

# **Restoration Genetics of Murray Mallee and Neotropical Forests**

**Martin F. Breed**

A thesis submitted in fulfilment of the  
requirements for the degree of

***Doctor of Philosophy***

School of Earth & Environmental Sciences  
University of Adelaide, Australia

February 2013

## Table of Contents

<b>SUMMARY .....</b>	<b>3</b>
<b>DECLARATION .....</b>	<b>6</b>
<b>PUBLISHED AND SUBMITTED WORKS INCLUDED IN THESIS .....</b>	<b>7</b>
<b>ACKNOWLEDGEMENTS .....</b>	<b>8</b>
<b>CHAPTER 1: INTRODUCTION.....</b>	<b>12</b>
<i>Thesis structure .....</i>	<i>12</i>
<i>Thesis aims and objectives.....</i>	<i>19</i>
<b>CHAPTER 2: FOREST FRAGMENTATION GENETICS.....</b>	<b>20</b>
<i>Breed M.F., Ottewell K.M., Gardner M.G., Dormontt, E.E., Lowe A.J.</i> <i>(submitted). Mating patterns and pollinator mobility are critical traits in</i> <i>forest fragmentation genetics. Heredity.....</i>	<i>20</i>
<b>CHAPTER 3: REPRODUCTIVE ASSURANCE SHIFTS IN MAHOGANY ....</b>	<b>63</b>
<i>Breed M.F., Gardner M.G., Ottewell K.M., Navarro C., Lowe A.J. (2012).</i> <i>Shifts in reproductive assurance strategies and inbreeding costs</i> <i>associated with habitat fragmentation in Central American mahogany.</i> <i>Ecol. Lett. 15(5), 444-452. ....</i>	<i>63</i>
<i>Media uptake .....</i>	<i>81</i>
<b>CHAPTER 4: POLLEN DIVERSITY MATTERS .....</b>	<b>82</b>
<i>Breed M.F., Marklund M.H.K., Ottewell K.M., Gardner M.G., Harris J.C.B.,</i> <i>Lowe A.J. (2012). Pollen diversity matters: revealing the neglected effect</i> <i>of pollen diversity on fitness in fragmented landscapes. Mol. Ecol. 21(24),</i> <i>5955-5968.....</i>	<i>82</i>
<b>CHAPTER 5: EUCALYPT RESISTANCE TO FRAGMENTATION .....</b>	<b>109</b>
<i>Breed M.F., Ottewell K.M., Gardner M.G., Marklund M.H.K., Stead M.G.,</i> <i>Harris J.C.B., Lowe A.J. (in press). Mating system and early viability</i> <i>resistance to habitat fragmentation in a bird-pollinated eucalypt. Heredity.</i> <i>DOI: 10.1038/hdy.2012.72.....</i>	<i>109</i>
<b>CHAPTER 6: ADAPTATION AND SCATTERED TREES.....</b>	<b>126</b>
<i>Breed M.F., Ottewell K.M., Gardner M.G., Lowe A.J. (2011). Clarifying</i> <i>climate change adaptation responses for scattered trees in modified</i> <i>landscapes. J. Appl. Ecol. 48(3), 637-641. ....</i>	<i>126</i>
<i>Faculty of 1000 Recommended Paper .....</i>	<i>139</i>
<b>CHAPTER 7: WHICH PROVENANCE AND WHERE? .....</b>	<b>141</b>
<i>Breed M.F., Stead M.G., Ottewell K.M., Gardner M.G., Lowe A.J. (2013).</i> <i>Which provenance and where? Seed sourcing strategies for revegetation</i> <i>in a changing environment. Cons. Genet. 14(1), 1-10.....</i>	<i>141</i>
<b>CONCLUSIONS .....</b>	<b>153</b>
<b>COMPLETE LIST OF PUBLICATIONS.....</b>	<b>157</b>
<b>BIBLIOGRAPHY .....</b>	<b>159</b>

## Summary

Fragmented tree populations are not expected to be as susceptible to small population paradigm effects (*e.g.* genetic drift) that generally dominate conservation genetics and restoration as many other taxa. The reasons for this are that trees tend to (1) undergo regular far-reaching gene flow, even in fragmented landscapes, (2) have many overlapping generations and (3) be long lived relative to when most habitat fragmentation occurred. These traits result in tree populations having great genetic inertia and thus they tend to maintain genetic diversity (as measured by numbers of alleles) despite significant habitat fragmentation.

