants did not flower during the experiment in sufficient numbers, reproductive output could not be tested. Fecundity may also be limiting to population persistence, and knowledge of seed output would allow classification of source and sink populations.

3.5.5 Conclusions

The aims of this study were to investigate whether *A. arboreum*, *A. haworthii* and *C. orbiculata* are close to their climatic limits on Banks Peninsula and to assess the potential for upward spread. There is evidence that climate is strongly limiting to plant performance across the region, and that Banks Peninsula represents a gradient from favourable climates to those beyond the species' cold tolerances. *Aeonium* populations have reached almost their maximum elevation, which is likely to be around 300 MASL. Interpretations for *C. orbiculata* are less certain and it is possible that populations could persist beyond their current maximum elevation. Winter mortality, relative growth and seedling establishment of *Aeonium* species are all limiting at high elevations, while only relative growth appears to be limiting for *C. orbiculata*. Because *C. orbiculata* is less restricted by habitat type and climate than the *Aeonium* species, it evidently poses the highest risk to Banks Peninsula of the three species.

Chapter 4 – Exploring the link between fecundity and climate in naturalized populations of alien Crassulaceae

4.1 Abstract

Fecundity is an important facet of plant invasions. It shapes range limits and determines whether populations can self-sustain, and sometimes favours non-native species over native or other introduced competitors. In turn, fecundity is usually affected by climate. Climate acts directly *e.g.* through floral vernalisation, or indirectly *e.g.* through growth rates or biotic interactions. Here, I examine fecundity in three succulent plants naturalized in New Zealand: *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. Knowledge is scarce regarding the species' reproductive rates or how climate affects them, and this is the first study to measure the species' fecundity in the introduced range. In this chapter, I investigate the climate-fecundity relationship in *A. arboreum*, *A. haworthii* and *C. orbiculata* across their current ranges on Banks Peninsula, a region that is a New Zealand hotspot for all three species. I surveyed rates of flowering, as well as inflorescences per plant, flowers per inflorescence and seeds per pod, in eight naturalized populations per species across a gradient of climatic conditions. Reproductive traits were modelled against climatic variables as well as maternal plant size to test for direct and indirect climatic effects. Direct effects of climate were only found in *A. arboreum* and *C. orbiculata*, predicting higher probability of flowering with increasing heat sum and solar radiation, respectively. The majority of variation in *A. haworthii* was not explained, and aspect was the only environmental predictor of inflorescences, flowers or seeds in any species. Potential indirect effects of climate were found in all species, as plant size was a predictor of at least one reproductive trait per species. Total seed output was highest for *C. orbiculata*, the most prolific invader of the three, producing approximately 190 000 seeds per capita on average. I found no evidence that climate is limiting to fecundity in any of the three species within the gradient studied, as direct effects were weak and the size-fecundity relationship was ambiguous. All three species produced numerous seeds, and small populations may still constitute considerable seed sources within the majority of climatic conditions currently occupied on Banks Peninsula.

Keywords: Crassulaceae, fecundity, climate, survey, invasions

4.2 Introduction

Reproductive traits are key determinants of distributions, abundance, and population dynamics in higher plant species (Howe & Smallwood 1982). The fecundity of non-native species is commonly used to forecast risk and range limits in invaded ranges (Willis & Hulme 2002; Walter *et al.* 2015), to investigate establishment success after introduction (Thompson *et al.* 2001; Pyšek *et al.* 2009; McGregor *et al.* 2012) and to inform pest management (Parker 2000; Wadsworth *et al.* 2000). The number of viable seeds produced by an individual fundamentally limits its number of offspring, while

on a larger scale, spatial patterns are often explained by dispersal (Harper 1977). Seed production and dispersal is, in turn, regulated by climate. Climatic constraints shape all species' distributions (Woodward 1987), where populations at range edges are sometimes sink populations, incapable of self-sustaining without immigration from nearby seed sources (Hargreaves *et al.* 2014). Any species' potential distribution therefore depends on the relationship of fecundity to climate. By ignoring this relationship, we may confound sink populations with suitable conditions, and in the context of invasions over-estimate future spread. Conversely, if no decline in fecundity or sink populations are present, it may be that the species is yet to reach climatic equilibrium in the invaded range (Hargreaves *et al.* 2014).

While total propagule pressure is a major determinant of spread of non-native species (Holle & Simberloff 2005; Lockwood *et al.* 2005), climate can inhibit or facilitate fecundity at many points on the continuum from flowering to seed dispersal. Climate can affect each stage differentially, and can influence fecundity either directly or indirectly. Direct climatic limitations include vernalisation or floral initiation through temperature (Taiz & Zeiger 1991), meeting temperature requirements for embryo development and seed maturation (Walck *et al.* 2011), or specific conditions for breaking seed dormancy, *e.g.* chilling (Baskin & Baskin 1998). Indirectly, climate can influence flowering by altering overall plant performance, resource allocation, and plant size, which is often a predictor of fecundity (Harper & White 1974; Herrera 1991). In addition, pollinators and dispersal agents may vary in abundance or behaviour according to climatic conditions (Hegland *et al.* 2009). In the absence of pollinators, many species are auto- or geitonogamous, but selfing can lower progeny fitness (Munguía-Rosas *et al.* 2013; Wright *et al.* 2013) and seed output (Zietsman 1998). As such, when identifying climatic constraints on fecundity it is useful to break reproduction down into discrete stages: probability of flowering, number or size of flowers, number and viability of seeds, *etc.* Doing so may reveal patterns and limitations otherwise masked by estimates of overall fecundity (Herrera 1991).

Variation in fecundity can be pivotal to invasion success, determining where and how rapidly different species spread, and their interactions with native competitors. Phenological differences are a predictor of invasion success in a number of species, where prolonged flowering offers an advantage over natives or other invaders (Goodwin *et al.* 1999; Cadotte & Lovett-Doust 2001; Lloret *et al.* 2005). In some non-native species, high nectar yields and bright floral blooms may offer an advantage by attracting pollinators, thus increasing seed yield (Ghazoul 2002). This is exacerbated when non-native, "showy" plants are preferentially planted as ornamentals over native species (Li *et al.* 2004). At the dispersal stage, traits of non-native species sometimes favour regeneration success, longer dispersal distances or attractiveness to foragers (Westcott & Fletcher 2011). It is not only relative to natives that non-native plants can have reproductive advantages; some species exhibit elevated fitness in the invaded range relative to their own native ranges, often attributed to release from natural enemies (Keane & Crawley 2002), and facilitating spread to novel environments (Edwards *et al.* 1998; Jakobs *et al.* 2004). It is therefore valuable to measure species' fecundity in the introduced range as it may

differ to the native range, and because invasion success is tied closely to reproductive output. Single measures of fecundity can assist in understanding the success of invasive species relative to other species, but by extending these measures along climate gradients encompassed by the species' distributions, we gain additional insight into their potential distributions.

In previous chapters, I examined the potential distributions of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* in New Zealand, and using a field experiment measured mortality, growth and germination along a climatic gradient on Banks Peninsula. For a complete understanding of the species' climatic limits on Banks Peninsula, it was important to test whether fecundity varies with, or is limited by, climate. For ethical and legal reasons the species were prevented from reproducing during the field experiment, so fecundity data were collected from wild populations. By measuring flowering and seed production along the climate gradient of the species' current distributions, I aimed to infer whether climate currently limits their reproduction and whether more widespread species have higher seed output. Fecundity may be particularly important to the invasion of these three species; their popularity as ornamentals is partly due to their large, colourful inflorescences, and non-native ornamentals may have a particularly strong advantage in New Zealand as the native flora are predominantly white-flowered, are not specialized, and are not "showy" (Lee *et al.* 2001). Propagule pressure from naturalized populations is also potentially high, as their numerous, wind-dispersed seeds could potentially travel long distances (van Rheede van Oudtshoorn & van Rooyen 1999). It was envisaged that this study would inform risk forecasting and future management of the target species.

4.2.1 Aims

1. To determine whether reproductive traits (probability of flowering, inflorescences per plant, flowers per inflorescence, and seeds per pod) of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* vary predictably along the climatic gradient encompassed by their current distribution on Banks Peninsula, and hence whether climatic constraints on fecundity might limit their current or potential distributions.
2. To determine which reproductive stages, and which climatic or non-climatic variables, most affect per capita seed production across Banks Peninsula.
3. To compare overall seed output per capita between species, under the hypothesis that less widespread species would produce fewer seeds.

4.3 Methods

4.3.1 Study species

As in previous chapters, I focussed on *Aeonium arboreum*, *A. haworthii* and *C. orbiculata*. Fecundity data for the three species are sparse, with no information for New Zealand except for the fact that they flower and produce viable seed readily (Webb *et al.* 1988). In their native ranges, *Aeonium* species

flower in spring or summer (Levin 2006), while *C. orbiculata* flowers in the dry season (Eller & Ferrari 1997). Pollination is thought to occur via wind, water droplets and generalist insects in the case of *Aeonium* species (Alamo *et al.* 1996), and sunbirds in the case of *C. orbiculata* (Zietsman 1998). All three species are also capable of self-pollination. The resulting seeds are wind-dispersed, numerous, and small (van Rheede van Oudtshoorn & van Rooyen 1999). There are no studies of seed size or output in *Aeonium* species, but *C. o. var. dactylopsis* reportedly produces an average 1500 seeds per flower in its native range when hand-pollinated, with a mean seed weight of 51 μ g (Zietsman 1998). Seed survival in other Crassulaceae species is low (< 2%) regardless of climate (Daws *et al.* 2007), and germination of other *Aeonium* species in their native range reportedly varies between 2 and 84% (Alamo *et al.* 1996). Low germination rates combined with the energy constraints associated with small seeds indicates an r-selection strategy, so in the absence of barriers, seeds should be numerous.

There are no previous studies of Crassulaceae species' fecundity in New Zealand, or their climatic constraints, although flowering of the non-native congener *A. canariense* (L.) Webb & Berthel. has been anecdotally linked to frost (Anon 1950). There is some evidence that flowering in *Aeonium* species is related to plant size. Jorgensen and Olesen (2001) describe deterministic modular growth in *Aeonium* species in the native range, based on the clear annual internodes of stem growth common to all species in the genera. They provide linear formulae for the probability of flowering based on the position of modules. However, these formulae are of limited use in New Zealand as they do not account for climatic limitation, were calculated in the native range, and counting all internodes can require uprooting the plant.

4.3.2 Study area

The study area for this chapter is Banks Peninsula, New Zealand, the region where field experiments were conducted (Chapter 3). All three species are found only in the warmest, driest parts of Banks Peninsula between 0 - 400 MASL, and mostly along the northern coastline (Figure 4.1a-c). While the species are likely to be limited by the climate gradient of Banks Peninsula, suitable habitat (*e.g.* cliffs, rock outcrops) is abundant. Furthermore, as demonstrated in Chapter 3, at least two of the species (*Aeonium* species) appear to be approaching their climatic limits in the region, consequently naturalized populations were expected to exhibit some climatic limitation near range margins. All three species ostensibly produce sufficient seed on Banks Peninsula to colonize and form self-sustaining populations; the region is where all three species were first described as naturalized (Healy 1959), and there are now more occurrence records on Banks Peninsula than elsewhere in New Zealand (Chapter 2). It is useful to measure seed output in the region to assist with population control by local authorities (Di Carter, *pers. comm.*, 2010). Further spread is of concern due to invasion of pasture by the toxic *C. orbiculata* (Botha & Penrith 2008), and colonization of the unique ecosystems of the cliffs and outcrops by all three species (Wiser & Buxton 2009; Holdaway *et al.* 2012).

4.3.3 Flowering surveys

Permanent transects were marked within eight distinct naturalized populations per species. Based on results of a preliminary presence-absence survey (Section C.1, Figure C.1), four main areas were chosen for each species, representing the range of temperature and precipitation across the three species' regional distributions. Unfortunately, following an earthquake in February 2011, the high elevation areas selected for *A. haworthii* and *C. orbiculata* became inaccessible. I was thus restricted to surveying between the warmest and driest areas in Sumner, and cooler and wetter areas in the northern and eastern bays (Figure 4.1a-c, Figure C.3). Within each of the four main areas, two survey sites were selected. They were intended to be paired replicates, but later investigation of temperature data revealed they were too different to be paired for analyses. Sites were chosen based on population size (requiring at least 50 individuals per site), and accessibility (*i.e.* some cliff populations were inaccessible). See Table C.1 for site descriptions. Estimated abundance and accessibility in wild populations across Banks Peninsula is shown in Figure C.2.

I chose fifty individuals as a minimum sample size to ensure replication across a number of life stages without limiting the study to the largest populations. The initial aim of the surveys was to measure variation in demographic parameters (including growth, survival and reproductive output) along a climate gradient, over the course of one year. Two problems led to focussing solely on reproductive output. Firstly, rock fall caused by the 2011 earthquake increased mortality, and plants were often missing or in different locations upon return the following year. Furthermore, size and life stage of surviving plants changed little between surveys. The growth rates and life expectancy of the species was unknown prior to surveying, and more rapid change was expected.

Surveys took place during peak flowering; December 2010 for *A. arboreum*, February 2011 for *A. haworthii* and March 2011 for *C. orbiculata* (all hereafter referred to as 2011), and at the same time one year following (hereafter referred to as 2012). Where populations occurred on vertical surfaces, *e.g.* cliffs or roadside cuttings, one 50 m permanent transect was placed at 1.4 m above the ground adjacent to the vertical surface. At sites where the ground could be traversed (*e.g.* in grassland, only applicable to *C. orbiculata*), five 10 m transects were placed at ground level at random points within each population. At each site 50 plants were tagged with cable ties, selecting the closest plant to each 1 m interval, and a random subset of 10 flowering individuals were given numbered tags (or mature plants if there were insufficient flowering plants). One Thermochron iButton[®] data logger was placed at the mid-point along the 50 m transect, or the mid-point along the third 10 m transect, recording temperature in degrees Celsius (°C). Data loggers were placed 5 cm above ground level, facing south, with a protective covering of aluminium foil to protect from precipitation and solar radiation. Temperature was recorded at four-hourly intervals beginning at 00:00, and was accurate to the nearest 0.5 °C. I recorded GPS co-ordinates (WGS 1984) at both ends of each transect.

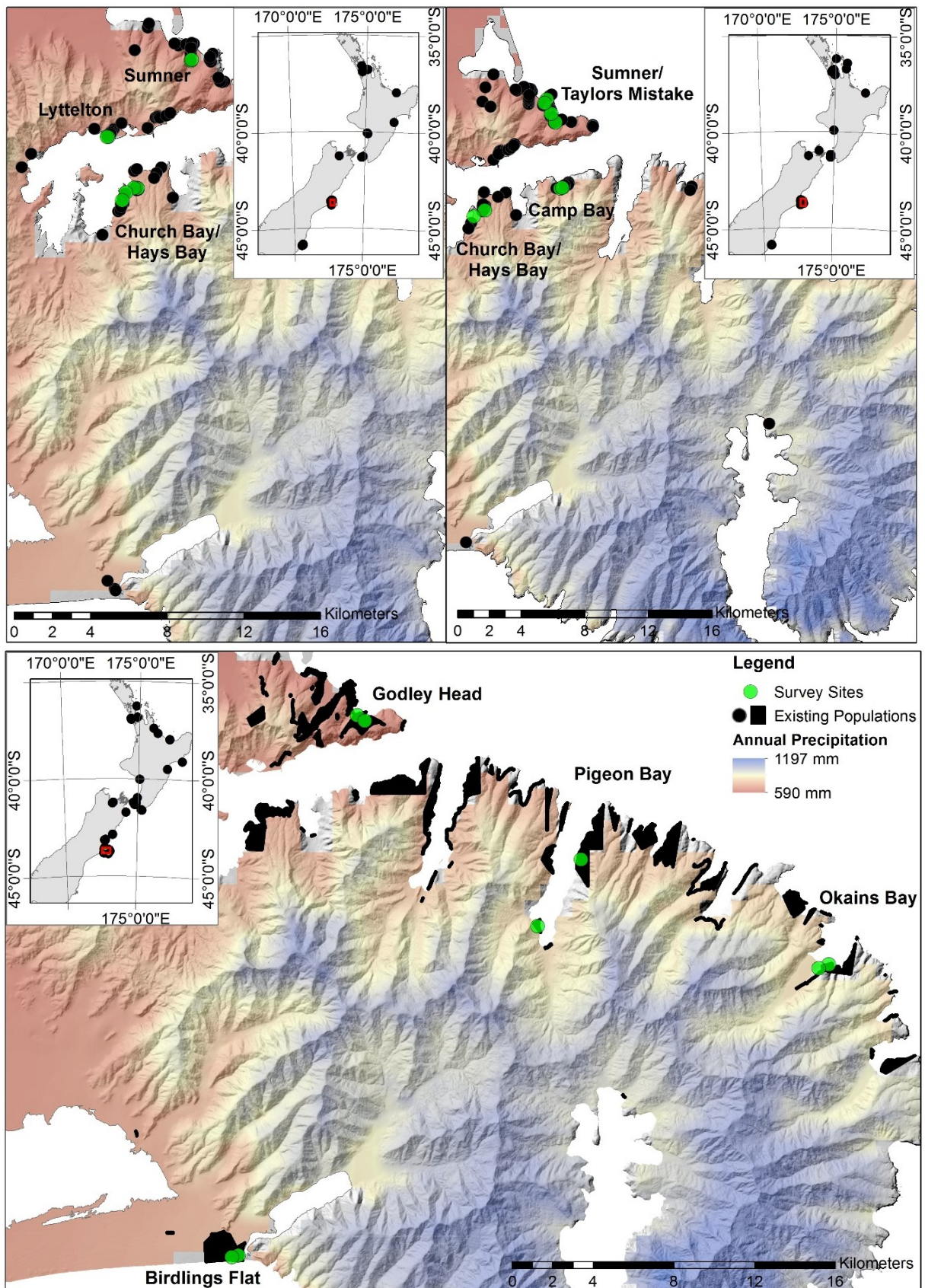


Figure 4.1 Populations of a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata* in Banks Peninsula and New Zealand (inset), and locations of survey sites (green points, general region labelled). Background layer shows annual precipitation, interpolated from Worldclim data, with shaded relief [(Hijmans *et al.* 2005), available at <http://www.worldclim.org/bioclim>].

For each of the 50 plants tagged, I recorded life stage as one of four categories (Table C.2) and if flowering, number of inflorescences. Life stage was intended for use in demographic measurements. I estimated the number of rosettes for *Aeonium* species, based on the reported relationship between branching modules and flowering (Jorgensen & Olesen 2000), and counted leaves along the main stem for *C. orbiculata*. After preliminary data analysis, it was apparent that number of rosettes and leaves were not reliable indicators of fecundity. In the second year of surveys, I additionally measured the height, width and breadth (cm) of each tagged plant, approximated to canopy volume (L, equation 1).

$$Volume = [(height \times width \times breadth) \times 10^{-3}] \quad (1)$$

In both years, detailed measurements were taken from each of the ten flowering plants with numbered tags. Umbels were counted on one randomly selected inflorescence per plant, flowers counted on three randomly selected umbels, and flowers per inflorescence estimated (equation 2, \bar{x} = sample mean).

$$Flowers|inflorescence = \bar{x} (flowers|umbel) \times (umbels|inflorescence) \quad (2)$$

Because of the reported correlation of stem growth and flowering in *Aeonium* species, I measured the previous years' internode length and new growth since the end of the previous summer (mm). For *C. orbiculata*, which lacks annual internodes, only canopy volume (L) was estimated.

4.3.4 Seed counts

In May 2011, before dehiscence, five inflorescences with fully developed seed pods were collected at each site. Inflorescences were randomly selected from distinct plants and were individually sealed in plastic bags for transport to the laboratory. In the laboratory, pods per inflorescence was estimated using the same methodology as described for flowers per inflorescence (Section 4.3.3). Number of seeds per pod was measured by weight based on sampling guidelines (International Seed Testing Association 2008), on scales accurate to 100 μ g. A homogenized 0.1 g sample of pod contents was collected for each site. *Aeonium* inflorescences were sampled by emptying equal numbers of pods from each until the mixed sample for each site reached 0.1 g. On average, 0.1 g equated to 50 pods of *A. arboreum* and 55 of *A. haworthii*. *Cotyledon orbiculata* pods are larger (0.1 g equated to, on average, 3 pods), so I instead emptied one pod from each inflorescence into the mixed sample. Homogenized samples were separated into seed and chaff by eye, and the components weighed. The average ratio of seed to chaff for each site was calculated using equation 3, where x = Seed to chaff ratio, y = Pure seed weight of sample (g) and z = Total weight of sample (g).

$$x = y/z \quad (3)$$

Next, 100 seeds were extracted from each mixed sample then weighed to estimate individual seed weight. Number of seeds per pod was measured for three pods on each inflorescence. Pods were randomly selected on the condition that they were closed and intact. Pods were emptied and content

weight was multiplied by the corresponding site seed to chaff ratio. The resulting pure seed weight of the sample was divided by the individual seed weight to estimate seeds per pod.

4.3.5 Climate variables

Flowering and seed production were modelled against climate. The following variables were used: frost days (below 0 °C), growing degree-days (GDD) at bases 5 and 10 °C, precipitation (mm), modelled solar radiation (KWh/m²), elevation (MASL) and aspect (N, E, S, W or NA on flat terrain). Growing degree days were chosen as plants generally respond to heat-sum variables (Wardlaw 1999), and bases 5 and 10 chosen as they are commonly used for warm-loving species, and the species' physiological limits were unknown. Number of frost days were used as the three species are thought to be frost-sensitive (Vogan 2003). Precipitation was included because the species are succulent xerophytes and may therefore be intolerant to excess precipitation (Jorgensen 2002), and solar radiation on the basis that sunlight is fundamental to plant growth (Monteith 1972) and at least one species is thought to be shade intolerant (Barker *et al.* 1997). Elevation appears to be a good predictor of the species' performance on Banks Peninsula (Chapter 3), although strong effects were not expected because of the loss of high-elevation sites described previously. Aspect was used as a proxy for solar radiation in the event that modelled solar radiation imperfectly captured site conditions, and because the species are mostly absent from south-facing slopes on the Peninsula. Climatic variation among survey sites is presented in Figure C.5. Temperature variables were calculated using data-logger measurements collected at each site, while precipitation data were obtained from the CliFlo database (National Institute of Water and Atmospheric Research 2014), using the nearest weather station to each site (Figure C.4). Solar radiation was modelled over the same years as the surveys in ArcMap 10.1, using the Solar Radiation Spatial Analyst tool (Fu & Rich 1999; Environmental Systems Research Institute 2011) and a 15 m DEM base layer. In addition to climate variables, I also included measurements related to maternal plant size, as the link to reproductive output is well-established (Harper & White 1974). Specific size measurements were canopy volume (L), and for *Aeonium* species, also internode length (mm).

Although peak flowering occurs at different times for each species, each climate variable was summed over the same period for all three species. This was to facilitate model comparison among species and incorporation into population models in subsequent chapters. All three species share a similar biology (succulent, xerophyte, CAM) and phylogeny, so it was assumed they would respond to similar climatic variables. Variables were summed over 6-monthly periods between the coldest month (July) and December, which marks peak flowering in survey populations of *A. arboreum* and the beginning of flowering for *A. haworthii* and *C. orbiculata*. To ensure that choice of time period did not affect model results, models were also fitted with 6-monthly heat sums prior to survey date for each species, and no differences in significant variables or model performance were found. It was not possible to sum variables over the same period for models of seed production because it would require using months before flowering or well after dehiscence for at least one of the species. Instead, seed

production was assumed to depend on conditions during flowering, due to pollinator availability and climatic requirements for embryo development. Climate variables for seed models were summed over the two-monthly peak flowering period relevant to each species (December - January for *A. arboreum*, January - February for *A. haworthii* and February - March for *C. orbiculata*). Additionally, number of pods per inflorescence was included as a variable under the hypothesis that vigorous plants would invest more energy into flowers and seeds, and that more flowers would attract more pollinators.

4.3.6 Model fitting

The summing of variables over 6 months necessitated that flowering was modelled using 2012 data only, as data loggers were not present at the sites prior to 2011 surveys. Having only one, or even two years' data is insufficient to test whether observations are representative of general trends. To address this problem, variation was compared among years and sites, where large yearly differences would demand less confidence in the generality of results. A one-way nested ANOVA tested for differences among years and sites in number of inflorescences, flowers and seeds. Flowering data were nested by *Year* | *Site*, and seed data by *Site* | *Inflorescence*. Differences in volumes and internode lengths among individuals and sites were also tested using this method. Differences in total number of flowering plants between sites were tested with a Chi-squared ANOVA [*anova* in base R (R Core Team 2014)] run against binomial generalized linear models (GLMs) of all surveyed individuals. Binomial GLMs were specified with the binary response variable *Flowering*, against the factor effects *Site*, and *Year + Site*. Variables (*y*) were log-standardized according to equation 4 (\bar{x} = mean, *s* = standard deviation).

$$\text{Log Standardized } y = \{\ln [y_i] - \bar{x} [\ln (y)]\} / \{2s [\ln (y)]\} \quad (4)$$

Flowering and seed production were modelled using generalized linear mixed models (GLMMs) in the R package *lme4* (Bates *et al.* 2014; R Core Team 2014). For each species, the response variables probability of flowering (*P[Flower]*), inflorescences per plant (*Inflorescences* | *Plant*), flowers per inflorescence (*Flowers* | *Inflorescence*) and seeds per pod (*Seeds* | *Pod*) were modelled. I fitted *P[Flower]* as a binomial GLMM, using data from all 50 tagged plants for the binary response variable *Flowering* (excluding plants that died). I modelled *Inflorescences* | *Plant*, *Flowers* | *Inflorescence* and *Seeds* | *Pod* as Poisson GLMMs. Two sets of models of *Inflorescences* | *Plant* were run for *Aeonium* species: one using data from all flowering plants, the second using the 10 subset plants, as only the subset data contained the predictor *internode length*. I tested whether *Inflorescences* | *Plant* within the subset was representative of the overall within-site variation using a Kolmogorov-Smirnov test. For *C. orbiculata* models of *Inflorescences* | *Plant*, all flowering plants were used. Flowers were only counted in the subset surveys, so those data were used in *Flowers* | *Inflorescence* models. All laboratory data were used for *Seeds* | *Pod* models.

Mixed models (GLMMs) contain random effects to account for pseudo-replication in the sampling design and associated unexplained variation, where separate intercepts are fitted for each random effect specified. For flowering models I specified *Site* as a random effect, and for seed models *Inflorescence* nested within *Site*. All except binomial models also had a random effect, *Odis*, to correct for overdispersion (Harrison 2014), where *Odis* is a vector of 1: n (n = number of samples). All climatic variables were standardised to a mean of zero and standard deviation of one, while plant size variables were log-standardized in the same way as for ANOVA variables. Model parameters (climatic and non-climatic variables) were tested against null models individually using a Chi-squared test. Significant variables were then added to the final model and removed in a backwards stepwise fashion. Model fit was assessed by calculating the marginal and conditional R^2 of each final model using the methods of Johnson (2014). This function estimates pseudo- R^2 using random and fixed effects (conditional), and fixed effects only (marginal). Marginal and conditional R^2 allow comparison between the amount of variation explained by variables of interest (fixed effects), unexplained differences between sampling units (random effects) and noise. For models of $P[Flower]$, I calculated the area under the receiver operating curve (AUC) with 95% confidence intervals, in the R package *pROC* (Robin *et al.* 2011; R Core Team 2014). The AUC conveys whether models are better at identifying true positives and negatives than chance without requiring a probability threshold, and is arguably a better measure of fit for binary data than R^2 . All fixed effect coefficients are reported with 95% confidence intervals, calculated using the *confint.merMod* function in *lme4*, with 500 bootstrapped replicates. Random effects are presented as mean, minimum and maximum values.

4.3.7 Model predictions

Mean seeds per capita were estimated as the product of mean predicted inflorescences, flowers and seeds of each species. All mean values in the text are reported \pm standard error (SE). For predictions, continuous parameters (*e.g.* mean volume of flowering plants) were set to mean values across all flowering plants, and the most representative category chosen for categorical variables (*e.g.* aspect). Confidence intervals were generated by bootstrapping each model 1000 times. Within each bootstrap replicate, predicted inflorescences, flowers and seeds were multiplied and the 1000 resulting values used to estimate mean seeds per capita and 95% confidence intervals. This stepwise method allowed prediction error to be compounded at each level of multiplication where models were non-independent. To measure the relative influence of each model parameter on total predicted seeds, I calculated elasticity values for each parameter. This identified potential driving variables of total fecundity on Banks Peninsula and which level of fecundity (*e.g.* seed or flower production) may be most limiting for the species. This definition of elasticity is used widely in economics, and was calculated according to equation 5, where Y = Predicted seeds per capita, X = Input parameter value and Δ is the change relative to the baseline. Parameters were altered relative to the baseline values used to predict mean seeds per capita. Continuous variables were changed between - 100% and

+ 100% of the baseline, and categorical variables were calculated for each separate value. The gradient of the smoothed line of the % change in Y vs X is the reported elasticity.

$$Elasticity = (\% \Delta Y) / (\% \Delta X) \quad (5)$$

4.4 Results

4.4.1 General patterns

At all but one site, 50 plants were tagged in the first year (total plants tagged in 2011 = 374 for *A. arboreum*, 400 for both *A. haworthii* and *C. orbiculata*). One *A. arboreum* site had fewer than 50 plants tagged due to small population size and lack of alternative survey sites. At all sites, 10 plants (80 in total) were sub-sampled for detailed measurements in 2011. However, of those 80 plants, only 24 *A. arboreum*, 30 *A. haworthii* and 44 *C. orbiculata* were re-sampled in 2012, and so the sample size for models of flowers and inflorescences was reduced. This was due partly to high mortality rates, primarily affecting *Aeonium* plants (Table 3.1). Mortality was higher for both *Aeonium* species than for *C. orbiculata*, but only a minority of deaths could be confirmed (where a plant could not be re-located in 2012, it was assumed dead). Mortality was highest for *A. arboreum*, as 50% of sites experienced moderate or large rock falls, where some or most of the cliff face had fallen away (Table C.1). Sample sizes were further reduced by the fact that not all flowering individuals tagged in 2011 flowered in 2012. Some flowered in only one of the two years, but a high proportion of *Aeonium* plants, and the majority of *C. orbiculata*, flowered in both (Table 4.1). In 2011, 17% of all *A. arboreum* plants surveyed produced flowers, and 9% in 2012. For *A. haworthii* in 2011 vs. 2012, 18% vs. 12% of plants flowered, and 35% vs. 42% for *C. orbiculata*. Binomial GLMs indicated significant differences between years in number of flowering plants for *A. haworthii* and *C. orbiculata* (Table 4.2). There was no significant yearly variation in *Flowers|Inflorescence* in any of the three species, or *Inflorescences|Plant* in *A. arboreum*. There were significant and strong site differences in all variables except *Flowers|Inflorescence* of *A. arboreum*. Boxplots of raw data (Figure C.6) indicate that the lack of significant site differences in this case may be due an extremely wide distribution of flowers per inflorescence at one site (CHB2). There were significant differences in *Seeds|Pod* among inflorescences and sites in all three species, with highest variation among sites.

4.4.2 Flowering probability

There were large among-site differences in proportion of flowering individuals: 0 - 23% of tagged *A. arboreum* flowered in 2012, and *A. haworthii* was similar, ranging from 2 - 36%. There were higher proportions of flowering plants in *C. orbiculata* than either *Aeonium* species, varying between 8 - 65% among sites (Figure C.6). The best predictor of $P[Flower]$ in all three species was canopy volume. Climatic variables were not good predictors of flowering when used alone for any of the species (marginal $R^2 < 0.2$), and were not significantly better than null models for either *Aeonium* species. Models including canopy volume for *A. arboreum* and *C. orbiculata* were significantly improved by

Table 4.1 Total numbers of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* flowering in 2011 (Y1) or 2012 (Y2) only, or both years. Mortality shown as % of all individuals, broken down into number of plants confirmed dead vs. not re-located. Number of samples for each models also provided.

| Species | Total no. flowering | | | Mortality | | | n (samples) in model | | | | |
|----------------------|---------------------|---------|------|-----------|-----------|-------|----------------------|------------------------|-------------------------|-------------|--|
| | Y1 only | Y2 only | Both | Confirmed | Not found | Total | <i>P</i> [Flower] | (Inflorescences plant) | (Flowers inflorescence) | (Seeds pod) | |
| <i>A. arboreum</i> | 38 | 10 | 25 | 84 | 20 | 28% | 269 | 24 | 24 | 122 | |
| <i>A. haworthii</i> | 39 | 14 | 35 | 17 | 49 | 16% | 335 | 29 | 30 | 123 | |
| <i>C. orbiculata</i> | 31 | 59 | 110 | 6 | 18 | 6% | 373 | 180 | 61 | 120 | |

Table 4.2 Analysis of variance (ANOVA) source tables, showing differences in fecundity among years (if applicable), sites, and plants (if applicable) for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. ANOVAs run for numbers of log-standardised *Inflorescences|Plant*, *Flowers|Inflorescence*, and *Seeds|Pod*. For total numbers flowering, columns show degrees of freedom, deviance, and residual degrees of freedom and deviance from a Chi-squared ANOVA of a binomial GLM with year and site effects. Significant results highlighted in bold and level denoted by asterisks (*), where; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Species | Source | Total number flowering | | | | <i>Inflorescences Plant</i> | | | | <i>Flowers Inflorescence</i> | | | | <i>Seeds Pod</i> | | | |
|----------------------|--------|------------------------|------|-----|-------------------|-----------------------------|----------------------|----------------------|-----------------|------------------------------|------|-----|----------------|------------------|------|----------------------|------------------|
| | | DF | Dev | RDF | RDev | DF | SS | MS | F | DF | SS | MS | F | DF | SS | MS | F |
| <i>A. arboreum</i> | Year | 1 | 1.9 | 641 | 540.1 | 1 | 5 x 10 ⁻³ | 5 x 10 ⁻³ | 0.1 | 1 | 0.8 | 0.8 | 3.4 | | | | |
| | Site | 7 | 39.2 | 634 | 500.9 *** | 6 | 12.3 | 2.1 | 21.4 *** | 6 | 2.8 | 0.5 | 2.1 | 7 | 21.8 | 3.1 | 84.2 *** |
| | Plant | | | | | | | | | | | | | 32 | 5.4 | 0.2 | 4.6 *** |
| | Resid | | | | | 69 | 6.6 | 0.1 | | 69 | 15.4 | 0.2 | | 82 | 3.0 | 3 x 10 ⁻² | |
| <i>A. haworthii</i> | Year | 1 | 4.3 | 734 | 720.5 * | 1 | 1.4 | 1.4 | 7.4 ** | 1 | 0.5 | 0.5 | 2.2 | | | | |
| | Site | 7 | 52.9 | 727 | 667.5 *** | 7 | 5.4 | 0.8 | 4.0 *** | 7 | 3.8 | 0.5 | 2.4 * | 7 | 13.0 | 1.9 | 170.5 *** |
| | Plant | | | | | | | | | | | | | 33 | 16.6 | 0.5 | 46.2 *** |
| | Resid | | | | | 82 | 15.7 | 0.2 | | 82 | 18.2 | 0.2 | | 82 | 0.9 | 0.1 | |
| <i>C. orbiculata</i> | Year | 1 | 11.8 | 770 | 1039.7 *** | 1 | 1.5 | 1.5 | 6.6 * | 1 | 0.2 | 0.2 | 1.1 | | | | |
| | Site | 7 | 81.5 | 763 | 958.3 *** | 7 | 3.7 | 0.5 | 2.4 * | 7 | 7.7 | 1.1 | 5.4 *** | 7 | 11.0 | 1.6 | 11.2 *** |
| | Plant | | | | | | | | | | | | | 32 | 7.5 | 0.2 | 1.7 * |
| | Resid | | | | | 125 | 28.1 | 0.2 | | 125 | 25.4 | 0.2 | | 80 | 11.2 | 0.1 | |

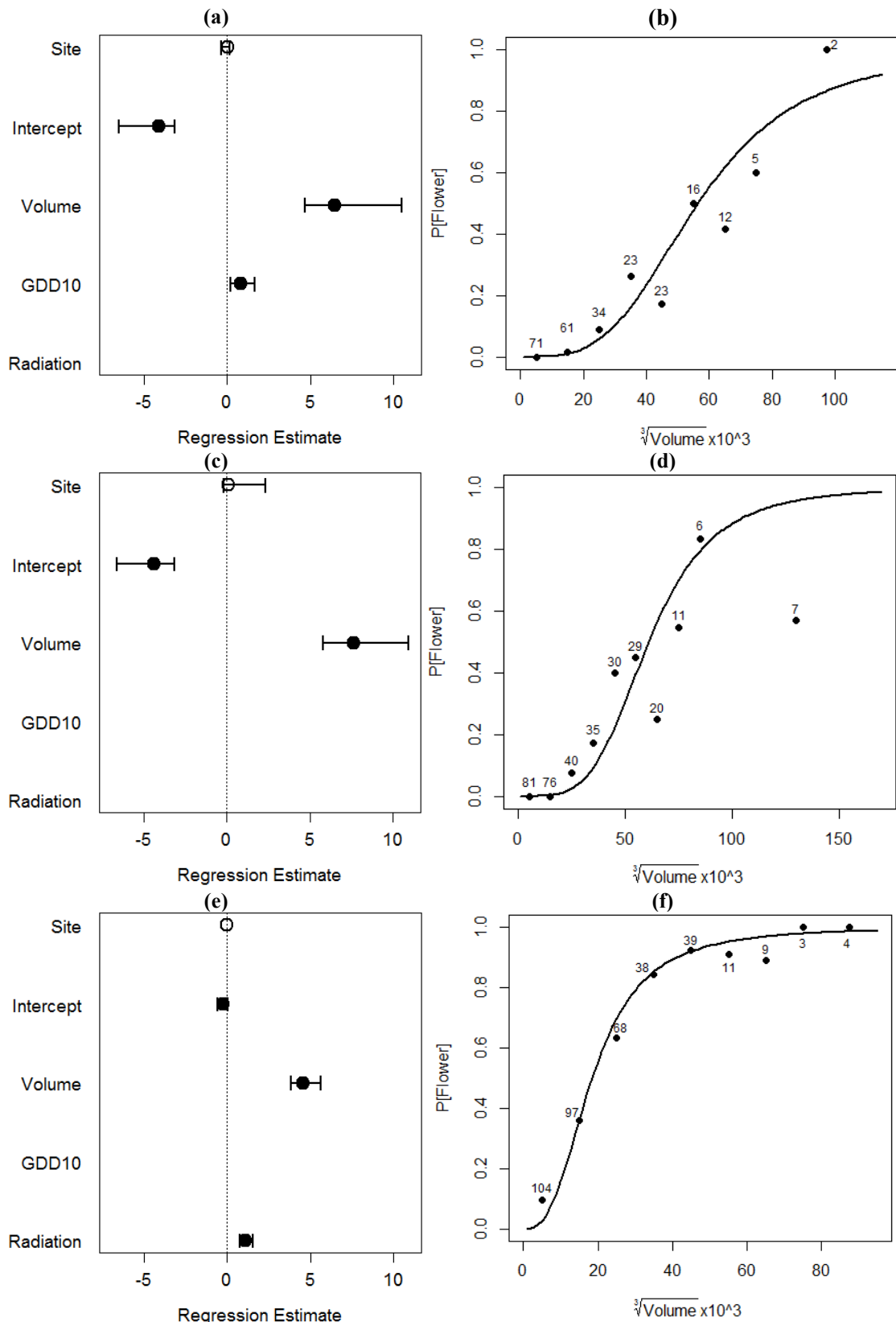


Figure 4.2 Coefficients and predictions of $P[Flower]$ GLMMs for *Aeonium arboreum* (a, b), *A. haworthii* (c, d) and *Cotyledon orbiculata* (e, f). Fixed effect coefficients shown with 95% confidence intervals (solid points), random effects with maximum and minimum values (hollow points). Plots b, d and f show modelled probability of flowering vs. canopy volume (lines). Axis rescaled to $\sqrt[3]{(Volume \times 10^3)}$, \approx plant height, for aesthetics. Proportion of plants flowering at midpoints of volume bins shown (points) with number of plants in bin (numbers).

the inclusion of, respectively, GDD10 and solar radiation, although canopy volume remained the principal explanatory variable (Figure 4.2a-c). Model predictions using mean climate variables where necessary, show that *Aeonium* plants were more likely to flower than not ($P[\text{Flower}] > 0.5$) when plants exceeded approximately 200 L. The same threshold for *C. orbiculata* was approximately 6 L. Models of $P[\text{Flower}]$ had high explanatory power; marginal R^2 were 0.75, 0.73 and 0.67 for *A. arboreum*, *A. haworthii* and *C. orbiculata* respectively. Models consistently assigned higher $P[\text{Flower}]$ to flowering over non-flowering plants (AUC = 0.91 ± 0.04 for *A. arboreum*, 0.94 ± 0.03 for *A. haworthii* and 0.91 ± 0.03 for *C. orbiculata*).

4.4.3 Inflorescences per plant

In 2011, across all sites *A. arboreum* produced a mean of 4.7 ± 0.8 (\pm SE) inflorescences per plant, between a minimum of 1 and maximum of 13. *Aeonium haworthii* individuals produced fewer inflorescences on average; 3.8 ± 1.0 , but had a wider range between 1 and 29. *Cotyledon orbiculata* produced more inflorescences than *Aeonium* species, with a mean of 9.1 ± 2.1 and between 1 and 88 per plant. For GLMMs of *A. haworthii* and *C. orbiculata*, it was necessary to remove the maximum observed value (one outlier for each model), as they strongly biased the results. Models of $\text{Inflorescences}|\text{Plant}$ were run for *Aeonium* species using both the full and sub-sampled datasets, as the sub-sampled dataset also included internode length as a potential variable. The sub-sampled data appeared to be representative of wider within-site variation; Kolmogorov-Smirnov tests on $\text{Inflorescences}|\text{Plant}$ revealed no significant differences between the two distributions. Variables related to plant size were the best predictors of number of inflorescences (Figure 4.3), specifically previous internode length for *A. arboreum*, and canopy volume for *C. orbiculata*. None of the variation in *A. haworthii* could be explained. Climate variables alone did not perform better than a null model for *Aeonium* species, and although precipitation performed better than null for *C. orbiculata*, it explained little variation (marginal $R^2 < 0.1$). The model for *C. orbiculata* predicted that larger plants produce more inflorescences (Figure 4.3d), while for *A. arboreum* higher stem growth in the previous year (longer internodes) predicted more inflorescences the following year (Figure 4.3c). It should be noted that internodes reflect growth from approximately May to April, with the main growing season in winter (Jorgensen & Olesen 2000). Therefore, the “new growth” measured at the time of surveying reflects less than a full years’ growth, which may explain why it is a poor predictor compared with previous years’ internodes. Model fit for $\text{Inflorescences}|\text{Plant}$ was lower than for $P[\text{Flower}]$, with marginal R^2 of 0.42 and 0.53 for *A. arboreum* and *C. orbiculata*, respectively. Conditional R^2 values were also low (0.56 and 0.59) indicating high noise in both datasets.

4.4.4 Flowers per inflorescence

Aeonium arboreum produced, on average, 534 ± 49 flowers per inflorescence in 2012 (mean \pm SE), between minimum of 108 and maximum of 2544. In contrast to the $\text{Inflorescences}|\text{Plant}$ results, *A. haworthii* produced fewer flowers than *A. arboreum*; on average 161 ± 17 , between 15 and 357

observed per inflorescence. *Cotyledon orbiculata* inflorescences produced the fewest flowers on average (137 ± 24) but ranged from 5 to a maximum of 630. There was no correlation between *Flowers|Inflorescence* and canopy volume or internode length in either *Aeonium* species. For *A. arboreum*, only aspect predicted number of flowers better than a null model, with slightly more flowers at west-facing sites, while north and east-facing sites were similar (Figure 4.4a & c). There are no predictions for south-facing aspects as none of the sub-sampled plants flowered in either year at the south-facing site. Again, none of the variation in *A. haworthii* could be explained. For *C. orbiculata*, *Flowers|Inflorescence* was best explained by canopy volume alone, and climate variables did not perform better than a null model, either in isolation or in addition to canopy volume. Performance of *Flowers|Inflorescence* models was the lowest in the study, with marginal R^2 of 0.29 for *A. arboreum* and 0.35 for *C. orbiculata*. Similar to *Inflorescences|Plant*, conditional R^2 values were also low (0.29 and 0.37), indicating a high degree of noise in the data not attributable to random or fixed effects.

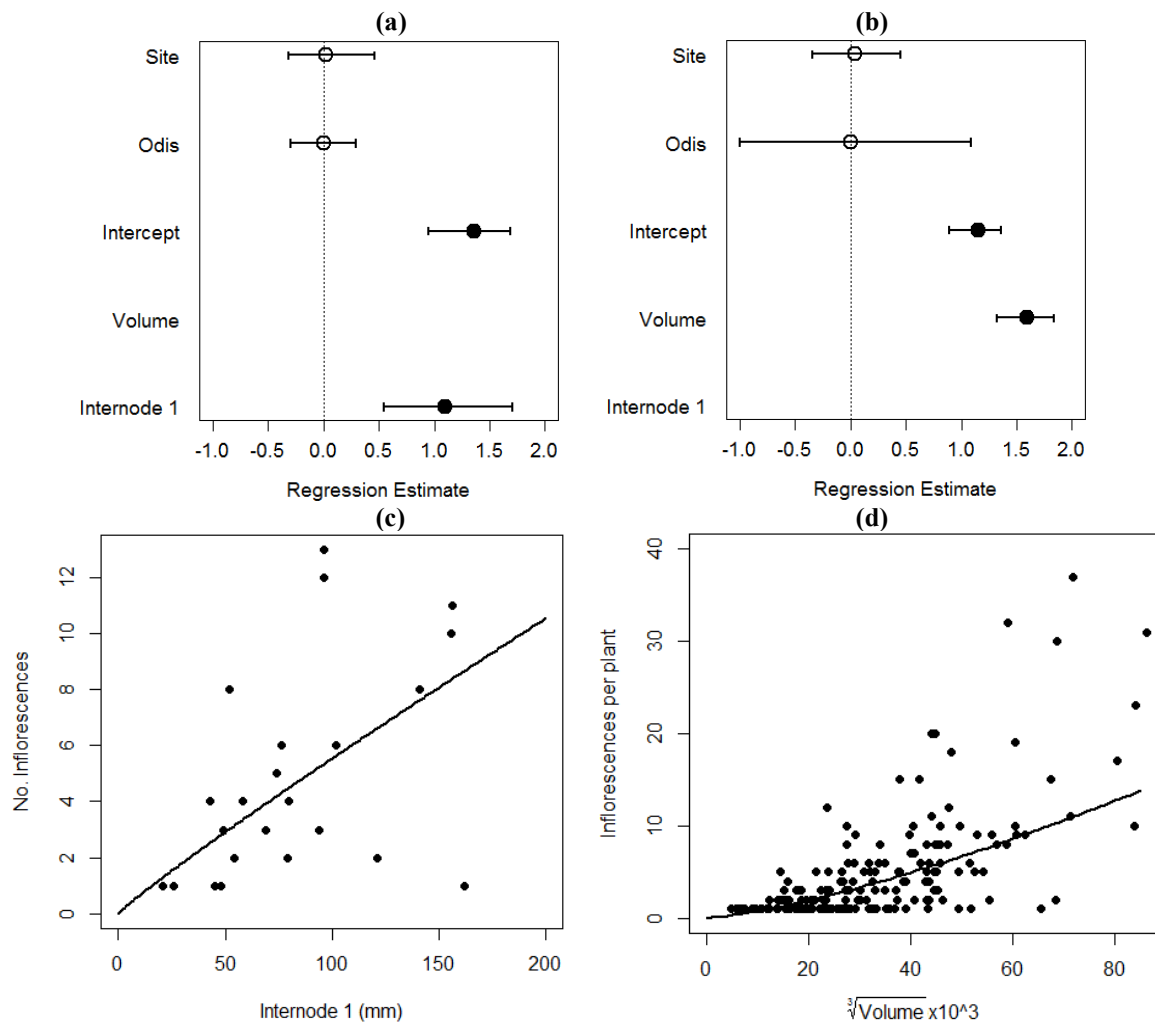


Figure 4.3 Outputs of *Inflorescences|Plant* GLMMs for *Aeonium arboreum* (a, c) and *Cotyledon orbiculata* (b, d). Plots a & b show model coefficients, solid points for fixed effects $\pm 95\%$ confidence intervals, hollow for random effects with maximum and minimum values. Plots c & d show predicted inflorescences (lines) vs. previous internode length (mm) and canopy volume (L), for *A. arboreum* (c) and *C. orbiculata* (d). Canopy volume axis rescaled to $\sqrt[3]{\text{Volume}} \times 10^3$ (\approx plant height) for aesthetics.

