

# From populations to communities: understanding changes in rainforest diversity through the integration of molecular, ecological and environmental data

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## Abstract

The progressive aridification of the Australian continent during the last 30 million years has considerably reduced the amount of habitat suited to broad-leaved vegetation. The fossil record suggests that much diversity has been lost in that period, and that the extreme climatic fluctuations of the Quaternary stressed the remaining refugial areas even further. Yet, despite the considerable transformation of the surrounding environment, the rainforest remnants scattered along the east coast still contain considerable levels of biodiversity and endemism. This complex matrix of remnants reflects a long and varied history of selective pressures, and represents an ideal setting for evolutionary studies. Although the conservatism of some rainforest lineages points to localised environmental stability, it also highlights the importance of adaptive potential and selective tolerance. A number of recent case studies show that the tension between persistence and dispersal (often in combination with other factors) is an important mechanism contributing to the survival and distribution of rainforest species. This paper discusses the benefits of linking molecular, ecological and environmental data to improve both interpretations and hypotheses of current (neo) and past (paleo) distributions and relationships among rainforest plants, and how this information can be used to improve conservation and management approaches. Understanding how species and communities have survived past environmental change will be a critical step in predicting likely responses to future threats. A selection of integrative research topics that are likely to increase our predictive capacity for future change are outlined.



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## Introduction: decline from dominance

Paleo-botanical studies suggest that during the Mid Eocene, closed canopy forests represented the dominant vegetation type across the Australian continent (Kershaw et al. 1991). Forests similar to those now restricted to the northern and wetter parts of Queensland were once widespread at much higher latitudes. As the Australian landmass separated from Antarctica in the Late Eocene, the formation of circumpolar currents increased the amount of moisture trapped at the South Pole as ice. This was followed by a global decline in temperature, and by increased aridification and retreat of rainforest vegetation continent-wide (Greenwood & Christophel 2005). By the Mid Miocene the extensive Western Australian paleo-drainage had dried. Rainforests disappeared from central Australia and were eventually restricted to wetter coastal habitats by the Late Miocene (Martin 2006). Evidence suggests that in the last 10 My the core rainforest areas of the Wet Tropics have remained relatively ecologically stable, while further fragmentation, aridification and loss of biodiversity took place at more southern latitudes (Kershaw et al. 2005).

Extensive macro- and micro-fossil records show that the Mid Eocene forests were dominated by families (such as Cunoniaceae, Elaeocarpaceae, Lauraceae, Myrtaceae and Proteaceae) that remain important in modern Australia (Greenwood & Christophel 2005). Floristically, rainforests are often considered as the living links to Australia's ancient past as they harbour a high concentration of primitive angiosperms (Webb & Tracey 1981). These paleo-endemics are vestiges of previously widespread taxa and are concentrated in the Wet Tropics and across the eastern border between Queensland and New South Wales (Whiffin & Hyland 1986). In some families only moderate morphological modifications have occurred during the last 55 My despite the major climatic adjustments that took place as the Australian continent traveled through 20° in latitude (Hill 2004). However, while some lineages have barely changed in morphology, the fossil record proves that their distribution has been considerably modified. For example, Oligocene and Miocene fossil floras from Victoria, New South Wales and southern and central Queensland contain endocarps of *Elaeocarpus clarkei* F.Muell. morphologically similar to the modern *E. bancroftii* F.Muell. & F.M.Bailey that is restricted to the Wet Tropics (Rozefelds & Christophel 1996, Greenwood & Christophel 2005).

Interestingly, the morphological adjustments that did take place were not necessarily in response to aridification. Hill (2004) suggested that the appearance of scleromorphy/xeromorphy in Proteaceae during the Mid Eocene (a period of high rainfall) was likely to be a response to nutrient deficient soils and/or higher light levels. These characteristics however, were an important source of evolutionary potential for adaptation to aridity, with increased diversification of sclerophyllous lineages taking place between 25 and 10 Mya (Crisp et al. 2004). More recently, molecular phylogenetic studies have contributed to the development of new hypotheses about previously unexpected relationships between dry-adapted and rainforest lineages. One such example is Tremandraceae, a former southern family of dry-adapted shrubs recently shown to be part of Elaeocarpaceae (comprising mostly rainforest trees), with the diversification of *Tetralthea*, the largest genus, putatively occurring during the major aridification phase of the Late Miocene (Crayn et al. 2006).

Because of the continental-scale climatic and environmental changes described, all remaining rainforest areas in Australia can be considered as refugia. Yet, despite covering

<1% of the land area, rainforests still contain a considerable portion of Australia's unique biodiversity (Adam 1992).

### **The extreme climatic events of the Quaternary**

The fossil record suggests that the greatest reduction in suitable rainforest habitat and diversity occurred before the Quaternary (Hill 2004). However, the most recent ice-age caused significant adjustments to species distributions worldwide, particularly during the last 700 Ky when climatic fluctuations were more intense (Hays et al. 1976). In Australia, rather than creating extensive ice sheets, ice-ages shaped the distribution of vegetation by increasing aridity, fire frequency and fire intensity (Bowman 2000). Paleo-climatic models suggest that the changes in temperature and moisture regimes caused by glacial maxima fragmented rainforest remnants into even smaller refugia (Nix 1991). As in most other areas around the globe, some species adapted to these new conditions or dispersed to more suitable locations, while others only persisted in marginal portions of their former range or became extinct (Hewitt 2000). Well-dated marine palynological records from northern Queensland suggest that throughout the late Cenozoic, complex rainforests occupied the wetter habitats and were surrounded by extensive drier araucarian forests that functioned as a transition to true sclerophyllous vegetation (Kershaw et al. 2005). In the last 200 Ky, increased climatic instability brought about greater environmental stress and vulnerability to fire, resulting in the replacement of the araucarian forest by true sclerophyllous vegetation dominated by eucalypts. The last glacial maximum was particularly intense, with severe and persistent fragmentation revealed by *Eucalyptus* intrusions in current Wet Tropics rainforest areas as recently as eight thousand years ago (Hopkins et al. 1993). The intensity of these more recent events is likely to have caused further extinctions (Kershaw 1994).

