# **Quaternary Climate Change**

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# Podocarpus elatus (Podocarpaceae)



Rohan Mellick School of Earth and Environmental Sciences University of Adelaide

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## ABSTRACT

Understanding the effect of Quaternary climate change on the distribution, diversity and divergence of *Podocarpus elatus* (R.Br. ex Endl.) will contribute to the conservation of the east Australian rainforests in light of increasing ecological damage, rapid human population growth and anthropogenic-induced global warming. To know how intraspecific diversification in a wide-ranging long-lived species is driven by climate change will improve our understanding of how climatic-drivers are involved in the evolutionary process.

This thesis examined the genetic consequences of Quaternary climate change in *Podocarpus elatus*, a long-lived rainforest conifer endemic to Australia. Firstly, eight polymorphic nuclear microsatellite and one chloroplast loci were isolated/characterised in *P. elatus*. I demonstrated the microsatellite primers could be applied to other podocarps (i.e. *P. grayi*, *P. lawrencei*, and *P. smithii*.).

The markers were used to investigate the genetic diversity and structure of *P. elatus* throughout the broad-distributional range. Populations throughout the east Australian rainforests were screened and two divergent regions separated by the dry Clarence River valley (New South Wales) were discovered (i.e. Clarence River Corridor). Niche modelling techniques were employed to verify the incidence of climatic/habitat divergence between the two regions.

Phylogeographic analysis and environmental niche modelling were combined to determine: (1) if post-glacial distributional dynamics could be described; (2) if the range-contractions suggested by southern fossil records are uniform across the entire distribution; and (3) if there is agreement between environmental niche modelling and molecular-based regional dynamics.

Niche-modelling indicated that at the Last Glacial Maximum (21 Ka), the habitats suiting the two genetically differentiated regions of *P. elatus* were geographically disjunct. The northern distributional region persisted through the LGM in a small refugial area, which during post-glacial periods has expanded. Conversely the southern range followed the opposite trend and has contracted since the LGM, but overall had greater genetic diversity. Coalescence-based analyses support these differential dynamics across the distribution of the species.

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The future climate-induced range shift of the two genetically differentiated regions of *P*. *elatus* were modelled and compared to coalescence-based inference of regional gene flow, genetic boundaries and expansion/contraction dynamics to provide information with regard to community response to climate cycles.

A total of 405 occurrence records were obtained to model species' distribution (21, 6, and 0 Ka) based on the current environment using MAXENT and forecasting future distribution (2050 A2) using an ensemble of thirteen atmospheric-oceanic global climate models. The analysis suggests the geographic shift in genetic diversity of *P. elatus* according to future climate change scenarios.

Together these data sources provide a means to predict future distribution of genetic diversity, and infer rainforest areas at increased risk of localised extinction. It was found that *P. elatus* is considerably more threatened than shown by its current distribution, and I suggest the use, and extension, of habitat corridors to accommodate future climate-induced range shift of fragmented rainforest habitats along the east coast of Australia.

## DECLARATION

I Rohan Mellick certify that 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 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. In addition, I certify that no part of this work will, in the future, be used in a submission for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree. 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 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 and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

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### STATEMENT OF CONTRIBUTION

### Chapter Two

Author contributions: Rohan Mellick collected material, generated the microsatellite library, screened clones, designed primers and wrote the manuscript. Carolyn Connelly supervised the microsatellite library generation. Maurizio Rossetto supervised the writing, screening of clones and primer design. Andrew Lowe, Robert Hill and Maurizio Rossetto funded the project.

### Chapter Three

Author contributions: Rohan Mellick, Andrew Lowe and Maurizio Rossetto conceived the ideas. Rohan Mellick collected samples, extracted DNA, completed the analyses, modelled the species' distribution and wrote the manuscript. Andrew Lowe and Maurizio Rossetto supervised the molecular analyses, interpretation of results and writing. Andrew Lowe, Robert Hill and Maurizio Rossetto funded the project.