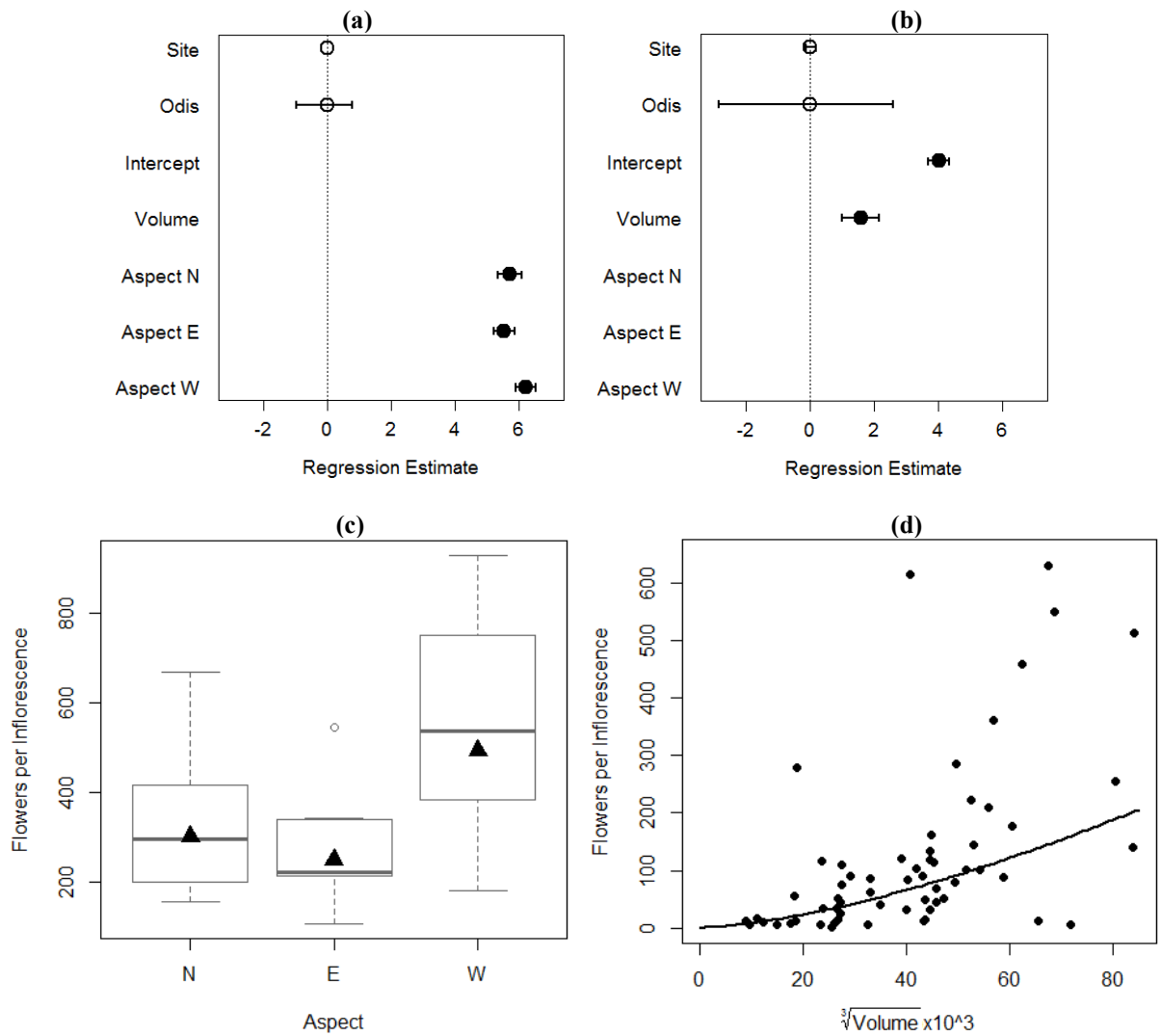


Figure 4.4 Outputs of *Flowers|Inflorescence* GLMMs for *Aeonium arboreum* (a, c) and *Cotyledon orbiculata* (b, d). Plots a & b show model coefficients, solid points for fixed effects with 95% confidence intervals, and hollow for random effects with maximum and minimum values. Plot c shows predicted number of *A. arboreum* flowers (triangular points) versus aspect, with observed values in boxplot. Plot d shows predicted number of *C. orbiculata* flowers (line) versus canopy volume (L). Axis rescaled to $\sqrt[3]{\text{Volume}} \times 10^3$, \approx plant height, for aesthetics, observed values shown as points.

4.4.5 Seed production

Seed samples indicated that in 2011, *Aeonium* species produced smaller seeds and more chaff than *C. orbiculata*. Seeds of *A. arboreum* were lightest at an estimated 20 μg per seed, with *A. haworthii* at 26 μg , and *C. orbiculata* at 29 μg . Mean percentage (\pm SE) of pure seed was similar for both *Aeonium* species ($32 \pm 6\%$ for *A. arboreum* and $31 \pm 6\%$ for *A. haworthii*), and much higher for *C. orbiculata* at $66 \pm 6\%$. There was considerable variation among sites, with a range of 9 – 51% pure seed for *A. arboreum* and 3 – 55% for *A. haworthii*. In contrast, *C. orbiculata* varied between 39 - 100% pure seed among sites. Climatic variables did not explain among-site variation, although with only one sample per site, low degrees of freedom are limiting. Mean number of *Seeds|Pod* was higher in *C. orbiculata* than either *Aeonium* species. On average, *A. arboreum* produced 31 ± 2 seeds per pod,

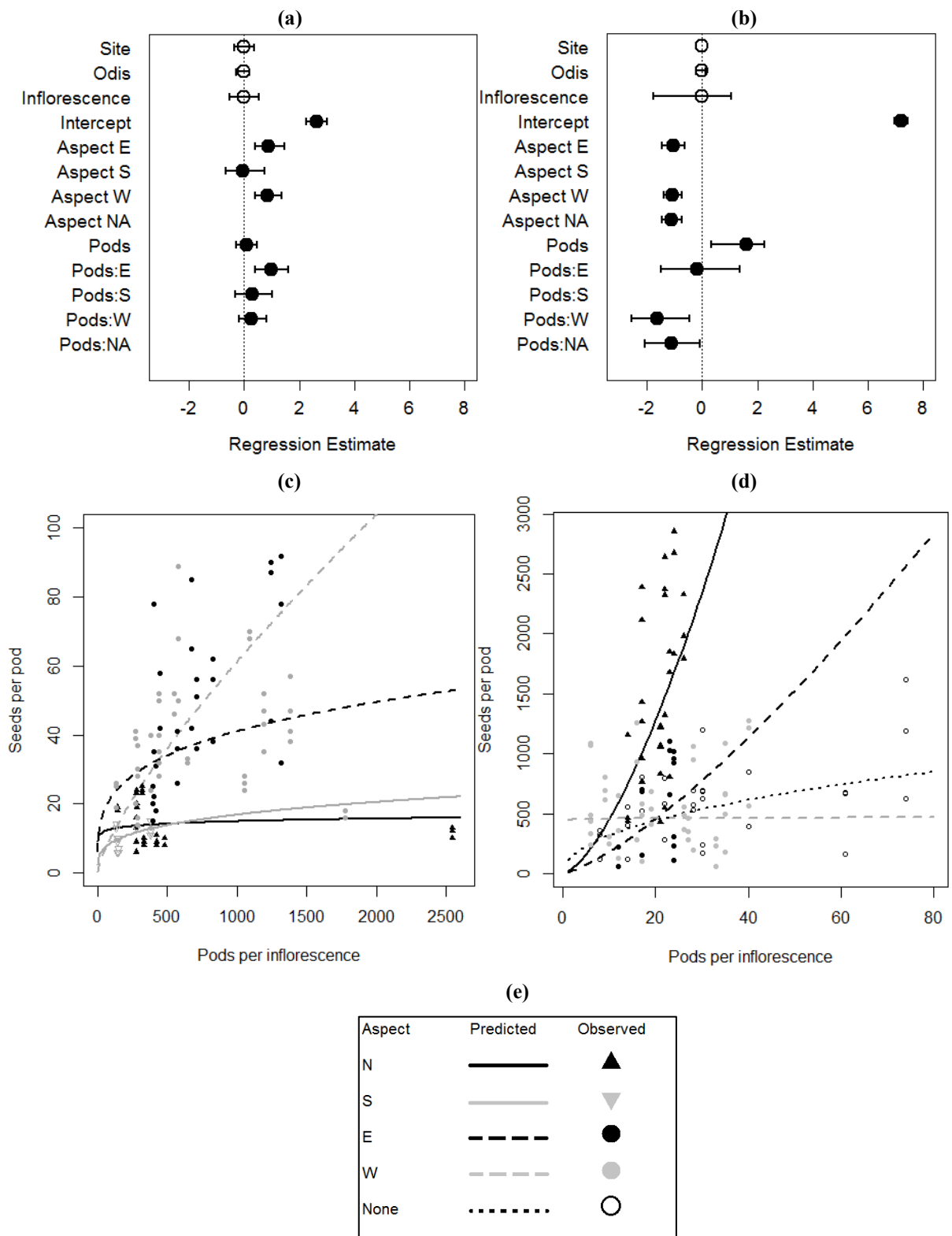


Figure 4.5 Outputs of *Seeds|Pod* GLMMs for *Aeonium arboreum* (a, c) and *Cotyledon orbiculata* (b, d) and legend for plots c & d (e). Plots a & b show GLMM coefficients, solid points for fixed effects with 95% confidence intervals, hollow points for random effects with maximum and minimum values. The reference category for aspect is north. Plots c & d show predicted number of seeds per pod, versus pods per inflorescence, in *A. arboreum* and *C. orbiculata* respectively. Lines show predictions for aspect category, points show observed data (see legend).

and *A. haworthii* produced 23 ± 2 . In contrast, *C. orbiculata* produced on average 812 ± 56 seeds, thanks to higher ratios of seed to chaff and larger pods. Again, no variables explained variation in *A. haworthii*, whereas the best models for *A. arboreum* and *C. orbiculata* were identical; the best explanatory variable was aspect (Figure 4.5a & c), with a marginal R^2 of 0.59 (*A. arboreum*) and 0.31 (*C. orbiculata*) when used alone. Models were improved significantly by the inclusion of pods per inflorescence, although it explained less variation than aspect (marginal R^2 of 0.14 for *A. arboreum* and 0.04 for *C. orbiculata* when used alone). Plots indicated a clear interaction effect between the two variables (Figure 4.5d & e), which was incorporated into the final models.

In general, pods per inflorescence and seeds per pod were positively correlated for both *A. arboreum* and *C. orbiculata*. In the case of *A. arboreum* the effect was strongest at west-facing, and to a lesser extent, east-facing sites. North and south-facing sites showed little to no relationship with pods per inflorescence, where seed numbers are predicted to be low, and near constant. For *C. orbiculata*, similar patterns occurred, but north and east-facing sites were more favourable and strongly related to pods per inflorescence, with west and “none” (*i.e.* flat gradient) close to constant (Figure 4.5c & d). Seed models performed better for *A. arboreum* than *C. orbiculata*, but for both species fixed effects explained most of the non-random variation; marginal vs. conditional R^2 values were 0.66 vs. 0.83 and 0.40 vs. 0.44 for each species respectively. There was a disparity between number of flowers per inflorescence in section 4.4.4 and number of pods per inflorescence in seed samples. This could have arisen from loss of pods after flowering or during transport, or because of sampling bias. Consequently, caution is warranted if extrapolating these models to higher numbers of seeds per pod.

4.4.6 Site differences in canopy volume

Table 4.3 Source tables for one-way ANOVAs on among-site differences in log-standardized canopy volume and internode length, for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. Analyses were run on second year data, both across all plants, and flowering plants only.

| Species | Source | Canopy volume (all plants) | | | | Internode length (flowering plants) | | | | Canopy volume (flowering plants) | | | |
|----------------------|--------|-------------------------------|------|-----|-----------------|--|-----|-----|--------------|-------------------------------------|------|--------------------|----------------|
| | | DF | SS | MS | F | DF | SS | MS | F | DF | SS | MS | F |
| <i>A. arboreum</i> | Site | 7 | 3.5 | 0.5 | 2.0 | 6 | 2.8 | 0.5 | 2.8 * | 6 | 0.9 | 0.2 | 6.5 *** |
| | Resid | 238 | 57.8 | 0.2 | | 17 | 2.9 | 0.2 | | 25 | 0.6 | 2×10^{-2} | |
| <i>A. haworthii</i> | Site | 7 | 21.2 | 3.0 | 15.9 *** | 7 | 3.6 | 0.5 | 3.1 * | 7 | 0.6 | 0.1 | 2.4 * |
| | Resid | 327 | 62.3 | 0.2 | | 22 | 3.6 | 0.2 | | 46 | 1.7 | 4×10^{-2} | |
| <i>C. orbiculata</i> | Site | 7 | 9.2 | 1.3 | 5.7 *** | | | | | 7 | 7.2 | 1.0 | 4.7 *** |
| | Resid | 365 | 83.4 | 0.2 | | | | | | 172 | 37.6 | 0.2 | |

Because plant size was a strong predictor at most reproductive stages, among-site differences in canopy volume (and internode length for *Aeonium* species) were investigated. In all three species, whether including all plants or just those flowering, there were significant differences among sites. I attempted to explain this site variation by running Gaussian GLMMs with a random site effect against climate variables, but found no significant relationships.

4.4.7 Total per capita fecundity

Predicted numbers of inflorescences, flowers and seeds were combined to predict mean seeds per plant (Table 4.4). Where aspect was a parameter I selected the aspect category which, if extrapolated, would represent favourable sites but without trending to extreme values (Figure 4.5c & d): for *A. arboreum* I selected east, and *C. orbiculata*, none. All predictions for *A. haworthii* were derived from null models representing means across all sites. Models predict that of the three species, *C. orbiculata* produces the most seeds per plant on average, due to numerous seeds per pod. *Aeonium haworthii*, meanwhile, is predicted to produce the fewest seeds; as although the species produces more inflorescences than *A. arboreum*, its inflorescences produce fewer flowers.

Table 4.4 Predicted mean inflorescences per plant, flowers per inflorescence and seeds per pods for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*, with 95% bootstrapped confidence intervals in brackets. Models use mean plant volume or internode length of all flowering plants, aspect set to east (*A. arboreum*) or none (*C. orbiculata*). Seeds per plant is the product of the three models.

| Species | Inflorescences | Flowers | Seeds | Seeds per plant |
|----------------------|----------------|-----------------|-----------------|-----------------------------|
| <i>A. arboreum</i> | 5 (3 - 6) | 254 (179 - 349) | 22 (12 - 36) | 25 826 (10 480 - 52 501) |
| <i>A. haworthii</i> | 3 (2 - 4) | 132 (102 - 167) | 13 (7 - 24) | 4 510 (2 118 - 8 922) |
| <i>C. orbiculata</i> | 5 (4 - 6) | 71 (52 - 97) | 521 (360 - 782) | 191 862 (104 562 - 364 852) |

Elasticities of GLMM parameters were calculated in reference to their effect on predicted seeds per plant. I tested all parameters in final models of inflorescences, flowers and seeds, for *A. arboreum* and *C. orbiculata*. For both species, aspect had most effect on predicted seeds per capita (Table 4.5). For *A. arboreum*, the effect of aspect on seeds per capita was strongest at the level of flowers per inflorescence. For *C. orbiculata*, only models of seeds per pod contained an aspect term, so variation at this level had the greatest effect on seeds per capita. Plant size parameters (*i.e.* internode length, volume and pods per inflorescence) had a minor effect on predicted seeds per capita at all levels of fecundity (inflorescences, flowers and seeds).

Table 4.5 Parameter elasticity values for GLMMs of inflorescences per plant, flowers per inflorescence and seeds per pod, calculated against predicted seeds per plant for *Aeonium arboreum* and *Cotyledon orbiculata*. Highest elasticity value per species is highlighted in bold.

| Model | Parameter | <i>A. arboreum</i> | <i>C. orbiculata</i> |
|------------------------------|-----------------------------------|--------------------|----------------------|
| <i>Inflorescences Plant</i> | Internode 1 | 0.14 | |
| | Volume | | 0.53 |
| <i>Flowers Inflorescence</i> | Aspect | 8.31 | |
| | Volume | | 0.23 |
| <i>Seeds Pod</i> | <i>Pods Inflorescence</i> | 0.79 | 0.34 |
| | Aspect | 4.11 | 21.62 |
| | Aspect* <i>Pods Inflorescence</i> | 1.65 | -3.70 |

4.5 Discussion

4.5.1 Direct climate limitation

Reproductive traits of *A. arboreum*, *A. haworthii* and *C. orbiculata* were highly variable among and within sites, and direct relationships with climate were weak across naturalized populations on Banks Peninsula. These are similar to the findings of Jorgensen (2002), who reports that vegetative and reproductive traits of four Canarian *Aeonium* species have a high degree of variability not explained by plant size, climate or phylogeny. Despite high noise in the data, probability of flowering in *A. arboreum* correlated positively with heat sum (GDD10), and plants at west-facing sites tended to produce more flowers per inflorescence and seeds per pod than at other aspects. *Cotyledon orbiculata* was more likely to flower at sites with higher modelled solar radiation, and pods contained most seeds at north-facing sites. These findings are consistent with the biogeography of the three species; all three originate in warmer climates than New Zealand, and Banks Peninsula represents the cooler extremes of their distributions (Chapter 2). Furthermore, *Cotyledon orbiculata* is likely to be shade intolerant as a result of its photoprotective epicuticular wax (Barker *et al.* 1997), which both *Aeonium* species lack (Stevens 1995). Although a slight effect of climate was observed on probability of flowering, no evidence was found that climate was limiting to reproduction as would be expected in marginal populations (*i.e.* seed was produced in large quantities at all sites).

In the case of *A. haworthii*, I was unable to explain variation in any reproductive trait except probability of flowering, despite large and highly significant differences among sites. In particular, among-site variation in number of seeds per pod was twice as high for *A. haworthii* as for *A. arboreum* (F-values of 170.5 vs. 84.2), yet there were no correlations between *A. haworthii* seeds per pod and climatic or non-climatic variables. This could be due to limitations in the survey design, which are discussed in detail later. However, the sampling design was identical for all three species, and variation was at least partially explained for all reproductive traits of *A. arboreum* and *C. orbiculata*. As an alternative explanation, reproductive traits of *A. arboreum* might exhibit stronger responses to plant size and climate than *A. haworthii* because of their evolutionary niches. Lems (1960) hypothesizes that *A. arboreum* is part of an older lineage of *Aeonium* than *A. haworthii* based on their respective growth forms, and that “older” forms which take longer to reach flowering maturity and produce larger inflorescences are adapted to milder, more stable climates in the native range. He argues that the group containing *A. haworthii*, which are found at higher elevations and more extreme conditions in the Canary Islands, flower at a younger age (producing fewer seeds per capita, as observed in this study) to maximise chances of reproduction in harsh climates. If this is the case, *A. haworthii* reproduction should be more adaptable to climate than *A. arboreum*.

According to sensitivity analyses, heat sum (GDD10) and solar radiation had minor impacts on per capita seed output compared with aspect. It was surprising that aspect was selected repeatedly as a significant variable over other, more biologically meaningful variables. Aspect was included in the

potential variables only as a proxy for solar radiation, in the event that the ArcMap model imperfectly captured real site conditions. Error in the model is one possible explanation for the importance of aspect. Alternatively, aspect could capture other variables related to solar radiation but imperfectly captured by total insolation (*e.g.* mid-day sun versus morning or afternoon sun). Because all three species flower in spring/summer they are assumed to be long-day plants (LDPs), and floral initiation by far-red light (which is higher in morning and afternoon) has been documented in a number of other LDPs (Taiz & Zeiger 1991). Many other environmental variables vary with aspect, but few are likely to affect the study species at the particular sites surveyed. One of these few is salinity: most sites were in the northern bays of the Peninsula, so perhaps north-facing sites tended to have higher salinity and sea spray. Alternatively, Lems (1960) reports that *A. arboreum* thrives on northeast facing slopes in the Canary Islands where plants are exposed to the humid trade wind. However, in this study *A. arboreum* performed better at west-facing sites, and in Canterbury the humid, prevailing wind is easterly (McGann 1983) while the characteristic “nor’wester” foehn wind is hot and dry (McGowan & Sturman 1996). As a consequence of how solar radiation and wind patterns change with aspect, soil moisture and organic matter also vary. In North Canterbury, soil on north-facing slopes is usually drier than on south-facing slopes (Radcliffe & Lefever 1981). Although soil may seem irrelevant to cliff-dwelling species, they often grow in small pockets of organic matter on rock faces. Equally, biotic interactions may vary with aspect: pollinators are often more active on sunny slopes (Weiss *et al.* 1988), and differences in community structure and vegetation may increase competition (Bennie *et al.* 2006; Warren II 2010). Jorgensen (2002) describes growth limitation in other *Aeonium* species with increasing longitude in the Canary Islands, hypothesized to reflect decreasing solar radiation and higher light competition. Overall, while aspect appears to be important and potentially limiting for *A. arboreum* and *C. orbiculata* at the study sites, the underlying mechanism is unclear and extrapolation of these results to other regions is discouraged.

4.5.2 Plant size – indirect climate limitation?

While direct relationships with climate were weak, plant size was a predictor of at least one reproductive trait in all three species. In most cases, canopy volume (L) was a better predictor than internode length (mm) or number of leaves/rosettes, neither of which correlated with volume. Only in one model of inflorescences per plant (*A. arboreum*) was internode length a better predictor than volume. Internode position (reported to correlate negatively with internode length) has been used to predict flowering probability in *A. haworthii* (Jorgensen & Olesen 2000), so it was surprising that length was a poor predictor. Despite its apparent importance, the relationship between plant size and reproductive traits is ambiguous. On one hand, positive size-fecundity relationships are found in many plant species (Aarssen & Taylor 1992), and some argue that it is a near-universal phenomenon (Herrera 1991). In turn, larger plants may attract more pollinators (Wyatt 1980; Gerber 1985), although flowers sometimes receive proportionally fewer visits (Klinkhamer *et al.* 1989; Herrera 1991). A site containing small individuals as a result of chance, non-climatic effects (*e.g.* competition)

or being more recently colonized (*i.e.* with many young individuals) should therefore produce fewer seeds per capita regardless of climate. Yet, the observed size-fecundity relationship could be an indirect result of climate (perhaps higher temperatures favour faster growth, or plants struggle to reach a minimum reproductive size in harsh environments).

Whether the size-fecundity relationship is a result of climate, demography or both, is unclear. I investigated by testing for significant differences among sites in all plants, and flowering plants only. There were significant differences among sites in canopy volumes of flowering *A. arboreum* individuals, but not in volumes of all plants. In other words, plants flowered at smaller sizes at some sites than at other sites. The size-fecundity differences among *A. arboreum* sites are therefore unlikely to be simply a result of population structure or chance. If some sites simply had many small, young plants size differences would be expected across populations as a whole, not just in flowering plants. However, this analysis alone cannot distinguish which sites are more favourable, as plants may also flower when small because of stress (Wada & Takeno 2010). In contrast, there were significant differences in plant size among overall populations and among flowering plants in both *A. haworthii* and *C. orbiculata*. This could indicate that in favourable climates growth is faster (thus, many individuals are large), and that plants flower when smaller under good conditions. But, population size structure may vary among the survey sites for numerous other reasons. These include variation in soil characteristics (some sites were loess banks, while others were bare rock), distance from shoreline and salinity, wind patterns, or disturbance (most notably, landslides). Rock type may be particularly important to these geophytic species, and the surveys covered seven geological units roughly grouped into loess, volcanic rock and gravel (Table C.1). Without prior knowledge on the effect of rock type on the study species, it is difficult to speculate as to its importance, although application of silicates has been shown to boost growth in *Kalanchoe* Adans. (MoonSook *et al.* 2012).

4.5.3 Implications for spread, and limitations

There are notable limitations to this study that reduce the generality of the results and that may have weakened detection of climatic effects. Peak flowering for each species was assumed to occur at the same time across sites, but climate is heavily linked with floral initiation [in addition to other variables *e.g.* day length (Taiz & Zeiger 1991)]. Sampling may therefore have occurred before peak flowering at some sites. Variation within both *Aeonium* species was particularly high, perhaps exacerbated by the frequency of natural hybrids. This is especially true for *A. arboreum*, which overlaps phenologically with *A. undulatum* [also common on the Peninsula (Webb *et al.* 1988)]. As a result, defining populations as belonging to one taxonomic unit can be troublesome. It is also possible that sampling plants near ground level has biased results for cliff populations; reproductive output at ground level could be unrepresentative of higher microsites where competition might be lower. The lack of strong climatic responses could indicate that other variables, *e.g.* relative humidity, are more limiting than temperature, precipitation or radiation. Even if the variables used were limiting, perhaps the time periods used for calculating sums were not the most appropriate, or microclimate variation within sites

was high and not captured by the data-loggers. Similarly, precipitation data were obtained from the nearest weather station, decreasing statistical power and accuracy in capturing rainfall at survey sites. The lack of accessible large populations resulted in sampling a climate gradient that, apparently, was insufficiently wide. Furthermore, the generality of the conclusions is lessened by having a single year of data and temporal extrapolation of these results is discouraged.

Limitations aside, it is possible to draw some inferences from the data. There was no evidence of limited fecundity in any sampled populations of *A. arboreum*, *A. haworthii* or *C. orbiculata* on Banks Peninsula. Namely, plants readily flowered and produced viable seeds at all sites, and direct climatic effects were minimal, contrary to expectations if some were marginal or edge populations. There were significant among-site differences in plant size and reproductive traits where plant size, growing degree-days and solar radiation had a minor impact on seeds per capita compared with aspect. The most potentially limiting reproductive trait for spread appears to be seeds per pod, as observed values had a wider range than number of inflorescences or flowers. Upper and lower 95% confidence intervals of mean seeds per pod differed by a higher factor than flowers or inflorescences, in all three species. Seed production is likely to influence spread of all three species strongly, as they are wind-dispersed, produce very small seeds with limited energy reserves, and evidence suggests potentially low rates of germination (Alamo *et al.* 1996).

There were also marked differences in mean predicted seeds per capita between the three species. The average *Aeonium arboreum* plant is predicted to produce over five times as many seeds as *A. haworthii*. This was surprising as both species have been naturalized for the same amount of time and have developed similar distributions. However, predicted *Aeonium* seeds per capita were consistent with the hypothesis of Lems (1960) that growth-form classes containing *A. haworthii* should flower younger and produce fewer seeds than those containing *A. arboreum*, as adapted responses to their native niches. In contrast, *Cotyledon orbiculata* produces many more seeds than either *Aeonium* species, over a predicted 190 000 per plant on average, across sampled populations. It is interesting to note that mean seeds per pod was lower than reported from open pollination experiments in the native range [521 vs. 1050 seeds per pod (Zietsman 1998)]. *Cotyledon orbiculata* has a much wider distribution in the region than either *Aeonium* species, and while additional factors may also have facilitated its spread (*e.g.* broader climatic tolerances and habitat preferences), high seed output is likely to have contributed significantly. From a management perspective, relatively small populations of *C. orbiculata* still constitute a considerable seed source, and could facilitate continued invasion subject to dispersal and germination.

4.5.4 Conclusions

The aims of this chapter were to assess evidence for direct or indirect climatic limitation to fecundity in the three study species, across their current ranges on Banks Peninsula. I found evidence of weak direct climatic responses in probability of flowering in all three species, but insufficient evidence to

conclude that fecundity is strongly climate limited within their current ranges. A strong relationship with plant size was found in all three species, but it is unclear whether this is an indirect response to climate. I also aimed to answer which stage of fecundity, and which variables, were most limiting to reproduction. In all three species, per capita seed output was most sensitive to variation in seeds per pod due to a wider range of observed values. Meanwhile, the variable with the greatest effect on *A. arboreum* and *C. orbiculata* seeds per capita was aspect, although it is unclear why some aspects are more favourable than others to the species. I was unable to explain variation in flowers, inflorescences or seeds produced by *A. haworthii*. The final aim was to assess whether more widespread species had highest fecundity, and there is some support for this hypothesis. *Cotyledon orbiculata* produces more seeds than either *Aeonium* species, a difference of 2 - 3 orders of magnitude. Nevertheless, *A. haworthii* produces fewer seeds than *A. arboreum* despite their similar distributions. Though the species' invasion success cannot be explained by fecundity alone, high seed production by *C. orbiculata* is likely to facilitate spread and merits consideration for control efforts.

Chapter 5 – Validating SDM projections against field data

5.1 Abstract

Correlative species distribution models (SDMs) are valuable tools in invasion ecology, but assessing the accuracy of their projections is not always straightforward. While the underlying algorithms are becoming increasingly sophisticated, the methods used to validate SDM projections remain largely static. Models of potential distributions are usually validated against occurrence data, but testing hypothetical scenarios against current conditions unfairly rewards over-fitted models. Instead, species' performance data and process-based models can be utilized to test and improve SDM projections. In this chapter, the concept of fundamental absences (where a species cannot occur due to limiting abiotic conditions) is introduced. Using this concept, I develop a novel approach to validating and refining SDM projections against climate-driven population models. Population models were used to predict whether climatic conditions in Banks Peninsula, New Zealand are conducive to self-sustaining populations of three non-native succulent species; *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. Pre-existing field data detailing how growth, mortality, germination and fecundity respond to climate were incorporated into an integral projection model (IPM), which was used to predict hypothetical population growth at 83 occupied and unoccupied locations in the region. Predicted population growth was used to infer fundamental presences and absences and to validate previous SDM projections of climatic suitability. Finally, SDM projections were refined to increase parsimony with IPM predictions. The results of this independent validation showed that the SDMs performed better than k-folds cross-validation using only occurrence data would suggest. Nonetheless, the SDMs over-predicted suitable climate, and I identify likely sources of error leading to the over-prediction. The use of validation techniques similar to those presented is encouraged in field of distribution modelling.

Keywords: BIOCLIM, IPM, population modelling, SDM, validation

5.2 Introduction

Advances in computing power have given ecologists access to a suite of methods for predicting how species respond to their environment. The most commonly used of these methods are correlative species distribution models [SDMs (Elith 2013)]. User-friendly software and freely-available input data make it relatively easy to project environmental suitability for a species (Ahmed *et al.* 2015), but despite a recent explosion in the SDM literature, there is ongoing debate around how trustworthy the ensuing projections are (Pearson & Dawson 2003; Jeschke & Strayer 2008; Sinclair *et al.* 2010; Warren 2012). There are a number concerns regarding the accuracy of SDM projections. For example, although it is well known that SDMs are sensitive to changes in input settings; such as sampling area (Merow *et al.* 2013), pseudo-absence sampling (Senay *et al.* 2013), corrections for bias (Syfert *et al.*

2013) and choice of environmental predictors (Araújo & Guisan 2006), these details are often omitted from published articles, preventing critical evaluation of their results (Yackulic *et al.* 2013). Furthermore, it is well-known that modellers should base their choice of algorithm on the ecology of the target species and question at hand (Aguirre-Gutiérrez *et al.* 2013; Kriticos *et al.* 2013). Yet, a survey of the modelling community found that SDMs are overwhelmingly chosen based on convenience (Ahmed *et al.* 2015), with algorithms developed in R (R Core Team 2014) and MaxEnt (Phillips *et al.* 2006) being most popular. Lozier *et al.* (2009), in a satirical exercise modelling Sasquatch distributions, draw attention to how easily spurious SDM results can be confused with meaningful ones when the species' biology is disregarded.

Aside from human error, SDMs have been criticized because of questionable underlying assumptions. These include the assumption that, 1) the environmental variables used correlate with and are representative of the species' requirements, 2) that these requirements are the same across space and time (Elith & Leathwick 2009), 3) that the species distribution is at equilibrium with the environment (Václavík & Meentemeyer 2012), and, 4) that adaptation and niche shifts are not occurring (Pearman *et al.* 2008). Any variable not included in the model, for example biotic interactions or dispersal, is assumed to either be non-limiting or to correlate with training variables (Godsoe & Harmon 2012). During invasions these assumptions are often violated (Elith *et al.* 2010) and so using SDMs in this context is inherently risky (Mesgaran *et al.* 2014). It should be noted that some SDMs explicitly include biotic interactions or dispersal [*e.g.* Bateman *et al.* (2012); Quinn *et al.* (2014)], and although this study focusses on climate-only SDMs the methods could also be applied to more complex models.

The accuracy of SDM projections is commonly assessed through cross-validation (Wenger & Olden 2012), whereby a random or otherwise-chosen subset of occurrence records are held back from each model run and used for testing. While this is convenient because the model can still use all data for training, cross-validation often gives an inflated measure of accuracy (Hijmans 2012). Independent validation of SDM results is generally considered to be superior (Dormann *et al.* 2012), ideally using independent survey data that is not spatially auto-correlated with training data (Araújo *et al.* 2005). This is rare in practice, as presence/absence survey data can be difficult to obtain (Jeschke & Strayer 2008), and if the aim is to produce informative projections it may be beneficial to use all available geographic regions for training, rather than handicap the SDM by denying it crucial information (Broennimann & Guisan 2008). Importantly, even independent validation generally requires information on where the species does not occur (absence data) in addition to presence locations, potentially rewarding over-fitted models (Rodda *et al.* 2011).

For model validation, known presences and absences are usually compared to projected suitable and unsuitable areas using confusion matrices and their derived metrics such as sensitivity and specificity (Allouche *et al.* 2006), or to continuous model scores using AUC (Fielding & Bell 1997). These metrics are commonly used in medicine to assess how well a clinical test detects a condition or disease

in patients (Zweig & Campbell 1993). Applying the same logic to SDMs, each patient becomes a grid cell in the landscape, each patient's health the presence or absence of the species, and each clinical test result is represented by the SDM score for the grid cell. Crucially, clinical tests aim to detect whether a patient currently has a condition, not predict whether a patient could potentially fall ill. Yet confusion matrices are often used to evaluate SDMs that aim not to project where invasive species currently are, but where they might occur in the future. For example, projections of species' climatic limits are assessed against how well they predict whether grid cells are currently occupied or not. Logically, the best possible model is then one that predicts suitability only where the species is already known to be, and over-fitted models are likely to be rewarded. False absences (*i.e.* the SDM predicts climatic unsuitability but the species is present) are good indicators of an unreliable model because if the species is present the environment is probably suitable. However, false absences can also be caused by sink populations, microhabitat and geo-referencing errors (Márcia Barbosa *et al.* 2013). Conversely, false presences (*i.e.* SDM predicts suitability but the species is absent) are entirely ambiguous as a species can be absent for many reasons, only one of which is environmental unsuitability. Reasons for a species being absent from suitable environments include geographic barriers, biotic interactions, dispersal patterns, non-climatic limitation, or it may simply not be detected (Lobo *et al.* 2010). Modelling invasions is particularly problematic, because typically the species is assumed to be expanding in its distribution (Elith *et al.* 2010) and there is no quantitative way to distinguish model error from climatically suitable, yet-to-be colonized, habitat. Despite these apparent contradictions, there are few examples of validating SDMs using anything other than distribution data.

Instead of distribution data, a better test of SDM performance is to compare projections with “bottom-up” approaches, for example, plant performance data, population models or the physiological requirements of the species (Kearney & Porter 2009). It might intuitively seem that if such data were available, such as if there was sufficient knowledge of physiological requirements to build a mechanistic model, it would be better to use bottom-up approaches to predict the species' potential distribution. Bottom-up approaches have been successfully applied to predicting species' distributions (Kearney & Porter 2004; Buckley 2008), but it is data-intensive and requires spatial projections of all relevant driving variables. Small errors and uncertainties are compounded with increasing model complexity, and as a result, bottom-up projections are not necessarily more accurate than top-down approaches (correlative SDMs). Consequently, the method should be chosen according to the aims of the study (Buckley *et al.* 2010). Some authors have combined bottom-up and top-down approaches to produce more detailed or dynamic projections, albeit most commonly using climatic SDMs combined with non-climatic metapopulation models (Anderson *et al.* 2009; Franklin *et al.* 2014). While such “hybrid” models can improve species' range forecasts and provide more detailed projections (Brook *et al.* 2009), they assume that both the top-down and bottom-up components are accurate. Errors in the underlying SDM projections will transfer to the hybrid projections, and Conlisk *et al.* (2013) show that the SDM is the largest source of uncertainty in hybrid models. While this does not discount the

usefulness of hybrid models, it is clear that there is still progress to be made in evaluating and improving SDM outputs, which is the focus of this study.

Alternatively, Kearney and Porter (2009) suggest using bottom-up approaches to define areas of unsuitability, against which SDMs could be validated and refined. This is distinct from validation using *pseudo-absences* [locations where the species is thought to be absent due to lack of records, though more complex pseudo-absence selection techniques exist *e.g.* Senay *et al.* (2013)] and *true absences* (where the species is known to be absent through surveys). To distinguish the methods presented here from pseudo-or true absences, I refer hereafter to *fundamental absences*, *i.e.* where evidence suggests that locations are outside of the fundamental niche of the species, where abiotic factors will prevent survival. Using fundamental absences to test SDM performance would give better insight into model accuracy but few studies have taken such an approach. Sheppard *et al.* (2014) compared SDM projections of climatic suitability for three non-native plants in New Zealand to performance in field trials, but unsuitability was not explicitly defined, and the results were not used to improve the model. Pattison and Mack (2008) used a similar method, correlating CLIMEX scores for *Triadica sebifera* (L.) Small in the USA with performance of seeds and young plants, and Aragón *et al.* (2010) used known physiological thresholds to validate model projections of *Diabrotica virgifera* J. L. LeConte in Europe. Morin and Thuiller (2009) predicted the distributions of 15 tree species using population models and SDMs, but it was a comparative study rather than a critical evaluation.

In this chapter, I demonstrate a novel method of validating and improving SDM projections in a scenario where it is unrealistic to develop landscape-scale simulations using a bottom-up approach. In Chapter 2, BIOCLIM (Nix 1986) was used to project suitable habitat in New Zealand for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*, based on their global distributions, climate and selected non-climatic factors. In recent years, BIOCLIM has declined in use and is often reported to perform poorly in comparison to other models, but I determined it was the most appropriate tool for modelling the three particular study species. In previous assessments of BIOCLIM, its performance was assessed using occurrence data (Elith *et al.* 2006; Hernandez *et al.* 2006; Wisz *et al.* 2008). The rectilinear envelope used by BIOCLIM will inevitably result in some over-prediction, but it is unclear to what degree its reportedly poor performance is a consequence of it being less prone to overfitting than more complex models. To test the accuracy of the SDM projections of the study species, I develop a climate-driven integral projection model (IPM) of population growth using existing performance data collected from Banks Peninsula, New Zealand (Chapter 3 and Chapter 4), and then test the IPM against independent occurrence data. Whereas most population modelling efforts aim to predict the growth of real populations of species, I aimed instead to identify where hypothetical populations could self-sustain. Population growth was predicted in the steady state and transformed into fundamental presences and absences, to identify where climate could support self-sustaining populations assuming otherwise ideal non-climatic conditions. Existing BIOCLIM projections of climatic suitability in the region of interest were tested against the fundamental presence/absence data,

and SDM projections were then refined to remove as much prediction error as possible. The principles of this method have been suggested by Kearney and Porter (2009), but to my knowledge have not been previously demonstrated.

5.2.1 Aims

1. Combine existing linear regressions of climate-dependent mortality, growth, germination and fecundity of the study species into a population model that predicts whether climate is amenable to self-sustaining populations on Banks Peninsula.
2. Validate existing BIOCLIM projections of climatic suitability on Banks Peninsula against projected population growth.
3. Improve BIOCLIM projections to more closely match population model predictions, and improve maps of climatic suitability on Banks Peninsula for the study species.

5.3 Methods

5.3.1 Study species

This study builds on previous research on three succulent perennials in the Crassulaceae family; *Aeonium arboreum*, *A. haworthii*, and *Cotyledon orbiculata*. Their potential distributions in New Zealand are likely to be climate limited due to the comparatively hot and dry conditions of the native ranges (Morocco, the Canary Islands and Southern Africa, respectively), and SDM projections (using BIOCLIM) have indicated that the species' distributions in New Zealand constitute a shift of the realized niches (Chapter 2). Nevertheless, continued spread in New Zealand is apparent on cliffs, roadsides and, in the case of *C. orbiculata*, grazing land, and the accuracy of SDM projections of climatic suitability was uncertain. Field studies confirmed that growth rates, survival and germination decline with increasingly cold and wet conditions in the study region (Chapter 3), but that plant size is also an important predictor of mortality (Chapter 3) and fecundity (Chapter 4). Surveys of naturalized populations in the study region indicated high mean seed output (approximately 26 000 seeds per capita for *A. arboreum*, 5000 for *A. haworthii* and 192 000 for *C. orbiculata*). Propagule pressure from naturalized populations is therefore likely to be high, and further spread appears likely. Although the relationships between plant performance and climate were established in previous chapters, the potential for new and existing populations to self-sustain across varying climatic conditions was not clear, nor was how the species' vital rates would interact to determine overall suitability under various climatic conditions.

5.3.2 Study area

As in the two preceding chapters, I focus on the region of Banks Peninsula, New Zealand, where previous field surveys and experiments on the study species were undertaken. Banks Peninsula

comprises approximately 1150 km² of hilly terrain extending from the coast south of Christchurch. All three target species have established numerous populations on Banks Peninsula, mostly along the northern coastline: the region contains 52% of all *Aeonium* occurrence records in New Zealand and 75% of *C. orbiculata* records. Because occurrence records on Banks Peninsula were used to train BIOCLIM, testing the projections in the same region is not a fully independent test of model performance. However, it was necessary to train the SDM using Banks Peninsula data because the region represents the wettest extremes of the species' realized niches. Testing projections on the Peninsula was also valuable because, as a key area of invasion for all three species, accurate projections of climatic limits are of interest to practitioners. Numerous training points in the test region ensures that this is a "best-case" scenario of model performance. The results should, however, not be extrapolated beyond the Peninsula because of the non-independence of test data.

The climate of the region is heterogeneous, with elevations ranging from 0 – 930 MASL, and precipitation averaging from 600 - 1200 mm per year [(Hijmans *et al.* 2005), available from <http://www.worldclim.org>]. Evidence suggests that this precipitation and elevation gradient extends beyond the limits of climatic suitability for all three species (Chapter 3). The Peninsula contains much suitable habitat for these succulent xerophytes, namely, volcanic cliffs and rock outcrops, roadside cuttings, loess banks and sparse grassland (Webb *et al.* 1988). At the scale of SDM projections (approximately 1 km²) there are few grid cells that do not contain suitable habitat, so it is assumed that on Banks Peninsula invasion is limited primarily by climate.

5.3.3 Integral projection models

Generalized Linear Mixed Models (GLMMs) were previously fitted to field experiment and survey data (Chapter 3 and Chapter 4) to describe climatic limitations to growth, mortality and fecundity [collectively called vital rates (Tuljapurkar & Caswell 2012)] for the three target species. In all three species, plant size (canopy volume) was a significant predictor of vital rates in addition to climate. The GLMMs were integrated into a single population model per species. Integral projection models (IPMs) were used, a technique developed by Easterling *et al.* (2000). The IPMs were used to predict whether the species are likely to form self-sustaining populations under given climatic conditions.

Population growth (λ ; λ) of *A. arboreum*, *A. haworthii* and *C. orbiculata* was modelled using IPMs because they offer distinct advantages over the more commonly-used matrix projection models (MPMs) in situations involving continuous state variables. In this case, plant size (canopy volume) was the state variable as it is a predictor of multiple vital rates. Although MPMs are useful when modelling population growth over discrete time periods, they are suited to organisms that can be divided into distinct classes based on age (Leslie matrices) or stage (Lefkovich matrices). In MPMs, each class has a unique probability of reproduction, mortality and transition to the next class. Where no natural divisions in the life cycle exist, constraining the state variable (*e.g.* age, canopy volume) into a matrix of few or arbitrary classes leads to over-inflated extinction risk, as MPMs ignore

variation within classes (Fox & Kendall 2002). Conversely, with too many class divisions, the calculations required to parametrize an MPM becomes impractical, with too few samples within each class to predict vital rates (Ellner & Rees 2006). Integral projection models provide a solution to this problem, and are well-described by Merow, Dahlgren, *et al.* (2014). All IPMs use the same principles as MPMs, but instead of individually calculating transition probabilities across a small matrix, linear regressions describing vital rates are integrated across a very large matrix of the state variable.

For clarity, it is necessary to qualitatively describe the structure and concepts behind IPMs before we continue. As a first step, an $n \times n$ matrix of state variable classes (*e.g.* plant size as canopy volume) is created by defining the maximum and minimum values. The number of cells in the matrix determines the cell size (*i.e.* interval between classes), often set to 1000×1000 , with each cell representing a class of plant sizes. Next, three kernels describing fecundity, growth and mortality are defined. These kernels combine multiple linear regressions of vital rates (*e.g.* probability of flowering, seeds per pod) and are dependent on the state variable of the initial matrix (*e.g.* canopy volume), with or without external driving variables (*e.g.* climate). Finally, the three kernels are integrated across the initial matrix of size classes, to create an IPM matrix of transition probabilities between cells in each time step. The locations within each cell where linear regressions are integrated are also defined by the user (usually the mid-point of each cell). Fitting a climate-driven IPM therefore requires only a few linear regressions describing vital rates as functions of the continuous state variable and climate.

5.3.4 Climate variables

Three IPMs were developed for predicting population growth (λ) at locations on Banks Peninsula, as a function of climate. The key driving climate variables in the underlying GLMMs included annual frost days (below 0 °C) and growing degree days (base 5 °C and 10 °C, hereafter referred to as GDD5 and GDD10). These variables are not available as spatial layers, so it was not feasible to project the IPMs across the entire Banks Peninsula. Instead, I ran the IPMs at point locations using temperature data from existing weather stations, field surveys and experiments. At 71 field sites I had previously recorded four-hourly temperature data (°C) using iButton™ data loggers, between December 2010 and November 2012 (Chapter 3 and Chapter 4). In addition, I downloaded daily maximum and minimum temperature from the 12 available weather stations between latitudes -43.325 and -43.900, and longitudes 172.294 and 173.131 decimal degrees (WGS 1984). Data were obtained from the CliFlo database [(National Institute of Water and Atmospheric Research 2014), <http://cliflo.niwa.co.nz/>]. Combining all temperature data from December 2010 – November 2012 provided 83 point locations with the climate data necessary to run the IPM (Table D.1).

At each point location, frost days, GDD5 and GDD10 were calculated from recorded daily maximum and minimum temperatures, and monthly solar radiation (KWh/m^2) was modelled at the same locations using the Solar Radiation tool in ArcMap 10.1 (Fu & Rich 1999; Environmental Systems Research Institute 2011). Not all weather stations record both temperature and precipitation, and only

temperature was recorded at the 71 field sites. I therefore estimated monthly precipitation (mm) for point locations without rainfall data, using the nearest neighbour station in the CliFlo database (14 stations total, Table D.1).

Time periods over which climate variables were summed (*e.g.* annual precipitation) were the same as were used in the original GLMMs. In other words, July-December climate totals were used to drive regressions in the fecundity kernels, December-June totals for survival kernels, and annual totals for the growth kernels. Finally, I used the means of climate variables (*e.g.* annual frost days) over December 2010 – November 2012 as the driving variables for the IPM at each point location. For predictions to be useful, the two-year means (December 2010 – November 2012) should be representative of longer-term averages at the sites. To test this assumption I compared the two-year means to five, ten and twenty-year means at the 12 weather stations, using a paired t-test with alpha levels adjusted using the Bonferroni correction. I then tested whether the trends recorded by data loggers were comparable to those recorded at weather stations over the same period (December 2010 – November 2012), by calculating mean correlation (r) between the residuals of the means of temperatures recorded by data loggers versus the nearest weather station. Both daily maximum and daily minimum temperatures were compared.

There were no significant differences in two, five, ten or twenty-year means of annual frost days at any of the weather station sites (Figure D.1, Table D.2). There were significant differences in annual GDD5 and GDD10, but between the two and five-year means only. Between December 2010 and November 2012, data loggers recorded more extreme temperatures than weather stations. In particular, maximum temperatures were higher (mean r of residuals = 0.54; Figure D.2). This is expected, as the weather stations are mostly low elevation and/or coastal, while data loggers were in exposed locations. Daily minimum temperatures were well correlated between data loggers and weather stations (mean r of residuals = 0.85; Table D.3). In summary, there was good evidence that the two-year climate means used in the IPMs were representative of longer-term trends.

5.3.5 IPM parameters

The IPMs were based on annual time steps, standard practice for long-lived perennial plants (Merow, Smith, *et al.* 2014). The models were run over one time step using the mean climate variables, beginning on 1st December and ended on 30th November to align with field experiments and surveys, where 1st December approximately marks the beginning of the flowering season for the species. Linear regressions for the fecundity and mortality kernels were identical to those described in Chapter 3 and Chapter 4, with random effects set to zero where applicable (Table 5.1).

Growth kernels were simpler than the regressions described in Chapter 3, because preliminary attempts to introduce a “rapid growth stage” as observed in the first year of the field experiments (Figure 3.4) led to unstable model behaviour. Instead, I fitted a model using a similar structure to the

growth kernels in the R package *IPMpack* (Metcalf *et al.* 2013). Canopy volumes (L) of plants at experimental sites in November 2011 and 2012 were used as the response variable “Volume_{*t+1*}”. Using stepwise backward selection, I fitted a GLMM with the random effects *Site* and *Source*, identical to those used in Chapter 3. I fitted fixed effects of annual climate variables and canopy volume (L) at previous time step (“Volume_{*t*}”). Marginal R² (Johnson 2014) of the growth models were 0.42 for *A. arboreum*, 0.21 for *A. haworthii* and 0.22 for *C. orbiculata*.