However, trees are not resistant to changes in the genetic diversity of their progeny (as measured by observed heterozygosity) as a result of habitat fragmentation. Habitat fragmentation can alter the mating patterns of individual trees by changing pollination dynamics (*e.g.* levels of selfing, pollen diversity) and these mating patterns directly influence the genetic makeup of progeny. Tree progeny are predicted to be particularly sensitive to mating pattern changes of their maternal plant since most tree species predominantly outcross, leading them to accumulate more genetic load than plants that regularly self-pollinate. Consequently, reduced pollen diversity is likely to reduce pollen competition or reduce heterosis effects within the observed generation; more selfing is expected to increase inbreeding depression.

Furthermore, for trees, these patterns remain to be examined in an experimental or quantitative way. Furthermore, discussions of these trends have often relied on theoretical arguments, rather than empirical data, paving the way for experimental investigations. Consequently, it was the primary goal of this thesis to examine some of these gaps in knowledge in an experimental and quantitative way.

Specifically the aims of this thesis were to:

1. Examine and quantify the impact of fragmentation and tree density on mating patterns, and how this may vary with pollinators of differing mobility
2. Determine the theoretical expectations and perform empirical tests of mating pattern-fitness relationships in trees
3. Explore the plant genetic resource management implications that arise from the observations in aims 1 and 2

In general the results showed that stands of trees that have experienced habitat fragmentation or are present in lower densities express a quantifiable negative shift in their mating patterns (*i.e.* they tend to self more and receive less pollen diversity). More mobile pollinators appear to buffer trees from these negative shifts in their mating patterns.

I present a theoretical guide to the mating pattern-fitness relationships in terms of habitat fragmentation. I found that an increase in selfing and a decrease in pollen diversity are both important factors that could be quantified as impacting on fitness of established seedlings.

Taken together, these findings suggest that seeds collected from larger, less fragmented and higher density stands have higher fitness. Consequently, collecting seeds from these stands should lead to better outcomes of *ex situ* and *in situ* conservation, restoration and revegetation plantings.

**Declaration**

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution to Martin Breed and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968.

The author acknowledges that copyright of published works contained within this thesis (as listed below) resides with the copyright holder(s) of those works.

I also give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library catalogue, the Australian Digital Thesis Program (ADTP) and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

Signed ..... Date: 12 March 2013

---

**Published and submitted works included in thesis**

1. **Breed M.F.**, Ottewell K.M., Gardner M.G., Dormontt E.E., Lowe A.J. (submitted). Mating patterns and pollinator mobility are the critical traits in forest fragmentation genetics: no longer a paradox, just looking in the wrong place. *Heredity*.
2. **Breed M.F.**, Gardner M.G., Ottewell K.M., Navarro C., Lowe A.J. (2012). Shifts in reproductive assurance strategies and inbreeding costs associated with habitat fragmentation in Central American mahogany. *Ecol. Lett.* **15**(5), 444-452.  
  
<http://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2012.01752.x/abstract>
3. **Breed M.F.**, Marklund M.H.K., Ottewell K.M., Gardner M.G., Harris J.C.B., Lowe A.J. (2012). Pollen diversity matters: revealing the neglected effect of pollen diversity on fitness in fragmented landscapes. *Mol. Ecol.* **21**(24), 5955-5968.  
  
<http://onlinelibrary.wiley.com.proxy.library.adelaide.edu.au/doi/10.1111/mec.12056/abstract>
4. **Breed M.F.**, Ottewell K.M., Gardner M.G., Marklund M.H.K., Stead M.G., Harris J.C.B., Lowe A.J. (in press). Mating system and early viability resistance to habitat fragmentation in a bird-pollinated eucalypt. *Heredity*. DOI: 10.1038/hdy.2012.72  
  
<http://www.nature.com/hdy/journal/vaop/ncurrent/full/hdy201272a.html>
5. **Breed M.F.**, Ottewell K.M., Gardner M.G., Lowe A.J. (2011). Clarifying climate change adaptation responses for scattered trees in modified landscapes. *J. Appl. Ecol.* **48**(3), 637-641.  
  
<http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2011.01969.x/abstract>
6. **Breed M.F.**, Stead M.G., Ottewell K.M., Gardner M.G., Lowe A.J. (2013). Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Cons. Genet.* **14**(1), 1-10.  
  
<http://link.springer.com/article/10.1007%2Fs10592-012-0425-z>

## Acknowledgements

Firstly I'd like to thank my supervisor Andy Lowe. He has been an excellent mentor over the years and I thank him for accepting me as a PhD student. He never stopped his dynamic style of encouragement and guidance, while also letting me plan my work quite freely.

Thanks also to Mike Gardner and Kym Ottewell, my co-supervisors. You have both provided excellent support and experienced guidance throughout my candidature.