#### Chapter Four

Author contributions: Rohan Mellick, Andrew Lowe and Maurizio Rossetto conceived the ideas. Rohan Mellick collected samples, extracted DNA, analysed the data, modelled the species' distribution, generated the coalescent-based model and wrote the manuscript. Chris Allen supervised the processing of environmental layers and completed the bathymetry extrapolation Andrew Lowe, Robert Hill and Maurizio Rossetto supervised the molecular analyses, interpretation of results and writing. Andrew Lowe, Robert Hill and Maurizio Rossetto funded the project.

#### Chapter Five

Author contributions: Rohan Mellick, Andrew Lowe and Maurizio Rossetto conceived the ideas. Rohan Mellick analysed the data, generated the coalescent-based model, modelled the species' distribution and wrote the manuscript. Chris Allen supervised the processing of environmental layers, completed the bathymetry extrapolation and helped with Figure 1 generation. Peter D. Wilson supplied future data and projected models onto the future ensemble. Maurizio Rossetto, Robert Hill and Andrew Lowe supervised the writing, analyses and interpretation of results. Andrew Lowe, Robert Hill and Maurizio Rossetto funded the project.

## CONTEXTUAL STATEMENT

This thesis has been submitted for assessment as a portfolio of publications (Chapter 2-5). The overall aim is to determine the level of genetic diversity and structure within naturally occurring populations of *Podocarpus elatus*, and establish if this is more strongly influenced by historic or contemporary drivers. I aim to describe via Environmental Niche Modelling (ENM), the past-current-future distributional dynamics of suitable habitat for *P. elatus*. I seek to correlate the observed fossil record and regional genetic boundaries to the inferred distributional dynamics, i.e. is palynology, the ENM-based, and molecular-based regional boundaries and expansion/contraction dynamics in *P. elatus* in agreement?

Furthermore, I attempt to combine knowledge of gene flow dynamics and future ENM of *P*. *elatus* to be applied to the conservation of these fragmented habitats. The application of molecular and ecological niche modelling techniques could guide the integration of the natural and artificial landscape with the aim of allowing unimpeded range shift in response to rapid climate change.

Chapter One (Literature review): a broad-contextual statement to frame the study for a broader audience in light of current knowledge and understanding.

Chapter Two (Almany, *et al.* 2009): we developed nine species-specific markers to explore the species' genetic diversity and structure.

Chapter Three (Mellick, *et al.* 2011): we determined diversity and structure of *P. elatus* through traditional molecular techniques to understand the effect of recent and historical habitat fragmentation on the observed intraspecific divergence. Two environmental niche models were developed for each genetic region and both were found to be statistically significant. The models suggested climatic-drivers were responsible for the species' intraspecific divergence.

Chapter Four (Mellick, *et al.* 2012): we inferred changes in paleodistribution in response to post-glacial warming by projecting the current model, from Chapter Three, onto the Last Glacial Maximum (21 Ka), Holocene Climatic Optimum (6 Ka) and Pre-Industrial climatic

estimates. We also incorporated traditional and coalescent-based molecular techniques to understand the species' demographic patterns.

Chapter Five (Mellick, *et al.* submitted): we inferred future distribution by projecting the current models onto a future climatic ensemble. We used traditional and coalescent-based molecular techniques to understand population divergence and ancestral gene flow (as a proxy to natural gene flow in the absence of anthropogenic effects), for the conservation of *P. elatus* rainforest habitat. We propose conservation strategies in the context of a rapidly changing environment.

Chapter Six: (Conclusion): this includes set sub-sections, summary information and future ideas for the study system. The latter includes conservation strategies, a phylogenetic hypothesis and author's remarks.

Linking past climatic divergence patterns of species, with well-defined environmental realms of tolerance will allow the forecasting of future threats from likely anthropogenic climate change. A changing climate has caused species to shift in range from ancestral to present-day distributions. The corresponding changes in diversity and structure are known to follow climatic patterns. In this thesis an inter-disciplinary methodology is explored in an attempt to correlate intra-specific divergence patterns to climate. Observing divergence patterns in the future from that inferred in the past will validate this methodology and shape future evolutionary and conservation research.