Table 5.1 Linear regressions of vital rates of *Aeonium arboreum* (AA), *A. haworthii* (AH) and *Cotyledon orbiculata* (CO), as used in IPMs. Parameters of each regression shown, and whether the regression was fitted to experimental (Chapter 3) or survey (Chapter 4) data. Model coefficients are available in Table S.1. Units are plant volume (L), elevation (MASL), precipitation (mm/year) Frost days, GDD and precipitation were 2-year annual means for each variable.

| Vital rate | Species | Parameters | Source | Thesis figure |
|------------------------------|---------|---|------------|---------------|
| P[Die] summer | AA | Volume + Elevation | Experiment | Figure 3.6 |
| | AH | Volume + Elevation | Experiment | Figure 3.6 |
| | CO | Volume | Experiment | Figure 3.6 |
| P[Die] winter | AA | Volume + Cumulative Frost Days | Experiment | Figure 3.7 |
| | AH | Volume + Cumulative Frost Days | Experiment | Figure 3.7 |
| | CO | Volume + Cumulative Frost Days | Experiment | Figure 3.7 |
| Volume _{<i>t+1</i>} | AA | Volume _{<i>t</i>} + Elevation + Elevation ² | Experiment | Table S.1 |
| | AH | Volume _{<i>t</i>} + Elevation + Frost | Experiment | Table S.1 |
| | CO | Volume _{<i>t</i>} + Elevation + Elevation ² | Experiment | Table S.1 |
| P[Flower] | AA | Volume + GDD10 | Surveys | Figure 4.2 |
| | AH | Volume | Surveys | Figure 4.2 |
| | CO | Volume + Solar Radiation | Surveys | Figure 4.2 |
| Inflorescences per plant | AA | Constant | Surveys | Table S.1 |
| | AH | Constant | Surveys | Table S.1 |
| | CO | Volume | Surveys | Figure 4.3 |
| Flowers per inflorescence | AA | Aspect | Surveys | Figure 4.4 |
| | AH | Constant | Surveys | Table S.1 |
| | CO | Volume | Surveys | Figure 4.4 |
| Seeds per pod | AA | Aspect + Pods + (Aspect*Pods) | Surveys | Figure 4.5 |
| | AH | Constant | Surveys | Table S.1 |
| | CO | Constant | Surveys | Table S.1 |
| Seedling success | AA | GDD5 + Frost Days + Precipitation | Experiment | Figure 3.3 |
| | AH | Elevation | Experiment | Figure 3.3 |
| | CO | Precipitation | Experiment | Figure 3.3 |

In linear regressions that contained aspect as a driving variable, I chose to predict vital rates for north-facing aspects to represent favourable conditions for all species. Assuming that the majority of grid cells on Banks Peninsula contain at least one north-facing slope, this mitigates the risk of under-predicting potential ranges. Canopy volume (*v*) was normalised by log-standardizing against the relevant original raw data (*y*) used in original linear regressions in Chapters 3 and 4, according to equation 1. Constant values, the observed means across all survey sites between December 2010 – November 2012, were used to describe inflorescences per plant in *A. arboreum*, all seed and flower production in *A. haworthii* and seeds per pod in *C. orbiculata*. Constant mean values were used for

Aeonium species where no strong relationships with plant volume or climate had been found during field surveys. For *C. orbiculata*, constant seeds per pod were used to prevent extreme values when extrapolating. In its native range, *C. orbiculata* var. *dactyloopsis* produces on average 1585 ovules per flower (Zietsman 1998), while the IPM predicted values of up to 15 890 seeds per pod. This was a result of extrapolating the relationship to larger inflorescences than were actually sampled, hence mean seeds per pod were used. The original regression for *C. orbiculata* is shown in equation 2, and because aspect was a driving variable, I again used the mean number of seeds at north-facing sites. The same regression was used to predict *A. arboreum* seeds per pod, but it did not lead to extreme predictions for this species, as seeds per pod was less variable, and flowers per inflorescence was more representative in the original dataset.

$$\text{Log Standardized Canopy Volume} = \{\ln [v_i] - \bar{x} [\ln (y)]\} / \{2s [\ln (y)]\} \quad (1)$$

$$\text{Seeds per Pod} = \text{Aspect} + \text{Pods per Inflorescence} + (\text{Aspect} \times \text{Pods per Inflorescence}) \quad (2)$$

5.3.6 IPM structure

Each vital rate regression was incorporated into one of the three kernels of the IPM: survival, growth or fecundity. For each of the 83 point locations, the kernels were integrated across the initial matrix of size classes of canopy volume to create a survival vector (S), and growth (G) and fecundity (F) matrices (see Figure D.3 for a simplified example of the model structure). The IPM matrix for each location showing transition probability among size classes of canopy volume, is calculated by first creating P , a growth and survival matrix (equation 3). Then, F is incorporated to make the IPM matrix (K , equation 4). Though a vector of initial conditions is usually supplied, eigenvectors and lambda (λ) were calculated from transition probabilities with no initial conditions, equivalent to population growth in the steady state. The steady state was used in order to answer whether a hypothetical population could self-sustain at point locations, including at current absences, without biasing the model with arbitrary initial conditions for species with unknown dispersal capabilities. Lambda is calculated using the *eigen* function in R's base package, as $\text{lambda} = \text{Re}(\text{eigen}(K)\$values[1])$. This function calculates the eigenvalues for the matrix and returns them as a vector sorted in decreasing order, where the dominant (largest) eigenvalue equals lambda.

$$P = G \times S \quad (3)$$

$$K = P + F. \quad (4)$$

The initial matrices of size classes were rescaled from the original state variable canopy volume (L), because it was difficult to see model behaviour in small plants. I instead used the state variable $\sqrt[3]{(\text{Volume} \times 10^3)}$, approximately equivalent to plant height. This did not alter model predictions as plant height was rescaled to canopy volume before input into the vital rate regressions. I defined the initial matrix as a 1000×1000 cell matrix between 2 cm and 55 cm height, based on observed sizes of seedlings and mature plants during surveys. Kernel functions were integrated using the simplest

option, the midpoint rule (Merow, Dahlgren, *et al.* 2014). In order to run the IPM on an annual time step, the survival kernel incorporated summer and winter mortality (equation 5). Growth kernels contained the linear regressions described in Table 5.1, which predict mean canopy volume at time $t+1$ based on volume at time t , plus climate. The distribution around the mean was Gaussian with a standard deviation of 5 cm, equivalent to the residual variances of the fitted growth models.

$$\text{Annual Survival} = (1-P[\text{Die}] \text{ winter}) \times (1-P[\text{Die}] \text{ summer}) \quad (5)$$

The fecundity kernel was driven by probability of reproduction $P[\text{Reproduce}]$ and per capita seed output. Probability of reproduction was defined according to equation 6. Establishment probability ($P[\text{Establish}]$) is often incorporated into IPMs as a constant, the probability of a seed landing in a favourable location for germination (Metcalf *et al.* 2013; Merow, Dahlgren, *et al.* 2014). I set establishment to $P[1]$ to model population growth under optimum conditions. Seedling success is the probability of germination and subsequent annual seedling survival (the models derived from field experiments, Chapter 3). If the IPMs for the three species were to be used for dynamic or temporally explicit projections, they should include a discrete seedling stage akin to a seed bank [see Ellner and Rees (2006)]. As predictions were static, I simplified flowering, germination and seedling survival to occur in the same time step with no seedling bank. Per capita seed output was calculated according to equation 7. The final fecundity kernel combines reproduction and seed output (equation 8), and predicts how many seeds per capita develop, germinate and survive to become seedlings. The resulting seedlings enter the IPM matrix as a normal distribution of individuals centred on the mean recruitment size, set to 2 cm height with a standard deviation of 1 cm.

$$P[\text{Reproduce}] = P[\text{Flower}] \times P[\text{Establish}] \times P[\text{Seedling Success}] \quad (6)$$

$$\text{Seed Output} = \text{Inflorescences per Plant} \times \text{Flowers per Inflorescence} \times \text{Seeds per Pod}. \quad (7)$$

$$\text{Fecundity} = P[\text{Reproduce}] \times \text{Seed Output} \quad (8)$$

5.3.7 Verification of IPMs

Predictions of the IPMs were assessed against true presences of the target species, and were considered reliable on the condition that λ was consistently > 1 at presence locations, in other words if positive population growth was predicted. Predicted λ at true absence locations was not used to test the IPMs because true absences are ambiguous; species may be absent from a location for a number of reasons not necessarily related to climate. Additionally, the species are still spreading in the region, so “false presences” are expected. However, both predicted λ at true presence and absence locations were used to assess the proportion of currently unoccupied sites with potential for invasion. Predictions were compared between species by calculating the Jaccard similarity index of λ scores, converted to fundamental presence/absence using a threshold of 1. Models were checked for spurious or biologically unrealistic behaviour by plotting the IPM (K) and growth (G) matrices, and the stable size distributions (the right eigenvectors). I checked and corrected for eviction, where individuals are

dropped from the matrix upon falling outside of the minimum or maximum size classes [see Williams *et al.* (2012)], by plotting the survival function and column sums of the growth and survival (P) matrix. Predicted P and K matrices, and stable size distributions at the 5th and 95th percentile locations when ranked by λ (*i.e.* “poor” and “good” sites), are shown in Figure D.4, Figure D.5 and Figure D.6.

To investigate which driving variables and plant size classes had most effect on λ , I ran perturbation and elasticity analyses on predictions at the 5th and 95th percentile locations. As sensitivities and elasticities were highly similar, only elasticity is presented. Elasticity measures the change in λ proportional to the change in each variable, thus accounting for the different scales (*e.g.* plant height vs. probabilistic regressions). The elasticity analysis is part of standard IPM code (Metcalf *et al.* 2013; Merow, Dahlgren, *et al.* 2014), and derives elasticity from the left and right eigenvectors of the matrix, indicating size classes that have most influence on λ . The perturbation analysis measures the relative influence of driving variables on λ (Caswell 2000), by changing each parameter in the IPM by a delta (Δ) value of 0.0001 (equation 9).

$$\text{Elasticity} = (\text{new } \lambda - \text{original } \lambda) / (\text{original } \lambda - \Delta) \quad (9)$$

5.3.8 Validation of BIOCLIM projections

The 83 predicted λ values for each species at each point location were used to validate BIOCLIM projections for Banks Peninsula (Chapter 2.4.3), on the assumption that the IPM represents a best estimate of true climatic suitability for each species. This assumption is defensible on the basis that all linear regressions in the IPMs are derived from high-power field data in the same region, with minimal extrapolation or additional assumptions, and the IPM predictions were shown to be reasonable before carrying out further analysis. I transformed BIOCLIM and IPM projections into binary projections of suitability. BIOCLIM has a natural threshold; scores of 0 indicate that climatic conditions are outside of the “envelope” defined by presence data and are presumably unsuitable. For the IPM scores, I used 1 as the threshold, where $\lambda < 1$ indicate that populations are not predicted to be self-sustaining due to negative population growth rate in the steady state. I resampled all IPM points onto a 30 arc-second raster grid aligned with BIOCLIM projections, taking the mean λ when multiple points fell within a grid cell. I then calculated confusion matrices to evaluate the performance of BIOCLIM (“prediction”) against the 83 IPM fundamental presences and absences (“reality”). For comparison with conventional validation techniques, I calculated confusion matrices using 5-fold cross-validated presence/absence data for Banks Peninsula (occurrence data shown in Appendix C).

The most common metrics calculated from confusion matrices are sensitivity and specificity [see Allouche *et al.* (2006) for a comprehensive explanation of these]. Sensitivity measures the proportion of presences correctly identified by the model, while specificity does the same for absences. These metrics may be misleading depending on the structure of the occurrence data. For example, with a 50:50 split of true presence and absence points within a predicted absence area (*i.e.* model likely to be

under-predicting) sensitivity and specificity could equal 75% (a “good” model) if there are three times as many presence points as absence points overall. Instead, Márcia Barbosa *et al.* (2013) propose the over- and under-prediction rates (OPR and UPR respectively). These metrics are the proportions of all predicted absences that contain true presences (OPR), and predicted presences that contain true absences (UPR). From the confusion matrices I calculated sensitivity, specificity, UPR, and OPR of BIOCLIM projections. To test whether true presences were likely to have high BIOCLIM scores, and vice versa, I calculated area under the ROC curve (AUC). A common, if somewhat arbitrary rule-of-thumb is that models are useful only if $AUC > 0.7$ (Greiner *et al.* 2000).

5.3.9 Improving BIOCLIM projections

The final aim was to improve BIOCLIM projections for Banks Peninsula. Assuming that the projections would not be perfect, there are two possibilities; that overall, BIOCLIM under-predicts climatic suitability on Banks Peninsula, or it over-predicts. If results showed BIOCLIM to be under-predicting, I aimed to input false absence locations (where $\lambda > 1$ but $BIOCLIM = 0$) back into the original SDMs as additional training presences, to extend projected range limits. This assumes that BIOCLIM under-predicts due to niche expansion in New Zealand and non-equilibrium distribution. In the case of over-prediction, I aimed to test whether presences and absences, as defined by the IPM, had significantly different BIOCLIM scores. This assumes that low BIOCLIM scores (*i.e.* the outer edges of the climatic envelope) represent marginal conditions that cannot support self-sustaining populations, and will not remove any over-prediction in the “core” envelope. To test whether the mean BIOCLIM scores were significantly different between fundamental presences and absences, I would run 1000 - fold bootstraps of BIOCLIM scores at fundamental presence and absence locations, plot the distributions, and perform a single-factor ANOVA of the BIOCLIM scores of the two groups. If fundamental presences and absences had significantly different scores to each other, I would recalculate the confusion matrices iteratively, raising the BIOCLIM threshold by 0.001 on each run between 0 and the maximum score. A new BIOCLIM threshold would then be chosen as the value that best distinguished fundamental presences from fundamental absences. For the recalculation of confusion matrices, fundamental and true presences were pooled to minimize the risk of raising the threshold too high and under-predicting suitable climate. The new threshold was to be the value with the lowest under prediction rate (UPR, described in section 5.3.8) within 0.01 of the maximum True Skill Statistic (TSS, equal to sensitivity plus specificity, minus 1). Maximising TSS would remove as much over-prediction from the BIOCLIM projections as possible, while keeping UPR as low would minimize risk of raising the threshold too high and removing truly suitable climate.

5.4 Results

5.4.1 IPM predictions

Across the 83 point locations used for IPM projections, lambda (λ) ranged from 0.64 - 7.43 for *A. arboreum*, 0.002 - 1.54 for *A. haworthii*, and 0.04 - 7.40 for *C. orbiculata*. The IPM predicted

Aeonium haworthii to have the lowest maximum λ of all species, and ranked plots of λ revealed an asymptotic curve. This is because seed output for *A. haworthii* was the lowest of all three species, producing fewer flowers and fewer seeds per flower. Furthermore, while probability of flowering increases with size in *A. haworthii* models, reproductive output is constant. Consequently, predicted reproductive output of *A. haworthii* in the steady state cannot increase once $P[\text{Flower}] \rightarrow 1$. Across the 83 sites, λ correlated positively but weakly among species (between the *Aeonium* species $r = 0.63$, between *C. orbiculata* and *A. arboreum* 0.50, and between *C. orbiculata* and *A. haworthii* 0.59). Converting λ to fundamental presence/absence revealed that, among species, there was a high degree of overlap in whether locations were classified as suitable or unsuitable (Jaccard Similarity = 0.87 between *Aeonium* species, 0.63 between *C. orbiculata* and both *Aeonium* species). All sites that were dissimilar between *C. orbiculata* and *Aeonium* species were predicted as suitable for the former, and unsuitable for the latter.

The IPMs predicted that at colder sites, growth rates are low, and as a result, mortality increases as individuals die back continuously (Figure D.5). As reproduction is size-dependent, low growth also results in little to no recruitment at unfavourable locations. Irrespective of plant size, survival is low at unfavourable sites, compounding the effect of low growth rates (Figure D.6). The IPMs predicted $\lambda > 1$ at the majority of known presence locations for all three species (Table 5.2). I investigated the remaining false absences (where $\lambda < 1$), and found three sources of error: cultivated populations, spatial scale, and possible marginal populations. With respect to cultivated populations, four locations (Birdling's Flat, Lincoln, Leeston, and "CKSE" in Central Christchurch) were predicted as unsuitable for at least one species. Though the species are present, they are single plants in outdoor gardens. Spatial scale was an issue for the IPM location "Greenwood Park 4" where $\lambda = 0.44$. *Cotyledon orbiculata* is present within the same grid cell as the IPM location, but approximately 100 m lower, and in small numbers. Finally, while *C. orbiculata* is present at both locations at Okains Bay, at one location the IPM predicted $\lambda = 0.95$. This particular location contains a small population with relatively poor performance (Figure C.6), and is potentially a marginal population, although other sources of error cannot be discounted. Overall, the majority of true presences in all three species were predicted to be self-sustaining. As described previously, false presences are not considered sources of error as the species are not at equilibrium.

Table 5.2 Verification of integral projection models of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*, run at 83 point locations on Banks Peninsula. Sites divided according to species' current presence or absence. Sites with predicted population growth (λ) > 1 were classified as suitable, < 1 were classified unsuitable.

| | Species present | | Species absent | |
|----------------------|-----------------|----------------|----------------|----------------|
| | IPM suitable | IPM unsuitable | IPM suitable | IPM unsuitable |
| <i>A. arboreum</i> | 26 | 1 | 16 | 40 |
| <i>A. haworthii</i> | 29 | 2 | 13 | 39 |
| <i>C. orbiculata</i> | 35 | 4 | 32 | 12 |

Table 5.3 Elasticity values of IPM parameters. Perturbation analyses conducted for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* at favourable sites (upper 95th percentile of λ) and unfavourable sites (lower 95th percentile of λ), with the three highest elasticities highlighted for each species.

| Stage | Parameter | Favourable site | | | Unfavourable site | | |
|-----------------|------------------------|------------------------|----------------------|------------------------|------------------------|------------------------|------------------------|
| | | <i>A. arboreum</i> | <i>A. haworthii</i> | <i>C. orbiculata</i> | <i>A. arboreum</i> | <i>A. haworthii</i> | <i>C. orbiculata</i> |
| Summer survival | Intercept | 0.02 | 0.02 | 0.42 | 0.06 | 0.68 | 0.04 |
| | Volume | - 0.01 | - 0.01 | - 0.30 | 0.02 | 0.19 | 0.02 |
| | Elevation | 0.01 | 0.01 | | - 0.02 | - 0.61 | |
| Winter survival | Intercept | 3.6×10^{-6} | 3.3×10^{-6} | $- 1.2 \times 10^{-7}$ | 0.53 | 2.48 | 2.09 |
| | Volume | $- 8.7 \times 10^{-6}$ | 3.3×10^{-6} | $- 1.2 \times 10^{-7}$ | 0.45 | 1.12 | 0.36 |
| | Frost | 1.6×10^{-6} | 3.4×10^{-6} | $- 1.2 \times 10^{-7}$ | - 0.76 | - 4.88 | - 2.22 |
| Growth | Intercept | 0.50 | 0.11 | 0.80 | 0.06 | 0.93 | 1.37 |
| | Elevation | 0.16 | 0.06 | 0.13 | - 0.02 | - 0.65 | - 0.29 |
| | Elevation ² | - 0.30 | | - 0.50 | - 0.03 | | - 1.40 |
| | Frost | | 0.07 | | | - 0.51 | |
| | Previous size | 0.13 | 0.12 | 0.06 | 0.26 | 2.53 | 1.73 |
| | SD | 0.20 | 0.14 | 0.59 | - 0.18 | 2.52 | 1.64 |
| P[Flower] | Intercept | - 1.53 | - 0.95 | - 0.06 | $- 5.9 \times 10^{-6}$ | $- 4.2 \times 10^{-5}$ | $- 1.1 \times 10^{-5}$ |
| | Volume | 0.41 | 0.19 | $- 4.5 \times 10^{-3}$ | $- 5.2 \times 10^{-6}$ | $- 4.2 \times 10^{-5}$ | $- 1.1 \times 10^{-5}$ |
| | GDD10 | - 0.86 | | | $- 5.7 \times 10^{-6}$ | | |
| Inflorescences | Radiation | | | - 0.01 | | | $- 1.1 \times 10^{-5}$ |
| | Intercept | 0.38 | 0.20 | 0.50 | $- 5.4 \times 10^{-6}$ | $- 4.2 \times 10^{-5}$ | $- 1.1 \times 10^{-5}$ |
| | Volume | | | - 0.28 | | | $- 1.1 \times 10^{-5}$ |
| Flowers | Intercept | 0.38 | 1.09 | 1.74 | $- 5.4 \times 10^{-6}$ | $- 4.2 \times 10^{-5}$ | $- 1.0 \times 10^{-5}$ |
| | Volume | | | - 0.45 | | | $- 1.1 \times 10^{-5}$ |
| Seeds | Intercept | 1.00 | 0.57 | 0.43 | $- 5.2 \times 10^{-6}$ | $- 4.2 \times 10^{-5}$ | $- 1.1 \times 10^{-5}$ |
| | Flowers | - 0.01 | | | $- 5.5 \times 10^{-6}$ | | |
| Germination | Intercept | - 1.51 | - 1.60 | - 4.02 | $- 6.3 \times 10^{-6}$ | $- 4.2 \times 10^{-5}$ | $- 1.2 \times 10^{-5}$ |
| | GDD5 | 0.81 | | | $- 5.5 \times 10^{-6}$ | | |
| | Frost | 0.54 | | | $- 5.5 \times 10^{-6}$ | | |
| | Precipitation | 0.16 | | 1.73 | $- 5.5 \times 10^{-6}$ | | $- 1.1 \times 10^{-5}$ |
| Recruit size | Elevation | | 0.74 | | | $- 4.2 \times 10^{-5}$ | |
| | Mean | 0.61 | 0.36 | 0.74 | $- 5.2 \times 10^{-6}$ | $- 4.2 \times 10^{-5}$ | $- 1.1 \times 10^{-5}$ |
| | SD | 0.38 | 1.1×10^{-3} | 0.06 | $- 5.4 \times 10^{-6}$ | $- 4.2 \times 10^{-5}$ | $- 1.1 \times 10^{-5}$ |
| Establishment | P[Establish] | 0.38 | 0.22 | 0.43 | $- 5.4 \times 10^{-6}$ | $- 4.2 \times 10^{-5}$ | $- 1.1 \times 10^{-5}$ |

5.4.2 Perturbation analyses

Elasticity plots of IPM matrices revealed that at favourable sites, λ was most affected by changes in the growth rates of small plants (*i.e.* less than 30 cm height, Figure D.7). When plants are small, minor increases in growth rates facilitates reproduction, and population growth increases rapidly. At unfavourable sites, changes to growth in medium-to-large plants had the most effect, as increases in growth at this stage reduces net die-back, allowing ongoing winter survival. Perturbation of individual parameters resulted in similar patterns to the matrix plots, where λ at favourable sites was most affected by parameters related to reproduction (Table 5.3). At unfavourable sites, parameters related to growth and survival affected λ most. Additionally, λ tended to be more sensitive to regression intercepts than to climate or volume parameters, particularly at favourable sites.

5.4.3 Validation of BIOCLIM projections

Predicted λ tended to be highest at low elevations or near coastlines for all three species. Notable exceptions were locations on the Canterbury plains, where IPMs of all three species commonly predicted $\lambda < 1$. Despite the low elevations, the plains more frequently experience sub-zero temperatures than sites on Banks Peninsula (up to 63 mean annual frost days at Christchurch Airport, while Banks Peninsula had maximum of 7). In the IPMs, frost days limit winter survival for all three species, growth for *A. haworthii*, and germination for *A. arboreum*. For both *Aeonium* species, all grid cells classified as unsuitable by BIOCLIM were predicted by the IPMs to be fundamental absences (Figure 5.1). In other words, UPR of BIOCLIM = 0. By extension, grid cells containing fundamental presences were projected as suitable by BIOCLIM in 100% of instances (sensitivity = 1). Sensitivity was also 1 for *C. orbiculata*, but the UPR could not be assessed because BIOCLIM predicted no unsuitable grid cells. However, in all three species a number of fundamental absences were incorrectly classified as suitable by BIOCLIM (*i.e.* specificity was low, between 0 – 0.4). As a proportion of all BIOCLIM cells predicted as suitable, 10 - 30% contained fundamental absences (OPR = 0.1 - 0.3).

The confusion matrices for BIOCLIM projections were repeated using occurrence data (Table 5.5), and despite the over-prediction of BIOCLIM, it performed better than traditional cross-validation techniques would have suggested. For example, cross-validation indicated misleadingly high over prediction rates (OPR) of 0.95 for both *Aeonium* species, and 0.89 for *C. orbiculata*. This was due to a large number of currently unoccupied grid cells along the coastlines, where BIOCLIM was penalized for projecting suitability, despite it being likely to be true.

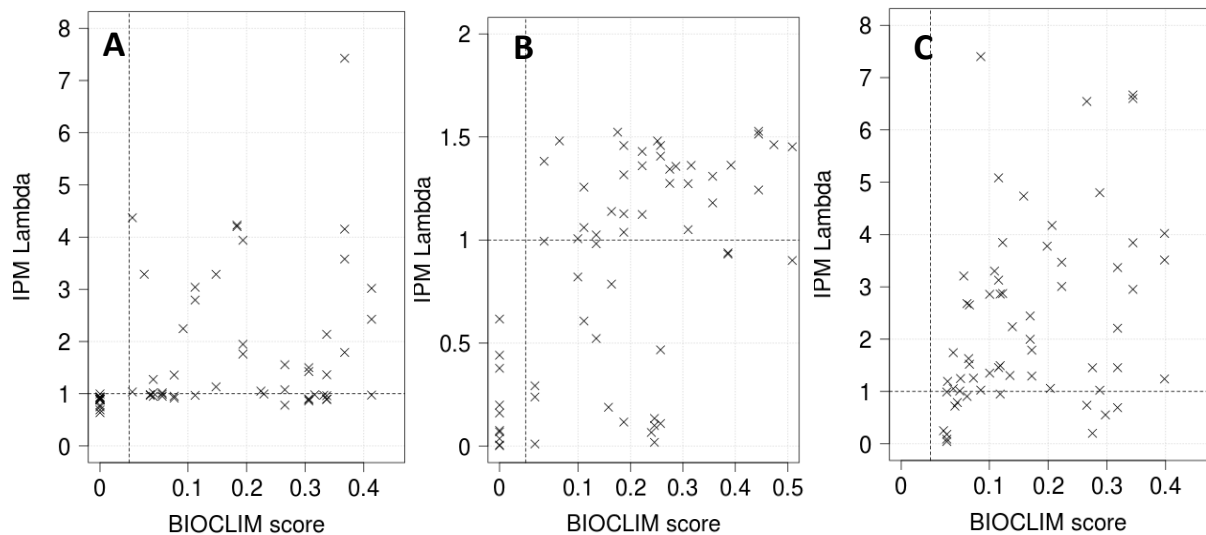


Figure 5.1 Graphical representation of confusion matrices validating BIOCLIM against IPM predictions. Points show BIOCLIM score vs. λ at each location where IPMs were run, for a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata*. Lines indicate where BIOCLIM > 0 (projected suitable by BIOCLIM) and $\lambda = 1$ (threshold for suitable/unsuitable in IPM). Because BIOCLIM scores all unsuitable sites as 0, lines are drawn at the lowest BIOCLIM score on Banks Peninsula.

5.4.4 Can BIOCLIM distinguish fundamental presences from absences?

In all three species, 100% of fundamental presences were correctly predicted by BIOCLIM, and areas projected as unsuitable by BIOCLIM are unlikely to sustain populations of the species. However, BIOCLIM clearly over-predicts both at the range limits (where BIOCLIM scores are low but > 0) and within the “core” climate (where BIOCLIM scores are high). Despite this over-prediction, AUCs were sufficient for the model to be classified as useful; 0.70 ± 0.13 for *A. arboreum*, 0.77 ± 0.12 for *A. haworthii* and 0.71 ± 0.20 for *C. orbiculata*. Therefore, while BIOCLIM ranked sites well in order of suitability, the threshold of 0 for defining unsuitability was too low. The ANOVA results (Table 5.4), confirmed that BIOCLIM scores at fundamental presence and absence locations were significantly different, with large F-ratios (especially in the case of *A. haworthii*). Bootstrapped distributions of mean BIOCLIM scores also revealed little overlap, indicating that true population means are likely to be significantly different (Figure D.8).

Table 5.4 Single factor ANOVA comparing BIOCLIM scores at fundamental presence and absence locations for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. Fundamental presences and absences distinguished by the threshold of $\lambda = 1$ for IPM predictions.

| Species | Factor | DF | SS | MS | F |
|----------------------|------------------|-----|------|------|-----------|
| <i>A. arboreum</i> | Binary λ | 1 | 0.13 | 0.13 | 7.71 ** |
| | Residuals | 78 | 1.33 | 0.02 | |
| <i>A. haworthii</i> | Binary λ | 1 | 0.29 | 0.29 | 16.18 *** |
| | Residuals | 81 | 1.46 | 0.02 | |
| <i>C. orbiculata</i> | Binary λ | 1 | 0.04 | 0.04 | 4.9 * |
| | Residuals | 133 | 1.19 | 0.01 | |

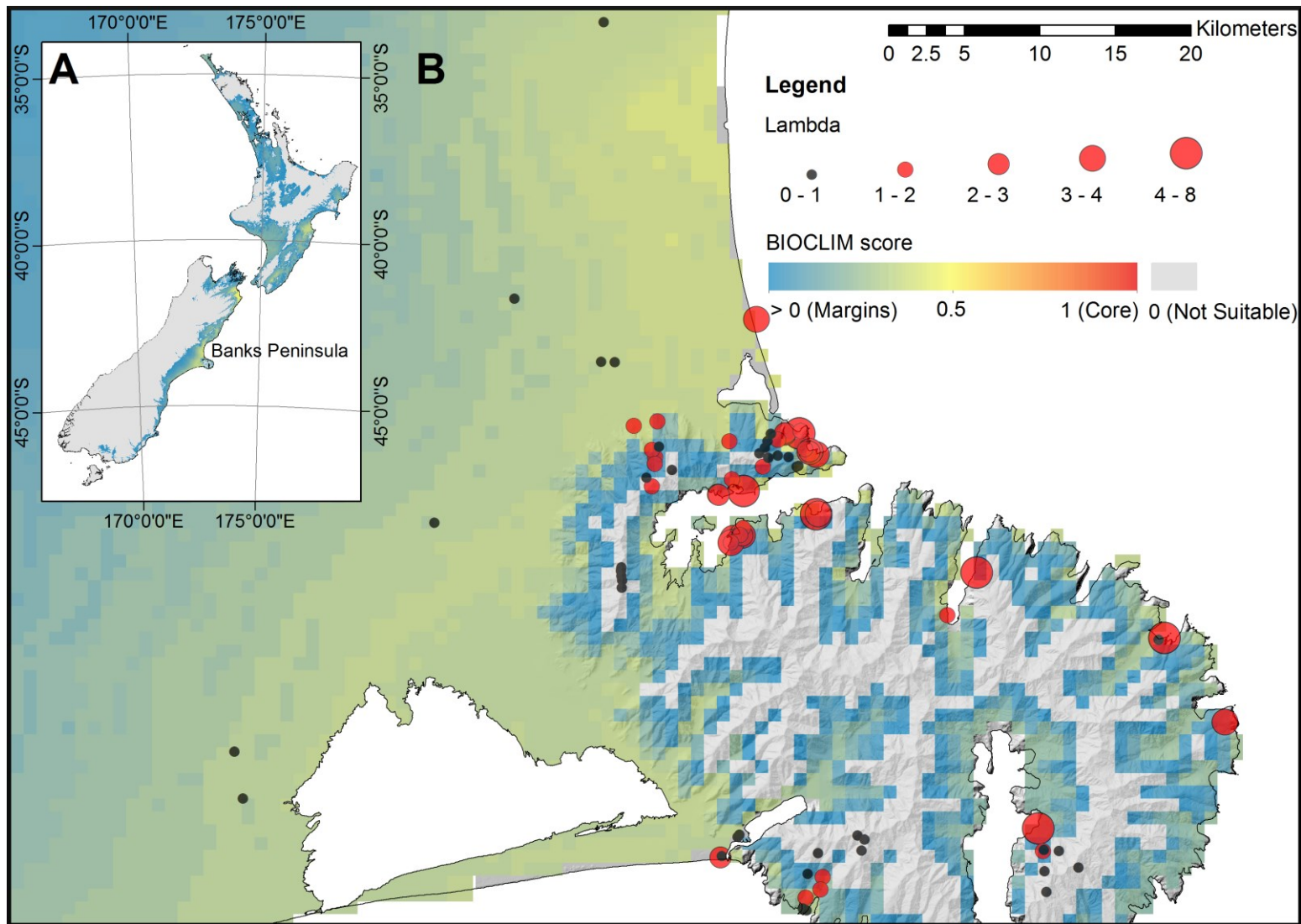


Figure 5.2a) New Zealand and b) Banks Peninsula BIOCLIM projections for *Aeonium arboreum*. Grey cells are projected as unsuitable by BIOCLIM. Predicted λ (IPM) for each species shown as graduated red points at each IPM location, black points represent $\lambda < 1$ (unsuitable). Shaded relief shown on Banks Peninsula.

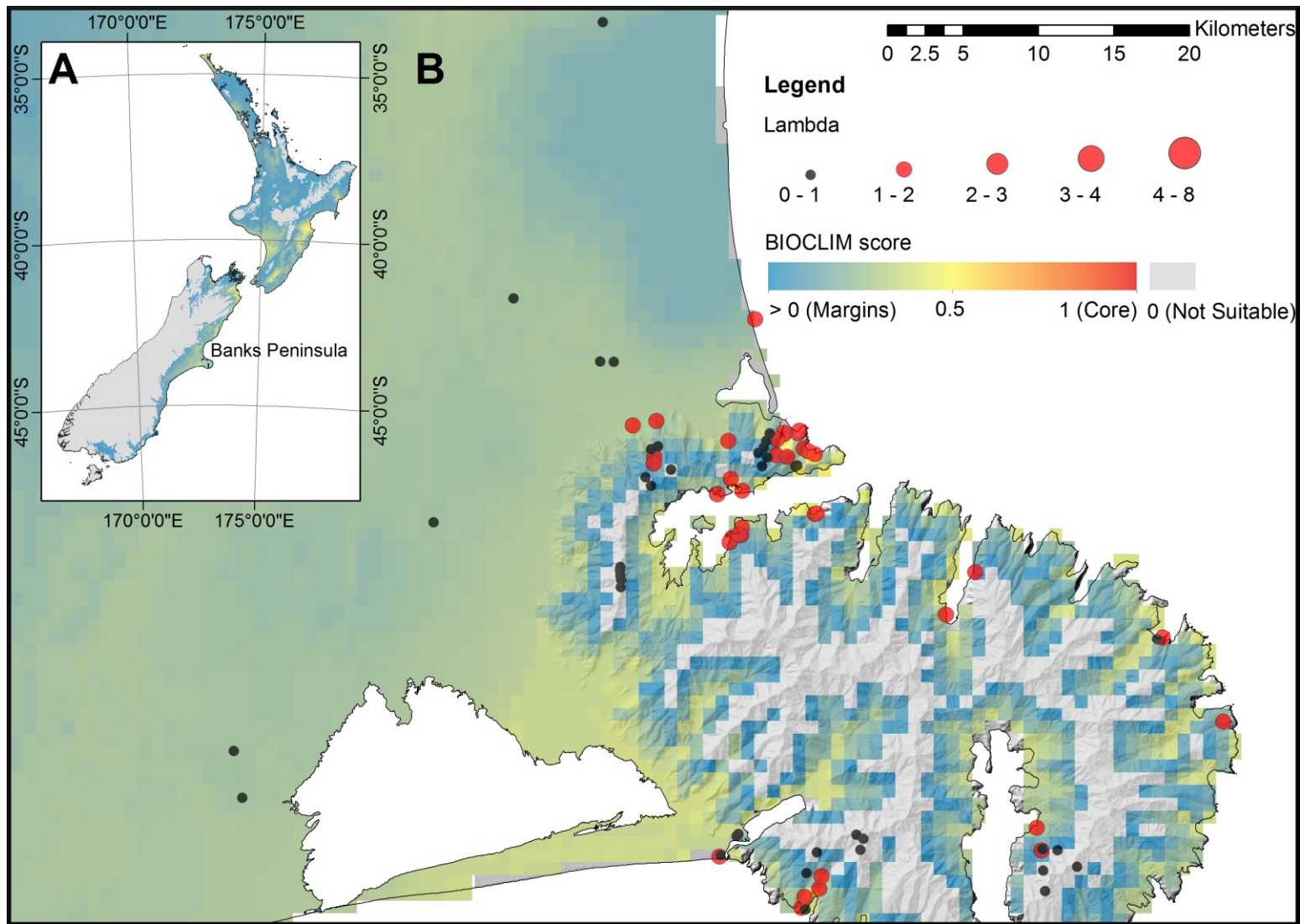


Figure 5.3a) New Zealand and **b)** Banks Peninsula BIOCLIM projections for *Aeonium haworthii*. Grey cells are projected as unsuitable by BIOCLIM. Predicted λ (IPM) for each species shown as graduated red points at each IPM location, black points represent $\lambda < 1$ (unsuitable). Shaded relief shown on Banks Peninsula.

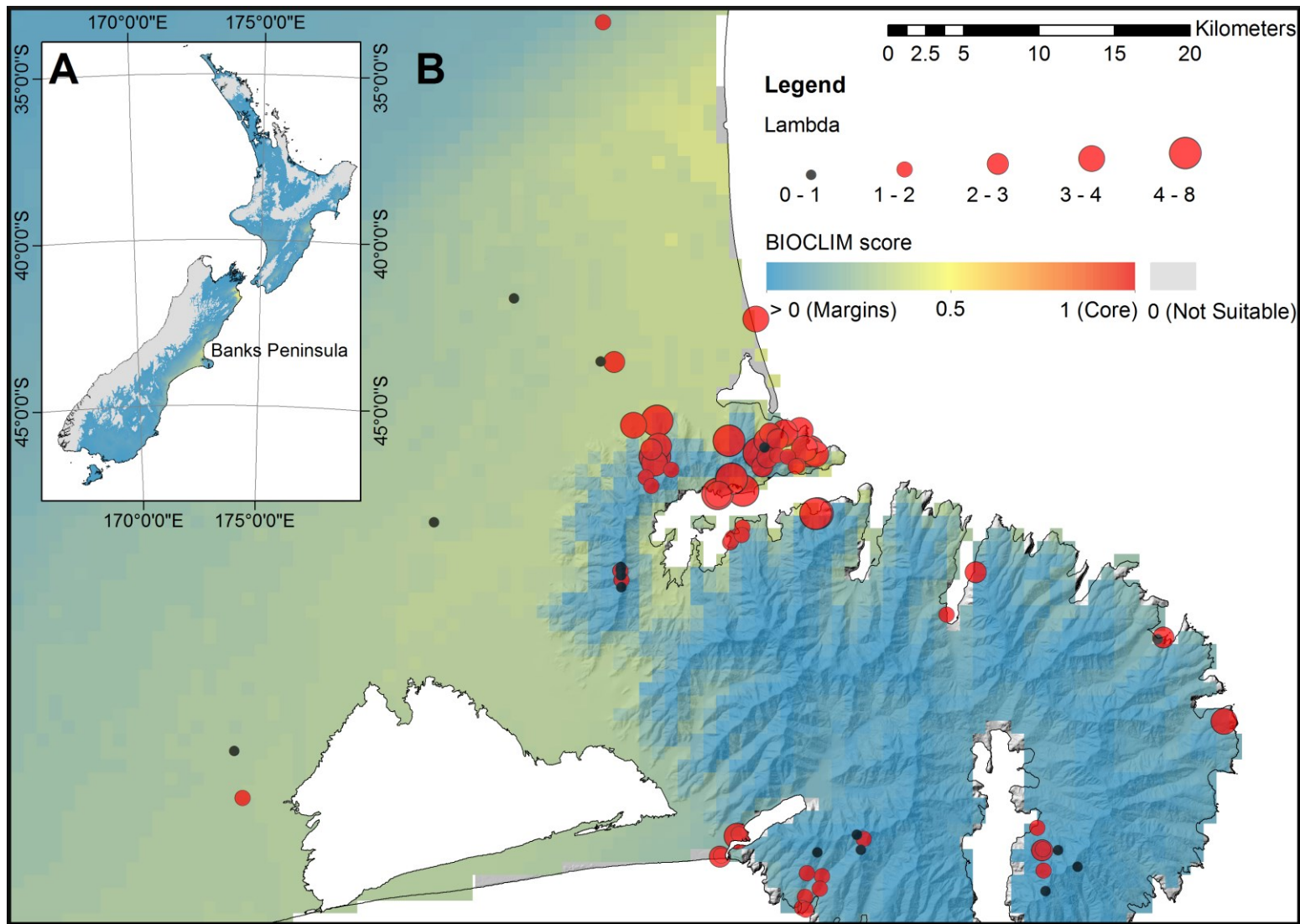


Figure 5.4a) New Zealand and b) Banks Peninsula BIOCLIM projections for *Cotyledon orbiculata*. Grey cells are projected as unsuitable by BIOCLIM. Predicted λ (IPM) for each species shown as graduated red points at each IPM location, black points represent $\lambda < 1$ (unsuitable). Shaded relief shown on Banks Peninsula.

5.4.5 Improving BIOCLIM projections for Banks Peninsula

Following the results of the previous analyses, I constrained BIOCLIM projections on Banks Peninsula by raising the threshold for unsuitability above the default of 0, to refine projections and remove as much over-prediction as possible. Confusion matrices were iteratively re-calculated (Figure D.9) by increasing thresholds as described in Section 5.3.9, maximising TSS while minimizing UPR. From this analysis the following new thresholds were chosen; 0.036 for *A. arboreum* and *A. haworthii*, and 0.046 for *C. orbiculata*. Projections for Banks Peninsula were then re-mapped as grid cells originally classified as unsuitable by BIOCLIM (assumed to be truly unsuitable), cells with BIOCLIM scores below the new thresholds (likely to be unsuitable), and those above the threshold (likely to be suitable, Figure 5.5). The new thresholds improved BIOCLIM performance for all three species by removing some over-prediction while retaining model sensitivity (Table 5.5). The updated projections are similar to the original BIOCLIM projections for both *Aeonium* species, removing only the highest elevation grid cells. However, suitable area for *A. arboreum* dropped by 22% after projection refinement, leading to the smallest predicted range of all three species. Fewest grid cells were removed for *A. haworthii*, resulting in the largest predicted suitable area of the three species (70% of Banks Peninsula). Refining projections was most effective in the case of *C. orbiculata*, excluding much of the wetter southern part of the Peninsula as “likely unsuitable”, whereas original BIOCLIM models were unable to exclude any grid cells as potential invasion sites. For *C. orbiculata*, final models indicate that climate is likely to be suitable in 63% of grid cells on the Peninsula.

Table 5.5 Sensitivity, specificity, under prediction rate (UPR) and over prediction rate (OPR), and projected suitable area (PSA, %), for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. All metrics calculated for Banks Peninsula only. Original models (unrefined BIOCLIM projections) validated against IPM predictions. The same metrics are shown for refined BIOCLIM projections, calculated against IPM predictions and true presences.

| Metric | <i>A. arboreum</i> | | | <i>A. haworthii</i> | | | <i>C. orbiculata</i> | | |
|-------------|--------------------|----------|---------|---------------------|----------|---------|----------------------|----------|---------|
| | Cross-Validated | Original | Refined | Cross-Validated | Original | Refined | Cross-Validated | Original | Refined |
| Sensitivity | 1 | 1 | 0.94 | 1 | 1 | 0.96 | 1 | 1 | 0.98 |
| Specificity | 0.26 | 0.41 | 0.47 | 0.22 | 0.33 | 0.47 | 0 | 0 | 0.54 |
| UPR | 0 | 0 | 0.17 | 0 | 0 | 0.13 | N/A | N/A | 0.30 |
| OPR | 0.95 | 0.28 | 0.27 | 0.95 | 0.27 | 0.24 | 0.89 | 0.10 | 0.05 |
| PSA | 73% | 73% | 51% | 77% | 77% | 70% | 100% | 100% | 63% |

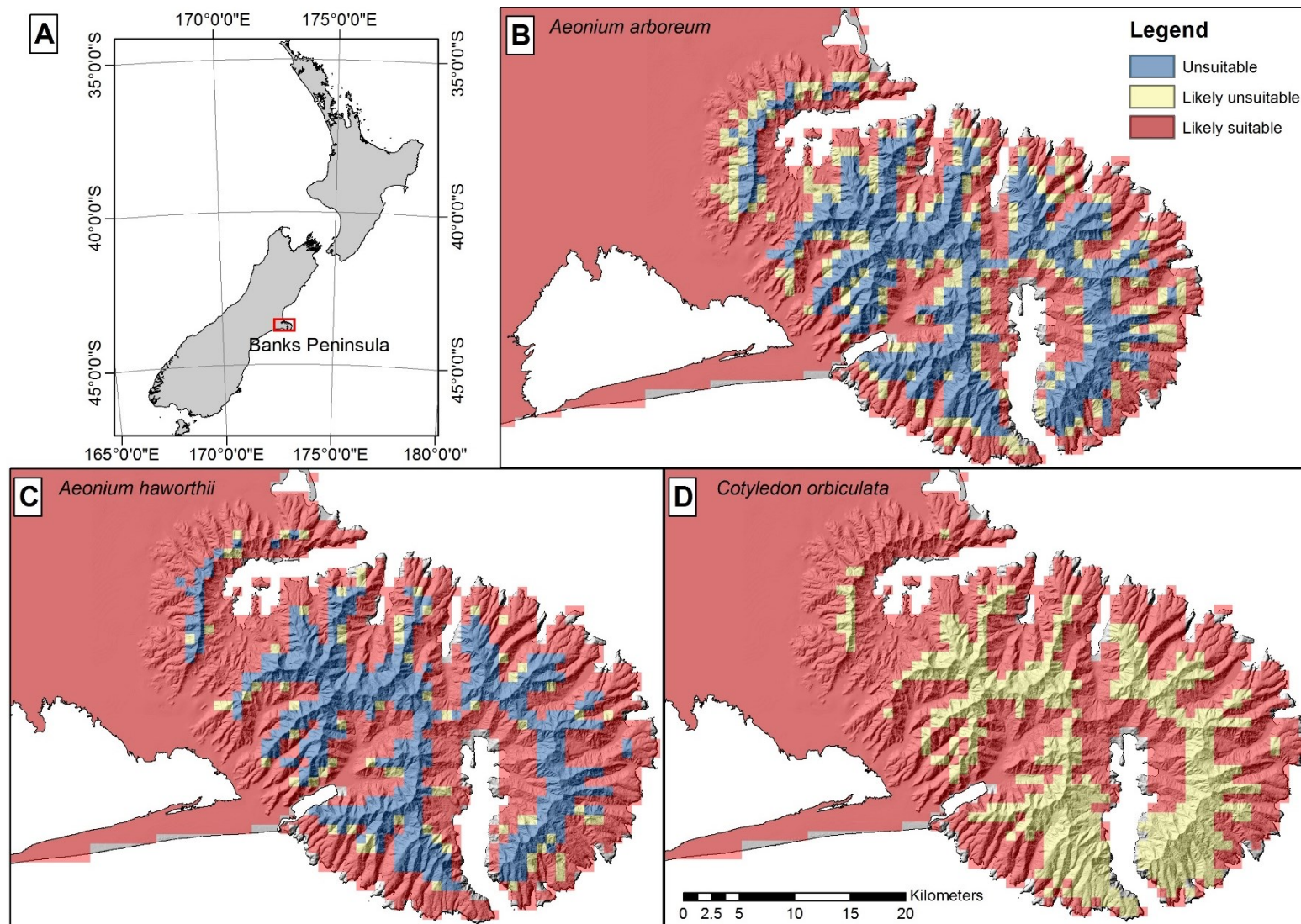


Figure 5.5 Refined BIOCLIM projections for b) *Aeonium arboreum*, c) *A. haworthii* and c) *Cotyledon orbiculata* on Banks Peninsula, with shaded relief, and extent indicator (a). Categories are: predicted unsuitable by BIOCLIM (blue, unsuitable), predicted suitable by BIOCLIM but below IPM-based threshold (yellow, likely unsuitable), and predicted suitable by BIOCLIM and above the IPM-based threshold (red, likely suitable).

5.5 Discussion

5.5.1 Accuracy of IPM and BIOCLIM projections

The IPM consistently predicted self-sustaining populations at the majority of true presence locations. At the few locations where predicted λ was less than 1, existing populations were small, cultivated or at lower elevations than the IPM point location. Because IPM performance was not assessed against true absences on Banks Peninsula, over-prediction of range limits by the IPM cannot be discounted. In fact, it is likely that running the IPM in the steady state, and as a closed system where all seeds have a chance to germinate, that λ values are optimistic. For these wind-dispersed species, seed rain may be lost from populations depending on elevation, barriers, shelter and wind direction (Okubo & Levin 1989). Further limitations are discussed in detail in Section 5.5.3. Despite potential over prediction, the regressions that underpin the IPM are derived from large-scale experiment and field data in the region of interest, and have a high degree of explanatory power (Section 3.4). The aim was not to predict actual rates of population growth in existing populations, but to provide meaningful delineation of climatic unsuitability assuming otherwise favourable conditions. The IPMs therefore appear sufficient to predict fundamental absences, with the caveat that they may still slightly over-predict range limits. It is worth noting that over-prediction is preferable to under-prediction in a pest risk context (Jiménez-Valverde *et al.* 2011). Predictions also align well with the known biology of the three species: they are thought to be frost sensitive (Vogan 2003), are likely to be close to their climatic limits on Banks Peninsula, and behaviour of the IPMs is consistent with the interpretation of the field experiment data (Section 3.4.4).

Validation of BIOCLIM against IPM predictions revealed unexpected behaviour in the SDM. It has previously been reported that BIOCLIM over-predicts suitable habitat (Elith *et al.* 2006; Hernandez *et al.* 2006; Wisz *et al.* 2008). Over-prediction occurs is because BIOCLIM fits a rectilinear envelope in climate space around all presence locations, with no interactions between climate variables, instead of building complex response curves to the variables (Booth *et al.* 2014). The simplicity of BIOCLIM was the reason it was used to model these species (Section 2.3.5), but some over-prediction was inevitable. On the other hand, BIOCLIM classifies as unsuitable any grid cell with one or more climate variable outside the bounding box of the envelope, whereas more complex models can extrapolate into novel climates. As a result, over-prediction within the “core” envelope, but under-prediction of range limits (*i.e.* the boundaries of the envelope) was expected, especially because there is evidence of a shift in the species’ realized niches in New Zealand (Section 2.4.1). Surprisingly, BIOCLIM over-predicted suitable climate both within the envelope (as demonstrated by the high projected suitability of the Canterbury Plains), as well as at range limits (IPMs predicted fundamental absences at lower elevations than BIOCLIM projected unsuitability). An important point is that BIOCLIM’s performance was better than indicated by the standard cross-validation using presence/absence data, because λ was positive at a number of locations where the species are not yet present. Most studies identifying poor performance of BIOCLIM have done so using occurrence data

(Hernandez *et al.* 2006; Wisz *et al.* 2008; Smith *et al.* 2013), which as demonstrated, may be misleading. Despite its over-prediction, BIOCLIM's projections were useful. Ranking sites by BIOCLIM scores aligned relatively well with λ , as demonstrated by the AUC scores (0.7 - 0.76) and Figure 5.1. Sensitivity was also perfect (100%) in all cases, and therefore where BIOCLIM projects unsuitability, there is good evidence that it can be trusted. The agreement between the two models also allowed BIOCLIM projections to be refined to more accurately reflect climatic range limits.

5.5.2 Why did BIOCLIM over-predict suitable climate?

Many studies have tested relative performance of SDMs (Elith *et al.* 2006; Hernandez *et al.* 2006; Aguirre-Gutiérrez *et al.* 2013), but it is difficult to infer the cause of poor model performance when they are evaluated against occurrence data. Non-climatic limitation and complex model algorithms may cloud sources of model error, and distinguishing whether the model is capturing real biological processes or is over-fitting is not straightforward. In this study, the use of fundamental absences combined with a simple SDM, tested within its training range, highlights issues that are likely to plague most correlative modelling efforts. These sources of model error can be broadly categorized into model algorithm, scale, input data and covariates.

The most obvious cause for the observed over-prediction is BIOCLIM itself. As described previously, the use of a rectilinear envelope and a simple algorithm (distance to the 50th percentile in climate space), results in a coarsely-defined niche. The model will include neighbouring areas of climate space in the envelope not represented by the species' distribution, as long as they are between the minima and maxima of climate variables. Additionally, the algorithm does not allow variable interactions. This emphasizes the need to carefully select an SDM according to the question at hand, and be aware of the limitations of each method (Kriticos *et al.* 2013). However, over-prediction was unexpectedly observed within the training range of the model and at the species' range limits (*i.e.* not in "corners" of the rectilinear envelope unrepresented by the species' distribution), so there must be additional sources of error aside from the BIOCLIM model.

A potential second source of error is differences in scale (grain size) between BIOCLIM and IPM projections, and that is not unique to this study. The SDM was fitted at 30 arc-seconds (WGS 1984, approximately 1 km²) while the IPM predicts population growth at just one point within the grid cell. Microhabitat conditions at the IPM point location might give inflated or deflated impressions of suitability relative to average conditions in the grid cell. It could therefore be argued that this study was not a fair test of BIOCLIM, but the problem of scale also applies to conventional tests of SDM performance, which use point occurrence data for verification (Sinclair *et al.* 2010). A possible solution could be to divide each grid cell into sub-samples and take the mean of all occurrences or, in this case, λ values across each cell, thus comparing average climate to average suitability, but this would require a quantity of data rarely available to modellers.