There are a number of people with whom I spent significant amounts of time discussing the development of the Australian components of my PhD. These include:

- Rob Murphy from Rural Solutions, Martin O'Leary from the State Herbarium of South Australia, Bruce Smith from Trees for Life and Michael Stead from the University of Adelaide. Rob, Martin, Bruce and Michael were instrumental in teaching me the skills of identifying mallee eucalypts in the field.
- Matt Coulter and Tina Miljanovic from Mt Lofty Botanic Gardens and Bruce Smith and Dennis Hayles from Trees for Life taught me how to overcome the challenges of rearing mallee eucalypt seedlings.
- Dennis Hayles from Trees for Life, Rob Murphy from Rural Solutions, Joe Stephens from Australian Wildlife Conservancy and Matt Kilby from Global Land Repairs taught me the skills of

how to design and implement a revegetation trial in semi-arid areas of Australia.

- Rob Murphy from Rural Solutions and Joe Stephens, Phil Scully, Kerryn Herman and Matt Hayward from Australian Wildlife Conservancy were very accommodating and flexible in helping me find locations to plant my trees.
- Next I must thank all those volunteers who helped me rear, plant and monitor >2500 eucalypt seedlings. These people include: Tom Hunt, Susie Pendle, Michael Stead, Duncan Jardine, Carlos Navarro, Kym Abrams, Bert Harris, Sarah Smith, Tessa Bradford, Bianca Dunker, Annabel Smith, Julie and Jack Paine, Andrea Ramirez, Catalina Sanchez, Jolene Scoble, Ian Matthews, Maria Marklund and my parents, Bill and Esther Breed.

I feel that I have many to thank for the academic development offered at The University of Adelaide over the last 3 years. In particular I would like to thank ACEBB and Environment Institute management committees for offering such stimulating seminars, workshops and symposia. Additionally, I would like to thank those in the Darling building, especially members of the Lowe Lab Group, for the many discussions about lab, field and general science topics. Thanks also to the TERN team on level 12 of the Schulz building for the entertaining and thought provoking weekly meetings.

I have also been lucky enough to spend a proportion of my PhD with researchers at Uppsala University, Sweden and Plant Genetics Institute, Florence, Italy. In Uppsala, I'm very grateful for the generous offer to be a visiting student during the Swedish summer of 2011. Specifically I thank Professor Jon Ågren and Professor Martin Lascoux for helping to organise my stay. Thanks again to Jon, as well as Yoshiaki Tsuda, Lára Hallson, Andreas Rudh and Shaun Boye for the many insightful discussions that took place during my visit to Sweden. I also thank Beppe Vendramin for his warm invitation to Florence and the many discussions about my PhD and beyond.

The Native Vegetation Council of South Australia (grant 09/10/27), Estate of the late Winifred Violet Scott Charitable Trust, Sir Mark Mitchell Foundation, Nature Foundation SA Inc., Field Naturalist Society of South Australia, National Climate Change Adaptation Research Facility, Australian Geographic Society, Biological Society of South Australia, Wildlife Preservation Society of Australia, Environment Institute and the Noel and Vivian Lothian Scholarships of 2010 and 2012 are gratefully acknowledged for their financial support. The University of Adelaide research branch staff was instrumental in helping me coordinate my grant applications.

Away from work, there have been four things that have kept my sanity over the last 3 years: rockclimbing, mountain biking, lunchtime volleyball and the support from my family. Thanks Bert, Nik, Tom and Matt for the many sessions out in the Adelaide Hills and those great

trips to the Gramps and Araps; long live the mulled wine, long weekends and Kachoong whippers. Thanks Shawn, Håkan, Lára and Pablo for the granite cranking around Uppsala and Stockholm. Thanks Duncan and Matt for those MTB sessions in the hills, long may they continue. Thanks so much to the SA Museum lunchtime volleyballers - Laurie, Ralph, Remko, Mark, Michael, David, David, Cam, Flavia, Ben, Em, Thierry - you are the highlight of my Mondays and Thursdays.

To my family:

Mum, Dad, Andrew and Matt: thank you all so much for providing such a stimulating life. Nature and science (not the journals!) are what come to mind when I think of my earliest and fondest childhood memories. Andrew and Matt, you have always inspired and motivated me to be the best I can be. Thank you both so much for the continued challenges of my views, sporting ability and knowledge.

Min älskling Maria: Du betyder allt för mig. Jag är ledsen för all tid min doktorsavhandling tog från dig. Ditt stöd och din kärlek gör mitt liv fantastiskt. Du är min kärlek, mitt hjärta, mitt allt!