Tangential to the issue of scale is that of input data. Most SDMs are calibrated on large data sets of occurrence records collated from online databases (e.g. GBIF, <http://www.gbif.org/>), and there is a wealth of literature detailing the ensuing biases and effect on model performance (Loiselle *et al.* 2007; Wolmarans *et al.* 2010; Syfert *et al.* 2013). Consequences of sampling bias should be less severe for simple profiling techniques such as BIOCLIM, because as long as the outer envelope is accurate, the species' distribution within it will only bias the relative scores of suitable grid cells, not whether sites are classified as suitable or unsuitable. In addition to sampling bias, taxonomic uncertainties, misidentification, and geo-referencing error could cause over-prediction. Although every effort was taken to clean the data prior to model training (section 2.3.2), the study species are difficult to identify. All *Aeonium* species hybridize readily and have high phenotypic plasticity (Lems 1960). *Cotyledon orbiculata* has a disputed taxonomy, where some consider that regional varieties should be classed unique species due to different habitat requirements (Van Jaarsveld & Koutnik 2004). Furthermore, most SDMs weight all occurrences equally, so single outlier points (e.g. plants under indoor cultivation or irrigation) can disproportionately influence projections (Kriticos *et al.* 2014). While I removed cultivated plants from the BIOCLIM training data, it is possible that some occurrences persisted in sink populations, or in microclimates within otherwise unsuitable grid cells. If so, BIOCLIM would over-predict range limits (Warren 2012), as the SDM was tested against whether grid cells could support self-sustaining, rather than sink, populations. These issues could be mitigated by weighting input data by abundance, and while some studies have incorporated abundance data into SDMs (de Villiers *et al.* 2013) that option is yet to be adopted widely.

A final source of uncertainty arises from climatic variables used in the SDMs. It is known that climatic predictors should be chosen to reduce autocorrelation and according to the requirements of the species (Elith 2013). I parameterised BIOCLIM using only five climatic variables, to minimize over-fitting. While additional variables might have reduced some over-prediction, the risk of underestimating range limits due to spurious correlations was deemed too high. A less obvious pitfall of climatic variables is whether they accurately reflect real climatic conditions in an area. Most SDM efforts base projected distributions on global interpolated data such as the freely-available Worldclim variables [(Hijmans *et al.* 2005), available at <http://www.worldclim.org/>]. The Worldclim dataset projects temperature and rainfall variables at up to 30 arc-second resolution interpolated from weather station point data, and is averaged over a 30 or 50 - year period depending on the location. Where coverage is low, the accuracy of the interpolated values is questionable (Soria-Auza *et al.* 2010) and areas such as Banks Peninsula with high climate variation over small areas (as a result of topography) may be poorly approximated by gridded climate data (Kriticos & Leriche 2010). In this study, BIOCLIM projections trained on long-term, average climate data (Worldclim) were tested against IPM predictions derived from 2-year averages at point locations. The IPM is immediately advantaged by using recorded data rather than interpolations, and more biologically meaningful variables (e.g. growing degree days, frost days). For example, no SDM of *A. arboreum* based on Worldclim data would differentiate the unsuitable Canterbury Plains from the suitable coastline of Banks Peninsula, because a key limiting variable

(frost days) is poorly represented by Worldclim's "Annual minimum temperature". For comparison, recorded annual frost days were 63 at Christchurch Airport and 0 at Hays Bay (equivalent elevations, but the former is unsuitable and the latter highly suitable), yet Worldclim estimates their mean minimum temperatures to be 1.7 °C and 1.3 °C respectively. Whether testing the SDM against a model driven by more accurate climate data is fair, depends on the question being asked. If that question is to evaluate how intrinsically good BIOCLIM is as a model, it would need to be compared with an IPM driven by the same Worldclim variables. But, this study was concerned with how BIOCLIM projections compare with reality, so the IPM should mirror field observations as closely as possible.

It was beyond the scope of this study to determine the relative impact of the potential sources of over-prediction, but the results demonstrate that validation against fundamental absences can give some insight into model reliability. While some over-prediction stems from the BIOCLIM algorithm, there are likely to be other sources of error common to all SDM studies, and comparing fundamental absence data against a selection of SDMs could disentangle the relative importance of scale, covariates, algorithm and training data. Regardless of the cause of the observed over-prediction, BIOCLIM nonetheless appeared to rank sites adequately by suitability. To refine projections, I demonstrated a simple method to remove a proportion of model over-prediction by altering the threshold for suitability, which is a novel approach to combining process-driven models with SDMs. By raising the threshold to better discriminate fundamental absences from both fundamental and true presences, I was able to reduce the predicted suitable area by between 7% and 37%, depending on the species, with minimal risk of under-predicting species' ranges. While this is an improvement on the original models, differences in specificity were minor because only range margins were adjusted and over-prediction within the core climate envelope remained. However, for *C. orbiculata* in particular, the refined projections may be useful for prioritizing areas for control. The implications for the future spread of the three species on Banks Peninsula are discussed in Chapter 6, within the context of the findings of previous chapters.

5.5.3 Limitations

Though the refined maps are an improvement on the original BIOCLIM projections, they are still a liberal estimate of range limits because only the outer extremes of the climate envelope were trimmed. Substantial over-prediction of suitable climate (e.g. the Canterbury Plains) remains. Furthermore, the IPM does not predict actual population growth rates, principally because at many locations there are currently no populations to model and seed rain is unknown. Lambda was modelled in the steady state over a 2-year period, using a closed system (*i.e.* no immigration or emigration) and the IPM assumed that all viable seeds had an opportunity to germinate. The IPMs used in this chapter were fully deterministic, and therefore may over-predict suitable conditions at range margins where populations may be vulnerable to environmental stochasticity (Parmesan *et al.* 2000; Hargreaves *et al.* 2014). While there is room for improvement in the IPMs, they provide a close approximation to actual climatic suitability for the study species, as they essentially combine multiple observations from high

powered field surveys into a single measure of suitability. As demonstrated, the IPMs provide a better measure of model performance than occurrence data alone, and allow more confident assertion of the species' climatic limits.

It is important to emphasize that the final projections represent climatic suitability only. Especially for succulent geophytes, many other environmental factors will determine whether a site is invaded including soils, rock type and land use. Very little is known about the dispersal capabilities of these species other than they produce microscopic ($\sim 500 \mu\text{m}$ length) wind-dispersed seeds. I have therefore assumed no barriers to dispersal. However, wind patterns may play a part in the direction and speed of invasion for these species. The question of non-climatic suitability could be addressed by applying the land use and habitat masks developed in Chapter 2, but at the scale of Banks Peninsula it would be beneficial to have prior knowledge of whether certain rock or soil types are suitable. Finally, the thresholding technique used here is somewhat experimental, and removes only those areas that are at the outer edges of the climatic envelope. Estimates could be improved substantially by using finer scale and more appropriate climate data informed by the field experiments, and using the IPM results as presence/absence data to feed an invaded range SDM for Banks Peninsula [a similar methodology to Elith *et al.* (2010)]. The methodology presented here is discussed further in Chapter 6, along with potential future work.

5.5.4 Conclusions

This study has demonstrated a novel method of integrating plant performance data with SDMs. Field data describing vital rates were used to parameterize a climate-driven IPM and predict population growth (λ) at 83 locations in the study region. The population parameters (λ) were then converted to fundamental presence/absence data, reflecting whether climatic conditions are conducive to self-sustaining populations. Fundamental presences/absences were used to validate and refine existing BIOCLIM projections, and this method could be applied to other SDMs to improve confidence in projections. I demonstrated that BIOCLIM was a better predictor of plant performance than would be indicated by conventional cross-validation techniques (using occurrence data) alone. However, I found that BIOCLIM over-estimated suitable climate not just within the core “envelope” but also, unexpectedly at range limits. Likely causes of over-prediction include coarse representation of the niche by BIOCLIM, differences in grain size of validation tools versus projections, and quality of climate and occurrence data in training the SDM. The latter three issues are likely to affect most correlative SDM efforts. The BIOCLIM projections were nonetheless useful as they ranked sites well, and I refined projections by iteratively raising the threshold to best fit IPM predictions. Thus, the over-prediction at range edges was minimized and projections of the species' potential distributions were improved. Where possible, I encourage the use of fundamental presence/absence data in addition to presence data, and in place of pseudo- or true absence data, for testing and improving SDMs of non-equilibrium species.

Chapter 6 - General discussion

6.1 Summary of findings

The aims of this thesis were to test the ability of correlative SDMs to predict real-world plant performance, and to integrate data from SDMs with survey and experimental data on actual plant performance to improve model projections. I applied this approach to three non-native succulent species naturalized in New Zealand; *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. My key questions were:

1. Are the current distributions of *A. arboreum*, *A. haworthii* and *C. orbiculata* in New Zealand climatically distinct from their distributions elsewhere, and what are their potential distributions as estimated using SDMs?
2. Is there evidence that climate limits the distributions of these species on Banks Peninsula, and how do demographic processes correlate with climate within and beyond the species' current distributions?
3. Is variation in fecundity in naturalized populations on Banks Peninsula related to variation in local climate?
4. How well do SDMs predict the actual performance of the target species on Banks Peninsula, and can field data be used to improve SDM projections?

I used simple correlative SDMs to project suitable climate for the three species globally, and in New Zealand (Chapter 2). The importance of non-climatic effects on the species' distributions was inferred via a combination of *a priori* reasoning and spatial analysis, and consequently climate-only models were refined by topography and land use. Results also indicated that the species' current distributions in New Zealand constituted a shift in their realized climatic niches. For the remainder of the thesis I focussed on climatic drivers within Banks Peninsula, Canterbury. A field transplant experiment (Chapter 3) provided evidence of strong climatic limitation to survival, germination and growth in all three species with increasing elevation. The responses of *Aeonium* species were similar and germination, growth and survival declined sharply above 300 - 400 MASL. Meanwhile, *C. orbiculata* was inconsistently limited by elevation and climatic covariates, and was mortality was predicted to be relatively low (< 75%) up to 300 m above current limits (681 MASL). Because growth and mortality were intrinsically linked, it was difficult to infer likely elevation limits for *C. orbiculata*. In contrast, surveys of naturalized populations (Chapter 4) uncovered scant evidence of climatic limitation to fecundity across the species' current distributions. Plant size was the most consistent predictor of fecundity, and it was unclear whether this was an indirect effect of climate. I integrated field data by incorporating the linear regressions of mortality, growth and fecundity against climate into an integral

projection model (IPM). Predicted lambda values from the IPM were converted into fundamental presence/absence data (*i.e.* whether self-sustaining populations were predicted), and used to validate the previous climate-only SDMs. The SDMs over-estimated climatic suitability, and so the suitability threshold was lowered to be as parsimonious as possible with predicted lambda. This reduced over-prediction of outer climatic limits in the region, and provided more realistic projections for Banks Peninsula. However, a significant amount of over-prediction remained within the suitable “envelope”. Potential causes of the over-prediction were discussed, most of which are likely to be relevant to all correlative SDM attempts. Because my final data chapter achieved many of the aims of a thesis “synthesis” chapter by drawing together the previous findings, I instead focus my discussion on the study species on Banks Peninsula, only briefly discussing the broader aspects of the modelling work.

6.2 Species distribution models vs. reality

6.2.1 How well did SDMs predict plant performance?

I was limited in my choice of SDM by the study species’ traits and the characteristics of the distribution data. Because of the disjunct distributions of the three species, I chose one of the oldest SDM algorithms, BIOCLIM (Nix 1986), a simple envelope or “boxcar” technique. This method avoided under-predicting suitable habitat at the expense of a high likelihood of over-prediction. Although cross-validation techniques used in Chapter 2 indicated that the SDM performed well, the IPM revealed substantial model over-prediction on Banks Peninsula. However, BIOCLIM was able to rank sites well enough in accordance with lambda to achieve a satisfactory AUC (> 0.7). It therefore provided a useful, but over-generous estimation of suitable climate and I demonstrated a simple method of eliminating as much of this over-projection as possible.

The relatively poor performance of BIOCLIM raises the question of whether it was, in fact, the best method for modelling the three species. I considered BIOCLIM the best option for a global model of the three species’ distributions, as the disjunct distributions would cause more complex models *e.g.* MaxEnt (Phillips *et al.* 2006), to under-predict potential ranges. Since then, another presence-only method, range-bagging (Drake 2015) has been developed, which might have been superior. Training the SDMs and niche analyses on global data demonstrated that the species’ New Zealand distributions are climatically distinct from their distributions elsewhere, and that the extent of their naturalization in New Zealand could not have been predicted prior to their introduction. However, the native ranges for all three species told us little about their potential distributions in New Zealand, and in the case of *C. orbiculata*, led to over-prediction of suitable climate because of the inclusion of frost-tolerant high elevation populations. In retrospect, a model trained on New Zealand data only [an invasive species distribution model, or iSDM; (Václavík & Meentemeyer 2009)] could have been informative as a follow-up to the global model. Removing the native ranges from training data would not sacrifice useful information, as the climatic conditions are so distinct, and would eliminate the problem of

disjunct distributions. An iSDM would allow the use of more complex algorithms that are less likely to over-estimate potential distributions (*e.g.* boosted regression trees, MaxEnt).

As discussed in Chapter 5, it was not possible to determine how much over-prediction stemmed from BIOCLIM itself, versus other sources of error common to all SDM studies. To recap, other potential sources of error are quality of occurrence data, accuracy of climate layers, and scale. Occurrence data may bias models where there are errors in species identification or confusion over taxonomy (Elith *et al.* 2013), sampling bias [though methods exist for minimizing bias *e.g.* Dorazio (2014)], or where species are persisting in otherwise unsuitable locations [for example plants in cultivation, or sink populations (Warren 2012)]. Climate layers do not always reflect true site conditions, as they are interpolated from weather station data and are often inaccurate where stations are rare (Niekerk & Joubert 2011). Scale introduces error when occurrence locations, which are usually point data, are not representative of the average conditions in the grid cell. Examples of this are populations persisting in microclimates, or where there is high climatic variation within the grid cell [*e.g.* Kriticos *et al.* (2014)]. Without further investigation, this discussion remains speculative, as it is not possible to attribute the proportion of error to each source. I encourage the consideration of the aforementioned sources of error in all modelling efforts, whether using complex or simple algorithms.

6.2.2 Improving SDM accuracy

This thesis has highlighted the importance of selecting an SDM algorithm based on species' traits and occurrence data, as well as performing prior niche analyses to identify disjunct or non-analog distributions. I have demonstrated an effective method of testing SDM projections against plant performance data, and argue for using fundamental absences in place of pseudo or true absences when modelling non-equilibrium species, if possible. However, drawing general conclusions on the accuracy of SDMs, and relative importance of sources of error, is difficult from this case study alone. More generality could be achieved by repeating the methods described in Chapter 5 for a selection of species, varying the quality of occurrence data, climate layers, grain size and SDM algorithm to identify the relative impact of each source of error on SDM performance. Although other studies have compared performance of different models and other error sources (Aguirre-Gutiérrez *et al.* 2013; Syfert *et al.* 2013; Qiao *et al.* 2015; Stoklosa *et al.* 2015), none have used fundamental absences, thus it is difficult to determine to what extent reportedly good models are simply overfitting the data.

Using fundamental presences and absences to validate SDMs is appealing, but may be difficult to implement widely. To parameterize the population model, predicted vital rates are required as a function of climate (or other variables included in the SDM being tested, such as soil), and this is data-intensive. The cost of gathering the necessary data may be prohibitive, and is at odds with the primary appeal of SDMs, namely, that they are fast and cheap. If a species is well studied, however, it could be possible to gather sufficient information from existing literature to parameterize a simple population model. In this case, more thorough validation of the population model would be required if it was

parameterized using data from other regions, but it could be a viable alternative to extensive field trials. Alternatively, other studies have used performance data for one or two vital rates alone to validate models, rather than predicting population growth (Pattison & Mack 2008; Sheppard *et al.* 2014). Although more cost-effective than developing full population models, performance data is reliable only if the limiting vital rate is known (*e.g.* germination), and it is difficult to determine where vital rates become limiting without an intuitive suitable/unsuitable binary classification, such as that provided by lambda. Furthermore, *a priori* assumptions of limiting processes may not always be correct. For example, based on existing literature I incorrectly expected annual internodes to be a good indicator of performance in *Aeonium* species.

In lieu of field experiments, surveys of wild populations could provide the necessary data if accidental release of the organism is too risky (*e.g.* the species is a restricted organism), but only under certain conditions. This is not valid for species that are far from equilibrium, such as the early stages of invasions (Thuiller *et al.* 2006; Wilson *et al.* 2007), and sampling marginal populations is desirable for robust extrapolation (Hargreaves *et al.* 2014). Identifying marginal populations prior to sampling is, admittedly, difficult. As a final alternative, laboratory-based studies are cheaper and more efficient than field studies, and could provide the necessary parameters for a climate-driven IPM or similar. This would be most practical for fast-growing annual species. But, responses observed in the laboratory may translate poorly to the field. In this scenario, it might be more useful to collect physiological data to parameterise a mechanistic model, though mechanistic models are not always superior to their simpler correlative counterparts due to compounding of error (Buckley *et al.* 2010).

6.3 The future of non-native Crassulaceae on Banks Peninsula

6.3.1 Climatic limitation

The second of the two central themes of this thesis was to define the climatic limits of *A. arboreum*, *A. haworthii* and *C. orbiculata* on Banks Peninsula. The field experiment established clear evidence of climatic limitation in the region. Regional spread cannot continue indefinitely, as all three species were limited to varying degrees by the elevation and precipitation gradient. High precipitation limited seedling establishment in *C. orbiculata* (and *A. arboreum* to a lesser extent), and is likely to mitigate spread of these species the wetter southeast parts of the region. High elevations were limiting to growth and survival for all three species, and for *Aeonium* species to seedling establishment also. The results of combining the field data into IPMs were consistent with previous findings in this thesis.

Overall, *Aeonium* species had clear climatic limits and the IPMs predicted negative population growth at most high-elevation or high-frost sites. Of the sites that the IPMs predicted to be suitable for *A. arboreum*, 38% are currently unoccupied, versus 31% for *A. haworthii*, indicating that further spread of both species is likely. Once the IPMs were used to refine the BIOCLIM projections, both *Aeonium* species had similar predicted range limits, and most high elevation or inland areas of Banks

Peninsula were excluded as potential invasion sites. The similarity of the two *Aeonium* species' potential distributions might appear surprising due to their different origins (Canary Islands vs. Morocco), but the *Aeonium* genus, while diverse, has low genetic diversity (Mes & T'Hart 1996). As a result, much of the genus' morphological variety may be due to phenotypic plasticity and flexible niche occupation (Jorgensen 2002). According to the refined projections of suitable climate, the main difference between the two species is that *A. haworthii* could persist at slightly higher elevations than *A. arboreum*, accounting for the difference in projected suitable area (51% of Banks Peninsula for *A. arboreum*, versus 70% for *A. haworthii*). This is consistent with their niches in the native range, where *A. arboreum* is found at lower elevations and is thought to be less adaptable to climatic extremes (Lems 1960). The final adjusted BIOCLIM projections indicated that, of the 871 30 arc-second grid cells surveyed (Figure C.1), only 5% of those predicted to be suitable currently contain *A. arboreum*, and 6% for *A. haworthii*.

The IPMs and BIOCLIM both predicted suitable climate at higher elevations for *Cotyledon orbiculata* than the *Aeonium* species, but climatic limits of this species were less clear-cut. Only 16 out of 83 IPM sites were predicted to be unsuitable, in contrast with 41 for both *Aeonium* species. Unsuitable sites for *C. orbiculata* were mainly those with highest elevation and precipitation. Out of the sites predicted to be suitable, 48% are currently unoccupied, indicating a greater potential for spread than either *Aeonium* species. Because the original BIOCLIM model classified the entire Peninsula as climatically suitable, the refined projections were less certain for *C. orbiculata*, but they eliminated the wettest and highest elevation sites in the region. The thresholding for *C. orbiculata* removed a much greater proportion of suitable grid cells for either *Aeonium* species, resulting in a similar projection to *A. haworthii*. Thus, the BIOCLIM projections for *C. orbiculata* were over-predicting to the greatest degree. The final projections indicated that approximately 63% of Banks Peninsula is likely to be climatically suitable, and of the grid cells surveyed, only 19% of those predicted to be suitable currently contain *C. orbiculata*.

6.3.2 Non-climatic limitation, implications for spread

Climatic limits are just one piece of the invasion puzzle, and the fact that *A. haworthii* has the greatest proportion of climatically suitable area does not necessarily mean it poses the greatest risk. Non-climatic effects will shape the distribution of each species, and these are discussed in Chapter 2.5 in relation to their global and New Zealand distributions, and Chapter 3.5 in relation to the elevation gradient on Banks Peninsula. Currently, much of how the species respond to non-climatic factors is unknown, but it is possible to draw the following conclusions. *Aeonium* species are likely to be restricted to similar habitats to each other and to where they currently occur. I expect spread within climatically suitable areas to be limited to cliffs, roadsides, and other bare or sparsely vegetated surfaces. Because the genus has no grazing defences it should remain absent in pasture (Jorgensen & Olesen 2001), and because of the low photosynthetic capacity of CAM, where interspecific competition is high (Luttge 2004). Climate will define the broad limits of the two species on the

Peninsula, preventing establishment inland or at high elevations, which is encouraging as the high elevation rock outcrops are refugia for a number of local and national endemic species (Wiser & Buxton 2009). Spread appears likely to continue around the coastline of the Peninsula, the volcanic cliffs of which are recognized as naturally uncommon ecosystems (Holdaway *et al.* 2012). The spread of *Aeonium* species should be slow in comparison to *C. orbiculata* as habitat is more limiting, thus lowering the probability of seed landing in suitable environments. Assuming only climate and habitat are limiting to both *Aeonium* species, and that other non-climatic effects are not relevant (*e.g.* substrate, anthropogenic effects), they should eventually form a patchy distribution around the coastline and up to around 400 MASL once they reach equilibrium.

On Banks Peninsula, *C. orbiculata* appears to be more limited by climate than by other factors. I expect spread to continue along the coastline and inland up to approximately 400 MASL in the northern bays, but as *C. orbiculata* is also limited by precipitation it is unlikely to spread far from the coast in the Southeast. It is found on a wide variety of substrates (Van Jaarsveld & Koutnik 2004), and in habitats that are common in the region (*i.e.* pasture, cliffs, outcrops and roadsides). *Cotyledon orbiculata* is likely to be absent under canopy because of the correlation between solar radiation and fecundity (Chapter 4) and the negative effect of canopy cover on growth (Chapter 3). Some small populations of *C. orbiculata* occur under pine on the Peninsula (*e.g.* survey site Pigeon Bay 2), but the plants have a distinct growth form with minimal branching and large leaves lacking epicuticular wax, consistent with the findings of Barker *et al.* (1997). I observed no flowering in these populations. I expect *C. orbiculata* to remain absent from the approximate 12% of the region covered by native forest, as it has a denser canopy than pine. As with *Aeonium* species, there are additional factors (*e.g.* soil type) that could be limiting to *C. orbiculata*. Based on the evidence collected in this thesis however, I expect *C. orbiculata* to eventually reach a less patchy, more widespread distribution than *Aeonium* species. Spread of *C. orbiculata* is likely to be more rapid as the probability of dispersing to suitable areas is higher, and vegetative spread by trampling in pasture may accelerate the process.

I therefore encourage the control of *C. orbiculata* on Banks Peninsula, both for economic and ecological reasons. The species poses a threat to the region's cliffs and outcrops, and associated rare species, but also could cause stock losses in the event of poisonings. All three species are probably too well established in the region to make eradication feasible, but further spread around the eastern bays could be contained. The southwestern bays are a particular cause for concern, as while the three species are currently absent, models indicate high climatic suitability and nearby populations of Birdling's Flat could provide a substantial seed source, especially for *C. orbiculata*. If possible, the three species should be removed from Birdling's Flat entirely. Raising awareness of *C. orbiculata*'s toxicity to livestock might encourage voluntary removal of the species by landowners.

6.4 Avenues for future research

6.4.1 Study species – some important unknowns

The climatic limits of *A. arboreum*, *A. haworthii* and *C. orbiculata* on Banks Peninsula have been established, but some unanswered questions remain that are relevant to their potential distributions. Quantifying seed bank longevity, seed dispersal, individual life span, and fecundity beyond current range limits for the three species would allow for temporally explicit projections of spread. More interestingly, the strength of biotic interactions and their effects on population dynamics remain unknown. While insect pollination occurs in all three species, *Aeonium* species are also pollinated abiotically, and all are also capable of autogamy (Alamo *et al.* 1996; Zietsman 1998). There are anecdotal tales of *C. orbiculata* being pollinated by New Zealand birds (Di Carter, *pers. comm.* 2010), which is plausible given that sunbirds are pollinators in its native range. If autogamy lowers seed output and progeny fitness in *Aeonium* species as it does in *C. orbiculata* (Zietsman 1998), pollinator interactions could strongly influence rates of spread for all three species.

Similarly, natural enemies and the effect of competition on the three species are unknown, though I hypothesized that interspecific competition is an important factor in habitat selection, given the low photosynthetic capacity of CAM plants. In the Canary Islands, *Aeonium* species are found only in specific habitats and regions, and Lems (1960) posits interspecific competition and adaptive radiation as underlying mechanisms. As a consequence of interspecific competition, I expect land use to be an important factor for all three species, and hypothesize that grazing facilitates *C. orbiculata* invasion by reducing competition and increasing vegetative spread. This hypothesis could be explicitly tested by grazing exclusion field trials [e.g. similar to studies of other succulents by Moolman and Cowling (1994) and Dean *et al.* (2015)] and would establish whether *C. orbiculata* can persist amongst vegetation without herbivores.

All three species have unanswered questions related to their taxonomy that merit further investigation. One of these is the effect of hybridization in *Aeonium* species, which hybridize readily (Jorgensen & Olesen 2001). Supposedly, natural hybrids are rare in the native ranges (Lems 1960) but on Banks Peninsula, they are common to the point that identification to species level can be difficult (Bill Sykes, *pers. comm.*, 2010). Natural hybrids might affect the genetic diversity of *Aeonium* populations and their climatic tolerances, thereby shaping range limits, as such studying the genetics of natural populations and testing climatic limitation in hybrids could be beneficial. Meanwhile, the taxonomy of *C. orbiculata* is highly contested (Van Jaarsveld & Koutnik 2004), with debates over classifying the five varietals as distinct species that are unlikely to be resolved soon (Ernst Van Jaarsveld, *pers. comm.*, 2014). In this thesis, I offered a hypothesis that the less-hardy regional populations of South African *C. orbiculata* such as those in coastal areas (Van Coller & Stock 1994) may be ancestral to those in New Zealand. Genetic or historical studies in New Zealand and South Africa could pinpoint the South African origins of New Zealand introductions. Such studies could improve projections of the

species' potential distributions by establishing whether the extremely frost-tolerant genotypes of *C. orbiculata* are present in New Zealand. Finally, and perhaps most interestingly, the apparent climatic niche shift in all three species in New Zealand relative to their global ranges merits further investigation. While New Zealand is undoubtedly novel climate for all three species, it is not feasible to distinguish realized from fundamental niche shifts from correlative approaches alone (Guisan *et al.* 2014). There are numerous reports of niche shifts during invasions (Broennimann *et al.* 2007; Mata *et al.* 2009; Gallagher *et al.* 2010), but the underlying mechanisms have rarely been investigated empirically (Petitpierre *et al.* 2012). Alien Crassulaceae in New Zealand could provide an ideal case study due to the dramatic climatic differences between ranges. Fully reciprocal transplant experiments between New Zealand and the native ranges would evidence whether the phenomenon can be considered a fundamental niche shift or not, while phylogenetic analyses could investigate underlying mechanisms, *e.g.* whether the shifts arise from evolutionary changes or are in fact a result of underlying phenotypic plasticity or exaptation. These species present an opportunity to improve our understanding of niche shifts and their mechanisms.

6.4.2 Limitations, and lessons learned

The majority of limitations have been discussed in corresponding chapters, but it is important to emphasize that the final refined projections for Banks Peninsula still over-predict suitable climate (over-prediction rate was 27%, 24% and 5% for *A. arboreum*, *A. haworthii* and *C. orbiculata*, respectively). Final projections also do not account for habitat suitability, thus they are valuable starting points but not predictions of spread. As discussed earlier, fine-scale iSDMs trained on the fundamental presence and absence points could improve projections for Banks Peninsula significantly. In addition, there is room for improvement in the IPMs. Some parameters were omitted (*e.g.* seed bank), population growth was predicted only in the steady state, and fecundity parameters were extrapolated from surveys. The IPMs could also be improved by running multiple simulations to estimate stable values of lambda that allow colonization. However, this would require temporally explicit projections that incorporate stochasticity, and an estimate of seed rain to un-colonized sites.

Some of the limitations of this thesis have highlighted issues to bear in mind in future work, the most important being choice of study species. While *A. arboreum*, *A. haworthii* and *C. orbiculata* are biologically interesting and of immediate concern to local practitioners, they are far from ideal species for a modelling exercise. In hindsight, other characteristics would have been desirable, for example, the species should not have highly restricted microhabitat requirements that are unlikely to be represented at a 1 km grid resolution, and should ideally not have a disjunct distribution in climate space or non-analog climate between the native and invaded ranges. A well-studied species would ensure a higher quality of distribution data in the native range, as well as sound *a priori* reasoning for choosing climatic variables and understanding the role of non-climatic effects. An annual or fast-growing species would maximise changes in demography or vital rates over a two-year field season.

Despite all of this, it was exciting to work with species that have scarcely been studied, and I am grateful for the opportunity to contribute to our understanding of the Crassulaceae.

6.5 Conclusions

To summarize, my four thesis objectives were answered as follows;

1. The current distributions of *A. arboreum*, *A. haworthii* and *C. orbiculata* in New Zealand are climatically distinct from their distributions elsewhere, and this constitutes a shift in at least the realized niches into cooler and wetter climatic conditions. I provided SDM projections of the species' potential distributions at a national scale, although it was necessary to use simple models.
2. Performance was strongly climate-limited along the gradient present on Banks Peninsula, and declined with increasing elevation and precipitation. Beyond the species' current distributions, at higher elevations, performance declined. The decline in performance was sharpest for *Aeonium* species, but none of the three species have yet reached climatic equilibrium.
3. Fecundity varied significantly within and among wild populations on Banks Peninsula, but very little of this variation was directly linked to climate. Plant size was the key predictor of fecundity, and across their current distributions in the region, climate does not appear to limit reproduction.
4. Testing SDMs against predicted population growth revealed that the SDMs over-predicted suitable climate, both at range edges and within the "climate envelope". It appeared unlikely that the over-prediction was solely because of the SDM algorithm. Scale, occurrence data and climate data are also likely sources of error, factors that are relevant to all SDM studies. Despite over-prediction, SDM and higher predicted population growth were ranked similarly, so projections were refined to improve estimates of range limits on Banks Peninsula.

Appendix A – Supporting information for Chapter 2

A.1 An example MaxEnt model

To illustrate the problem of creating response curves to frequency distributions that are clustered and disjunct in climate space, I ran a model in MaxEnt v.3.3.3k (Phillips *et al.* 2006) for a hypothetical species. I created a samples with data (SWD) file for a species “Y”, with 300 occurrences at arbitrary latitude and longitudes (WGS 1984). In the SWD file was only one variable of interest, “X”, which was assigned values at each occurrence location to produce the disjunct frequency distribution shown in Figure A1. In the same SWD file, I created 10 000 background occurrences, again with arbitrary latitude and longitudes, with values of X equally distributed across the range. I ran two models trained on this data. The first was run using linear and quadratic features only, to create smooth, “biologically reasonable” response curves that would be a robust choice when extrapolating. The second model was run using all “auto-features”, the commonly-used default settings. I used only one replicate per run, and did not project the models. Response curves to variable X were exported and plotted against frequency distributions in R (R Core Team 2014). Using either smoothed curves (a), or complex responses (b), MaxEnt will under-predict the range of suitable climates for species Y. I emphasize that this is not confined to MaxEnt; other SDMs may produce similar responses (Webber *et al.* 2011).

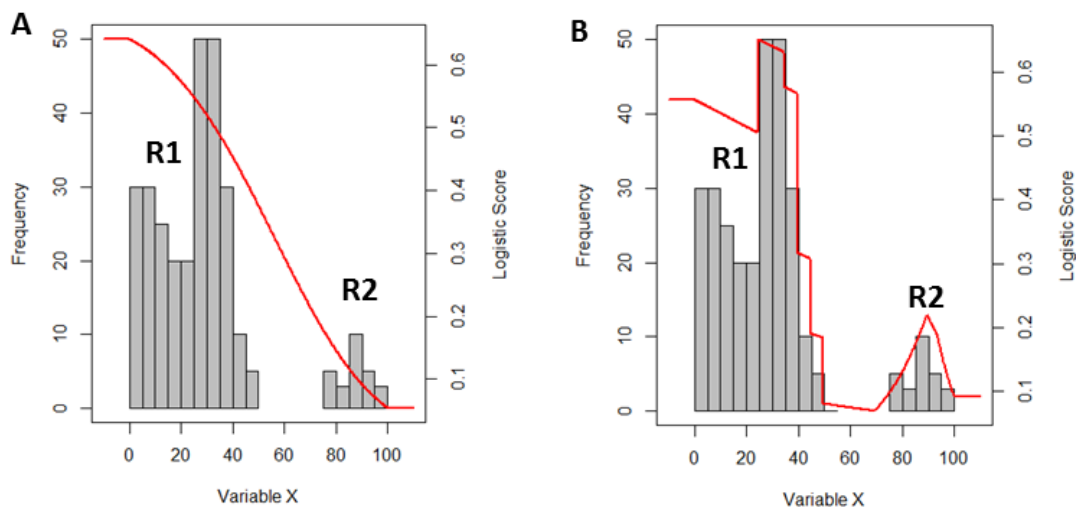


Figure A.1 Distribution of species Y in relation to a climatic variable X. Response curves (red) generated by a MaxEnt model with linear and quadratic features only (a), and all “auto-features” (b). In region 1 (R1), the species is most prevalent and occupies a wide range of climates, but can tolerate conditions in region 2 (R2) although it is less prevalent. Values of X between R1 and R2 are assumed to be climatically suitable. In a), suitable habitat in R2 is under-predicted, while in b), climate space between R1 and R2 is under-predicted.

A.2 Supporting data for study species

Table A.1 Sources and number of occurrence records collected for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*, before data cleaning and resampling.

| Type | Source | <i>A. arboreum</i> | <i>A. haworthii</i> | <i>C. orbiculata</i> | Available at: |
|--|--|--------------------|---------------------|----------------------|---|
| Data Portals | GBIF | 209 | 105 | 555 | http://data.gbif.org |
| | NZVH | 26 | 46 | 18 | http://www.virtualherbarium.org |
| | NZBRN | 1 | 1 | 4 | http://www.nzbrn.org.nz |
| | SANBI | | | 305 | http://sibis.sanbi.org |
| | BIOTA (Jürgens <i>et al.</i> 2011) | | | 7 | http://www.biota-africa.org |
| Herbaria (Digitised and non-digitised specimens) | CHR | 16 | 15 | 19 | http://www.landcareresearch.co.nz/resources/collections/allan-herbarium |
| | WAIK | | | 1 | http://www.nzherbaria.org.nz/herb_details.asp?NZHerb_ID=16 |
| | WELTU | | | 1 | http://www.victoria.ac.nz/sbs/research/facilities/herbarium |
| Articles | Healy (1959) | 3 | | | http://rsnz.natlib.govt.nz/ |
| | Mason (1978) | | | 1 | http://bts.nzpcn.org.nz/ |
| | Molloy (1980) | | | 1 | http://bts.nzpcn.org.nz/ |
| | Sykes (1992) | | 3 | | http://bts.nzpcn.org.nz/ |
| | Cameron (1996) | | | 3 | http://bts.nzpcn.org.nz/ |
| | Burrows (2001) | | | 1 | https://sites.google.com/site/nznaturalsciences/home/archived-issues |
| Surveys | Wilson (1983) | | | 7 | https://nvs.landcareresearch.co.nz/Data/DatasetDetails/2424/13248 |
| | Carter (2006) | | 32 | 79 | https://nvs.landcareresearch.co.nz/Data/DatasetDetails/2370/10859 |
| | Ministerio de Agricultura Alimentación y Medio Ambiente (2005) | | 50 | | http://www.magrama.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/atlas_manual_habitats_espanioles.aspx |
| | Carter (2014) | | 1 | 65 | |
| | Pannell (2010) | 41 | 36 | 186 | |
| Personal communication | Broker, Gary (2010) | | | 2 | |
| | Carter, Di (2011) | | | 13 | |
| | Jackson, Jill (2010) | | | 1 | |
| | Hulme, Philip (2012) | | | 2 | |
| | Rentoul, Sandy (2010) | | | 1 | |
| | Smith, Kathryn (2010) | | | 1 | |
| | Smith, Paula (2010) | | | 2 | |
| | Waghorn, Robin (2010) | | | 7 | |
| | Ater, Mohammed (2011) | 7 | | | |
| | Fennane, Mohammed (2011) | 2 | | | |
| Other | Google Street View | 6 | 10 | 3 | http://maps.google.com |
| | Bramwell & Bramwell (1990) | | NA | | |

Table A.2 Regions and Köppen-Geiger (KG) classes sampled within for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* niche analyses, and number of samples taken.

| Species | Sampling areas | Background samples | Main climate KG classes | Precipitation/temperature KG sub-classes |
|----------------------|------------------|--------------------|-------------------------|--|
| <i>A. arboreum</i> | Australia | 22 609 | Arid | Desert, hot |
| | Balearic Islands | | | Steppe, cold |
| | Canary Islands | | | Steppe, hot |
| | Madeira | | | |
| | Malta | | Warm temperate | Fully humid, warm summer |
| | Morocco | | | Summer dry, hot summer |
| | New Zealand | | | Summer dry, warm summer |
| | Portugal | | | |
| | Spain | | | |
| | U.S.A. | | | |
| <i>A. haworthii</i> | Australia | 13 676 | Arid | Steppe, cold |
| | Canary Islands | | Warm temperate | |
| | France | | | Fully humid, warm summer |
| | New Zealand | | | Summer dry, hot summer |
| | Spain | | | Summer dry, warm summer |
| | U.S.A. | | | |
| <i>C. orbiculata</i> | Angola | 35 924 | Arid | Desert, cold |
| | Australia | | | Desert, hot |
| | Corsica | | | Steppe, cold |
| | Lesotho | | | Steppe, hot |
| | Namibia | | Warm temperate | |
| | New Zealand | | | Fully humid, hot summer |
| | Mozambique | | | Fully humid, warm summer |
| | South Africa | | | Summer dry, hot summer |
| | Spain | | | Summer dry, warm summer |
| | Swaziland | | | Winter dry, hot summer |
| | U.S.A. | | | Winter dry, warm summer |

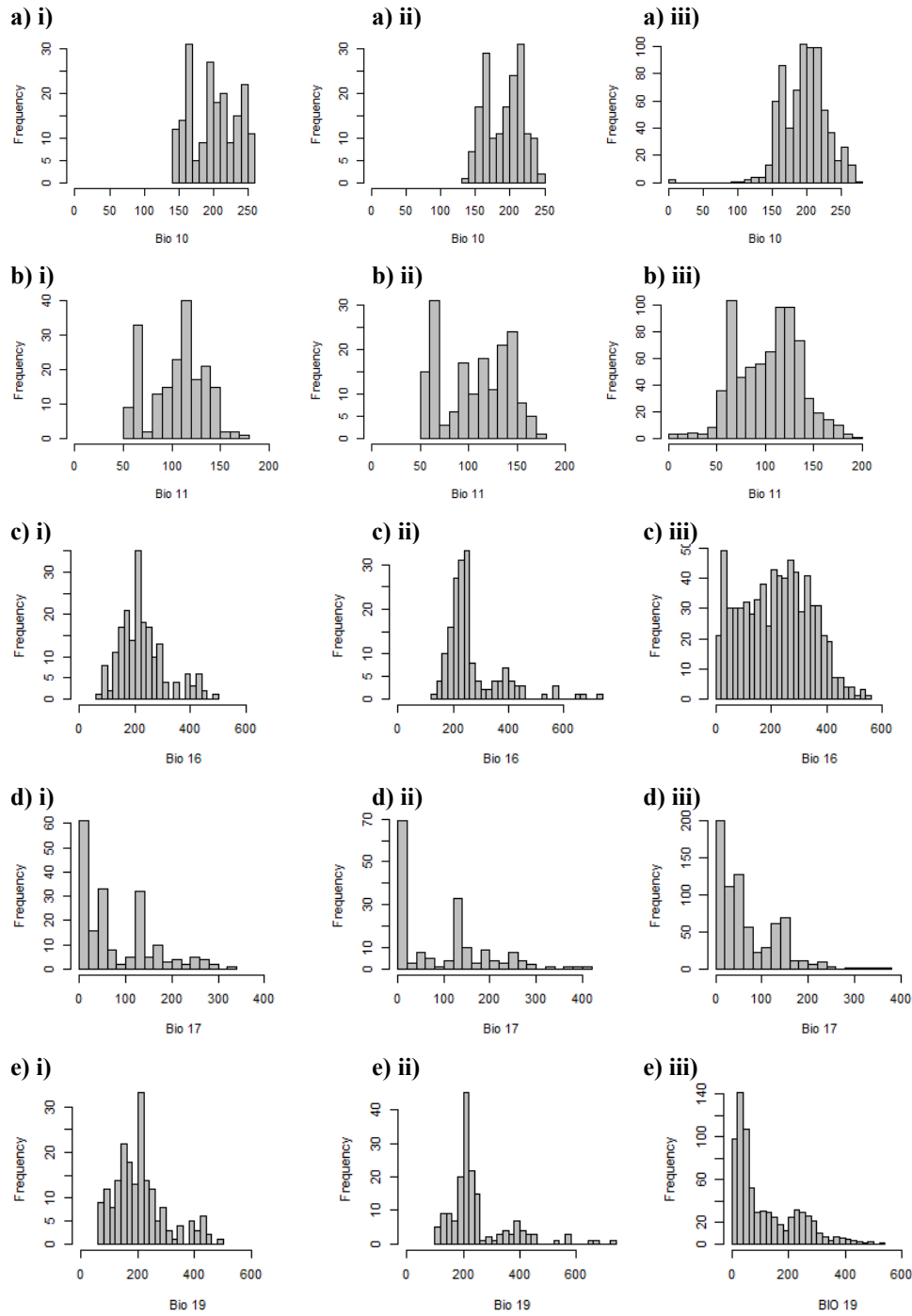


Figure A.2 Frequency histograms of the five bioclimatic variables used in niche analysis and models of target species, at all global occurrence points. Plots shown for i) *Aeonium arboreum*; ii) *A. haworthii* and iii) *Cotyledon orbiculata*. Variables are: a) BIO10 (Mean temperature of the warmest quarter, $^{\circ}\text{C} \times 10$); b) BIO11 (mean temperature of the coldest quarter, $^{\circ}\text{C} \times 10$); c) BIO16 (Precipitation of the wettest quarter, mm); d) BIO17 (Precipitation of the driest quarter, mm); e) BIO19 (Precipitation of the coldest quarter, mm).

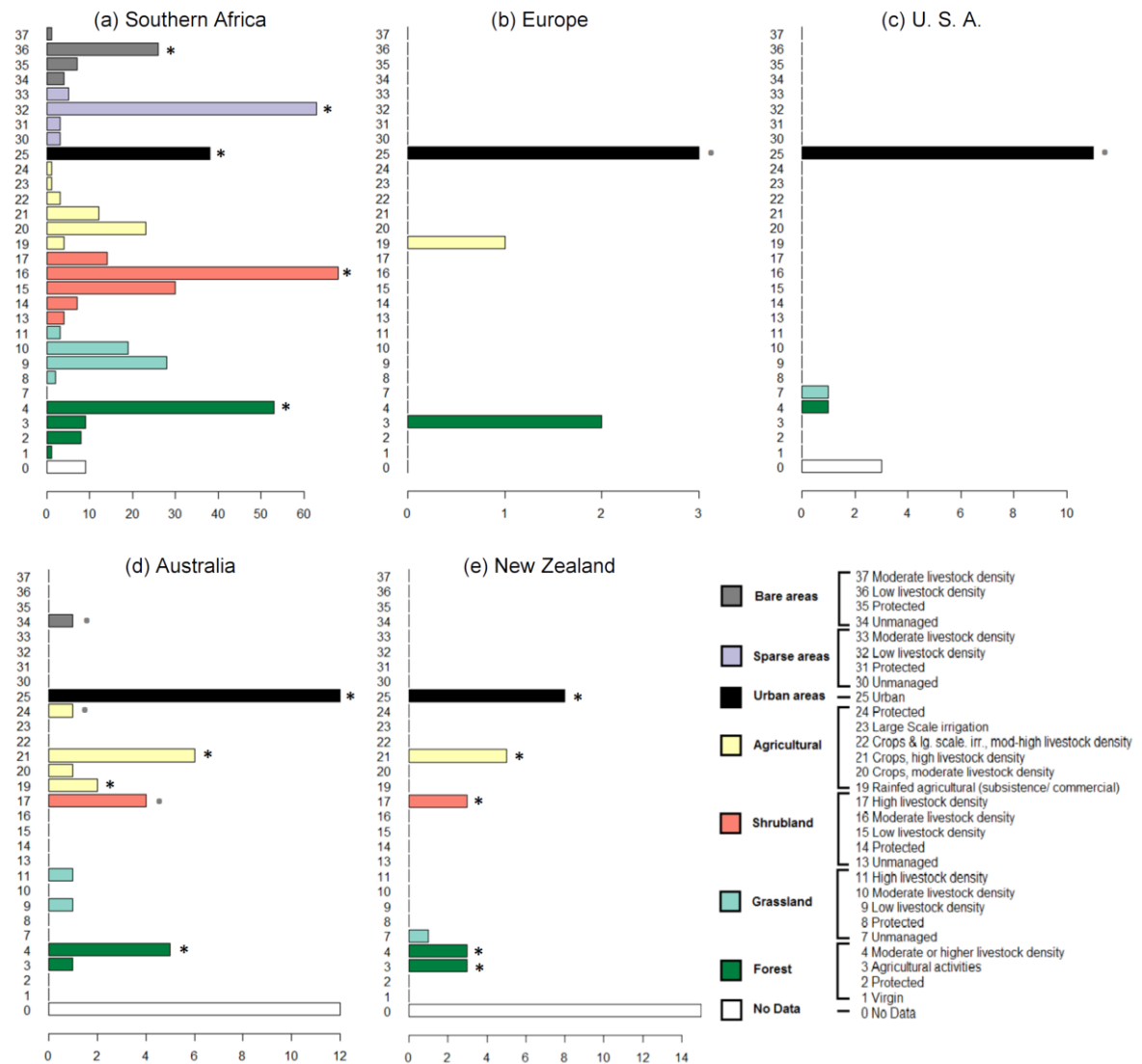


Figure A.3 Frequency of land use classification (Nachtergaele & Petri 2008) in grid cells (5 arc-minutes) containing *Cotyledon orbiculata* in a) Southern Africa (South Africa, Lesotho, Swaziland, Namibia, Mozambique, Angola); b) Europe (Corsica, Spain); c) the U.S.A.; d) Australia and e) New Zealand. Asterisks denote significance of land use type given its proportional area, according to Fisher's exact test (* = $p < 0.05$, * = $p < 0.01$).

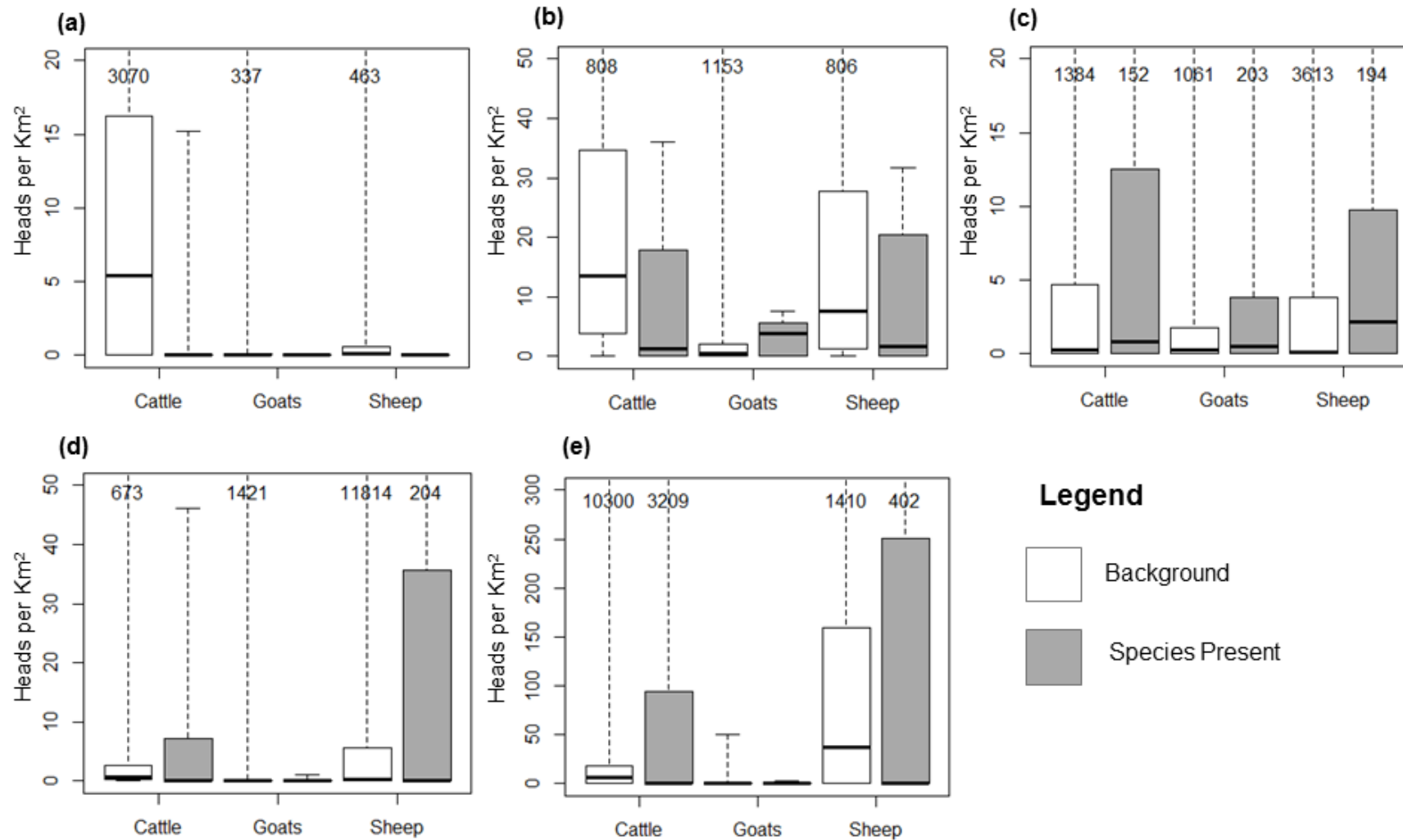


Figure A.4 Density of cattle, goats and sheep (heads per km²) in grid cells (0.05 decimal degrees) containing *Cotyledon orbiculata* (grey) versus randomly-selected background points (white) in a) U.S.A., b) Europe (Corsica, Spain), c) Southern Africa (South Africa, Lesotho, Swaziland, Namibia, Mozambique, Angola), d) Australia and e) New Zealand. Maximum density shown where whiskers extend beyond axes. Data courtesy of GLW (Robinson *et al.* 2014).

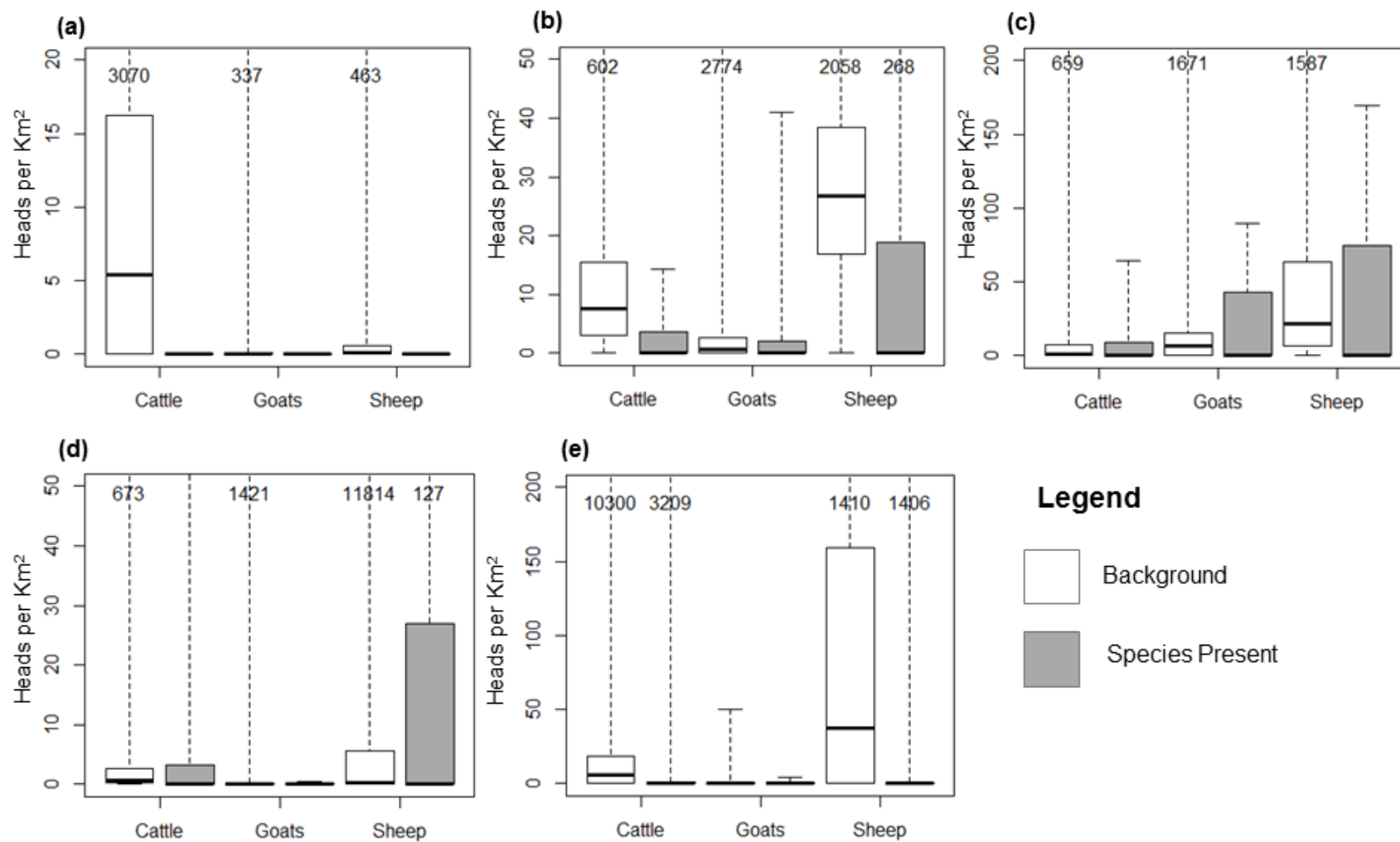


Figure A.5 Livestock density of cattle, goats and sheep expressed as heads per km² in grid cells (0.05 decimal degrees) containing *Aeonium arboreum* (grey) versus randomly-selected background points (white) in a) U.S.A., b) Europe (Spain, Portugal, Balearic Islands, Malta), c) Macaronesia (Canary Islands, Morocco, Madeira), d) Australia and e) New Zealand. Maximum values shown where whiskers extend beyond plots. Data courtesy of GLW (Robinson *et al.* 2014).

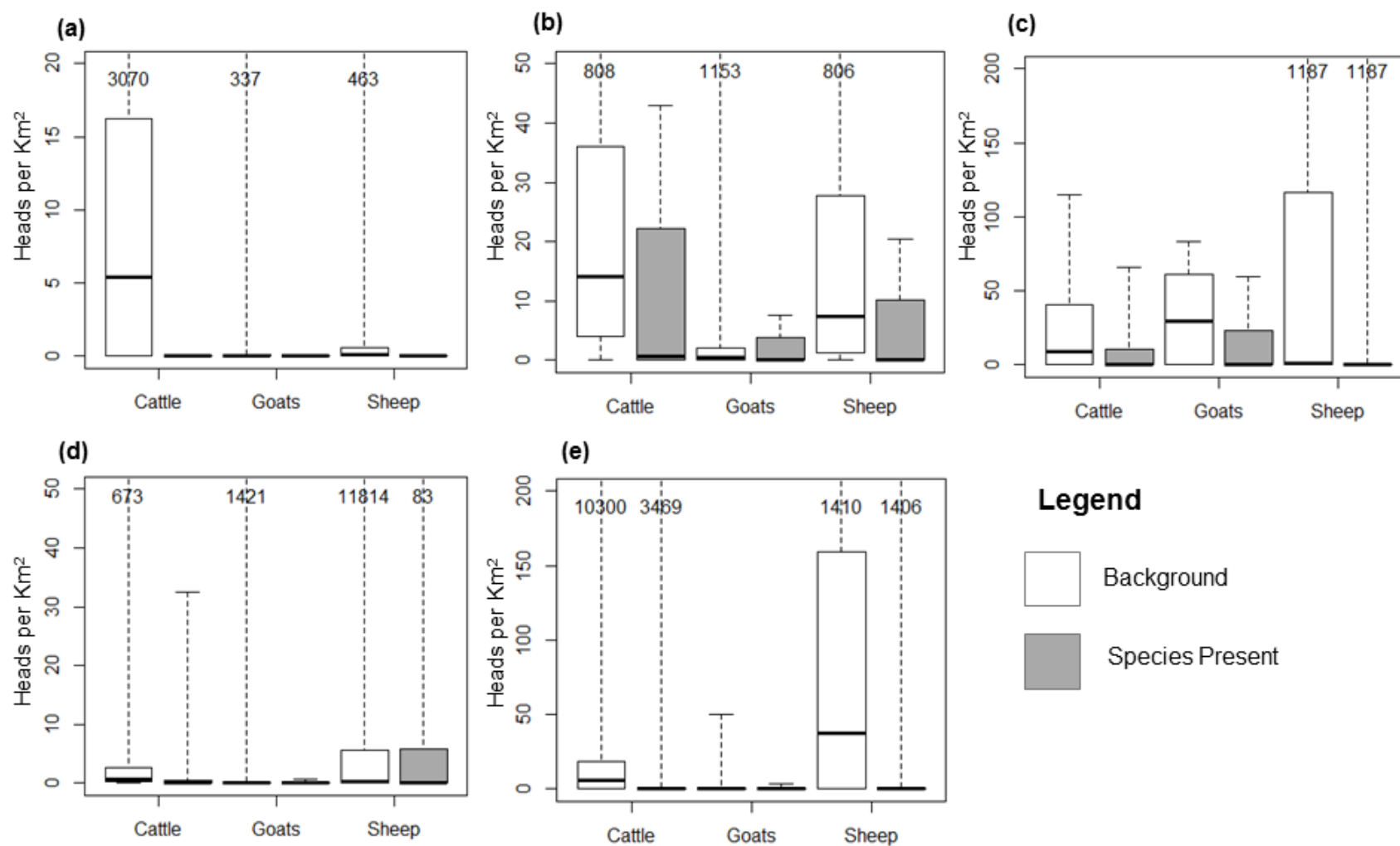
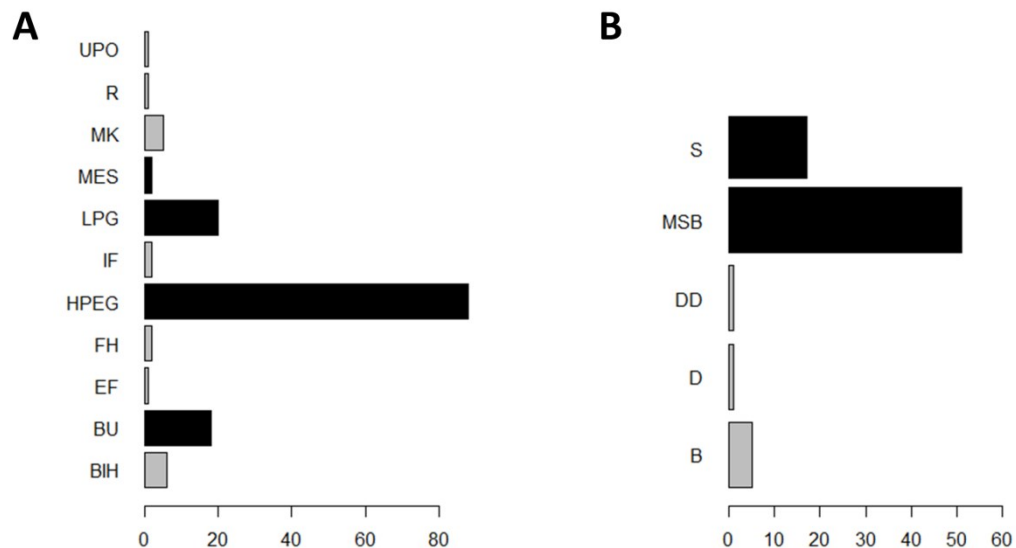


Figure A.6 Livestock density of cattle, goats and sheep expressed as heads per km² in grid cells (0.05 decimal degrees) containing *Aeonium haworthii* (grey) versus randomly-selected background points (white) in a) U.S.A., b) Europe (Spain, France), c) Macaronesia (Canary Islands), d) Australia and e) New Zealand. Maximum values shown where whiskers extend beyond plots. Data courtesy of GLW (Robinson *et al.* 2014).



Key to A:

Urban Park/Open (UPO); River (R); Manuka/Kanuka (MK); Mixed Exotic Shrubland (MES); Low Production Grassland (LPG); Indigenous Forest (IF); High Production Exotic Grassland (HPEG); Forest Harvested (FH); Exotic Forest (EF); Built Up (BU); Broadleaved Indigenous Hardwood (BIH)

Key to B:

Sheep (S); Mixed Sheep and Beef (MSB); Dry Dairying (DD); Dairy (D); Beef (B)

Figure A.7 a) Frequency of *Cotyledon orbiculata* occurrence records in land cover classes (Ministry for the Environment & Landcare Research 2014) and b) farm types (excluding non-farmland) according to Agribase™ (AsureQuality 2006). Black bars indicate statistical significance ($p < 0.01$) of *C. orbiculata* frequency, given total occurrences and the proportional area of each class in New Zealand, according to a one-tailed binomial test.

Table A.3 Description of land cover classes (Ministry for the Environment & Landcare Research 2014) that spatially intersect *Cotyledon orbiculata* occurrence records in New Zealand. Class descriptions summarized from Thompson *et al.* (2003).

| Class | Name | Description |
|-------|----------------------------------|--|
| UPO | Urban Park/Open | Open, mown, grassed amenity areas within or associated with BU. |
| R | River | Natural and modified rivers, creeks, canals and channels over 30 m wide. |
| MK | Manuka/Kanuka | Indigenous shrubland, often lightly grazed. Early successional scrub on previously forested land with history of burning. |
| MES | Mixed Exotic Shrubland | Single-species or mixed introduced exotic shrubs and climbers. |
| LPG | Low Production Grassland | Exotic or indigenous grassland, low vegetation vigour. Lower soil fertility, low fertilizer application, seasonal drought or short growing season. Usually managed for sheep and beef grazing, steep slopes. |
| IF | Indigenous Forest | Indigenous tall forest canopy species, identified from ground surveys. |
| HPEG | High Production Exotic Grassland | Intensively managed exotic grassland, with good vegetation vigour. Usually rotationally grazed. Fertilizer and irrigation may be used. |
| FH | Forest Harvested | Areas of forest showing evidence of harvesting since LCDB1. |
| EF | Exotic Forest | Exotic forest other than <i>Pinus radiata</i> , e.g. Douglas fir, <i>Acacia</i> or <i>Eucalyptus</i> . |
| BU | Built Up | CBDs, suburbs, commercial/industrial, hard surfaces e.g. roads, paved areas. |
| BIH | Broadleaved Indigenous Hardwood | Usually high rainfall areas, also low-growing coastal broadleaved forest. Mixture of native broad leaved hardwood species. |

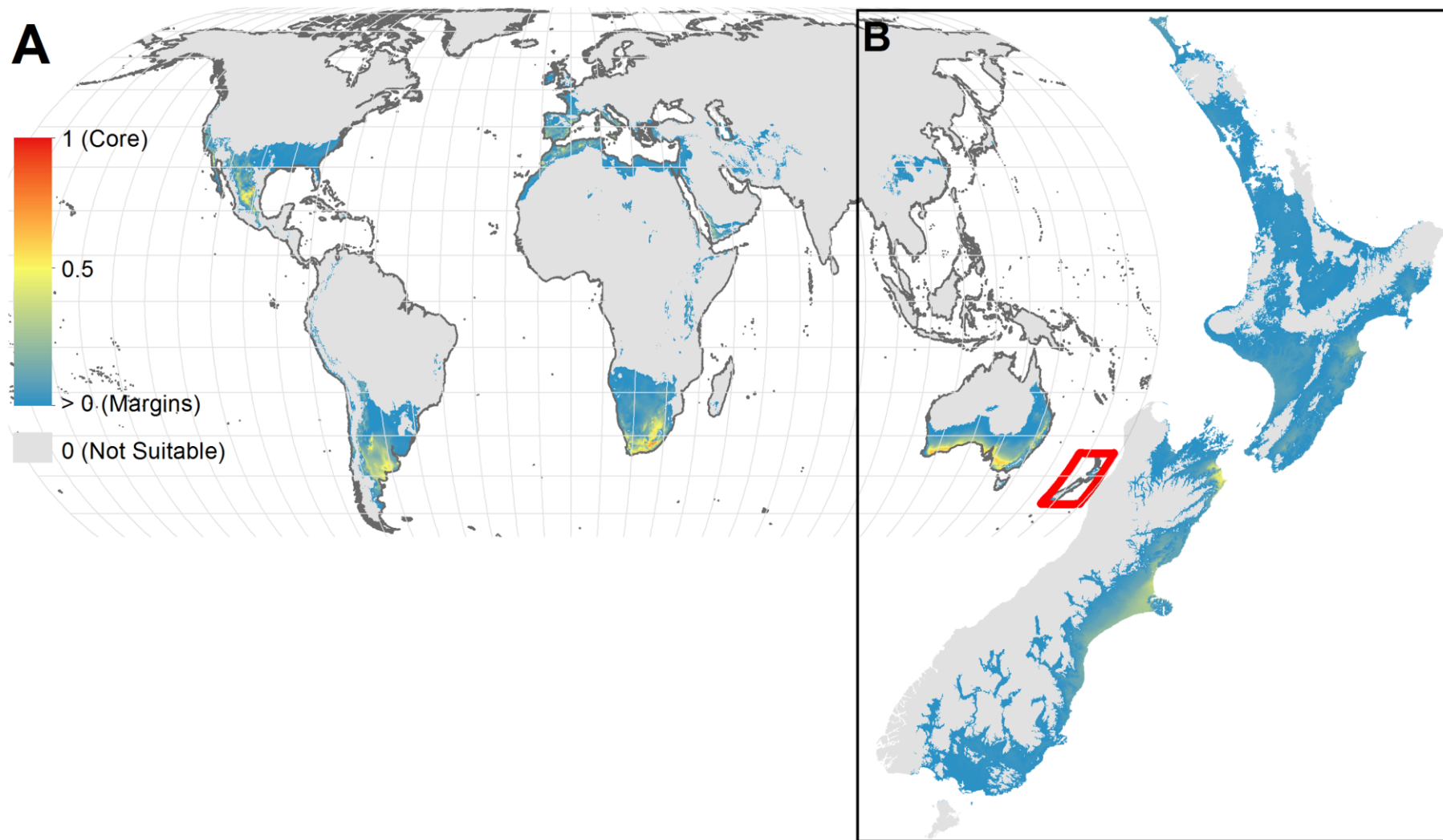


Figure A.8 Global a) and New Zealand b) projections of BIOCLIM models for *Cotyledon orbiculata*, trained on subset of all occurrence data, with 7 points removed from the most extreme high elevations in Lesotho. BIOCLIM scores are percentiles of the species' distributions in climate space. Scores approaching 1 signify similarity to the species' 50th percentile in climate space ("core" climate), and 0 signifies that the cell is outside of the species' rectilinear hypervolume.

Appendix B – Supporting information for Chapter 3

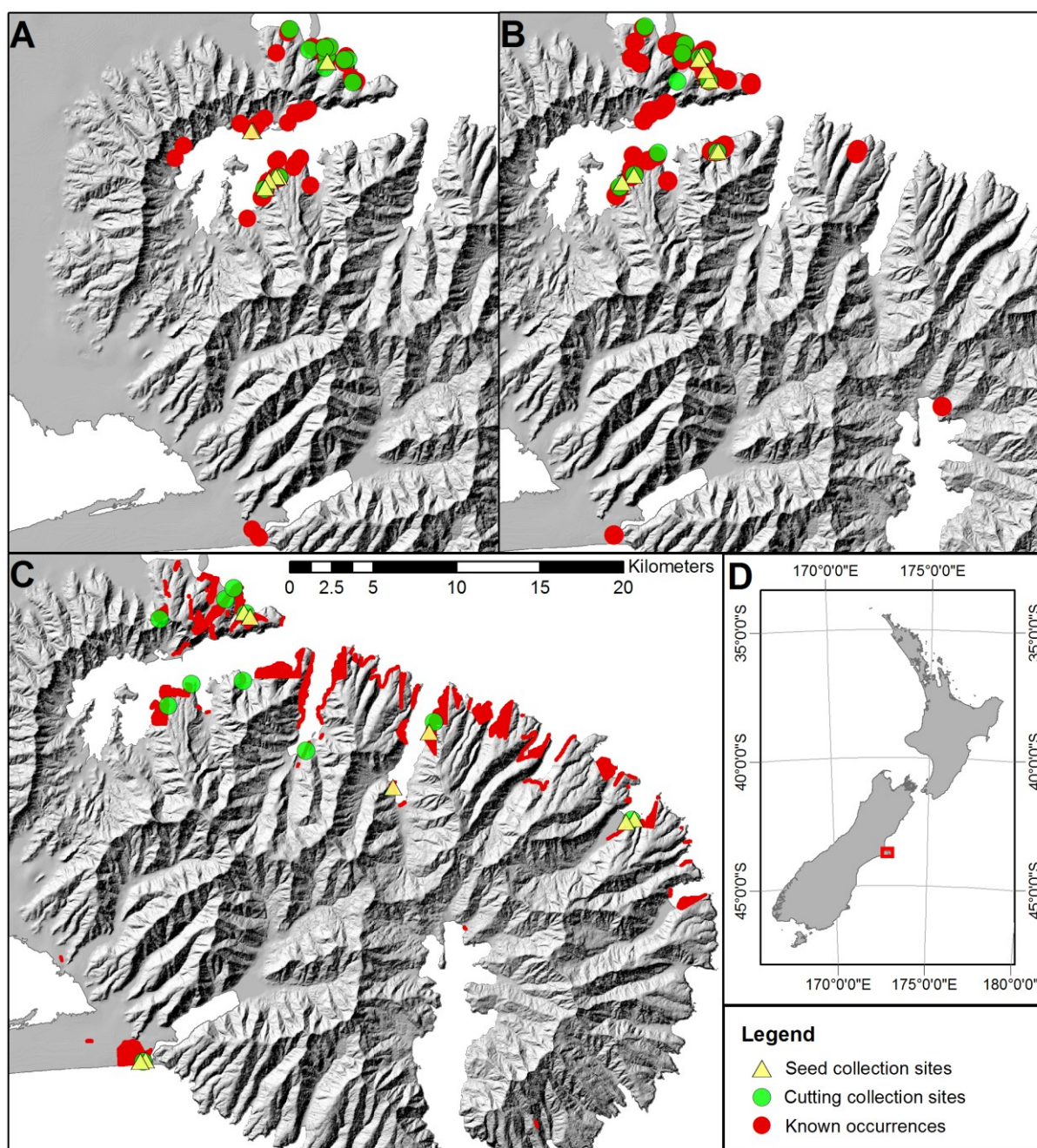


Figure B.1 Map of current distributions, cutting collection sites and seed collection sites, for a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata* on Banks Peninsula. Location of Banks Peninsula relative to New Zealand also shown (d).

Table B.1 Source list for Banks Peninsula distribution data of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*.

| Type | Source | <i>A. arboreum</i> | <i>A. haworthii</i> | <i>C. orbiculata</i> | Available at: |
|------------------------|-----------------------|--------------------|---------------------|----------------------|---|
| Data Portals | GBIF | 25 | 32 | 9 | http://data.gbif.org |
| | NZVH | 21 | 35 | | http://www.virtualherbarium.org |
| Herbaria* | CHR | 9 | 5 | 9 | http://www.landcareresearch.co.nz/resources/collections/allan-herbarium |
| | WAIK | | | 1 | http://www.nzherbaria.org.nz/herb_details.asp?NZHerb_ID=16 |
| Articles | Healy (1959) | 1 | | | http://rsnz.natlib.govt.nz/ |
| | Burrows (2001) | | | 1 | https://sites.google.com/site/nznaturalsciences/home/archived-issues |
| Surveys | Wilson (1983) | | | 7 | https://nvs.landcareresearch.co.nz/Data/DatasetDetails/2424/13248 |
| | Carter (2006) | | 32 | 79 | https://nvs.landcareresearch.co.nz/Data/DatasetDetails/2370/10859 |
| | Carter (2014) | | 1 | 65 | |
| | Pannell (2010) | 41 | 36 | 186 | |
| Personal communication | Broker, Gary (2010) | | | 2 | |
| | Carter, Di (2011) | | | 13 | |
| | Jackson, Jill (2010) | | | 1 | |
| | Rentoul, Sandy (2010) | | | 1 | |
| | Smith, Kathryn (2010) | | | 1 | |
| | Smith, Paula (2010) | | | 2 | |
| | Waghorn, Robin (2010) | | | 7 | |

*Including digitised and non-digitised specimens

Table B.2 Details of all numbered sites in Figure 3.1. “Use” distinguishes between weather stations used for precipitation data (P), and field sites used for cuttings only (C), seeds only (S), or both (CS). Longitude and latitude in decimal degrees (WGS 84), elevation in MASL. Aspect (cardinal direction) and % overhead canopy cover (CC) measured at field sites only. Asterisks (*) denote sites where CC is caused by trees (as opposed to low garden features at seed sites). “Precip.WS” indicates the weather station used for precipitation data at each field site.

| No. | Site ID | Use | Full name | Long. | Lat. | Elev. | Aspect | CC | Precip.WS |
|-----|---------|-----|----------------------------|----------|----------|-------|--------|-----|-----------|
| 1 | AE | P | Akaroa EWS | 172.9657 | -43.8094 | 45 | - | - | N/A |
| 2 | B1 | CS | Bowenvale 1 | 172.6551 | -43.5816 | 239 | S | 0 | CG |
| 3 | B2 | C | Bowenvale 2 | 172.6493 | -43.5833 | 40 | W | 0 | CG |
| 4 | B3 | C | Bowenvale 3 | 172.6519 | -43.5878 | 67 | W | 0 | CG |
| 5 | B4 | C | Bowenvale 4 | 172.6517 | -43.5916 | 67 | W | 0 | CG |
| 6 | B5 | CS | Bowenvale 5 | 172.6445 | -43.6000 | 358 | N | 0 | GB |
| 7 | B6 | CS | Bowenvale 6 | 172.6654 | -43.5953 | 340 | N | 0 | GB |
| 8 | BF1 | CS | Birdling's Flat 1 | 172.7182 | -43.8141 | 8 | N/A | 0 | MB |
| 9 | BF2 | CS | Birdling's Flat 2 | 172.7197 | -43.8126 | 7 | N/A | 0 | MB |
| 10 | CG | P | Christchurch Gardens | 172.6190 | -43.5310 | 7 | - | - | N/A |
| 11 | CK1 | CS | Coopers Knob 1 | 172.6236 | -43.6532 | 477 | W | 0 | LS |
| 12 | CK2 | CS | Coopers Knob 2 | 172.6233 | -43.6551 | 471 | N | 0 | LS |
| 13 | CK3 | CS | Coopers Knob 3 | 172.6234 | -43.6556 | 476 | W | 0 | LS |
| 14 | CK4 | CS | Coopers Knob 4 | 172.6236 | -43.6584 | 532 | N | 0 | LS |
| 15 | CK5 | CS | Coopers Knob 5 | 172.6242 | -43.6610 | 552 | W | 0 | LS |
| 16 | CK6 | CS | Coopers Knob 6 | 172.6240 | -43.6653 | 479 | W | 32* | LS |
| 17 | CP | S | CP (Lyttelton) | 172.7149 | -43.6011 | 60 | S | 97 | LH |
| 18 | EW | S | EW (Cashmere) | 172.6345 | -43.5690 | 40 | W | 43 | CG |
| 19 | FT | S | FT (Charteris Bay) | 172.7136 | -43.6386 | 35 | N | 20 | LS |
| 20 | GB | P | Governor's Bay | 172.6504 | -43.6278 | 274 | - | - | N/A |
| 21 | GP1 | CS | Greenwood Park 1 | 172.7465 | -43.5741 | 200 | E | 0 | LH |
| 22 | GP2 | CS | Greenwood Park 2 | 172.7527 | -43.5776 | 167 | E | 0 | LH |
| 23 | GP3 | CS | Greenwood Park 3 | 172.7403 | -43.5936 | 234 | E | 0 | LH |
| 24 | GP4 | CS | Greenwood Park 4 | 172.7418 | -43.5825 | 319 | E | 0 | GB |
| 25 | GP5 | CS | Greenwood Park 5 | 172.7440 | -43.5785 | 305 | N | 0 | GB |
| 26 | GP6 | CS | Greenwood Park 6 | 172.7445 | -43.5884 | 285 | E | 0 | LH |
| 27 | GPWT | S | Greenwood Park Water Tanks | 172.7372 | -43.5856 | 370 | N | 0 | LH |
| 28 | JK | S | JK (Huntsbury) | 172.6537 | -43.5664 | 80 | W | 62 | CG |
| 29 | JN | S | JN (Church Bay) | 172.7238 | -43.6300 | 75 | N | 54 | LS |
| 30 | LBBA | P | Le Bons Bay AWS | 173.1190 | -43.7460 | 236 | - | 42* | N/A |
| 31 | LH | P | Lyttelton Harbour | 172.7240 | -43.6080 | 5 | - | - | N/A |
| 32 | LS | P | Living Springs | 172.6468 | -43.6464 | 38 | - | - | N/A |
| 33 | MB | P | Magnet Bay | 172.7440 | -43.8440 | 6 | - | - | N/A |
| 34 | MP1 | CS | Misty Peaks 1 | 172.9696 | -43.8226 | 153 | N | 42* | AE |
| 35 | MP2 | CS | Misty Peaks 2 | 172.9703 | -43.8222 | 148 | W | 56* | AE |
| 36 | MP3 | CS | Misty Peaks 3 | 172.9709 | -43.8348 | 516 | S | 0 | AE |
| 37 | MP4 | CS | Misty Peaks 4 | 172.9722 | -43.8472 | 642 | E | 0 | LBBA |
| 38 | MP5 | CS | Misty Peaks 5 | 172.9825 | -43.8228 | 527 | W | 0 | AE |
| 39 | MP6 | CS | Misty Peaks 6 | 172.9989 | -43.8326 | 653 | N | 0 | LBBA |
| 40 | OK | P | Okuti | 172.8096 | -43.7895 | 61 | - | - | N/A |
| 41 | RH | S | RH (Heathcote) | 172.7127 | -43.5784 | 40 | N | 32 | LH |
| 42 | SH1 | C | Scarborough Hill 1 | 172.7524 | -43.5871 | 78 | W | 0 | LH |
| 43 | SH2 | C | Scarborough Hill 2 | 172.7610 | -43.5879 | 295 | E | 0 | LH |
| 44 | SH3 | C | Scarborough Hill 3 | 172.7678 | -43.5936 | 180 | E | 0 | LH |
| 45 | SH4 | C | Scarborough Hill 4 | 172.7693 | -43.5932 | 180 | S | 0 | LH |
| 46 | TO1 | CS | Te Oka 1 | 172.7883 | -43.8379 | 130 | E | 60* | MB |
| 47 | TO2 | CS | Te Oka 2 | 172.7864 | -43.8454 | 60 | E | 0 | MB |
| 48 | TO3 | CS | Te Oka 3 | 172.7749 | -43.8578 | 39 | E | 0 | MB |
| 49 | TO4 | CS | Te Oka 4 | 172.7718 | -43.8569 | 38 | W | 0 | MB |
| 50 | TO5 | CS | Te Oka 5 | 172.7743 | -43.8502 | 61 | W | 0 | MB |
| 51 | TO6 | CS | Te Oka 6 | 172.7760 | -43.8361 | 316 | E | 0 | MB |
| 52 | TO7 | CS | Te Oka 7 | 172.7845 | -43.8238 | 483 | E | 0 | OK |
| 53 | TO8 | CS | Te Oka 8 | 172.8169 | -43.8133 | 681 | E | 0 | OK |
| 54 | TO9 | CS | Te Oka 9 | 172.8228 | -43.8158 | 616 | W | 0 | OK |
| 55 | TO10 | CS | Te Oka 10 | 172.8202 | -43.8225 | 567 | W | 0 | OK |

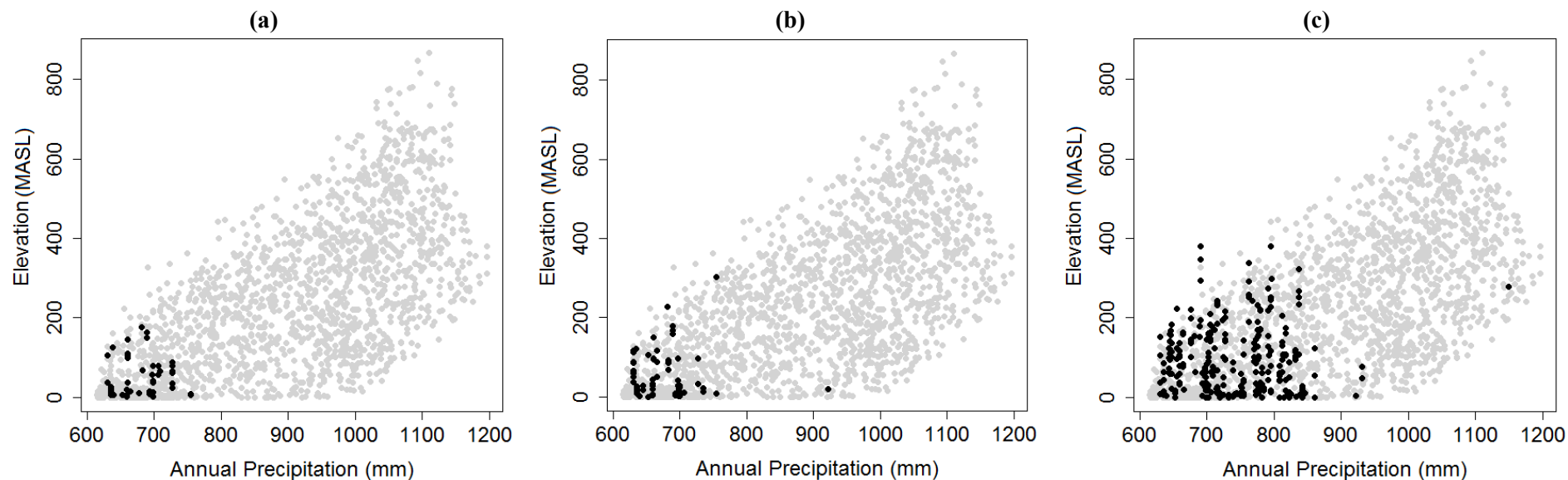


Figure B.2 Elevation (MASL) versus total annual precipitation (mm) on Banks Peninsula, taken from 30-arc-second Worldclim layers [(Hijmans *et al.* 2005), available at <http://www.worldclim.org>]. Grey points show values for entire Peninsula, black points show values at recorded presence locations of a) *Aeonium arboreum* b) *A. haworthii* and c) *Cotyledon orbiculata*.

Table B.3 Individual seed weight of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*, and weight of seed and chaff estimated to contain 100 seeds, according to seed source site. Also given are results of tetrazolium tests, as percentages of seeds found to be fully stained (viable, high vigour) and pale stained (viable, low vigour).

| Species | Site | Seed weight (µg) | Content weight 100 seeds (g) | Full stain % | Pale stain % | Total viable % |
|----------------------|--------------------|------------------|------------------------------|--------------|--------------|----------------|
| <i>A. arboreum</i> | Church Bay 1 | 20 | 4.4×10^{-3} | 65 | 23 | 88 |
| | Church Bay 2 | 20 | 7.9×10^{-3} | 70 | 11 | 81 |
| | Hays Bay 1 | 20 | 5.7×10^{-3} | 57 | 25 | 82 |
| | Hays Bay 2 | 20 | 2.3×10^{-2} | 49 | 28 | 77 |
| | Lyttelton 1 | 20 | 6.8×10^{-3} | 55 | 39 | 94 |
| | Lyttelton 2 | 20 | 1.4×10^{-2} | 51 | 31 | 82 |
| | Sumner 1 | 20 | 3.9×10^{-3} | 52 | 30 | 82 |
| | Sumner 2 | 20 | 4.0×10^{-3} | 56 | 24 | 80 |
| <i>A. haworthii</i> | Camp Bay 1 | 26 | 4.7×10^{-3} | 42 | 37 | 79 |
| | Camp Bay 2 | 26 | 7.2×10^{-3} | 46 | 27 | 73 |
| | Church Bay | 26 | 1.6×10^{-2} | 10 | 16 | 26 |
| | East Sumner 1 | 26 | 8.6×10^{-3} | 45 | 34 | 79 |
| | East Sumner 2 | 26 | 1.2×10^{-2} | 17 | 29 | 46 |
| | Hays Bay | 26 | 7.0×10^{-3} | 48 | 26 | 74 |
| | Taylor's Mistake 1 | 26 | 1.0×10^{-1} | 42 | 34 | 76 |
| | Taylor's Mistake 2 | 26 | 5.4×10^{-3} | 44 | 29 | 73 |
| <i>C. orbiculata</i> | Birdling's Flat 1 | 29 | 3.6×10^{-3} | 35 | 34 | 69 |
| | Birdling's Flat 2 | 29 | 4.0×10^{-3} | 34 | 19 | 53 |
| | Godley Head 1 | 29 | 4.6×10^{-3} | 45 | 40 | 85 |
| | Godley Head 2 | 29 | 2.9×10^{-3} | 53 | 37 | 90 |
| | Okains Bay 1 | 29 | 5.0×10^{-3} | 52 | 35 | 87 |
| | Okains Bay 2 | 29 | 5.0×10^{-3} | 43 | 31 | 74 |
| | Pigeon Bay 1 | 29 | 5.1×10^{-3} | 51 | 46 | 97 |
| | Pigeon Bay 2 | 29 | 7.4×10^{-3} | 47 | 41 | 88 |

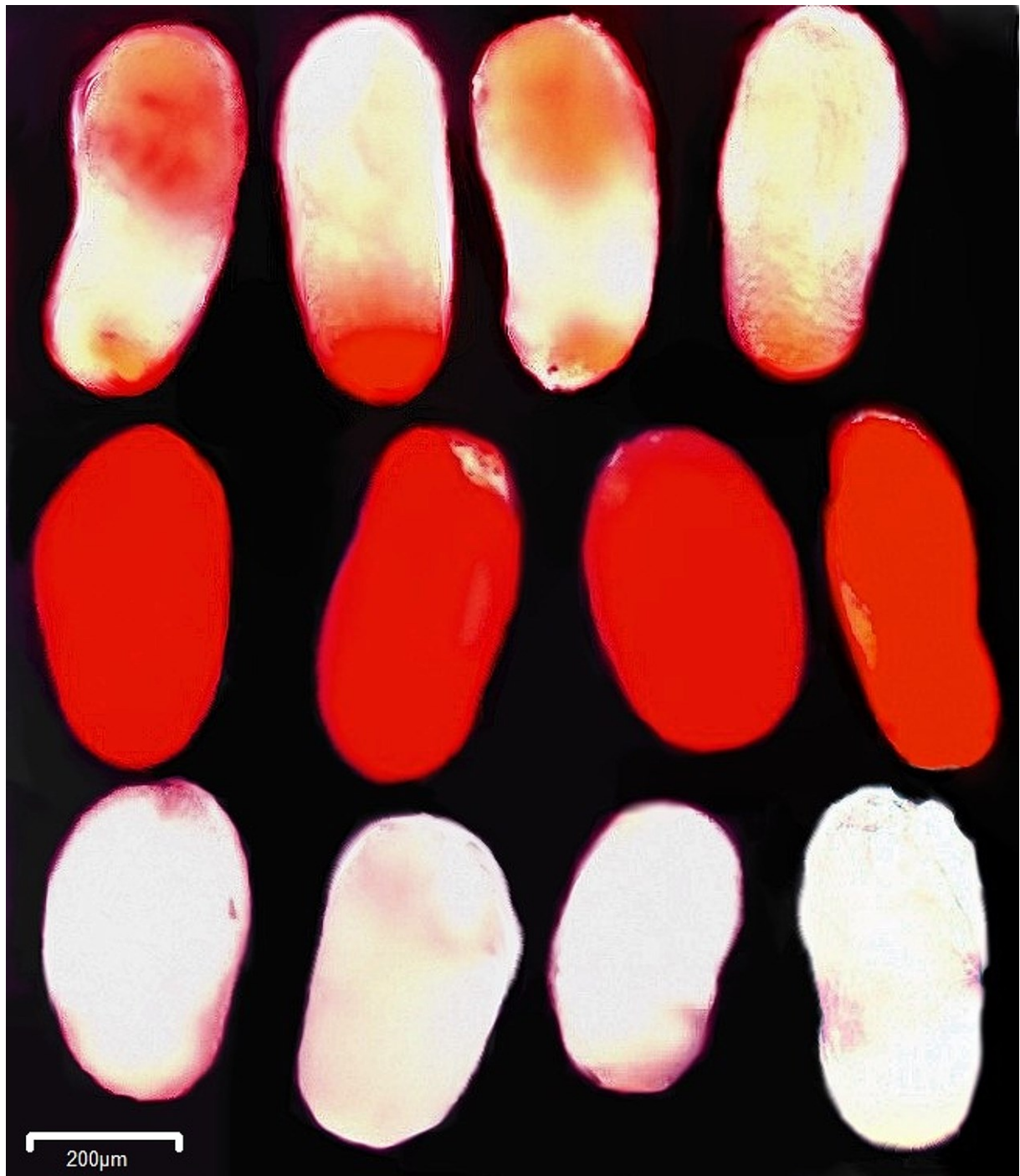


Figure B.3 *Cotyledon orbiculata* seeds under microscope at 100 × magnification. Seeds have been stained with TTC and seed coat removed. Top row show pale and partial staining and are non-viable due to necrosis of vital tissue. Middle row show full staining indicating viability and high vigour. Bottom row show no staining and are completely non-viable.

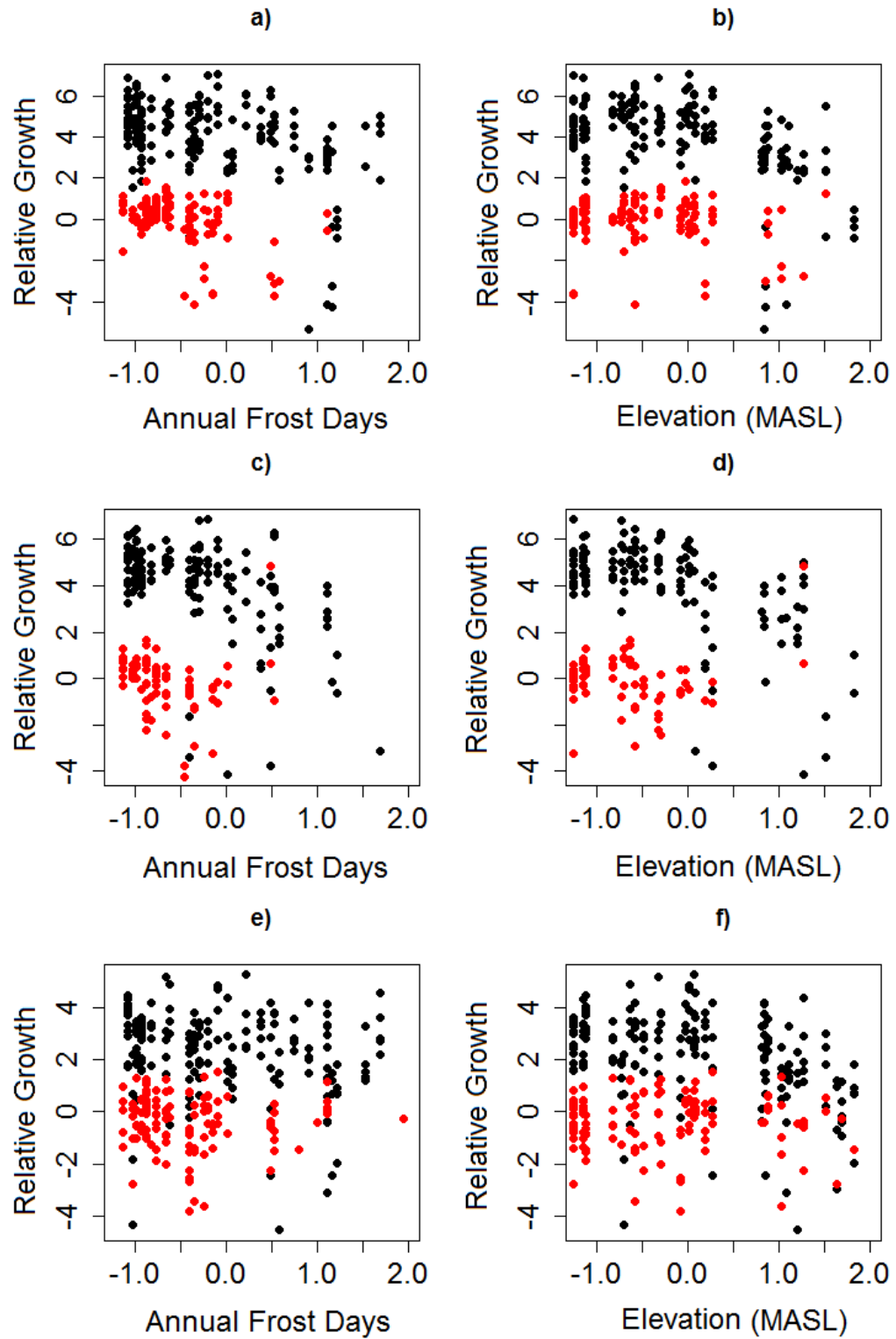


Figure B.4 Scatterplots showing similar relationships between relative growth, calculated as $[\ln(\text{Volume}_{t+1}) - \ln(\text{Volume}_t)]$, and annual frost days and elevation, in both years of field experiment. Year one indicated by black points, year two by red points. Shown for *Aeonium arboreum* (a, b) *A. haworthii* (c, d) and *Cotyledon orbiculata* (e, f).

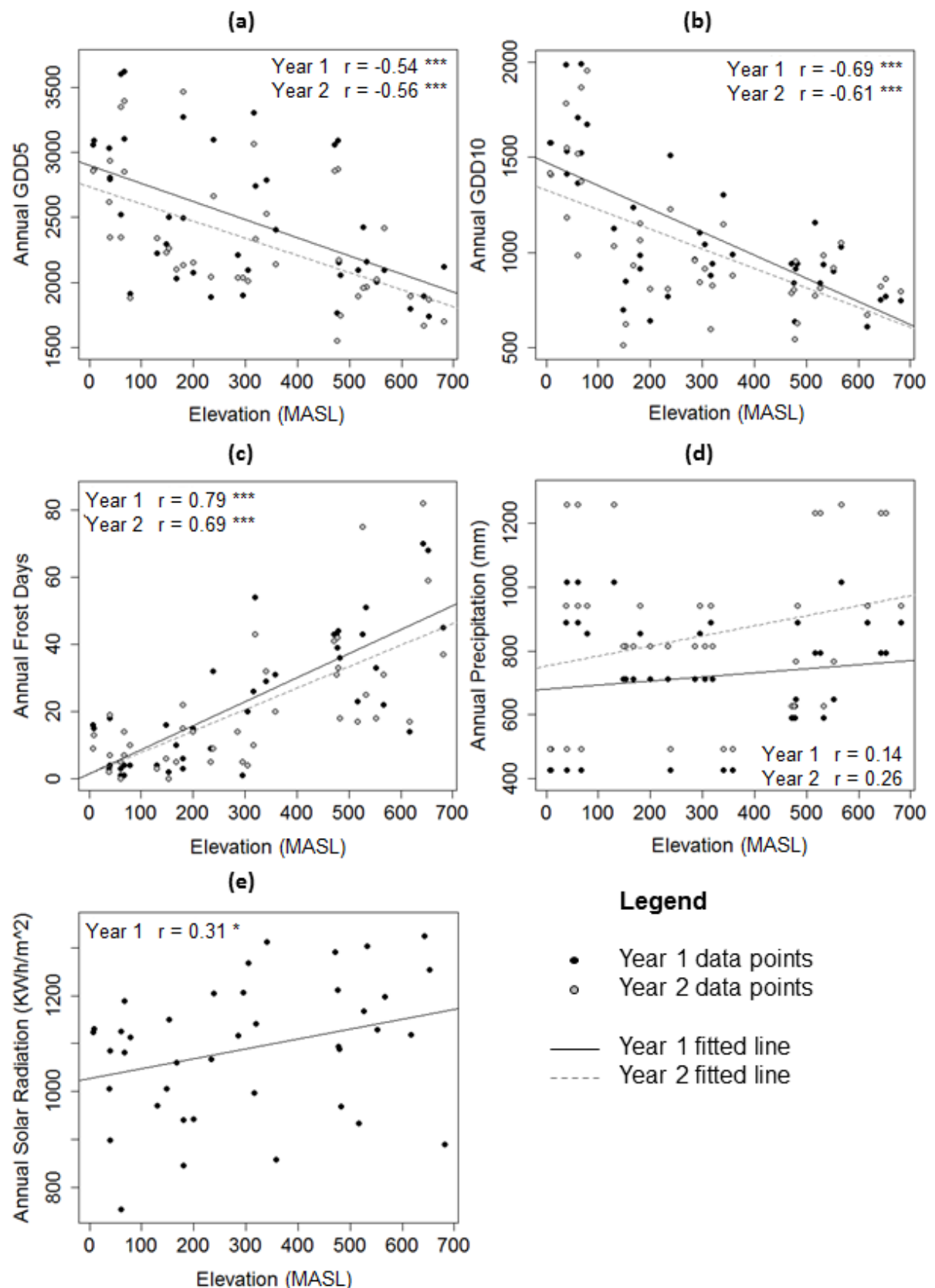


Figure B.5 Correlations of elevation with five annual climatic variables (a-e) at field transplant sites, over both years. Seed tray only sites not used due to incomplete year one data. Only one year of data presented for solar radiation (e) due to negligible differences between years. Pearson's correlation coefficient (r) and statistical significance indicated in figures, by * ($p < 0.05$), ** ($p < 0.01$), or *** ($p < 0.001$).

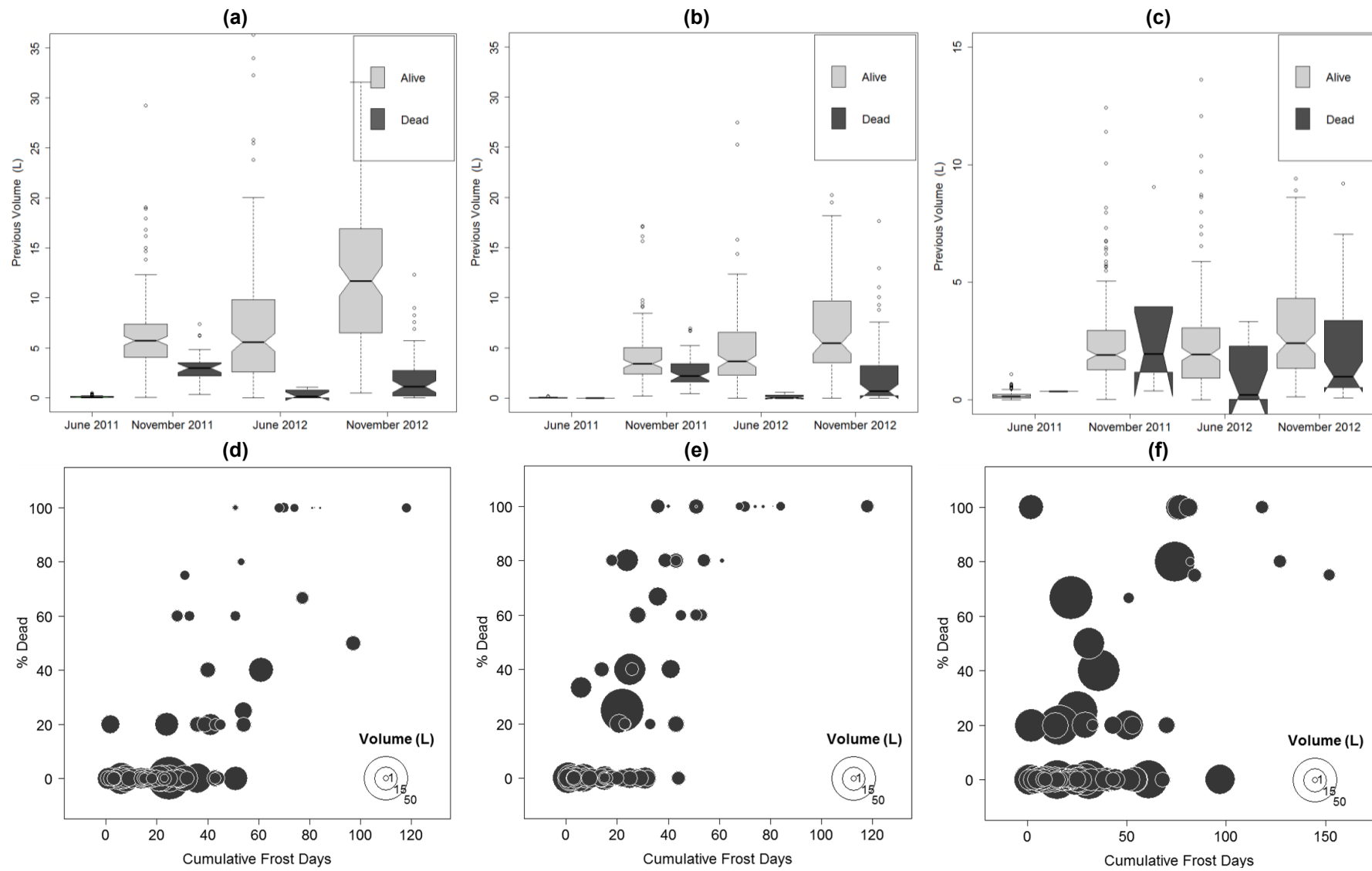


Figure B.6 Canopy volume (L) at previous measurement interval of a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata*, grouped by survival. Relationship between mean canopy volume, cumulative frost days and % deaths per site, of d) *A. arboreum*, e) *A. haworthii* and f) *C. orbiculata*.

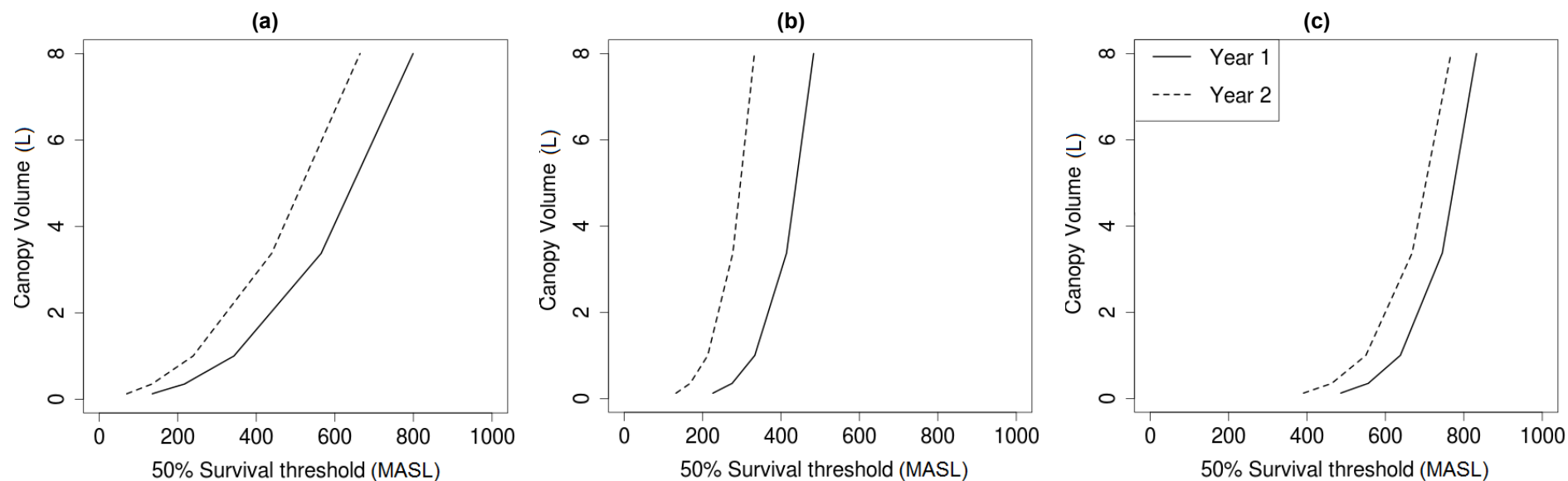


Figure B.7 Canopy volume required for 50% survival at a given elevation, in years 1 and 2, according to final models for a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata*. Predictions generated along a hypothetical gradient where frost increases linearly with elevation, and shade is set to zero.

Appendix C - Supporting information for Chapter 4

C.1 Road survey methodology

A presence/absence survey of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* was conducted on Banks Peninsula in 2010. I aimed to cover as much of the region as possible, encompassing a representative sample of all habitats and land use types. It was bounded by the end of Kaitorete spit in the West (- 43.856, 172.378 decimal degrees WGS 1984), Mount Pleasant in the North (- 43.555, 172.715), Le Bons Bay in the East (- 43.742, 173.102) and Waihuakina Bay in the South (- 43.898, 172.947). Surveys took place between January and April 2010, covering 844 grid cells of 30 arc-seconds (approximately 39% of the Peninsula's total area). I focussed in particular on areas pre-selected as likely to contain Crassulaceae or suitable habitat, based on species traits. Likely habitat included rocky outcrops, roadsides, sea-facing cliffs and areas close to population centres. I surveyed all bays, headlands and areas containing large rocky outcrops, as much as was accessible by road or foot and feasible within the time. To maximise efficiency over the large study area, surveys were conducted primarily along roadsides, driving slowly and stopping when *A. arboreum*, *A. haworthii* or *C. orbiculata* were seen. I recorded the species, GPS co-ordinates and estimated population size on the commonly used DAFOR scale (Dominant, Abundant, Frequent, Occasional, and Rare). Where road access was not possible, public walking tracks were used. I also surveyed some sea-facing cliffs by boat. All major roads, bays and likely presence locations were covered. Despite the inherent bias of road surveys, this method was used as all three species are often found on roadside cuttings, where surrounding dense vegetation or forest may be unsuitable. To minimise bias I took care to survey the main habitat types found in the region: grazing land, reserves, native and exotic forest, residential areas and seashore. I also covered a range of elevations between 0 and 800 MASL, aiming to survey as many rock outcrops as possible. A prior vegetation survey of all rock outcrops above 500 MASL on Banks Peninsula found no exotic Crassulaceae (Wiser & Buxton 2009), thus outcrops above 500 MASL were excluded and I focussed mainly on lower elevations. The resulting presence/absence data was combined with pre-existing occurrence data collected from external sources (Table B.1, total 32 additional grid cells) to map the species' distributions on Banks Peninsula and to select survey sites.

C.2 Supporting data

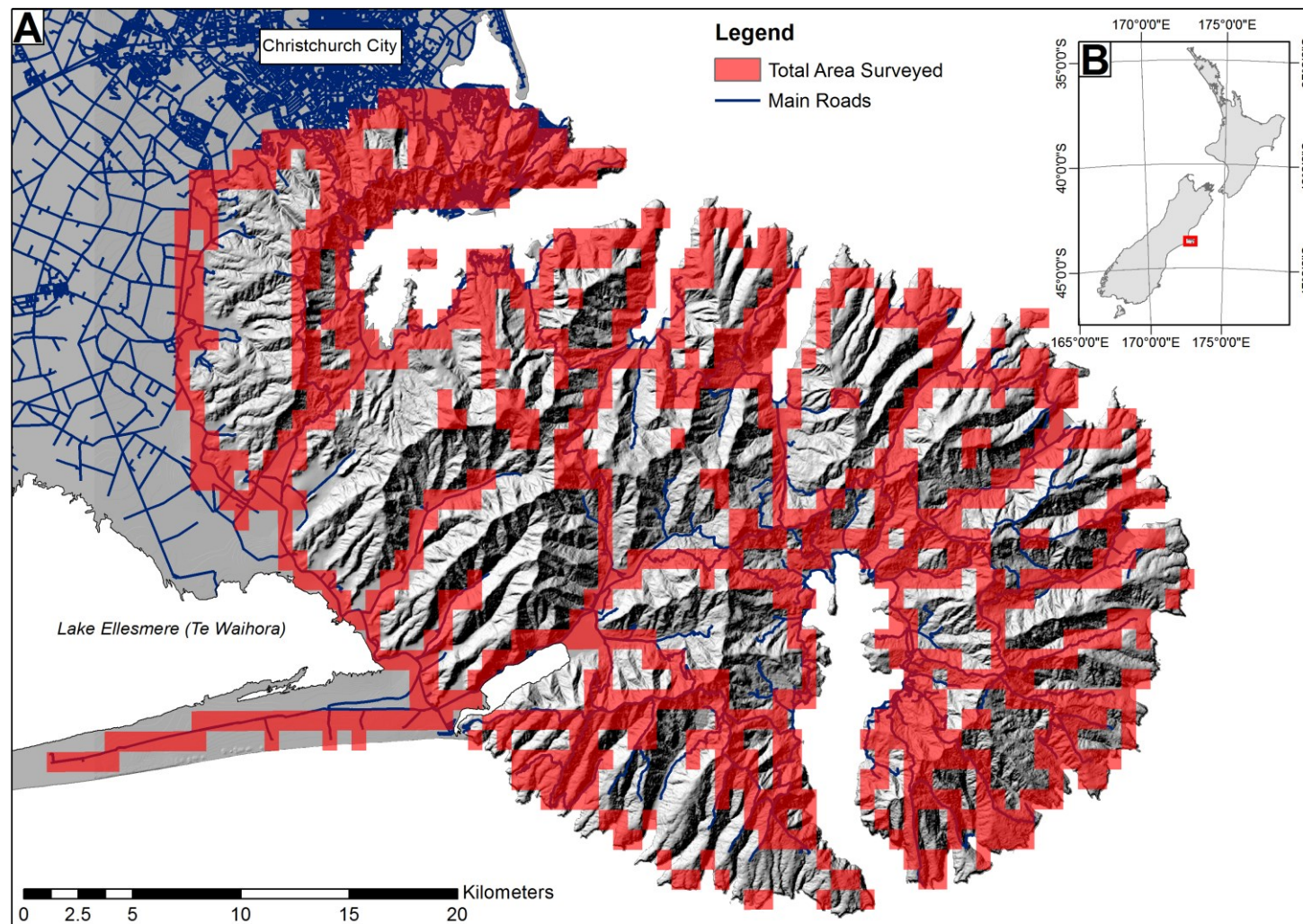


Figure C.1 All 30 arc-second cells surveyed for *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* on Banks Peninsula, b) extent indicator.

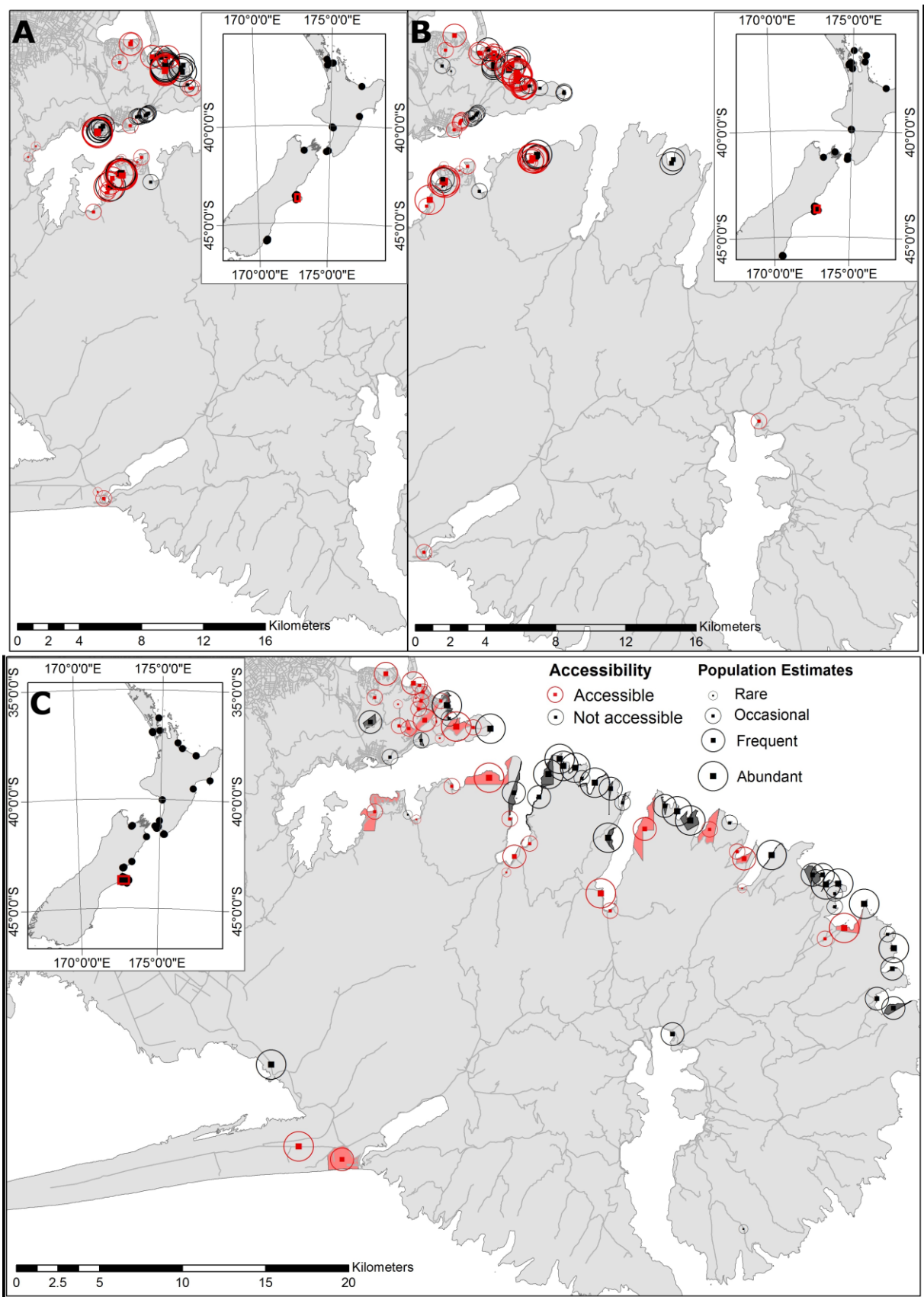


Figure C.2 Maps of populations of a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata* on Banks Peninsula. Inset maps show New Zealand presences of each species. Points on Banks Peninsula scaled by population size (Abundant = extensive, constant; Frequent = extensive, scattered; Occasional = few, scattered; Rare = one individual). Red points indicate accessible populations, black points inaccessible (e.g. cliffs). Road centrelines shown in dark grey.

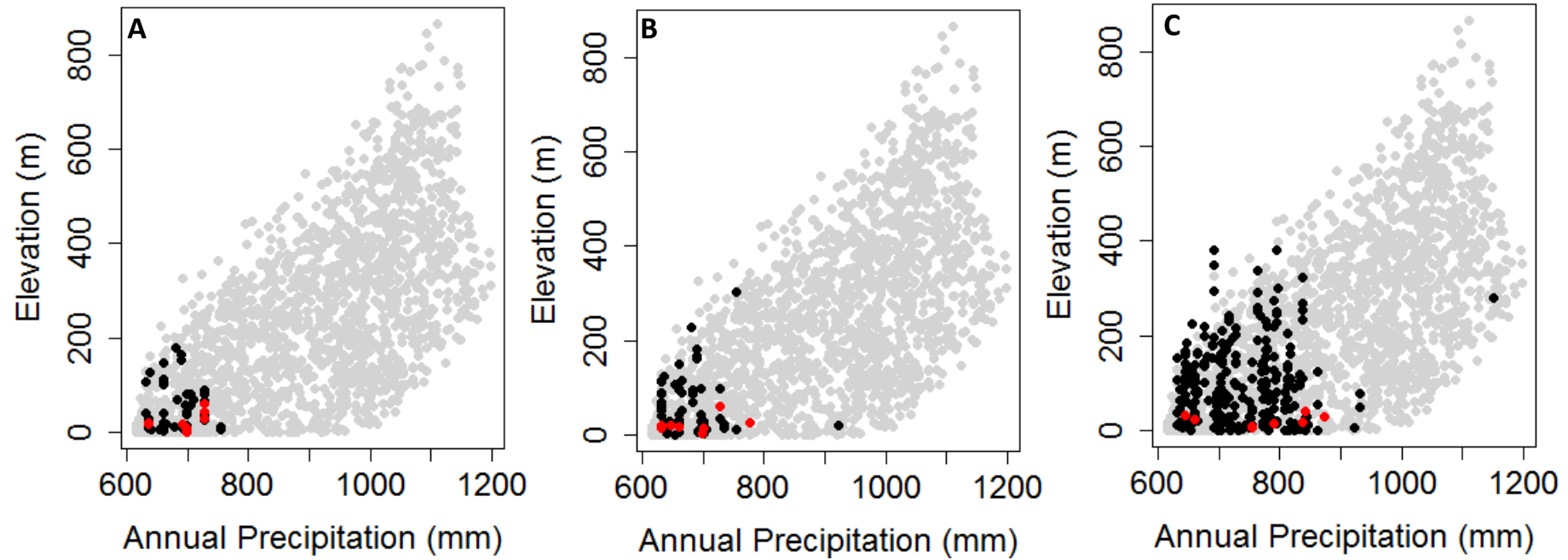


Figure C.3 Elevation vs. annual precipitation gradient across Banks Peninsula (grey), and at known populations of a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata* (black), and at sites chosen for surveys (red). Precipitation data taken from 30 arc-second Worldclim layer [(Hijmans *et al.* 2005), available at <http://www.worldclim.org/bioclim>].

Table C.1 Details of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* survey sites. Longitude and latitude given in decimal degrees (WGS 1984), elevation in MASL, aspect to the nearest cardinal point. Habitat and earthquake (EQ) damage are visual assessments, geological units from G.N.S. Science (2014). Categories of EQ damage are none, rock fall (RF) or landslides (LS), divided into small (S), moderate (M) and large (L).

| Species | Site | ID | Latitude | Longitude | Elevation | Aspect | Geological Unit | Habitat | EQ Damage |
|----------------------|---------------------------|------|----------|-----------|-----------|--------|----------------------------|-----------------------------------|-----------|
| <i>A. arboreum</i> | Church Bay 1 | CHB1 | -43.6344 | 172.7230 | 61 | W | Diamond Harbour Volcanics | Inland cliffs, exotic shrubs | RF (M) |
| | Church Bay 2 | CHB2 | -43.6342 | 172.7207 | 43 | N | Diamond Harbour Volcanics | Roadside loess, exotic shrubs | LS (S) |
| | Hays Bay 1 | HB1 | -43.6364 | 172.7155 | 27 | N | Allandale Rhyolite | Roadside loess, exotic shrubs | None |
| | Hays Bay 2 | HB2 | -43.6400 | 172.7129 | 17 | W | Allandale Rhyolite | Roadside loess, exotic shrubs | None |
| | Lyttelton Beach | LB | -43.6101 | 172.7034 | 0 | W | Governors Bay Andesite | Coastal cliffs, exotic shrubs | RF (S) |
| | Lyttelton Car Park | LCP | -43.6101 | 172.7041 | 8 | S | Governors Bay Andesite | Coastal cliffs, exotic shrubs | RF (L) |
| | North Sumner | NS | -43.5739 | 172.7582 | 18 | E | Lyttelton Volcanics | Inland cliffs, exotic shrubs | RF (L) |
| | South Sumner | SS | -43.5745 | 172.7579 | 15 | E | Lyttelton Volcanics | Inland cliffs, exotic shrubs | RF (M) |
| <i>A. haworthii</i> | Camp Bay 1 | CAB1 | -43.6226 | 172.7820 | 3 | N | Lyttelton Volcanics | Coastal cliffs, sparse vegetation | None |
| | Camp Bay 2 | CAB2 | -43.6221 | 172.7834 | 14 | N | Lyttelton Volcanics | Coastal clifftop, under pine | None |
| | Church Bay | CHB | -43.6348 | 172.7229 | 61 | W | Diamond Harbour Volcanics | Inland cliffs, exotic shrubs | RF (M) |
| | East Sumner Lifeboat | ESL | -43.5720 | 172.7715 | 13 | W | Lyttelton Volcanics | Coastal cliffs, exotic shrubs | RF (M) |
| | East Sumner Wading Pool | ESWP | -43.5740 | 172.7699 | 20 | W | Lyttelton Volcanics | Inland cliffs, exotic shrubs | RF (M) |
| | Hays Bay | HB | -43.6383 | 172.7143 | 26 | W | Allandale Rhyolite | Roadside loess, exotic shrubs | None |
| | Taylor's Mistake Beach | TMB | -43.5850 | 172.7781 | 17 | W | Lyttelton Volcanics | Coastal loess, sparse tussock | None |
| | Taylor's Mistake Roadside | TMR | -43.5801 | 172.7750 | 19 | E | Lyttelton Volcanics | Roadside loess, exotic shrubs | None |
| <i>C. orbiculata</i> | Birdlings Flat 1 | BF1 | -43.8260 | 172.7013 | 4 | NA | Holocene Shoreline Deposit | Beach shingle, exotic shrubs | None |
| | Birdlings Flat 2 | BF2 | -43.8253 | 172.7053 | 8 | NA | Holocene Shoreline Deposit | Beach shingle, depleted grass | None |
| | Godley Head 1 | GH1 | -43.5845 | 172.7795 | 21 | N | Lyttelton Volcanics | Coastal loess, grazed tussock | LS (S) |
| | Godley Head 2 | GH2 | -43.5869 | 172.7841 | 32 | N | Lyttelton Volcanics | Coastal loess, grazed tussock | LS (S) |
| | Okains Bay 1 | OB1 | -43.6958 | 173.0690 | 27 | W | Akaroa Volcanics | Coastal cliffs, sparse vegetation | None |
| | Okains Bay 2 | OB2 | -43.6975 | 173.0628 | 17 | W | Akaroa Volcanics | Coastal cliffs and grassland | None |
| | Pigeon Bay 1 | PB1 | -43.6490 | 172.9167 | 14 | E | Akaroa Volcanics | Coastal loess, grazed tussock | None |
| | Pigeon Bay 2 | PB2 | -43.6788 | 172.8900 | 39 | W | Mid Pleistocene Loess | Roadside loess, under pine | None |

Table C.2 Life stage categories used in surveys of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* on Banks Peninsula.

| Life stage | <i>A. arboreum</i> | <i>A. haworthii</i> | <i>C. orbiculata</i> |
|-----------------------|---|---|---|
| Seedling | ≤ one order of branching, stems not woody | < 5 cm tall, or if greater, no branching | < 10 cm tall, no branching, leaves < 4 cm long |
| Juvenile | ≥ one order of branching, thick woody stems, no evidence of flowering | ≥ two orders of branching, > 5 cm tall, no evidence of flowering | > 10 cm tall, one order of branching, large leaves, no evidence of flowering |
| Adult (not flowering) | Previous years' inflorescences visible or multi branched and > 30 cm tall | Previous years' inflorescences visible or fully developed into dense subshrub | Previous years' inflorescences visible or multi branched with fully formed leaves |
| Adult (flowering) | New inflorescences visible | New inflorescences visible | New inflorescences visible |

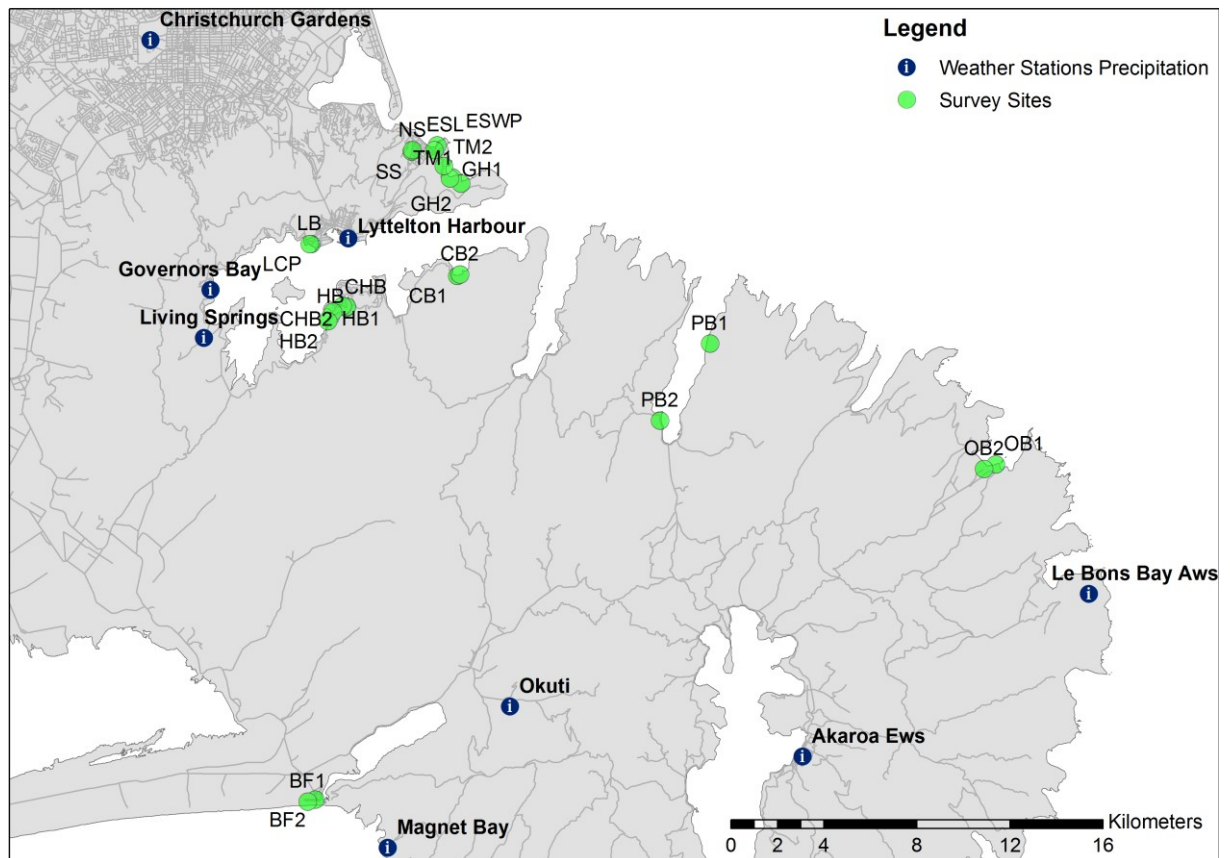


Figure C.4 Map of weather stations on Banks Peninsula ($n = 8$, dark blue points) with precipitation data for 2010 - 2012, the time period of flowering surveys. Survey sites ($n = 24$) shown as green points, all points labelled by site or station name, roads indicated by grey lines. Weather station data available from CliFlo (National Institute of Water and Atmospheric Research 2014).

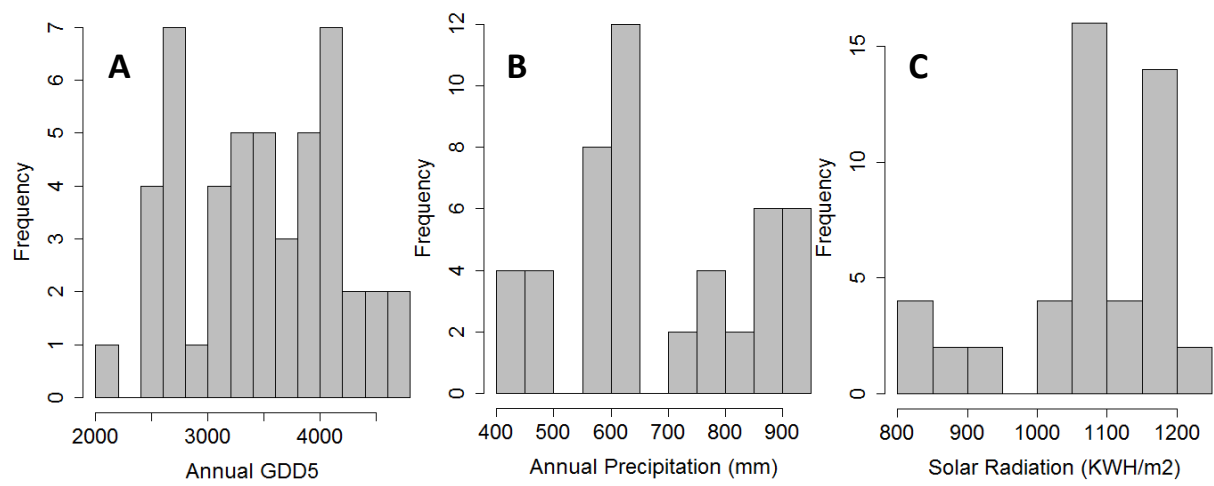


Figure C.5 Histograms of a) annual growing degree days base 5 (GDD5), b) annual precipitation (mm), and c) annual solar radiation (KWh/M²), at survey sites of all three target species. Data shown for both years of surveys. Temperature data taken from site data loggers, precipitation from the nearest weather station, and solar radiation modelled in ArcMap 10.1.

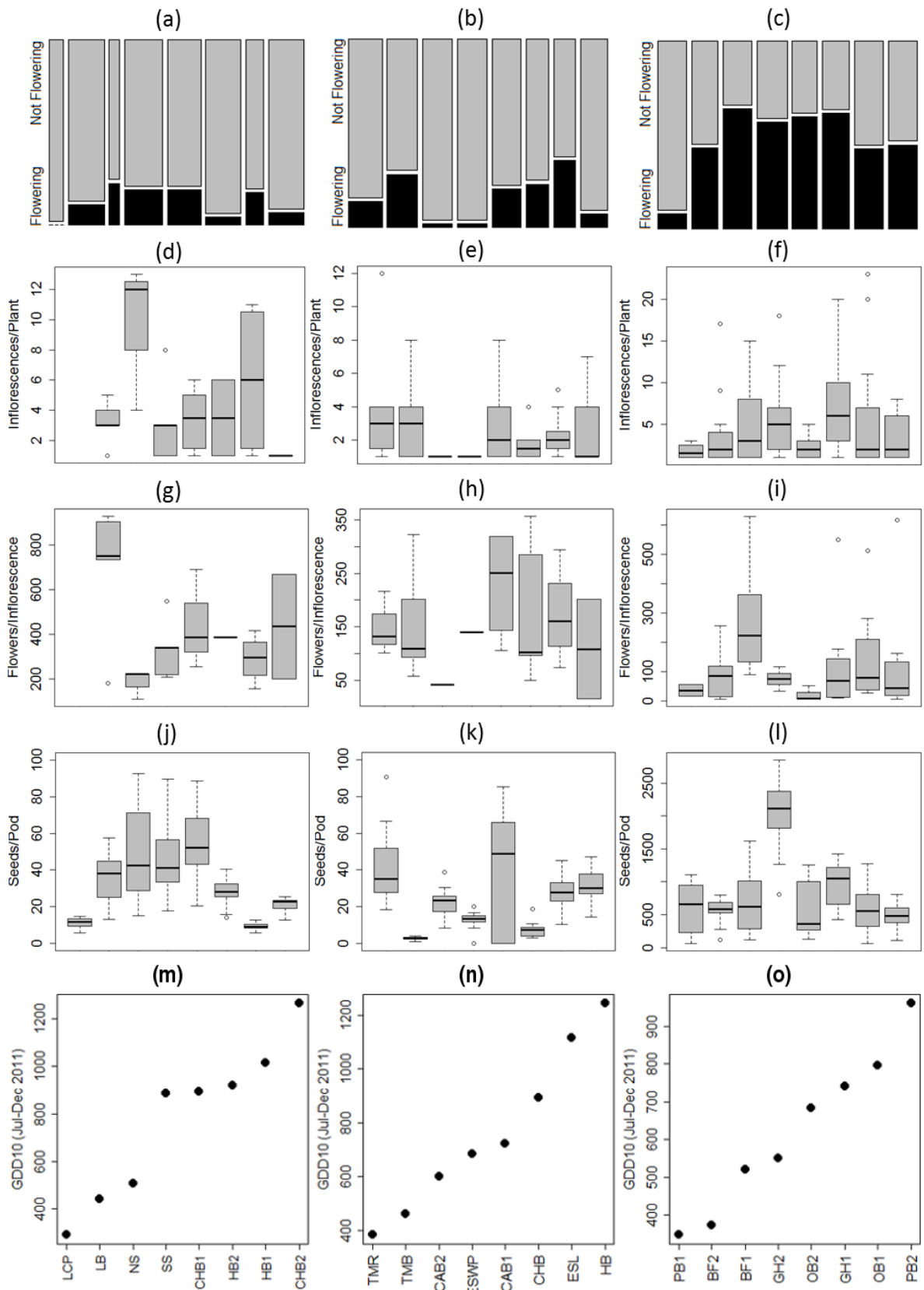


Figure C.6 Mosaic plots (a-c) and boxplots (d-l) of measured reproductive traits at survey sites in 2012. Columns, from left to right: *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*. Rows, from top to bottom: proportion of all plants flowering (black) and not flowering (grey) with thickness of bars scaled to sample size; and on flowering plants, inflorescences per plant; flowers per inflorescence; seeds per pod. Survey sites ordered by increasing GDD10, shown for each site (m-o).

Appendix D- Supporting information for Chapter 5

Table D.1 List of all point locations for which IPMs were run. Type denotes whether site is a weather station (WS; data available at <http://cliflo.niwa.co.nz/>), or a field experiment (FE) or survey site (FS; see Chapter 3 and Chapter 4). Longitude and latitude in decimal degrees (WGS 1984), elevation in MASL. Precip.WS denotes the ID of the weather station used for precipitation values for each site, also available through CliFlo, * denotes weather stations used for precipitation data only not listed in table, full names given below table. Species present indicates which species (*Aeonium arboreum*, *A. haworthii*, *Cotyledon orbiculata*) are present within the same 30-arc-second grid cell as the site.

| Site ID | Type | Full name | Long. | Lat. | Elev. | Precip.WS | Species present |
|---------|------|--------------------------------|----------|----------|-------|-----------|-----------------|
| AE | WS | Akaroa EWS | 172.9657 | -43.8094 | 45 | AE | Aa Ah Co |
| B1 | FE | Bowenvale 1 | 172.6551 | -43.5816 | 239 | CG | - |
| B2 | FE | Bowenvale 2 | 172.6493 | -43.5833 | 40 | CG | - |
| B3 | FE | Bowenvale 3 | 172.6519 | -43.5878 | 67 | CG | - |
| B4 | FE | Bowenvale 4 | 172.6517 | -43.5916 | 67 | CG | - |
| B5 | FE | Bowenvale 5 | 172.6445 | -43.6000 | 358 | GB* | - |
| B6 | FE | Bowenvale 6 | 172.6654 | -43.5953 | 340 | GB* | - |
| BF1 | FE | Birdlings Flat 1 | 172.7182 | -43.8141 | 8 | MB* | - |
| BF1_S | FS | Birdlings Flat 1 Survey | 172.7043 | -43.8261 | 4 | MB* | Aa Ah Co |
| BF2 | FE | Birdlings Flat 2 | 172.7197 | -43.8126 | 7 | MB* | - |
| BF2_S | FS | Birdlings Flat 2 Survey | 172.7053 | -43.8254 | 8 | MB* | Aa Ah Co |
| CA | WS | Christchurch Aero | 172.5370 | -43.4930 | 37 | CA | - |
| CAB1 | FS | Camp Bay 1 | 172.7835 | -43.6220 | 3 | LH | Ah Co |
| CAB2 | FS | Camp Bay 2 | 172.7852 | -43.6219 | 14 | LH | Ah Co |
| CG | WS | Christchurch Gardens | 172.6190 | -43.5310 | 7 | CG | - |
| CHB | FS | Church Bay | 172.7230 | -43.6344 | 61 | LS* | Aa Ah Co |
| CHB1 | FS | Church Bay 1 | 172.7230 | -43.6344 | 61 | LS* | Aa Ah Co |
| CHB2 | FS | Church Bay 2 | 172.7212 | -43.6343 | 43 | LS* | Aa Ah Co |
| CK1 | FE | Coopers Knob 1 | 172.6236 | -43.6532 | 477 | LS* | - |
| CK2 | FE | Coopers Knob 2 | 172.6233 | -43.6551 | 471 | LS* | - |
| CK3 | FE | Coopers Knob 3 | 172.6234 | -43.6556 | 476 | LS* | - |
| CK4 | FE | Coopers Knob 4 | 172.6236 | -43.6584 | 532 | LS* | - |
| CK5 | FE | Coopers Knob 5 | 172.6242 | -43.6610 | 552 | LS* | - |
| CK6 | FE | Coopers Knob 6 | 172.6240 | -43.6653 | 479 | LS* | - |
| CKSE | WS | Christchurch Kyle St EWS | 172.6077 | -43.5307 | 6 | CKSE | Ah |
| CNBP | WS | Christchurch New Brighton Pier | 172.7350 | -43.5060 | 12 | CG | Aa Ah Co |
| CP | FE | CP (Lyttelton) | 172.7149 | -43.6011 | 60 | LH | Aa Ah Co |
| ESL | FS | East Sumner Lifeboat | 172.7711 | -43.5724 | 13 | CG | Aa Ah Co |
| ESWP | FS | East Sumner Wading Pool | 172.7698 | -43.5740 | 20 | CG | Aa Ah Co |
| EW | FE | EW (Cashmere) | 172.6345 | -43.5690 | 40 | CG | Aa Ah |
| FT | FE | FT (Charteris Bay) | 172.7136 | -43.6386 | 35 | LS* | Aa Ah Co |
| GH1 | FS | Godley Head 1 | 172.7787 | -43.5847 | 21 | CG | Aa Ah Co |
| GH2 | FS | Godley Head 2 | 172.7837 | -43.5866 | 32 | CG | Aa Ah Co |
| GP1 | FE | Greenwood Park 1 | 172.7465 | -43.5741 | 200 | LH | - |
| GP2 | FE | Greenwood Park 2 | 172.7527 | -43.5776 | 167 | LH | Aa Ah Co |
| GP3 | FE | Greenwood Park 3 | 172.7403 | -43.5936 | 234 | LH | - |
| GP4 | FE | Greenwood Park 4 | 172.7418 | -43.5825 | 319 | GB* | Co |
| GP5 | FE | Greenwood Park 5 | 172.7440 | -43.5785 | 305 | GB* | - |
| GP6 | FE | Greenwood Park 6 | 172.7445 | -43.5884 | 285 | LH | Co |
| GPWT | FE | Greenwood Park Water Tanks | 172.7372 | -43.5856 | 370 | LH | Co |
| HB | FS | Hays Bay | 172.7145 | -43.6376 | 26 | LS* | Aa Ah Co |
| HB1 | FS | Hays Bay 1 | 172.7154 | -43.6363 | 27 | LS* | Aa Ah Co |
| HB2 | FS | Hays Bay 2 | 172.7136 | -43.6388 | 17 | LS* | Aa Ah Co |
| JK | FE | JK (Huntsbury) | 172.6537 | -43.5664 | 80 | CG | Aa Ah |
| JN | FE | JN (Church Bay) | 172.7238 | -43.6300 | 75 | LS* | Aa Ah Co |

| | | | | | | | |
|------|----|-------------------------|----------|----------|-----|------|----------|
| LB | FS | Lyttelton Beach | 172.7032 | -43.6101 | 0 | LH | Aa Ah |
| LBBA | WS | Le Bons Bay AWS | 173.1190 | -43.7460 | 236 | LBBA | Co |
| LBE | WS | Lincoln Broadfield EWS | 172.4704 | -43.6262 | 18 | LBE | Co |
| LCP | FS | Lyttelton Car Park | 172.7037 | -43.6103 | 8 | LH | Aa Ah |
| LH | WS | Lyttelton Harbour | 172.7240 | -43.6080 | 5 | LH | Aa Ah Co |
| LHCC | WS | Leeston Harts Creek CWS | 172.3116 | -43.7894 | 12 | LHCC | - |
| LR | WS | Leeston RAWS | 172.3049 | -43.7615 | 15 | LR | Co |
| MP1 | FE | Misty Peaks 1 | 172.9696 | -43.8226 | 153 | AE | - |
| MP2 | FE | Misty Peaks 2 | 172.9703 | -43.8222 | 148 | AE | - |
| MP3 | FE | Misty Peaks 3 | 172.9709 | -43.8348 | 516 | AE | - |
| MP4 | FE | Misty Peaks 4 | 172.9722 | -43.8472 | 642 | LBBA | - |
| MP5 | FE | Misty Peaks 5 | 172.9825 | -43.8228 | 527 | AE | - |
| MP6 | FE | Misty Peaks 6 | 172.9989 | -43.8326 | 653 | LBBA | - |
| NS | FS | North Sumner | 172.7585 | -43.5736 | 18 | CG | Aa Ah Co |
| OB1 | FS | Okains Bay 1 | 173.0695 | -43.6959 | 27 | LBBA | Co |
| OB2 | FS | Okains Bay 2 | 173.0644 | -43.6970 | 17 | LBBA | Co |
| PB1 | FS | Pigeon Bay 1 | 172.8913 | -43.6822 | 14 | LBBA | Co |
| PB2 | FS | Pigeon Bay 2 | 172.9153 | -43.6571 | 39 | LBBA | Co |
| RE | WS | Rangiora EWS | 172.6111 | -43.3286 | 23 | RE | - |
| RH | FE | RH (Heathcote) | 172.7127 | -43.5784 | 40 | LH | - |
| SH1 | FE | Scarborough Hill 1 | 172.7524 | -43.5871 | 78 | LH | Ah Co |
| SH2 | FE | Scarborough Hill 2 | 172.7610 | -43.5879 | 295 | LH | Co |
| SH3 | FE | Scarborough Hill 3 | 172.7678 | -43.5936 | 180 | LH | Co |
| SH4 | FE | Scarborough Hill 4 | 172.7693 | -43.5932 | 180 | LH | Co |
| SLA | WS | Sugar Loaf AWS | 172.6490 | -43.6050 | 466 | GB* | - |
| SS | FS | South Sumner | 172.7583 | -43.5745 | 15 | CG | Aa Ah Co |
| TMB | FS | Taylor's Mistake Beach | 172.7783 | -43.5848 | 17 | CG | Aa Ah Co |
| TMR | FS | Taylor's Mistake Road | 172.7747 | -43.5831 | 19 | CG | Aa Ah Co |
| TO1 | FE | Te Oka 1 | 172.7883 | -43.8379 | 130 | MB* | - |
| TO2 | FE | Te Oka 2 | 172.7864 | -43.8454 | 60 | MB* | - |
| TO3 | FE | Te Oka 3 | 172.7749 | -43.8578 | 39 | MB* | - |
| TO4 | FE | Te Oka 4 | 172.7718 | -43.8569 | 38 | MB* | - |
| TO5 | FE | Te Oka 5 | 172.7743 | -43.8502 | 61 | MB* | - |
| TO6 | FE | Te Oka 6 | 172.7760 | -43.8361 | 316 | MB* | - |
| TO7 | FE | Te Oka 7 | 172.7845 | -43.8238 | 483 | OK* | - |
| TO8 | FE | Te Oka 8 | 172.8169 | -43.8133 | 681 | OK* | - |
| TO9 | FE | Te Oka 9 | 172.8228 | -43.8158 | 616 | OK* | - |
| TO10 | FE | Te Oka 10 | 172.8202 | -43.8225 | 567 | OK* | - |

* GB = Governors Bay; MB = Magnet Bay; LS = Living Springs; OK = Okuti

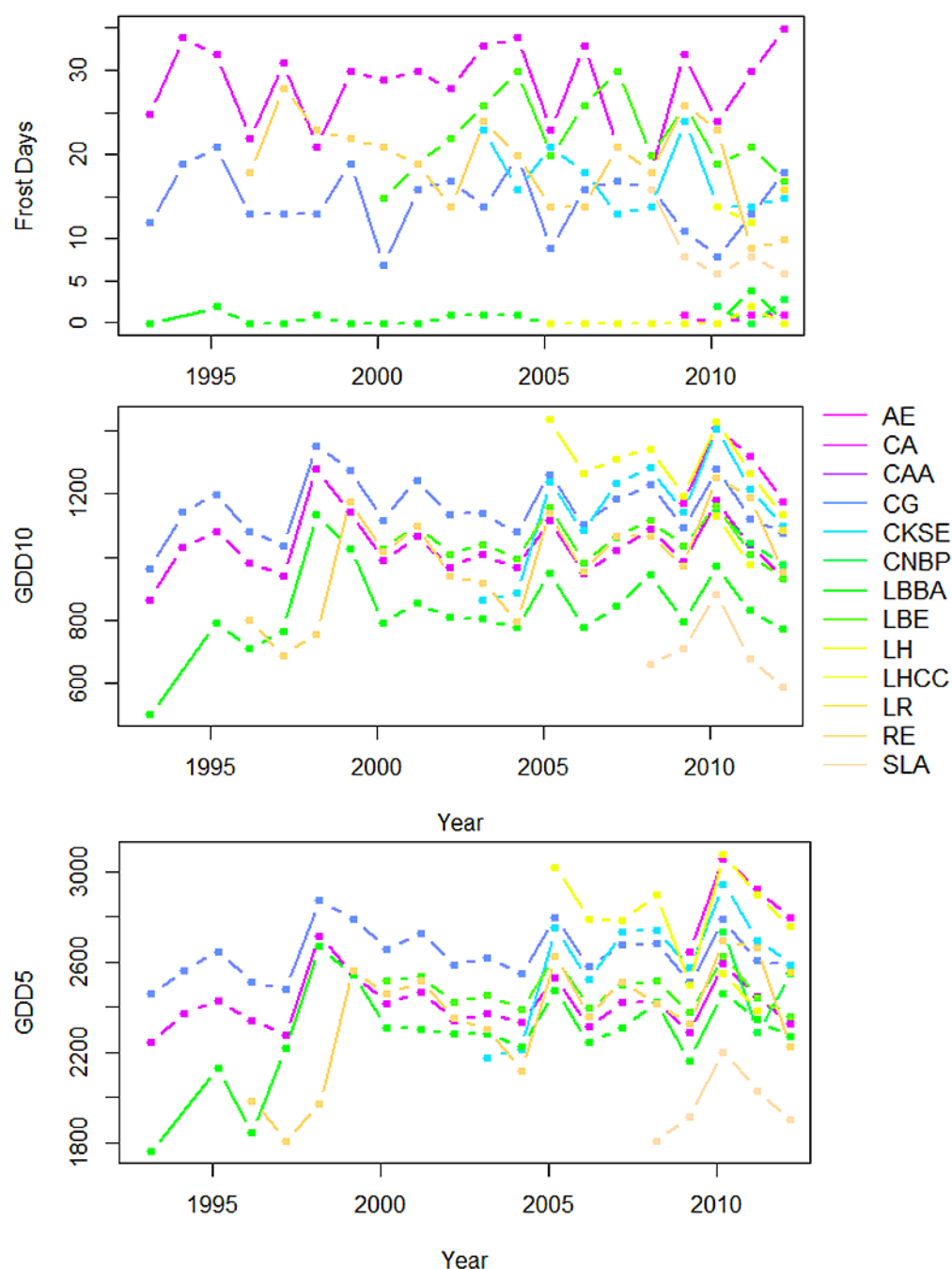


Figure D.1 Annual frost days, GDD10 and GDD5 from 1992-2012, at weather stations used as IPM locations (see Table D.1 for abbreviations)

Table D.2 Paired t-test results for mean annual frost days, GDD5 and GDD10 at weather stations used as IPM locations. Results given for 2-year versus 5-year, 10-year and 20-year means, with degrees of freedom (DF), t and p-values. Significant results indicated in bold.

| Variable | Two vs Five Year | | | Two vs Ten Year | | | Two vs Twenty Year | | |
|----------|------------------|------|----------------------------|-----------------|------|------|--------------------|--------|------|
| | DF | t | p | DF | t | p | DF | t | p |
| Frost | 9 | 0.38 | 0.71 | 6 | 0.70 | 0.51 | 4 | 0.51 | 0.64 |
| GDD5 | 9 | 3.23 | 0.01 | 6 | 0.86 | 0.42 | 4 | - 0.94 | 0.40 |
| GDD10 | 9 | 8.03 | 2 x 10⁻⁵ | 6 | 2.07 | 0.08 | 4 | 0.10 | 0.93 |

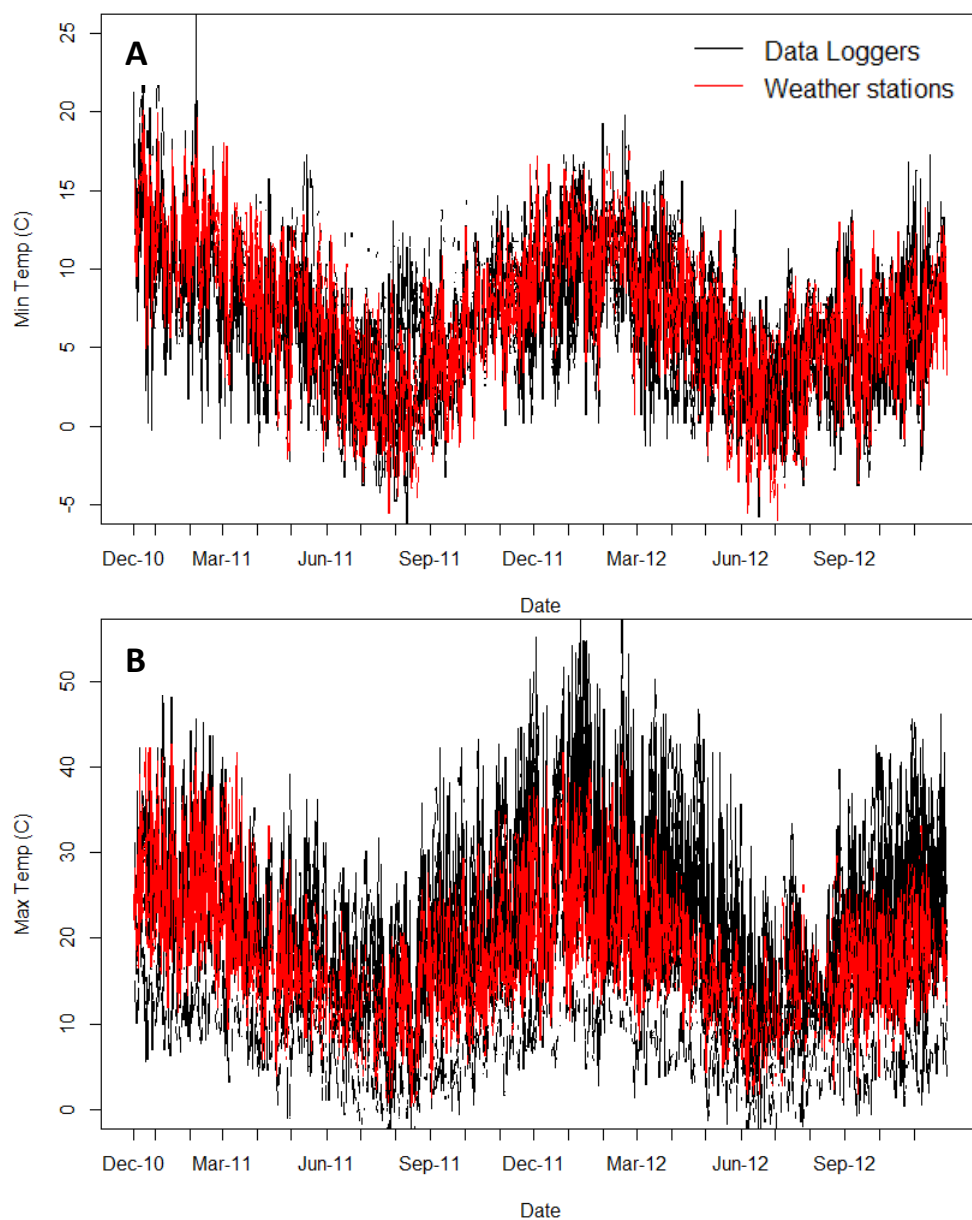


Figure D.2 a) Daily minimum and b) daily maximum temperatures, between December 2010 and November 2011, at sites with data loggers (black) and at weather stations (red).

Table D.3 Minimum, mean and maximum correlations (r) between data logger sites and the nearest weather station over 2011-2012. Minimum and maximum temperature rescaled as residuals of the site sample mean before calculating correlation coefficient.

| Temperature °C | Minimum r | Mean r | Maximum r |
|----------------|-------------|----------|-------------|
| Daily Minimum | 0.56 | 0.85 | 0.92 |
| Daily Maximum | 0.38 | 0.54 | 0.67 |

a) Population Vector

$$\begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}$$

The initial population is given in a vector, where each value is the number of individuals in each size class. In the IPM, this would have length 1000, all with values being 0.

b) Survival Vector

$$\begin{bmatrix} S_0 \\ S_1 \\ S_2 \\ S_3 \\ S_4 \end{bmatrix}$$

The survival vector gives the probability of an individual in each size class surviving the time step. Applied to the IPM, this would have 1000 values, each one calculated by integrating the survival kernel as a function of plant size and site variables.

c) Growth Matrix

$$\begin{bmatrix} P_{0,0} & P_{1,0} & P_{2,0} & P_{3,0} & P_{4,0} \\ P_{0,1} & P_{1,1} & P_{2,1} & P_{3,1} & P_{4,1} \\ P_{0,2} & P_{1,2} & P_{2,2} & P_{3,2} & P_{4,2} \\ P_{0,3} & P_{1,3} & P_{2,3} & P_{3,3} & P_{4,3} \\ P_{0,4} & P_{1,4} & P_{2,4} & P_{3,4} & P_{4,4} \end{bmatrix}$$

The growth matrix gives the probability of an individual transitioning to another size class in each time step (for example, the probability of an individual of size 2 becoming size 3 is represented here by $P_{2,3}$. In the IPM, this is a matrix of 1000 x 1000 cells, with each cell value calculated by integrating the growth kernel as a function of plant size and site variables.

d) Fecundity Matrix

$$\begin{bmatrix} 0 & F_{1,0} & F_{2,0} & F_{3,0} & F_{4,0} \\ 0 & 0 & F_{2,1} & F_{3,1} & F_{4,1} \\ 0 & 0 & 0 & F_{3,2} & F_{4,2} \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

The fecundity matrix gives the number of new individuals produced per existing individuals in each size class. In this example, I have imagined that new individuals produced in each time step may vary in size between size classes 0 and 2, and size classes 1-4 can reproduce. For example, the number of new offspring of size 1 produced by an individual of size 4 is given by $F_{4,1}$. The same applies to the IPM, where the matrix measures 1000 x 1000 and cell values are calculated by integrating the fecundity kernel, along with the minimum size & probability distribution of new offspring.

Figure D.3 Structure of a Lefkovitch Matrix Model (size-structured). Lefkovitch matrices are conceptually similar to IPMs. In this example, there are 5 size classes, 4 of which are reproductive, and individuals may grow, shrink or stay the same size in each time step. Graphical representations of the IPM results of these components are given in Figure D.4, Figure D.5 and Figure D.6 (the reader should note that the matrices are transposed in the IPM, but the same concepts apply).

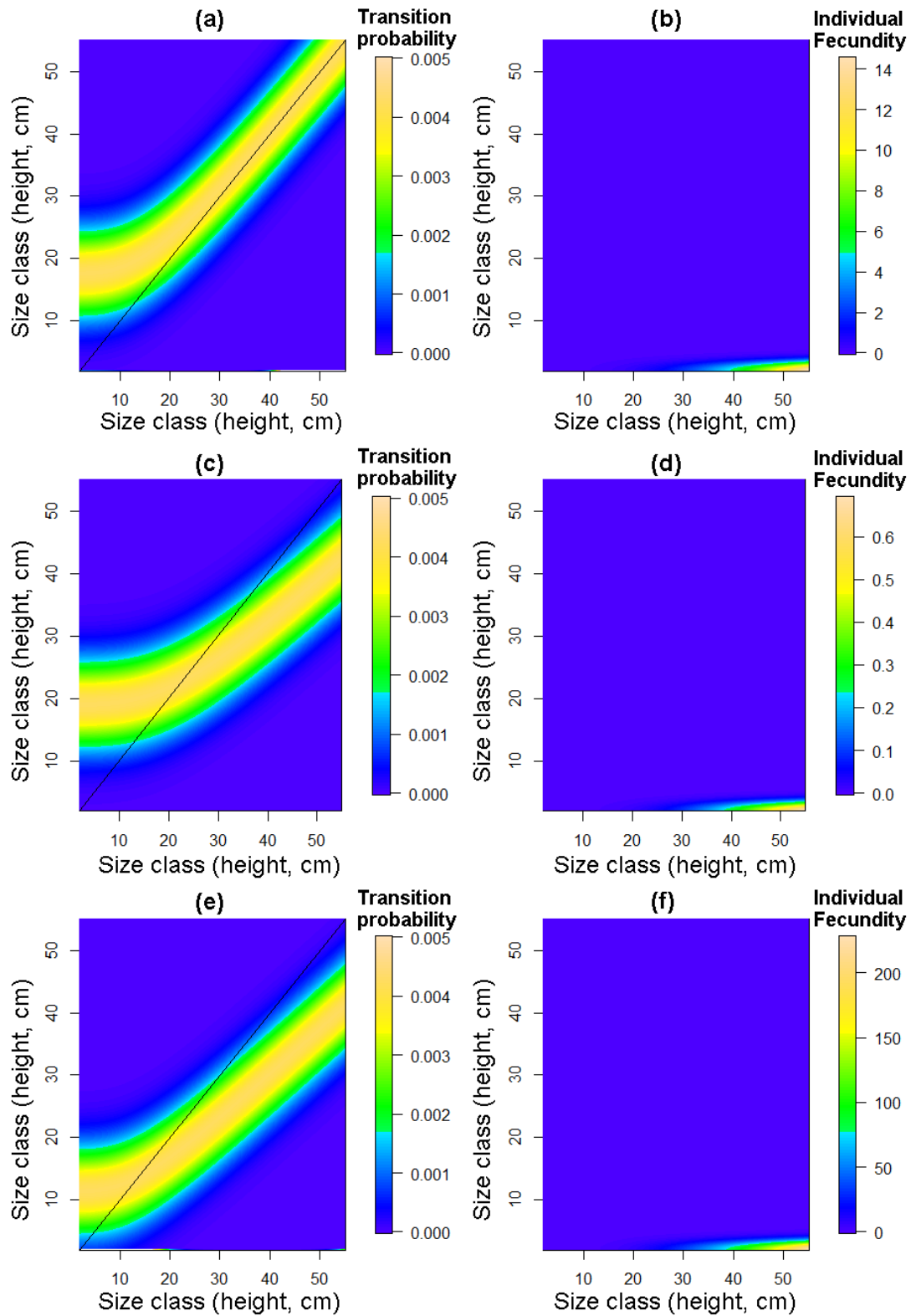


Figure D.4 Growth matrices (left) and fecundity matrices (right) at climatically good sites (upper 95th percentile of λ) for *Aeonium arboreum* (OB1; a, b), *A. haworthii* (LCP; c, d) and *Cotyledon orbiculata* (LB; e, f). Unit of plant size is cm (approximately equal to height). Colours show transition probabilities between size classes (growth matrices) and individual fecundity (fecundity matrices).

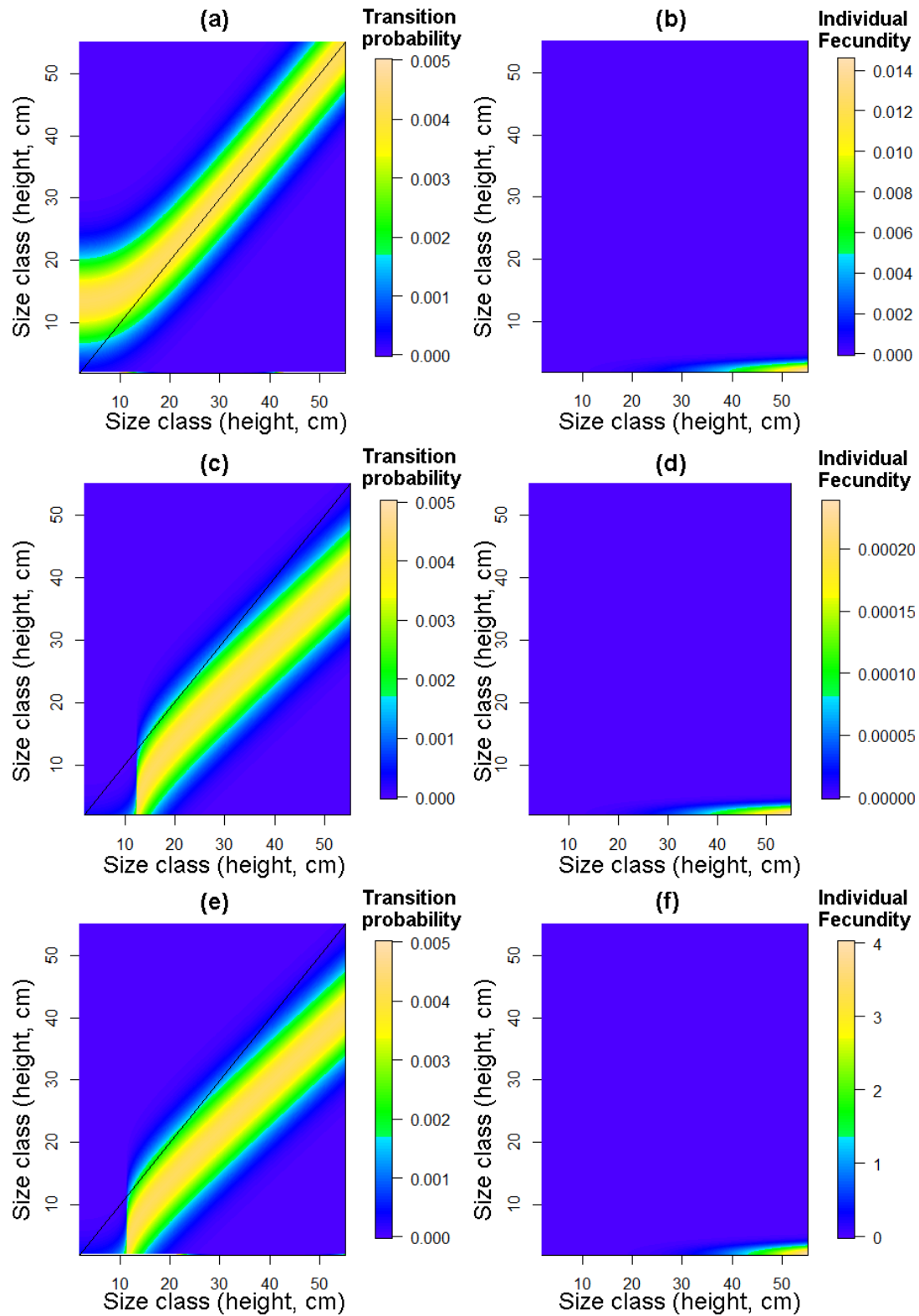


Figure D.5 Growth matrices (left) and fecundity matrices (right) at climatically poor sites (lower 95th percentile of λ) for *Aeonium arboreum* (MP5; a, b), *A. haworthii* (TO8; c, d) and *Cotyledon orbiculata* (TO8; e, f). Unit of plant size is cm (approximately equal to height). Colours show transition probabilities between size classes (growth matrices) and individual fecundity (fecundity matrices).

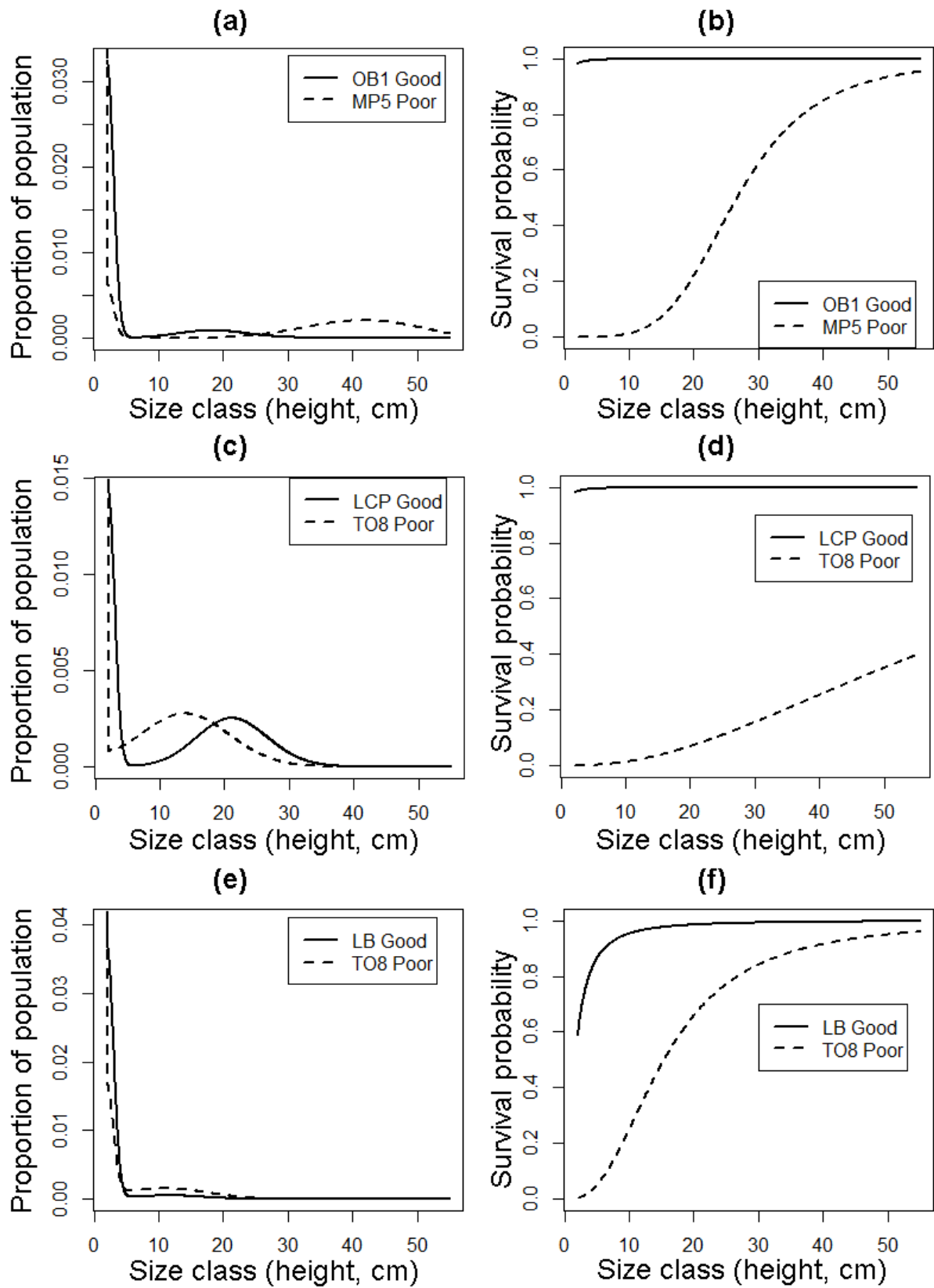


Figure D.6 Stable size distributions (left) and probability of survival versus plant size (right) for IPMs of *Aeonium arboreum* (a, b), *A. haworthii* (c, d) and *Cotyledon orbiculata* (e, f), at climatically “good” and “poor” sites (upper and lower 95th percentiles of λ). Site ID indicated in legend, size classes based on plant height (cm).

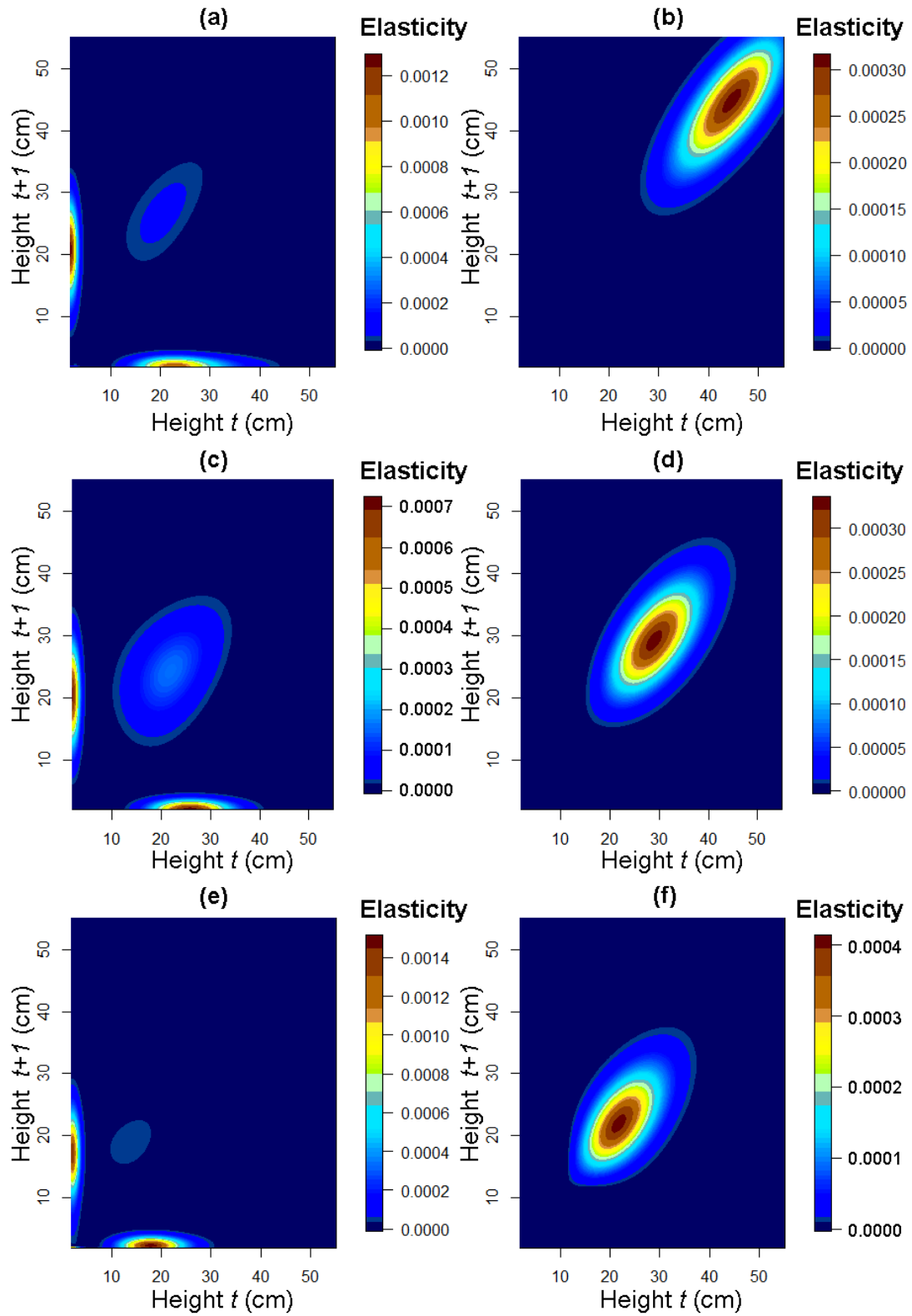


Figure D.7 Elasticity plots of IPM matrices at climatically good sites (left, upper 95th percentile of λ) and poor sites (right, lower 95th percentile of λ) for *Aeonium arboreum* (a, b), *A. haworthii* (c, d) and *Cotyledon orbiculata* (e, f). Plant size units are cm (height).

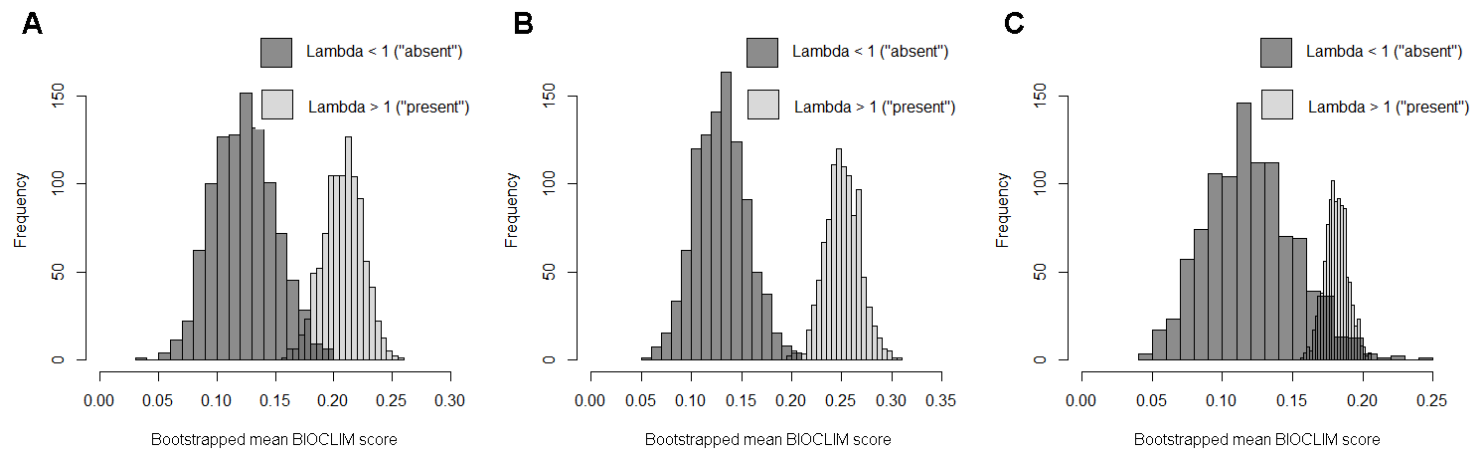


Figure D.8 Bootstrapped distributions ($n=1000$) of mean BIOCLIM scores at IPM locations where $\lambda > 1$ (climate suitable) and < 1 (climate unsuitable), for a) *Aeonium arboreum*, b) *A. haworthii* and c) *Cotyledon orbiculata*.

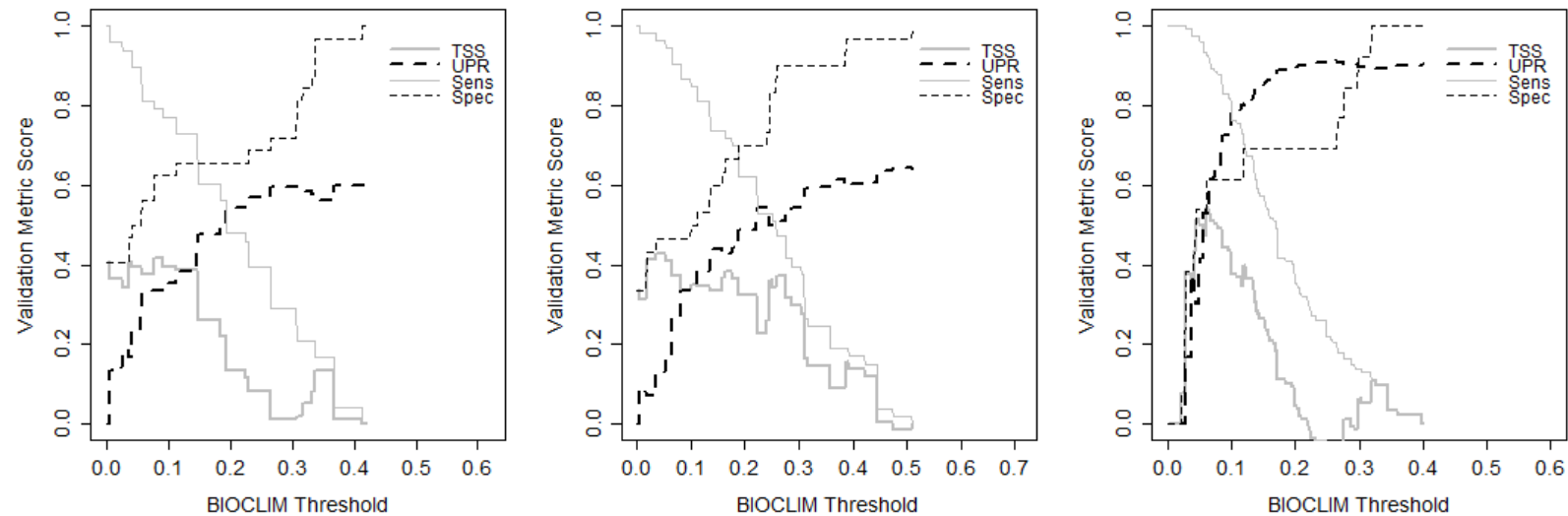


Figure D.9 True skill statistic (TSS), under prediction rate (UPR), sensitivity and specificity of BIOCLIM projections assessed against IPM predictions and true presences, after iterative raising of suitability threshold, for a) *Aeonium arboreum*, b) *A. haworthii* and *Cotyledon orbiculata*.

Appendix E - Herbicide trial results

E.1 Rationale

In November 2012, at the end of the field transplant experiment on Banks Peninsula (Chapter 3), all field sites were sprayed with herbicide and left in place for six weeks. Plants were sprayed primarily to minimize chance of escape and to comply with the requirements of the permission to propagate *C. orbiculata* granted by MPI. However, there is no quantitative data on herbicide effectiveness against *Aeonium arboreum*, *A. haworthii* or *Cotyledon orbiculata*, so although spraying may be an option for future control of the species, time and resources are likely to be wasted trialling different control options. To investigate, I tested the effectiveness of six different herbicides against the study species. After six weeks, plant damage was assessed, plant material removed and sites re-sprayed with the most affective of the six herbicides.

E.2 Methods

Each site was sprayed with one of the six herbicides commonly used by the Port Hills Rangers for weed control. Base herbicides were Glyphosate 1% (Roundup); Picloram 0.6% (Grazon) and Metsulfuron-Methyl 1% (Escort) in aqueous solution. Because it was possible that water-based herbicides might fail to penetrate the waxy leaves of the study species, I trialled each herbicide with and without additional penetrant (Pulse™ for Roundup, and Silmaxx™ for Escort and Grazon). I assigned herbicides randomly to sites within bins of low, medium and high elevation, balancing number of sample sizes between treatments. Each site was sprayed using a hand-held sprayer in dry conditions, at a rate of 1 L solution per 4 m². After 6 weeks, I returned and recorded mortality and plant damage on a scale of 0 – 5 (**Error! Reference source not found.**), excluding plants that were dead prior to spraying. Individuals were recorded as dead only if severe internal cellular damage was found, as over the course of the experiment individuals had regenerated from dried stems.

Table E.1 Scale used for visual assessment of damage to *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata* six weeks after herbicide treatment.

| Score | Description |
|-------|---|
| 0 | No visible damage |
| 1 | Mild damage to leaf margins |
| 2 | Mild damage to whole plant, or severe damage to leaf margins |
| 3 | Moderate damage to whole plant |
| 4 | Severe damage to whole plant, or almost dead |
| 5 | Dead – severe internal cellular damage, no chance of recovery |

E.3 Results

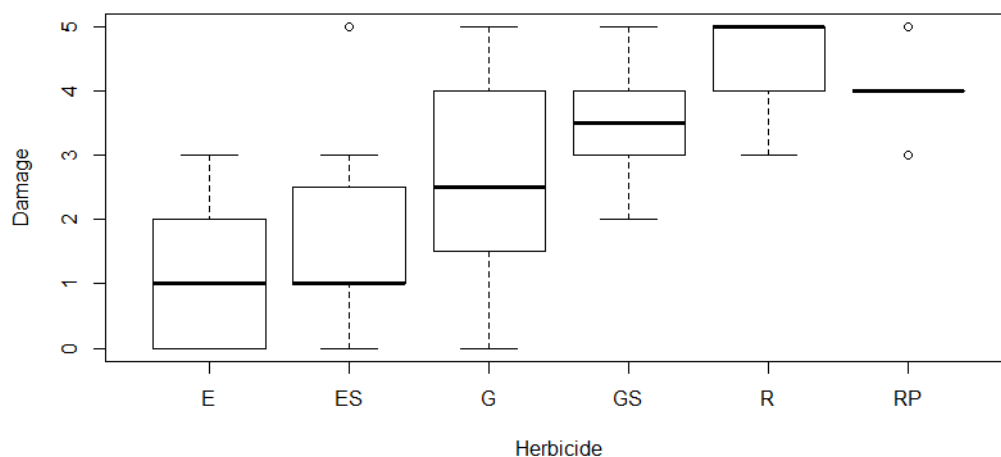


Figure E.1 Damage to *Aeonium arboreum* plants (0 = no damage, 5 = complete mortality, see Table E.1) after spraying with Escort (E), Escort with Silmaxx (ES), Grazon (G), Grazon with Silmaxx (GS), Roundup (R), and Roundup with Pulse (RP).

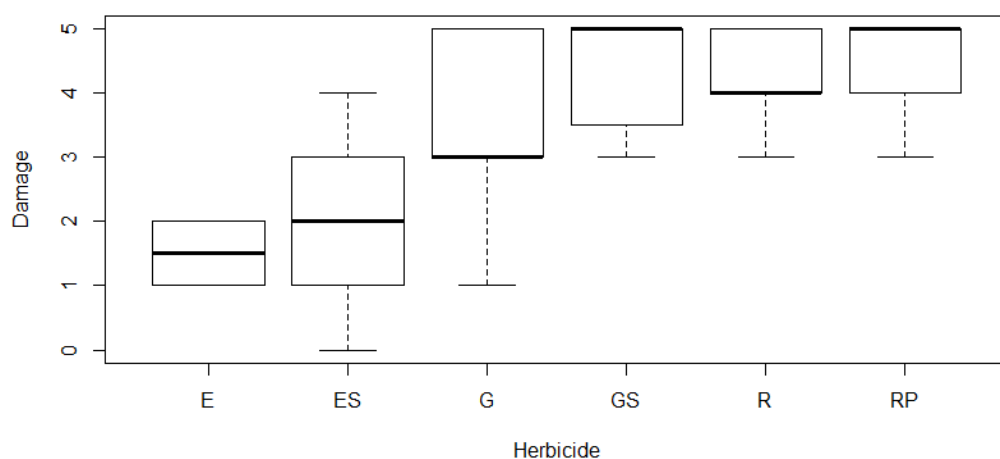


Figure E.2 Damage to *Aeonium haworthii* plants (0 = no damage, 5 = complete mortality, see Table E.1) after spraying with Escort (E), Escort with Silmaxx (ES), Grazon (G), Grazon with Silmaxx (GS), Roundup (R), and Roundup with Pulse (RP).

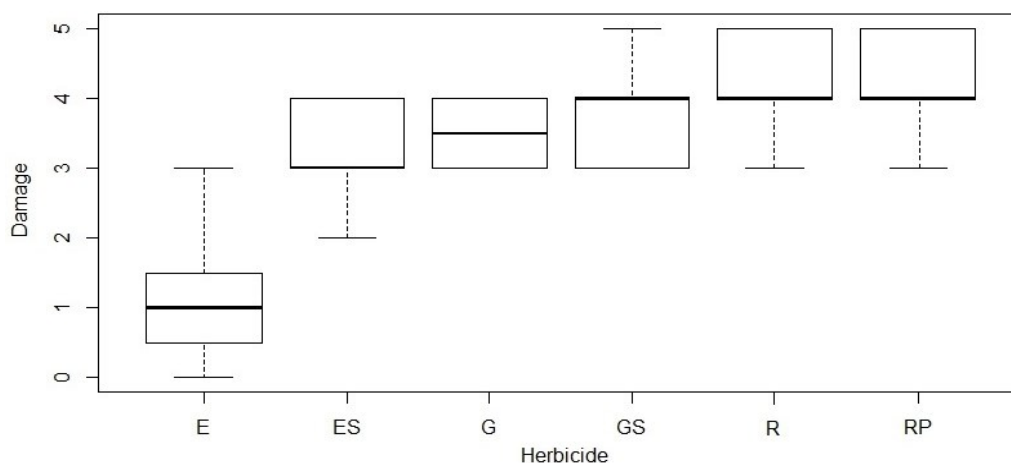


Figure E.3 Damage to *Cotyledon orbiculata* plants (0 = no damage, 5 = complete mortality, see Table E.1) after spraying with Escort (E), Escort with Silmaxx (ES), Grazon (G), Grazon with Silmaxx (GS), Roundup (R), and Roundup with Pulse (RP).









| Site / Herbicide | Before herbicide treatment | After herbicide treatment |
|----------------------------|---|--|
| TO2 / Escort |  |  |
| MP2 / Escort Silmaxx |  |  |
| B3 / Grazon |  |  |
| TO7 / Grazon Silmaxx |  |  |



Figure E.4 Examples of before and six weeks after herbicide treatment at selected field sites. Commercial name of herbicide given in table, site names correspond to Table B.2.

E.4 Summary

Glyphosate (Roundup) was the most effective of the three base herbicides, causing severe damage or complete mortality to the majority of plants in all three species. Addition of the penetrant Pulse increased effectiveness of Glyphosate against *A. haworthii*. Grazon (Picloram) was also relatively effective against *A. haworthii*, especially with the addition of Silmaxx, but was only lethal to minority of *A. arboreum* and *C. orbiculata* plants. Escort had a very minor effect on plant health, though with the addition of Silmaxx it was nearly as effective as Grazon against *C. orbiculata*. Based on these results I tentatively recommend Glyphosate, with or without Pulse, for control of the three species. However, it would be beneficial to repeat similar trials in wild populations.

Supplementary materials

S.1 - IPM coefficients

Table S.1 Coefficients used in IPMs of *Aeonium arboreum*, *A. haworthii* and *Cotyledon orbiculata*.

| Coefficient | Value | | |
|---|--------------------|---------------------|----------------------|
| | <i>A. arboreum</i> | <i>A. haworthii</i> | <i>C. orbiculata</i> |
| Summer Survival Intercept | 4.939 | 4.335 | 3.104 |
| Summer Survival Slope (Volume ι) | 1.602 | 2.224 | 1.824 |
| Summer Survival Slope (Elevation) | -1.424 | -1.580 | |
| Winter Survival Intercept | 4.370 | 3.039 | 7.515 |
| Winter Survival Slope (Volume ι) | 4.013 | 1.713 | 1.633 |
| Winter Survival Slope (Cumulative Frost) | -7.726 | -8.185 | -13.489 |
| Growth Intercept | 7479.518 | 3176.283 | 2711.492 |
| Growth Slope (Elevation) | -1802.254 | -1213.649 | -308.353 |
| Growth Slope (Elevation ²) | -2615.438 | | -826.492 |
| Growth Slope (Annual Frost) | | -1737.254 | |
| Growth Slope (Volume ι) | 0.922 | 0.413 | 0.404 |
| Growth SD | 5 | 5 | 5 |
| P[Flower] Intercept | -4.100 | -4.434 | -0.257 |
| P[Flower] Slope (Volume ι) | 6.461 | 7.669 | 4.593 |
| P[Flower] Slope (GDD10) | 0.802 | | |
| P[Flower] Slope (Radiation) | | | 1.079 |
| Germination Intercept | -7.983 | -7.337 | -9.346 |
| Germination Slope (GDD5) | 1.111 | | |
| Germination Slope (Annual Frost) | -2.913 | | |
| Germination Slope (Annual Precipitation) | -1.329 | | -2.453 |
| Germination Slope (Elevation) | | -2.575 | |
| Establishment Probability | 1 | 1 | 1 |
| Recruit Size Mean | 2 | 2 | 2 |
| Recruit Size SD | 1 | 1 | 1 |
| Inflorescences per Plant Intercept | 1.360 | 0.912 | 1.151 |
| Inflorescences per Plant Slope (Volume ι) | | | 1.592 |
| Flowers per Inflorescence Intercept | 5.707 | 4.882 | 4.029 |
| Flowers per Inflorescence Slope (Volume ι) | | | 1.593 |
| Seeds per Pod Intercept | 2.654 | 2.580 | 7.202 |
| Seeds per Pod Slope (Pods per Inflorescence) | 0.101 | | 1.617 |

S.2 - R code for IPMs, adapted from Merow, Dahlgren, *et al.* (2014)

```
### Read in parameters, variables and mean/sd log volumes ###
vols<-read.table("mean_log_vols.txt", header=T, sep="\t")
vols<-subset(vols, Species=="Species")
attach(vols)
params<-read.table("params.txt", header=T, sep="\t") # coefficients
elevg<-read.table("elev_growth.txt", header=T, sep="\t") ## variables

##### define the matrix #####
min.size=2 # minimum height observed
max.size=55 # maximum height observed
n=1000 # number of cells in matrix
b=min.size+c(0:n)*(max.size-min.size)/n # boundary points
y=0.5*(b[1:n]+b[2:(n+1)]) # mesh points
h=y[2]-y[1] # step size

Math.cbrt <- function(x) {
  sign(x) * abs(x)^(1/3)
} # function for cube root for rescaling volume to height

##### run the matrix #####
ld<-as.data.frame(setNames(replicate(83, numeric(1),simplify=F),
names(elevg))) # make empty lambda data frame

### create loop and run matrix for each site ###
## presented below for A. arboreum. For other species modify kernels ##

for(i in 1:83){

## survival kernel
s.x=function(x, params) {
  us= exp(params$ssurv.int+params$ssurv.slopeE*elevs[,i]+
    params$ssurv.slopeV*((log(x^3)-smlv)/sslv))
  ssurv=us/(1+us) # summer survival
  ws=exp(params$wsurv.int+params$wsurv.slopeV*((log(x^3)-wmlv)/wslv)+
    params$wsurv.slopeF*cumfrost[,i])
  wsurv=ws/(1+ws) # winter survival
  return(ssurv*wsurv) # annual survival
}

## growth kernel
g.yx = function (xp, x, params) {
  (dnorm(xp, mean=
Math.cbrt(params$growth.int+params$growth.slopeE*elevg[,i]+
  params$growth.slopeE2*(elevg[,i]^2)+params$growth.slopeS*(x^3)),
  sd=params$growth.sd))
} # calculate growth, translate back to height for matrix

## fecundity kernel step 1
# P(reproduce) flowering * germination probability
p.reproduce = function (x, params) {
  (exp(params$pfl.int+params$pfl.slopeV*((log(x^3)-fmlv)/fslv)+
    params$pfl.slopeG*gddl0[,i]))
  /(1+(exp(params$pfl.int+params$pfl.slopeV*((log(x^3)-
    fmlv)/fslv)+params$pfl.slopeG*gddl0[,i])))*)
```



```

      (exp(params$germ.int+params$germ.slopeG*gdd5[,i]+params$germ.slopeF*
annfrost[,i]+params$germ.slopeP*precip[,i]))
    / (1+(exp(params$germ.int+params$germ.slopeG*gdd5[,i]
      +params$germ.slopeF*annfrost[,i]+params$germ.slopeP*precip[,i])))
  }

## final fecundity kernel
# p(reproduce) x seed output
f.yx<-function(xp,x, params) {
  p.reproduce(x,params)*
  params$establishment.prob*
  dnorm(xp, mean=params$recruit.size.mean, sd=params$recruit.size.sd)*
  exp(params$inf.pl.int)*exp(params$fl.inf.int)*
  (exp(params$seed.int+params$seed.slopeP*((log(params$fl.inf)-sdmlv)/
sds1v)))
}

### apply kernels to matrix ###
G = h*outer(y,y,g.yx, params=params) # growth matrix
S = s.x(y, params=params) # survival matrix
Fc = h*outer(y,y,f.yx, params=params) # fecundity matrix
P=G # placeholder; redefine P on next line
for (j in 1:(n)) {
  G[1,j]<-G[1,j]+1-sum(G[,j])
  P[,j]<-G[,j]*S[j]
} # growth/survival matrix
K=P+Fc # full IPM matrix

### write lambdas ####

ld[,i]<-(lam=Re(eigen(K)$values[1]))

}

```

References

- Aarssen, L.W. & Taylor, D.R. (1992) Fecundity allocation in herbaceous plants. *Oikos*, **65**, 225-232.
- Aguirre-Gutiérrez, J., Carvalheiro, L.G., Polce, C., van Loon, E.E., Raes, N., Reemer, M. & Biesmeijer, J.C. (2013) Fit-for-purpose: species distribution model performance depends on evaluation criteria – Dutch hoverflies as a case study. *PLoS ONE*, **8**, e63708.
- Ahmed, S.E., McInerny, G., O'Hara, K., Harper, R., Salido, L., Emmott, S. & Joppa, L.N. (2015) Scientists and software – surveying the species distribution modelling community. *Diversity and Distributions*, **21**, 258-267.
- Aikio, S., Duncan, R.P. & Hulme, P.E. (2010) Lag-phases in alien plant invasions: separating the facts from the artefacts. *Oikos*, **119**, 370-378.
- Alamo, E.C., Aguilar, M.d.A., Arencibia, M.C.L. & De La Torre, W.W. (1996) Estudio seminal, germinativo y de plántulas de la flora vascular endémica canaria. I. Crassulaceae (1a parte). *Vieraea*, **25**, 7-30.
- Alexander, J.M., Edwards, P.J., Poll, M., Parks, C.G. & Dietz, H. (2009) Establishment of parallel altitudinal clines in traits of native and introduced forbs. *Ecology*, **90**, 612-622.
- Alexander, J.M., Kueffer, C., Daehler, C.C., Edwards, P.J., Pauchard, A., Seipel, T., Consortium, M., Arévalo, J., Cavieres, L., Dietz, H., Jakobs, G., McDougall, K., Naylor, B., Otto, R., Parks, C.G., Rew, L. & Walsh, N. (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences*, **108**, 656-661.
- Alexander, J.M., Naylor, B., Poll, M., Edwards, P.J. & Dietz, H. (2009) Plant invasions along mountain roads: the altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges. *Ecography*, **32**, 334-344.
- Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223-1232.
- Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W. & Brook, B.W. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society of London B: Biological Sciences*, **276**, 1415-1420.
- Angert, A.L. & Schemske, D.W. (2005) The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. *Evolution*, **59**, 1671.
- Anon (1866) Cure for corns. *Nelson Evening Mail*, p. 3. New Zealand.
- Anon (1871) Horticultural society's show. *Evening Post*, p. 2. New Zealand.
- Anon (1920) The garden: hardy flowers. *New Zealand Herald*, p. 2. New Zealand.
- Anon (1950) *Aeonium canariensis*. *The Journal of the Cactus and Succulent Society of New Zealand*, Vol. 3, pp. 7-8.
- Aragón, P., Baselga, A. & Lobo, J.M. (2010) Global estimation of invasion risk zones for the western corn rootworm *Diabrotica virgifera virgifera*: integrating distribution models and physiological thresholds to assess climatic favourability. *Journal of Applied Ecology*, **47**, 1026-1035.
- Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677-1688.
- Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693-695.
- Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504-1513.
- Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527-1539.
- AsureQuality (2006) AgriBase enhanced LCDB2. Auckland, New Zealand.
- Auckland Regional Council (2007) Regional pest management strategy 2007-2012 for the Auckland region. Ministry of Primary Industries, Auckland, New Zealand: Author.
- Badano, E.I., Villarroel, E., Bustamante, R.O., Marquet, P.A. & Cavieres, L.A. (2007) Ecosystem engineering facilitates invasions by exotic plants in high-Andean ecosystems. *Journal of Ecology*, **95**, 682-688.

- Baret, S., Maurice, S., Bourgeois, T.L. & Strasberg, D. (2004) Altitudinal variation in fertility and vegetative growth in the invasive plant *Rubus alceifolius* Poiret (Rosaceae), on Réunion island. *Plant Ecology*, **172**, 265-273.
- Barker, D.H., Seaton, G.G.R. & Robinson, S.A. (1997) Internal and external photoprotection in developing leaves of the CAM plant *Cotyledon orbiculata*. *Plant, Cell & Environment*, **20**, 617-624.
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J. & Villalobos, F. (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling*, **222**, 1810-1819.
- Baskin, C.C. & Baskin, J.M. (1998) Types of seed dormancy. *Seeds* (eds C.C. Baskin & J.M. Baskin), pp. 27-47. Academic Press, San Diego.
- Bateman, B.L., VanDerWal, J., Williams, S.E. & Johnson, C.N. (2012) Biotic interactions influence the projected distribution of a specialist mammal under climate change. *Diversity and Distributions*, **18**, 861-872.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4, R package version 1.1-7, <http://CRAN.R-project.org/package=lme4>.
- Bennie, J., Hill, M.O., Baxter, R. & Huntley, B. (2006) Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology*, **94**, 355-368.
- Black, C.C. (1973) Photosynthetic carbon fixation in relation to net CO₂ uptake. *Annual Review of Plant Physiology*, **24**, 253-286.
- Boffa Miskell (2007) Banks Peninsula landscape study. Final report for Christchurch City Council, Christchurch, New Zealand: Author.
- Bonhomme, R. (2000) Bases and limits to using 'degree.day' units. *European Journal of Agronomy*, **13**, 1-10.
- Booth, T.H., Nix, H.A., Busby, J.R. & Hutchinson, M.F. (2014) BIOCLIM : the first species distribution modelling package, its early applications and relevance to most current MAXENT studies. *Diversity and Distributions*, **20**, 1-9.
- Botha, C.J. (2013) Krimpsiekte in South Africa: historical perspectives. *Journal of the South African Veterinary Association*, **84**, 1-5.
- Botha, C.J., Crafford, J.E., Butler Jr, V.P., Stojanovic, M.N. & Labuschagne, L. (2007) A potential krimpsiekte vaccine. *Onderstepoort Journal of Veterinary Research*, **74**, 307-314.
- Botha, C.J. & Penrith, M.L. (2008) Poisonous plants of veterinary and human importance in southern Africa. *Journal of Ethnopharmacology*, **119**, 549-558.
- Bradley, B.A., Blumenthal, D.M., Wilcove, D.S. & Ziska, L.H. (2010) Predicting plant invasions in an era of global change. *Trends in Ecology & Evolution*, **25**, 310-318.
- Bramwell, D. & Bramwell, Z.I. (1990) *Flores silvestres de las Islas Canarias*, 3 edn. Editorial Rueda, Madrid, Spain.
- Breiman, L. (2001) Random forests. *Machine Learning*, **45**, 5-32.
- Breiman, L., Friedman, J., Stone, C.J. & Olshen, R.A. (1984) *Classification and regression trees*. CRC Press.
- Briere, J.-F., Pracros, P., Roux, A.-Y.L. & Pierre, J.-S. (1999) A novel rate model of temperature-dependent development for arthropods. *Environmental Entomology*, **28**, 22-29.
- Broennimann, O., Fitzpatrick, M.C., Heenan, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C.H. & Guisan, A. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, **21**, 481-497.
- Broennimann, O. & Guisan, A. (2008) Predicting current and future biological invasions: both native and invaded ranges matter. *Biology Letters*, **4**, 585-589.
- Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701-709.
- Brook, B.W., Akcakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G. & Araujo, M.B. (2009) Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters*, **5**, 723-725.
- Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028-2043.
- Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597-623.

- Brown, K.A., Spector, S. & Wu, W. (2008) Multi-scale analysis of species introductions: combining landscape and demographic models to improve management decisions about non-native species. *Journal of Applied Ecology*, **45**, 1639-1648.
- Buckley, Lauren B. (2008) Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *The American Naturalist*, **171**, E1-E19.
- Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010) Can mechanism inform species' distribution models? *Ecology Letters*, **13**, 1041-1054.
- Burrows, C. (2001) Additions to the flora of Otamahua/Quail Island. *Canterbury Botanical Society Journal*, **35**, 87-89.
- Cadotte, M.W. & Lovett-Doust, J. (2001) Ecological and taxonomic differences between native and introduced plants of southwestern Ontario. *Écoscience*, **8**, 230-238.
- Cameron, E.K. (1996) North Piha, Whites Beach and Fishermans Rock. *Auckland Botanical Society Journal*, **51**, 11-20.
- Carpenter, G., Gillison, A.N. & Winter, J. (1993) DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity & Conservation*, **2**, 667-680.
- Carter, D. (2006) Port Hills and Banks Peninsula rock outcrop surveys 2006-2010. Christchurch City Council, Christchurch, New Zealand.
- Carter, D. (2014) Banks peninsula coastal cliffs aerial vegetation survey, October 2012. pp. 1-10. Christchurch City Council, Christchurch, New Zealand.
- Caswell, H. (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, **81**, 619-627.
- Cohen, J. (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, **41**, 687-699.
- Collevatti, R.G., Terribile, L.C., Lima-Ribeiro, M.S., Nabout, J.C., de Oliveira, G., Rangel, T.F., Rabelo, S.G. & Diniz-Filho, J.A.F. (2012) A coupled phylogeographical and species distribution modelling approach recovers the demographical history of a neotropical seasonally dry forest tree species. *Molecular Ecology*, **21**, 5845-5863.
- Collingham, Y.C., Wadsworth, R.A., Huntley, B. & Hulme, P.E. (2000) Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. *Journal of Applied Ecology*, **37**, 13-27.
- Conlisk, E., Syphard, A.D., Franklin, J., Flint, L., Flint, A. & Regan, H. (2013) Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. *Global Change Biology*, **19**, 858-869.
- Daws, M.I., Kabadajic, A., Manger, K. & Kranner, I. (2007) Extreme thermo-tolerance in seeds of desert succulents is related to maximum annual temperature. *South African Journal of Botany*, **73**, 262-265.
- de Villiers, M., Hattingh, V. & Kriticos, D.J. (2013) Combining field phenological observations with distribution data to model the potential distribution of the fruit fly *Ceratitis rosa* Karsch (Diptera: Tephritidae). *Bulletin of Entomological Research*, **103**, 60-73.
- Dean, C., Day, J., Gozlan, R.E. & Diaz, A. (2015) Grazing vertebrates promote invasive swamp stonecrop (*Crassula helmsii*) abundance. *Invasive Plant Science and Management*, **8**, 131-138.
- DeFerrari, C.M. & Naiman, R.J. (1994) A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. *Journal of Vegetation Science*, **5**, 247-258.
- Department of Agriculture and Fisheries (2013) Mother-of-millions (*Bryophyllum delagoense*). Department of Agriculture and Fisheries, Queensland Government, Queensland, Australia: Author.
- Di Febbraro, M., Lurz, P.W.W., Genovesi, P., Maiorano, L., Girardello, M. & Bertolino, S. (2013) The use of climatic niches in screening procedures for introduced species to evaluate risk of spread: a case with the American Eastern grey squirrel. *PLoS ONE*, **8**, e66559.
- Dorazio, R.M. (2014) Accounting for imperfect detection and survey bias in statistical analysis of presence-only data. *Global Ecology and Biogeography*, **23**, 1472-1484.
- Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B. & Singer, A. (2012) Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, **39**, 2119-2131.
- Drake, J.M. (2014) Ensemble algorithms for ecological niche modeling from presence-background and presence-only data. *Ecosphere*, **5**, 76.

- Drake, J.M. (2015) Range bagging: a new method for ecological niche modelling from presence-only data. *Journal of The Royal Society Interface*, **12**, 20150086.
- Drake, J.M., Randin, C. & Guisan, A. (2006) Modelling ecological niches with support vector machines. *Journal of Applied Ecology*, **43**, 424-432.
- Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000) Size-specific sensitivity: applying a new structured population model. *Ecology*, **81**, 694-708.
- Ebeling, S.K., Welk, E., Auge, H. & Bruelheide, H. (2008) Predicting the spread of an invasive plant: combining experiments and ecological niche model. *Ecography*, **31**, 709-719.
- Edwards, K.R., Adams, M.S. & Kvet, J. (1998) Differences between European native and American invasive populations of *Lythrum salicaria*. *Applied Vegetation Science*, **1**, 267-280.
- Elith, J. (2013) Predicting distributions of invasive species. *arXiv preprint*. arXiv:1312.0851.
- Elith, J. & Graham, C.H. (2009) Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography*, **32**, 66-77.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.M., Townsend Peterson, A., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129-151.
- Elith, J., Kearney, M. & Phillips, S. (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, **1**, 330-342.
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677-697.
- Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802-813.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43-57.
- Elith, J., Simpson, J., Hirsch, M. & Burgman, M.A. (2013) Taxonomic uncertainty and decision making for biosecurity: spatial models for myrtle/guava rust. *Australasian Plant Pathology*, **42**, 43-51.
- Eller, B.M. & Ferrari, S. (1997) Water use efficiency of two succulents with contrasting CO₂ fixation pathways. *Plant, Cell & Environment*, **20**, 93-100.
- Ellner, Stephen P. & Rees, M. (2006) Integral projection models for species with complex demography. *The American Naturalist*, **167**, 410-428.
- Elton, C.S. (1927) *Animal Ecology*. The MacMillan Company, New York, NY, USA.
- Environmental Systems Research Institute (2011) ArcGIS Desktop: Release 10. ESRI, Redlands, CA.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38-49.
- Fort, J., Cherel, Y., Harding, A.M.A., Egevang, C., Steen, H., Kuntz, G., Porter, W.P. & Grémillet, D. (2010) The feeding ecology of little auks raises questions about winter zooplankton stocks in North Atlantic surface waters. *Biology Letters*, **6**, 682-684.
- Fourcade, Y., Engler, J.O., Rödder, D. & Secondi, J. (2014) Mapping species distributions with MaxEnt using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. *PLoS ONE*, **9**, e97122.
- Fox, G.A. & Kendall, B.E. (2002) Demographic stochasticity and the variance reduction effect. *Ecology*, **83**, 1928-1934.
- Franklin, J. (2010) Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, **16**, 321-330.
- Franklin, J., Regan, H.M. & Syphard, A.D. (2014) Linking spatially explicit species distribution and population models to plan for the persistence of plant species under global change. *Environmental Conservation*, **41**, 97-109.
- Friedman, J.H. (1991) Multivariate adaptive regression splines. *The Annals of Statistics*, **19**, 1-67.
- Fu, P. & Rich, P.M. (1999) Design and implementation of the Solar Analyst: an ArcView extension for modeling solar radiation at landscape scales. *Proceedings of the Nineteenth Annual ESRI User Conference*, pp. 1-31.
- Fuller, T.C. & McClintock, E. (1988) Crassulaceae, Stonecrop Family. *Poisonous Plants of California* pp. 124-127. University of California Press, Oakland, CA, USA.

- G.N.S. Science (2014) New Zealand geology web map. URL <http://data.gns.cri.nz/geology/> [accessed 06/01/2015].
- Gallagher, R.V., Beaumont, L.J., Hughes, L. & Leishman, M.R. (2010) Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *Journal of Ecology*, **98**, 790-799.
- Gerber, M.A. (1985) The relationship of plant size to self-pollination in *Mertensia ciliata*. *Ecology*, **66**, 762-772.
- Ghazoul, J. (2002) Flowers at the front line of invasion? *Ecological Entomology*, **27**, 638-640.
- Gitay, H., Roxburgh, S.H. & Wilson, J.B. (1991) Species-area relations in a New Zealand tussock grassland, with implications for nature reserve design and for community structure. *Journal of Vegetation Science*, **2**, 113-118.
- Givnish, T.J. (1984) Leaf and Canopy Adaptations in Tropical Forests. *Physiological Ecology of Plants of the Wet Tropics* (eds E. Medina, H.A. Mooney & C. Vazquez-Yanes), pp. 51-84. Springer, Netherlands.
- Godsoe, W. (2010) Regional variation exaggerates ecological divergence in niche models. *Systematic Biology*, **59**, 298-306.
- Godsoe, W. & Harmon, L.J. (2012) How do species interactions affect species distribution models? *Ecography*, **35**, 811-820.
- Golicher, D., Ford, A., Cayuela, L. & Newton, A. (2012) Pseudo-absences, pseudo-models and pseudo-niches: pitfalls of model selection based on the area under the curve. *International Journal of Geographical Information Science*, **26**, 2049-2063.
- González-Moreno, P., Diez, J.M., Richardson, D.M. & Vilà, M. (2015) Beyond climate: disturbance niche shifts in invasive species. *Global Ecology and Biogeography*, **24**, 360-370.
- Goodwin, B.J., McAllister, A.J. & Fahrig, L. (1999) Predicting invasiveness of plant species based on biological information. *Conservation Biology*, **13**, 422-426.
- Gould, S.J. & Vrba, E.S. (1982) Exaptation - a missing term in the science of form. *Paleobiology*, **8**, 4-15.
- Greiner, M., Pfeiffer, D. & Smith, R.D. (2000) Principles and practical application of the receiver-operating characteristic analysis for diagnostic tests. *Preventive Veterinary Medicine*, **45**, 23-41.
- Griffith, T.M. & Watson, M.A. (2006) Is evolution necessary for range expansion? Manipulating reproductive timing of a weedy annual transplanted beyond its range. *The American Naturalist*, **167**, 153-164.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*, 1 edn. John Wiley and Sons, New York, NY, USA.
- Grime, J.P. & Hunt, R. (1975) Relative growth-rate: its range and adaptive significance in a local flora. *Journal of Ecology*, **63**, 393-422.
- Grinnell, J. (1917) The niche-relationships of the California thrasher. *The Auk*, **34**, 427-433.
- Groves, R.H., Lonsdale, M. & Boden, R. (2005) *Jumping the garden fence: invasive garden plants in Australia and their environmental and agricultural impacts*. WWF Australia, Ultimo, NSW, Australia.
- Guichard, S., Guis, H., Tran, A., Garros, C., Balenghien, T. & Kriticos, D.J. (2014) Worldwide niche and future potential distribution of *Culicoides imicola*, a major vector of bluetongue and African horse sickness viruses. *PLoS ONE*, **9**, e112491.
- Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C. & Kueffer, C. (2014) Unifying niche shift studies: insights from biological invasions. *Trends in Ecology & Evolution*, **29**, 260-269.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993-1009.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P. & Buckley, Y.M. (2013) Predicting species distributions for conservation decisions. *Ecology Letters*, **16**, 1424-1435.
- Haider, S., Alexander, J.M. & Kueffer, C. (2011) Elevational distribution limits of non-native species: combining observational and experimental evidence. *Plant Ecology & Diversity*, **4**, 363-371.
- Hampe, A. (2004) Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography*, **13**, 469-471.

- Hargreaves, A.L., Samis, K.E. & Eckert, C.G. (2014) Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *The American Naturalist*, **183**, 157-173.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London, New York, San Francisco.
- Harper, J.L. & White, J. (1974) The demography of plants. *Annual Review of Ecology and Systematics*, **5**, 419-463.
- Harris, S. & Reynolds, Y. (2004) *Cotyledon orbiculata* L. . *PlantZAfrica*. South African National Biodiversity Institute URL <http://www.plantzafrica.com/plantcd/cotyledorbic.htm> [accessed 08/12/2014].
- Harrison, X.A. (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, **2**.
- Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized Additive Models*. CRC Press.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C. & Thomson, D. (2005) The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters*, **8**, 91-101.
- Healy, A.J. (1959) Contributions to a knowledge of the adventive flora of New Zealand: No. VIII. - The "succulent" element of the adventive flora. *Transactions and Proceedings of the Royal Society of New Zealand*, **87**, 229-234.
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009) How does climate warming affect plant-pollinator interactions? *Ecology Letters*, **12**, 184-195.
- Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, **29**, 773-785.
- Herrera, C.M. (1991) Dissecting factors responsible for individual variation in plant fecundity. *Ecology*, **72**, 1436-1448.
- Hijmans, R.J. (2012) Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. *Ecology*, **93**, 679-688.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.
- Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2014) dismo: Species distribution modeling. R package version 1.0-5. <http://CRAN.R-project.org/package=dismo>.
- Hirzel, A.H., Hausser, J., Chessel, D. & Perrin, N. (2002) Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology*, **83**, 2027-2036.
- Holdaway, R.J., Wiser, S.K. & Williams, P.A. (2012) Status assessment of New Zealand's naturally uncommon ecosystems. *Conservation Biology*, **26**, 619-629.
- Holle, B.V. & Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212-3218.
- Holt, R.D. & Keitt, T.H. (2005) Species' borders: a unifying theme in ecology. *Oikos*, **108**, 3-6.
- Hopkins, A.D. (1920) The bioclimatic law. *Journal of the Washington Academy of Sciences*, **10**, 34-40.
- Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201-228.
- Hulme, P.E. (2007) Biological Invasions in Europe: Drivers, Pressures, States, Impacts and Responses. *Biodiversity Under Threat*, Vol. 25 (eds R. Hester & R.M. Harrison), pp. 56-80. The Royal Society of Chemistry, Cambridge, England.
- Hulme, P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, **46**, 10-18.
- Hulme, P.E. (2011) Addressing the threat to biodiversity from botanic gardens. *Trends in Ecology & Evolution*, **26**, 168-174.
- Hulme, P.E. & Barrett, S.C.H. (2013) Integrating trait- and niche-based approaches to assess contemporary evolution in alien plant species. *Journal of Ecology*, **101**, 68-77.
- Hussey, B.M.J., Keighery, G.J., Dodd, J., Lloyd, S.G. & Cousens, R.D. (2007) *Western Weeds, a Guide to the Weeds of Western Australia*, 2 edn. The Weeds Society of Western Australia (Inc.).

- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, **22**, 415-427.
- International Seed Testing Association (2008) Testing seeds by weighed replicates. *International Rules for Seed Testing*. ISTA.
- Jakobs, G., Weber, E. & Edwards, P.J. (2004) Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity and Distributions*, **10**, 11-19.
- Jeschke, J.M. & Strayer, D.L. (2008) Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Sciences*, **1134**, 1-24.
- Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P. & Lobo, J.M. (2011) Use of niche models in invasive species risk assessments. *Biological Invasions*, **13**, 2785-2797.
- Johnson, P.C.D. (2014) Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. *Methods in Ecology and Evolution*, **5**, 944-946.
- Jorgensen, T.H. (2002) The importance of phylogeny and ecology in microgeographical variation in the morphology of four Canarian species of *Aeonium* (Crassulaceae). *Biological Journal of the Linnean Society*, **76**, 521-533.
- Jorgensen, T.H. & Olesen, J.M. (2000) Growth rules based on the modularity of the Canarian *Aeonium* (Crassulaceae) and their phylogenetic value. *Botanical Journal of the Linnean Society*, **132**, 223-240.
- Jorgensen, T.H. & Olesen, J.M. (2001) Adaptive radiation of island plants: evidence from *Aeonium* (Crassulaceae) of the Canary Islands. *Perspectives in Plant Ecology, Evolution and Systematics*, **4**, 29-42.
- Jürgens, N., Schmiedel, U., Haarmeyer, D.H., Dengler, J., Finckh, M., Goetze, D., Gröngroft, A., Hahn, K., Koulibaly, A., Luther-Mosebach, J., Muche, G., Oldeland, J., Petersen, A., Porembski, S., Rutherford, M.C., Schmidt, M., Sinsin, B., Strohbach, B.J., Thiombiano, A., Wittig, R. & Zizka, G. (2011) The BIOTA biodiversity observatories in Africa—a standardized framework for large-scale environmental monitoring. *Environmental Monitoring and Assessment*, **184**, 655-678.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, **17**, 164-170.
- Kearney, M. (2012) Metabolic theory, life history and the distribution of a terrestrial ectotherm. *Functional Ecology*, **26**, 167-179.
- Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334-350.
- Kearney, M. & Porter, W.P. (2004) Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, **85**, 3119-3131.
- Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B. & Rebelo, T.G. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560-563.
- Klinkhamer, P.G.L., de Jong, T.J. & de Bruyn, G.-J. (1989) Plant size and pollinator visitation in *Cynoglossum officinale*. *Oikos*, **54**, 201-204.
- Kollmann, J. & Bañuelos, M.J. (2004) Latitudinal trends in growth and phenology of the invasive alien plant *Impatiens glandulifera* (Balsaminaceae). *Diversity and Distributions*, **10**, 377-385.
- Körner, C. (2003) Life Under Snow: Protection and Limitation. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems* pp. 47-62. Springer-Verlag, Berlin, Germany.
- Körner, C. (2007) The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, **22**, 569-574.
- Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A.K., Augeri, D.M., Cheyne, S.M., Hearn, A.J., Ross, J., Macdonald, D.W., Mathai, J., Eaton, J., Marshall, A.J., Semiadi, G., Rustam, R., Bernard, H., Alfred, R., Samejima, H., Duckworth, J.W., Breitenmoser-Wuersten, C., Belant, J.L., Hofer, H. & Wilting, A. (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions*, **19**, 1366-1379.
- Kriticos, D., Morin, L. & Webber, B. (2014) Taxonomic uncertainty in pest risks or modelling artefacts? Implications for biosecurity policy and practice. *NeoBiota*, **23**, 81-93.

- Kriticos, D.J., Brunel, S., Ota, N., Fried, G., Oude Lansink, A.G.J.M., Panetta, F.D., Prasad, T.V.R., Shabbir, A. & Yaacoby, T. (2015) Downscaling pest risk analyses: identifying current and future potentially suitable habitats for *Parthenium hysterophorus* with particular reference to Europe and North Africa. *PLoS ONE*, **10**, e0132807.
- Kriticos, D.J., Le Maitre, D.C. & Webber, B.L. (2013) Essential elements of discourse for advancing the modelling of species' current and potential distributions. *Journal of Biogeography*, **40**, 608-611.
- Kriticos, D.J. & Leriche, A. (2010) The effects of climate data precision on fitting and projecting species niche models. *Ecography*, **33**, 115-127.
- Landcare Research (2015) New Zealand soils portal. *New Zealand Soils*. URL <https://soils.landcareresearch.co.nz/> [accessed 16/01/2015]
- Langer, M.R., Weinmann, A.E., Lötters, S., Bernhard, J.M. & Rödder, D. (2013) Climate-driven range extension of *Amphistegina* (Protista, Foraminiferida): models of current and predicted future ranges. *PLoS ONE*, **8**, e54443.
- Larcher, W. (2005) Climatic constraints drive the evolution of low temperature resistance in woody plants. *Journal of Agricultural Meteorology*, **61**, 189-202.
- Le Roux, J.J., Strasberg, D., Rouget, M., Morden, C.W., Koordom, M. & Richardson, D.M. (2014) Relatedness defies biogeography: the tale of two island endemics (*Acacia heterophylla* and *A. koa*). *New Phytologist*, **204**, 230-242.
- Lee, D.E., Lee, W.G. & Mortimer, N. (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Australian Journal of Botany*, **49**, 341-356.
- Leger, E.A., Espeland, E.K., Merrill, K.R. & Meyer, S.E. (2009) Genetic variation and local adaptation at a cheatgrass (*Bromus tectorum*) invasion edge in western Nevada. *Molecular Ecology*, **18**, 4366-4379.
- Leist, N. & Krämer, S. (2003) *ISTA working sheets on tetrazolium testing*, 1 edn. International Seed Testing Association.
- Lemmon, P.E. (1956) A spherical densiometer for estimating forest overstory density. *Forest Science*, **2**, 314-320.
- Lems, K. (1960) Botanical notes on the Canary Islands II. The evolution of plant forms in the islands: *Aeonium*. *Ecology*, **41**, 1-17.
- Lesotho Meteorological Services (2013) Climate of Lesotho. *Lesotho Meteorological Services* URL <http://lesmet.org.ls/cimatology/climate-lesotho> [accessed 16/01/2015].
- Levin, D.A. (2006) Flowering phenology in relation to adaptive radiation. *Systematic Botany*, **31**, 239-246.
- Li, Y., Cheng, Z., Smith, W.A., Ellis, D.R., Chen, Y., Zheng, X., Pei, Y., Luo, K., Zhao, D., Yao, Q., Duan, H. & Li, Q. (2004) Invasive ornamental plants: problems, challenges, and molecular tools to neutralize their invasiveness. *Critical Reviews in Plant Sciences*, **23**, 381-389.
- Lloret, F., Médail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambdon, P. & Hulme, P.E. (2005) Species attributes and invasion success by alien plants on Mediterranean islands. *Journal of Ecology*, **93**, 512-520.
- Lobo, J.M., Jiménez-Valverde, A. & Hortal, J. (2010) The uncertain nature of absences and their importance in species distribution modelling. *Ecography*, **33**, 103-114.
- Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223-228.
- Loik, M.E. & Nobel, P.S. (1993) Exogenous abscisic acid mimics cold acclimation for cacti differing in freezing tolerance. *Plant Physiology*, **103**, 871-876.
- Loiselle, B.A., Jørgensen, P.M., Consiglio, T., Jiménez, I., Blake, J.G., Lohmann, L.G. & Montiel, O.M. (2007) Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes? *Journal of Biogeography*, **35**, 105-116.
- Lösch, R. & Kappen, L. (1981) The cold resistance of Macaronesian Sempervivoideae. *Oecologia*, **50**, 98-102.
- Lozier, J.D., Aniello, P. & Hickerson, M.J. (2009) Predicting the distribution of Sasquatch in western North America: anything goes with ecological niche modelling. *Journal of Biogeography*, **36**, 1623-1627.

- Lozier, J.D. & Mills, N.J. (2011) Predicting the potential invasive range of light brown apple moth (*Epiphyas postvittana*) using biologically informed and correlative species distribution models. *Biological Invasions*, **13**, 2409-2421.
- Lutge, U. (2004) Ecophysiology of Crassulacean acid metabolism (CAM). *Annals of Botany*, **93**, 629-652.
- Mackey, B.G. & Lindenmayer, D.B. (2001) Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography*, **28**, 1147-1166.
- Márcia Barbosa, A., Real, R., Muñoz, A.R. & Brown, J.A. (2013) New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Diversity and Distributions*, **19**, 1333 - 1338.
- Marini, L., Gaston, K.J., Prosser, F. & Hulme, P.E. (2009) Contrasting response of native and alien plant species richness to environmental energy and human impact along alpine elevation gradients. *Global Ecology and Biogeography*, **18**, 652-661.
- Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., Low-Choy, S., McBride, M. & Mengersen, K. (2012) Eliciting expert knowledge in conservation science. *Conservation Biology*, **26**, 29-38.
- Mason, R. (1978) Gore Bay and Port Robinson - miscellaneous notes. *Canterbury Botanical Society Journal*, **12**, 33-34.
- Mata, R.A., Tidon, R., Côrtes, L.G., Marco, P. & Diniz-Filho, J.A.F. (2009) Invasive and flexible: niche shift in the drosophilid *Zaprionus indianus* (Insecta, Diptera). *Biological Invasions*, **12**, 1231-1241.
- McConnaughay, K.D.M. & Coleman, J.S. (1999) Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology*, **80**, 2581-2593.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*, 2nd edn. CRC Press.
- McFadden, D. (1973) Conditional Logit Analysis of Qualitative Choice Behaviour. *Frontiers in Econometrics* (ed P. Zarembka), pp. 105-142. Academic Press, Waltham, MA, USA.
- McGann, R.P. (1983) The climate of Christchurch. Vol. 167(2). New Zealand Meteorological Service, Wellington, New Zealand.
- McGowan, H.A. & Sturman, A.P. (1996) Regional and local scale characteristics of foehn wind events over the South Island of New Zealand. *Meteorology and Atmospheric Physics*, **58**, 151-164.
- McGregor, K.F., Watt, M.S., Hulme, P.E. & Duncan, R.P. (2012) What determines pine naturalization: species traits, climate suitability or forestry use? *Diversity and Distributions*, **18**, 1013-1023.
- McInerny, G.J. & Etienne, R.S. (2012) Ditch the niche - is the niche a useful concept in ecology or species distribution modelling? *Journal of Biogeography*, **39**, 2096-2102.
- Médail, F. & Quézel, P. (1999) The phytogeographical significance of S.W. Morocco compared to the Canary Islands. *Plant Ecology*, **140**, 221-244.
- Merow, C., Dahlgren, J.P., Metcalf, C.J.E., Childs, D.Z., Evans, M.E.K., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R. & McMahon, S.M. (2014) Advancing population ecology with integral projection models: a practical guide. *Methods in Ecology and Evolution*, **5**, 99-110.
- Merow, C., LaFleur, N., Silander Jr, J.A., Wilson, A.M. & Rubega, M. (2011) Developing dynamic mechanistic species distribution models: predicting bird-mediated spread of invasive plants across Northeastern North America. *The American Naturalist*, **178**, 30-43.
- Merow, C., Smith, M.J., Edwards, T.C., Guisan, A., McMahon, S.M., Normand, S., Thuiller, W., Wüest, R.O., Zimmermann, N.E. & Elith, J. (2014) What do we gain from simplicity versus complexity in species distribution models? *Ecography*, **37**, 1267-1281.
- Merow, C., Smith, M.J. & Silander, J.A. (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, **36**, 1058-1069.
- Mes, T.H.M. & T'Hart, H. (1996) The evolution of growth-forms in the Macaronesian genus *Aeonium* (Crassulaceae) inferred from chloroplast DNA RFLPs and morphology. *Molecular Ecology*, **5**, 351-363.
- Mesgaran, M.B., Cousens, R.D. & Webber, B.L. (2014) Here be dragons: a tool for quantifying novelty due to covariate range and correlation change when projecting species distribution models. *Diversity and Distributions*, **20**, 1147-1159.
- Metcalf, C.J.E., McMahon, S.M., Salguero-Gómez, R. & Jongejans, E. (2013) IPMpack: an R package for integral projection models. *Methods in Ecology and Evolution*, **4**, 195-200.

- MetService (2010) New Zealand climate. Meteorological Service of New Zealand URL <http://www.metservice.com> [accessed 16/01/2015].
- Michod, R.E. (1979) Evolution of life histories in response to age-specific mortality factors. *The American Naturalist*, **113**, 531-550.
- Ming, D.S., Hillhouse, B.J., Guns, E.S., Eberding, A., Xie, S., Vimalanathan, S. & Towers, G.H.N. (2005) Bioactive compounds from *Rhodiola rosea* (Crassulaceae). *Phytotherapy Research*, **19**, 740-743.
- Ministerio de Agricultura Alimentación y Medio Ambiente (2005) Atlas y manual de interpretación de los hábitat Españoles. Ministerio de Agricultura, Alimentación y Medio Ambiente, Dirección General de Calidad y Evaluación Ambiental y Medio Natural.
- Ministry for Primary Industries (1993) Biosecurity Act. Wellington, New Zealand.
- Ministry for Primary Industries (2015) Unwanted Organisms register MPI Biosecurity New Zealand URL <http://www.biosecurity.govt.nz/pests/registers/uor> [accessed 01/12/2015].
- Ministry for the Environment & Landcare Research (2014) Land Cover Database version 4.0. [Vector polygon layer] Retrieved from: <https://lris.scinfo.org.nz>.
- Molloy, B.P.J. (1980) The Flora of Gore Bay, Port Robinson and Manuka Bay. *Canterbury Botanical Society Journal*, **14**, 58-68.
- Monteith, J.L. (1972) Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology*, **9**, 747-766.
- Moolman, H.J. & Cowling, R.M. (1994) The impact of elephant and goat grazing on the endemic flora of South African succulent thicket. *Biological Conservation*, **68**, 53-61.
- MoonSook, S., HyeJin, O., JuYeon, S., MiYoung, L., Sivanesan, I. & ByoungRyong, J. (2012) Effect of silicon source and application method on growth of *Kalanchoe 'Peperu'*. *Korean Journal of Horticultural Science & Technology*, **30**, 250-255.
- Morin, X. & Thuiller, W. (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, **90**, 1301-1313.
- Mort, M.E., Levens, N., Randle, C.P., Van Jaarsveld, E. & Palmer, A. (2005) Phylogenetics and diversification of *Cotyledon* (Crassulaceae) inferred from nuclear and chloroplast DNA sequence data. *American Journal of Botany*, **92**, 1170-1176.
- Mort, M.E., Soltis, D.E., Soltis, P.S., Francisco-Ortega, J. & Santos-Guerra, A. (2001) Phylogenetic relationships and evolution of Crassulaceae inferred from matK sequence data. *American Journal of Botany*, **88**, 76-91.
- Munguia-Rosas, M.A., Campos-Navarrete, M.J. & Parra-Tabla, V. (2013) The effect of pollen source vs. flower type on progeny performance and seed predation under contrasting light environments in a cleistogamous herb. *PLoS ONE*, **8**.
- Nachtergaele, F. & Petri, M. (2008) Mapping land use systems at global and regional scales for land degradation assessment analysis. *LADA Technical Report*. Global Environment Facility, United Nations Environment Programme, Food and Agriculture Organization of the United Nations.
- National Institute of Water and Atmospheric Research (2014) CliFlo: NIWA's national climate database on the web. URL <http://cliflo.niwa.co.nz> [accessed 07/08/2015].
- Nghindinwa, K.C. (2009) *Why are some species invasive? Determining the importance of species traits across three invasion stages and enemy release of southern African native plants in New Zealand*. Master of Science, Lincoln University, New Zealand.
- Niekerk, A.v. & Joubert, S.J. (2011) Input variable selection for interpolating high-resolution climate surfaces for the Western Cape. *Water SA*, **37**, 271-279.
- Nix, H.A. (1986) A Biogeographic Analysis of Australian Elapid Snakes. *Atlas of Elapid Snakes of Australia: Australian Flora and Fauna* (ed R. Longmore), pp. 4-15. Bureau of Flora and Fauna, Canberra, Australia.
- Nobel, P.S. (1981) Influence of freezing temperatures on a cactus, *Coryphantha vivipara*. *Oecologia*, **48**, 194-198.
- Ogle, K. & Reynolds, J.F. (2004) Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia*, **141**, 282-294.
- Ojewole, J.A.O. (2005) Antinociceptive, anti-inflammatory and antidiabetic effects of *Bryophyllum pinnatum* (Crassulaceae) leaf aqueous extract. *Journal of Ethnopharmacology*, **99**, 13-19.
- Okubo, A. & Levin, S.A. (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology*, **70**, 329-338.

- Paíaro, V., Mangeaud, A. & Pucheta, E. (2007) Alien seedling recruitment as a response to altitude and soil disturbance in the mountain grasslands of central Argentina. *Plant Ecology*, **193**, 279-291.
- Parker, I.M. (2000) Invasion dynamics of *Cytisus scoparius*: A matrix model approach. *Ecological Applications*, **10**, 726-743.
- Parmesan, C., Root, T.L. & Winig, M.R. (2000) Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, **3**, 443-450.
- Pattison, R.R. & Mack, R.N. (2008) Potential distribution of the invasive tree *Triadica sebifera* (Euphorbiaceae) in the United States: evaluating CLIMEX predictions with field trials. *Global Change Biology*, **14**, 813-826.
- Pauchard, A. & Alaback, P.B. (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conservation Biology*, **18**, 238-248.
- Pauchard, A., Kueffer, C., Dietz, H., Daehler, C.C., Alexander, J., Edwards, P.J., Arévalo, J.R., Cavieres, L.A., Guisan, A., Haider, S., Jakobs, G., McDougall, K., Millar, C.I., Naylor, B.J., Parks, C.G., Rew, L.J. & Seipel, T. (2009) Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, **7**, 479-486.
- Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008) Niche dynamics in space and time. *Trends in Ecology & Evolution*, **23**, 149-158.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361-371.
- Pearson, R.G. & Dawson, T.P. (2004) Bioclimate envelope models: what they detect and what they hide — response to Hampe (2004). *Global Ecology and Biogeography*, **13**, 471-473.
- Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Townsend Peterson, A. (2006) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102-117.
- Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007) Updated world map of the Koppen-Geiger climate classification. *Hydrology and Earth System Sciences*, **11**, 1633-1644.
- Peña-Gómez, F.T., Guerrero, P.C., Bizama, G., Duarte, M. & Bustamante, R.O. (2014) Climatic niche conservatism and biogeographical non-equilibrium in *Eschscholzia californica* (Papaveraceae), an invasive plant in the Chilean mediterranean region. *PLoS ONE*, **9**, e105025.
- Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C. & Guisan, A. (2012) Climatic niche shifts are rare among terrestrial plant invaders. *Science*, **335**, 1344-1348.
- Pheloung, P.C., Williams, P.A. & Halloy, S.R. (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management*, **57**, 239-251.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231-259.
- Pilon-Smits, E.a.H., Hart, H.t. & Brederode, J.v. (1996) Evolutionary Aspects of Crassulacean Acid Metabolism in the Crassulaceae. *Crassulacean Acid Metabolism* (eds D.K. Winter & D.J.A.C. Smith), pp. 349-359. Springer Berlin Heidelberg.
- Pimentel, D., Zuniga, R. & Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273-288.
- Pitt, J.P.W., Worner, S.P. & Suarez, A.V. (2009) Predicting Argentine ant spread over the heterogeneous landscape using a spatially explicit stochastic model. *Ecological Applications*, **19**, 1176-1186.
- Podger, F.D., Mummery, D.C., Palzer, C.R. & Brown, M.J. (1990) Bioclimatic analysis of the distribution of damage to native plants in Tasmania by *Phytophthora cinnamomi*. *Australian Journal of Ecology*, **15**, 281-289.
- Poulos, H.M., Chernoff, B., Fuller, P.L. & Butman, D. (2012) Ensemble forecasting of potential habitat for three invasive fishes. *Aquatic Invasions*, **7**, 59-72.
- Price, T.D., Qvarnström, A. & Irwin, D.E. (2003) The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 1433-1440.

- Prince, S.D. & Carter, R.N. (1985) The geographical distribution of prickly lettuce (*Lactuca serriola*): III. Its performance in transplant sites beyond its distribution limit in Britain. *Journal of Ecology*, **73**, 49-64.
- Pyšek, P., Jarošík, V., Hulme, P.E., Kühn, I., Wild, J., Arianoutsou, M., Bacher, S., Chiron, F., Didžiulis, V., Essl, F., Genovesi, P., Gherardi, F., Hejda, M., Kark, S., Lambdon, P.W., Desprez-Loustau, M.-L., Nentwig, W., Pergl, J., Poboljšaj, K., Rabitsch, W., Roques, A., Roy, D.B., Shirley, S., Solarz, W., Vilà, M. & Winter, M. (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences*, **107**, 12157-12162.
- Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I., Tichý, L., Danihelka, J., Chrtek jun, J. & Sádlo, J. (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions*, **15**, 891-903.
- Qiao, H., Soberón, J. & Peterson, A.T. (2015) No silver bullets in correlative ecological niche modelling: insights from testing among many potential algorithms for niche estimation. *Methods in Ecology and Evolution*, **6**, 1126-1136.
- Quinn, A., Gallardo, B. & Aldridge, D.C. (2014) Quantifying the ecological niche overlap between two interacting invasive species: the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena rostriformis bugensis*). *Aquatic Conservation: Marine and Freshwater Ecosystems*, **24**, 324-337.
- R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Radcliffe, J.E. & Lefever, K.R. (1981) Aspect influences on pasture microclimate at Coopers Creek, North Canterbury. *New Zealand Journal of Agricultural Research*, **24**, 55-56.
- Randin, C.F., Jaccard, H., Vittoz, P., Yoccoz, N.G. & Guisan, A. (2009) Land use improves spatial predictions of mountain plant abundance but not presence-absence. *Journal of Vegetation Science*, **20**, 996-1008.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93-107.
- Roberts, W., Harrod, O., Mitterdorfer, B. & Pheloung, P. (2011) Regulating invasive plants and use of weed risk assessments. *Current Opinion in Environmental Sustainability*, **3**, 60-65.
- Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C. & Müller, M. (2011) pROC: An open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*, **12**, 77.
- Robinson, T.P., Wint, G.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D'Aietti, L., Hay, S.I. & Gilber, M. (2014) Mapping the global distribution of livestock. *PLoS ONE*, **9**, e96084.
- Rodda, G.H., Jarnevich, C.S. & Reed, R.N. (2011) Challenges in identifying sites climatically matched to the native ranges of animal invaders. *PLoS ONE*, **6**, e14670.
- Ross, L.C., Lambdon, P.W. & Hulme, P.E. (2008) Disentangling the roles of climate, propagule pressure and land use on the current and potential elevational distribution of the invasive weed *Oxalis pes-caprae* L. on Crete. *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 251-258.
- Rousselet, J., Imbert, C.-E., Dekri, A., Garcia, J., Goussard, F., Vincent, B., Denux, O., Robinet, C., Dorkeld, F., Roques, A. & Rossi, J.-P. (2013) Assessing species distribution using Google Street View: a pilot study with the pine processionary moth. *PLoS ONE*, **8**, e74918.
- Royal Horticultural Society (2014) Find a plant. *RHS Gardening*. URL <https://www.rhs.org.uk/plants> [accessed 16/10/2014].
- Royle, J.A., Chandler, R.B., Yackulic, C. & Nichols, J.D. (2012) Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods in Ecology and Evolution*, **3**, 545-554.
- Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M., O'Connor, M.I. & Rice, W.R. (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution*, **22**, 465-471.

- Schoener, T.W. (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, **51**, 408-418.
- Scott, G. & Springfield, E.P. (2004) *Cotyledon orbiculata*. *Pharmaceutical monographs for 60 South African plant species used as traditional medicines*. South African National Biodiversity Institute (SANBI) URL <http://www.plantzafrica.com/medmonographs/> [accessed 01/12/2015].
- Seipel, T., Alexander, J.M., Daehler, C.C., Rew, L.J., Edwards, P.J., Dar, P.A., McDougall, K., Naylor, B., Parks, C., Pollnac, F.W., Reshi, Z.A., Schroder, M. & Kueffer, C. (2015) Performance of the herb *Verbascum thapsus* along environmental gradients in its native and non-native ranges. *Journal of Biogeography*, **42**, 132-143.
- Senay, S.D., Worner, S.P. & Ikeda, T. (2013) Novel three-step pseudo-absence selection technique for improved species distribution modelling. *PLoS ONE*, **8**, e71218.
- Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415-436.
- Shelford, V.E. (1931) Some concepts of bioecology. *Ecology*, **12**, 455-467.
- Sheppard, C.S., Burns, B.R. & Stanley, M.C. (2014) Predicting plant invasions under climate change: are species distribution models validated by field trials? *Global Change Biology*, **20**, 2800-2814.
- Sinclair, S.J., White, M.D. & Newell, G.R. (2010) How useful are species distribution models for managing biodiversity under future climates? *Ecology and Society*, **15**(8).
- Smith, A.B., Santos, M.J., Koo, M.S., Rowe, K.M.C., Rowe, K.C., Patton, J.L., Perrine, J.D., Beissinger, S.R. & Moritz, C. (2013) Evaluation of species distribution models by resampling of sites surveyed a century ago by Joseph Grinnell. *Ecography*, **36**, 1017-1031.
- Smith, C., van Klinken, R.D., Seabrook, L. & McAlpine, C. (2012) Estimating the influence of land management change on weed invasion potential using expert knowledge. *Diversity and Distributions*, **18**, 818-831.
- Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 19644-19650.
- Soons, J.M., Moar, N.T., Shulmeister, J., Wilson, H.D. & Carter, J.A. (2002) Quaternary vegetation and climate changes on Banks Peninsula, South Island, New Zealand. *Global and Planetary Change*, **33**, 301-314.
- Soria-Auza, R.W., Kessler, M., Bach, K., Barajas-Barbosa, P.M., Lehnert, M., Herzog, S.K. & Böhner, J. (2010) Impact of the quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from Bolivia. *Ecological Modelling*, **221**, 1221-1229.
- Stevens, J.F. (1995) 4. Chemotaxonomy of the Eurasian Sedoideae and Sempervivoideae. *Evolution and Systematics of the Crassulaceae* (eds H.t. Hart & U. Eggli), pp. 45-75. Backhuys Publishers, Leiden, The Netherlands.
- Stokland, J.N., Halvorsen, R. & Støa, B. (2011) Species distribution modelling - effect of design and sample size of pseudo-absence observations. *Ecological Modelling*, **222**, 1800-1809.
- Stoklosa, J., Daly, C., Foster, S.D., Ashcroft, M.B. & Warton, D.I. (2015) A climate of uncertainty: accounting for error in climate variables for species distribution models. *Methods in Ecology and Evolution*, **6**, 412-423.
- Strubbe, D., Broennimann, O., Chiron, F. & Matthysen, E. (2013) Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. *Global Ecology and Biogeography*, **22**, 962-970.
- Stuckey, I.H. & Curtis, O.F. (1938) Ice formation and the death of plant cells by freezing. *Plant Physiology*, **13**, 815-833.
- Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A. & Wiegand, T. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, **101**, 58-67.
- Sutherst, R.W. (2013) Pest species distribution modelling: origins and lessons from history. *Biological Invasions*, **16**, 239-256.

- Sutherst, R.W. & Bourne, A.S. (2009) Modelling non-equilibrium distributions of invasive species: a tale of two modelling paradigms. *Biological Invasions*, **11**, 1231-1237.
- Sutherst, R.W. & Maywald, G.F. (1985) A computerised system for matching climates in ecology. *Agriculture, Ecosystems & Environment*, **13**, 281-299.
- Sutherst, R.W., Maywald, G.F. & Bourne, A.S. (2007) Including species interactions in risk assessments for global change. *Global Change Biology*, **13**, 1843-1859.
- Syfert, M.M., Smith, M.J. & Coomes, D.A. (2013) The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS ONE*, **8**, e55158.
- Sykes, W.R. (1992) Succulent plants on Rangitoto Island. *Auckland Botanical Society Journal*, **47**, 6-16.
- T'Hart, H. (1997) Diversity within Mediterranean Crassulaceae. *Lagasalia*, **19**, 93-100.
- Tait, A.B. (2007) *Climate Maps*. NIWA Ltd, Wellington.
- Taiz, L. & Zeiger, E. (1991) The Control of Flowering. *Plant Physiology* pp. 513-531. The Benjamin/Cummings Publishing Company, Inc, California.
- Takahara, T., Minamoto, T. & Doi, H. (2013) Using environmental DNA to estimate the distribution of an invasive fish species in ponds. *PLoS ONE*, **8**, e56584.
- Tessarolo, G., Rangel, T.F., Araújo, M.B. & Hortal, J. (2014) Uncertainty associated with survey design in species distribution models. *Diversity and Distributions*, **20**, 1258-1269.
- Thompson, K., Hodgson, J.G., Grime, J.P. & Burke, M.J.W. (2001) Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. *Journal of Ecology*, **89**, 1054-1060.
- Thompson, S., Grüner, I. & Gapare, N. (2003) LCDB2 - Illustrated guide to target classes. pp. 1-126. Ministry for the Environment, New Zealand.
- Thuiller, W., Richardson, D.M., Rouget, M., Procheş, Ş. & Wilson, J.R.U. (2006) Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology*, **87**, 1755-1769.
- Townsend Peterson, A. (2011) *Ecological Niches and Geographic Distributions (MPB-49)*. Princeton University Press, NJ, USA.
- Townsend Peterson, A. & Soberón, J. (2012) Species distribution modeling and ecological niche modeling: getting the concepts right. *Natureza & Conservação*, **10**, 102-107.
- Tsoar, A., Allouche, O., Steinitz, O., Rotem, D. & Kadmon, R. (2007) A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions*, **13**, 397-405.
- Tuljapurkar, S. & Caswell, H. (2012) *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems*. Springer Science & Business Media.
- Václavík, T. & Meentemeyer, R.K. (2009) Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions? *Ecological Modelling*, **220**, 3248-3258.
- Václavík, T. & Meentemeyer, R.K. (2012) Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. *Diversity and Distributions*, **18**, 73-83.
- Van Collier, A. & Stock, W.D. (1994) Cold tolerance of the southern African succulent, *Cotyledon orbiculata* L. across its geographical range. *FLORA*, **189**, 89-94.
- Van Der Veken, S., Rogister, J., Verheyen, K., Hermy, M. & Nathan, R. (2007) Over the (range) edge: a 45-year transplant experiment with the perennial forest herb *Hyacinthoides non-scripta*. *Journal of Ecology*, **95**, 343-351.
- van Ham, R.C.H.J. (1995) Phylogenetic Relationships in the Crassulaceae Inferred from Chloroplast DNA Variation. *Evolution and Systematics of the Crassulaceae* pp. 16-29. Backhuys Publishers, Leiden, The Netherlands.
- Van Jaarsveld, E. & Koutnik, D. (2004) *Cotyledon and Tylecodon*. Umdaus Press, Hatfield, South Africa.
- van Rheede van Oudtshoorn, K. & van Rooyen, M.W. (1999) Dust Diaspores. *Dispersal Biology of Desert Plants* p. 38. Springer-Verlag, Berlin, Germany.
- Varela, S., Rodríguez, J. & Lobo, J.M. (2009) Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena. *Journal of Biogeography*, **36**, 1645-1655.
- Venette, R.C., Kriticos, D.J., Magarey, R.D., Koch, F.H., Baker, R.H.A., Worner, S.P., Gómez Raboteaux, N.N., McKenney, D.W., Dobesberger, E.J., Yemshanov, D., De Barro, P.J.,

- Hutchison, W.D., Fowler, G., Kalaris, T.M. & Pedlar, J. (2010) Pest risk maps for invasive alien species: a roadmap for improvement. *BioScience*, **60**, 349-362.
- Vicente, J., Randin, C.F., Gonçalves, J., Metzger, M.J., Lomba, Á., Honrado, J. & Guisan, A. (2011) Where will conflicts between alien and rare species occur after climate and land-use change? A test with a novel combined modelling approach. *Biological Invasions*, **13**, 1209-1227.
- Vogan, R. (2003) *Flora: The Gardener's Bible*. David Bateman Ltd, Auckland, New Zealand.
- Wada, K.C. & Takeno, K. (2010) Stress-Induced Flowering. *Plant Signaling & Behavior*, **5**, 944-947.
- Wadsworth, R.A., Collingham, Y.C., Willis, S.G., Huntley, B. & Hulme, P.E. (2000) Simulating the spread and management of alien riparian weeds: Are they out of control? *Journal of Applied Ecology*, **37**, 28-38.
- Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K. & Poschlod, P. (2011) Climate change and plant regeneration from seed. *Global Change Biology*, **17**, 2145-2161.
- Walker, P.A. & Cocks, K.D. (1991) HABITAT: A procedure for modelling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography Letters*, **1**, 108-118.
- Walter, J.A., Meixler, M.S., Mueller, T., Fagan, W.F., Tobin, P.C. & Haynes, K.J. (2015) How topography induces reproductive asynchrony and alters gypsy moth invasion dynamics. *Journal of Animal Ecology*, **84**, 188-198.
- Wardlaw, I.F. (1999) 14.3.2 Thermal Time. *Plants in Action* (eds P. Kriedemann, B.J. Atwell & C.N.G. Turnbull). Macmillan Education Australia Pty Ltd, Melbourne, Australia.
- Warren, D.L. (2012) In defense of 'niche modeling'. *Trends in Ecology & Evolution*, **27**, 497-500.
- Warren, D.L. (2013) 'Niche modeling': that uncomfortable sensation means it's working. A reply to McNerny and Etienne. *Trends in Ecology & Evolution*, **28**, 193-194.
- Warren II, R.J. (2010) An experimental test of well-described vegetation patterns across slope aspects using woodland herb transplants and manipulated abiotic drivers. *New Phytologist*, **185**, 1038-1049.
- Webb, C.J., Sykes, W.R. & Garnock-Jones, P.J. (1988) Crassulaceae. *Flora of New Zealand. Vol. IV. Naturalised Pteridophytes, Gymnosperms, Dicotyledons*, Vol. IVpp. 1-1288. Botany Division, Department of Scientific and Industrial Research (DSIR), Christchurch, New Zealand.
- Webber, B.L., Maitre, D.C.L. & Kriticos, D.J. (2012) Comment on "Climatic niche shifts are rare among terrestrial plant invaders". *Science*, **338**, 193-193.
- Webber, B.L., Yates, C.J., Le Maitre, D.C., Scott, J.K., Kriticos, D.J., Ota, N., McNeill, A., Le Roux, J.J. & Midgley, G.F. (2011) Modelling horses for novel climate courses: insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. *Diversity and Distributions*, **17**, 978-1000.
- Weiss, S.B., Murphy, D.D. & White, R.R. (1988) Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology*, **69**, 1486-1496.
- Wenger, S.J. & Olden, J.D. (2012) Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution*, **3**, 260-267.
- Westcott, D.A. & Fletcher, C.S. (2011) Biological invasions and the study of vertebrate dispersal of plants: Opportunities and integration. *Acta Oecologica*, **37**, 650-656.
- Wharton, T.N. & Kriticos, D.J. (2004) The fundamental and realized niche of the Monterey Pine aphid, *Essigella californica* (Essig) (Hemiptera: Aphididae): implications for managing softwood plantations in Australia. *Diversity and Distributions*, **10**, 253-262.
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A. & Snyder, M.A. (2009) Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences*, **106**, 19729-19736.
- Williams, J.L., Miller, T.E.X. & Ellner, S.P. (2012) Avoiding unintentional eviction from integral projection models. *Ecology*, **93**, 2008-2014.
- Willis, S.G. & Hulme, P.E. (2002) Does temperature limit the invasion of *Impatiens glandulifera* and *Heracleum mantegazzianum* in the UK? *Functional Ecology*, **16**, 530-539.
- Wilson, H.D. (1983) Banks Peninsula botanical survey 1983-1988. Maurice White Native Forest Trust, Christchurch, New Zealand.
- Wilson, H.D. (1986) The surprising botany of Banks Peninsula. *Auckland Botanical Society - The Lucy Cranwell Lecture* Auckland University
- Wilson, H.D. (1993) Bioclimatic zones and Banks Peninsula. *Canterbury Botanical Society Journal*, **27**, 22-29.

- Wilson, J.R.U., Richardson, D.M., Rouget, M., Procheş, Ş., Amis, M.A., Henderson, L. & Thuiller, W. (2007) Residence time and potential range: crucial considerations in modelling plant invasions. *Diversity and Distributions*, **13**, 11-22.
- Wiser, S.K. & Buxton, R.P. (2009) Montane outcrop vegetation of Banks Peninsula, South Island, New Zealand. *New Zealand Journal of Ecology*, **33**, 164.
- Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H. & Guisan, A. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, **14**, 763-773.
- Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P. & Svenning, J.-C. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, **88**, 15-30.
- Witt, A.B.R. (2004) Initial screening of the stem-boring weevil *Osphilia tenuipes*, a candidate agent for the biological control of *Bryophyllum delagoense* in Australia. *BioControl*, **49**, 197-209.
- Witt, A.B.R. & Nongogo, A.X. (2011) The impact of fire, and its potential role in limiting the distribution of *Bryophyllum delagoense* (Crassulaceae) in southern Africa. *Biological Invasions*, **13**, 125-133.
- Wolmarans, R., Robertson, M.P. & Van Rensburg, B.J. (2010) Predicting invasive alien plant distributions: how geographical bias in occurrence records influences model performance. *Journal of Biogeography*, **37**, 1797-1810.
- Woodward, F.I. (1987) *Climate and plant distribution*. Cambridge University Press, Cambridge, England.
- Wright, S.I., Kalisz, S. & Slotte, T. (2013) Evolutionary consequences of self-fertilization in plants. *Proceedings of the Royal Society B: Biological Sciences*, **280**.
- Wyatt, R. (1980) The reproductive biology of *Asclepias tuberosa*: I. Flower number, arrangement, and fruit-set. *New Phytologist*, **85**, 119-131.
- Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, J.A., Nichols, J.D., Campbell Grant, E.H. & Veran, S. (2013) Presence-only modelling using MaxEnt: when can we trust the inferences? *Methods in Ecology and Evolution*, **4**, 236-243.
- Zaniewski, A.E., Lehmann, A. & Overton, J.M. (2002) Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling*, **157**, 261-280.
- Zietsman, P.C. (1998) Pollination biology of *Cotyledon orbiculata* L. var. *dactyloopsis* Toelken (Crassulaceae). *Navorsinge Van Die Nasionale Museum Bloemfontein*, **14**, 81-96.
- Zweig, M.H. & Campbell, G. (1993) Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clinical Chemistry*, **39**, 561-577.