During the brief inter-glacials (such as the one we are currently in) climatic conditions improved and refugial populations could expand into newly available habitat. The success of post-glacial expansions depended on a range of factors such as recruitment and dispersal potential, and played an important role in defining modern-day distribution patterns. Extensive palynological records from the Northern Hemisphere show that tree species responded differently to climate change, tracking their individual habitat requirements according to their dispersal capability (Hewitt 1996). During this expansion process, transitional plant communities that were considerably different to current ones were established with the help of small populations that persisted within microclimate pockets in areas otherwise considered as unsuitable. Recent studies suggest that a predicted loss of 'core' habitat does not necessarily imply population extinction (although it certainly implies greater vulnerability), and that in order to understand temporal distributional changes of plant communities, it is essential to appreciate the tolerance of single species to environmental fluctuations (Stewart & Lister 2001). Similar species-level palynological records have not yet been identified for the Australian paleo-flora, as the focus of most studies has been on broad vegetation structure. As we await more detailed palynological investigations on rainforest taxa, we can assume that suitable circumstances existed for the survival of small refugial populations along the eastern coast of Australia.

## The molecular revolution: fine-scale evolutionary dynamics

Paleo-ecological, biogeographic and systematic studies have provided valuable information on the evolutionary and distributional shifts that shaped the Australian flora. However, if we are interested in the factors impacting on the survival/extinction of species, we must also consider the fine-scale influence of selective biotic and abiotic processes. The advances in molecular genetics over the past 20 years have significantly contributed to this goal. For example, reciprocally monophyletic populations (evolutionary significant units) can be identified by sampling selected loci prone to high substitution rates but non-recombinant and uni-parentally inherited (Moritz 1994). These genetically distinct groups identify historically isolated populations and define the location of barriers to gene flow (such as those established by changing climatic conditions). The availability of complementary fossil and molecular data and the recent development of improved analytical approaches (Sanderson 2003) provide the opportunity to explore the temporal dimension of these evolutionary processes.

Comparative studies on co-distributed species can make use of the genetic signatures left by different expansion patterns to identify the locations of refugia, the factors affecting expansion patterns and the adaptive potential of these taxa. In the Northern Hemisphere, haplotypic data from a range of maternally-inherited chloroplast loci have been used to track post-glacial re-colonisation patterns in a considerable number of tree species, confirming models previously suggested by palynological data (Petit et al. 2005). Interestingly, comparative studies in *Quercus* have concluded that during the last glaciation a more complex matrix of localised refugia (and consequently greater genetic diversity) was maintained in California than in Western Europe, highlighting how habitat availability and different life-history combinations can influence re-colonisation outcomes (Grivet et al. 2006). Similar studies are still limited in Australia. An overview of plastid DNA variation across the natural range of Tasmanian eucalypts from section *Maidenaria* showed that genetic variation correlates more with geography than taxonomy (McKinnon et al. 2001). This regional haplotype-sharing pattern suggests that extensive hybridisation took place among local eucalypts following the latest ice age (McKinnon et al. 2004), a pattern reminiscent of that found in the European oaks (Petit et al. 2002).

## An Australian rainforest perspective

Australian rainforest habitats provide an ideal setting for evolutionary studies (Schneider et al. 1998). They have high amounts of taxonomic diversity and endemism and, as suggested by fossil evidence, include ancient lineages that have been continuously present in the region (Hill 2004, Greenwood & Christophel 2005). Furthermore, rainforests are currently distributed across a matrix of differentially sized and spaced remnants that reflect a long and varied history of environmental disturbance and selective pressures (Moritz & McDonald 2005).

Until recently, most of the molecular research investigating the history and dynamics of Australian rainforests was focused on the fauna of the Wet Tropics. Phylogeographic studies on a number of low-vagility vertebrates (including habitat-specialist birds, lizards and frogs) detected significant genetic disjunction between populations distributed across a previously identified (Nix 1991) biogeographic barrier, the Black Mountain Corridor (BMC, a strip of low-lying land between Cairns and Mossman that

interrupts the Great Dividing Range; Schneider et al. 1998). Molecular divergence was ascribed to multiple vicariance episodes mostly near the BMC area, with the majority of speciation events originating before the Pleistocene. This suggests that the climatic fluctuations of the Quaternary generally emphasised existing divergence patterns rather than creating new ones (Schneider et al. 1998, Schneider & Williams 2005). The shallow genetic divergences measured between single putative refugia, and the lower genetic diversity in southern populations also suggest that a loss of suitable habitat during glacial maxima (and likely decline in species richness) was followed by rapid re-colonisation (Moritz & McDonald 2005). As these events are affected by the ecological characteristics of each species, it has been suggested that future studies should also pay attention to the ecological factors likely to impart selective constraints rather than focus on geographic isolation alone (Schneider et al. 1999).

The available fossil evidence from the Australian rainforest flora also points to an historical decline in diversity, although limited examples of recent speciation exist within southern rainforests (Rossetto 2005, Savolainen et al. 2006). To date, no phylogeographic research on the Australian rainforest flora has been published. However, a few studies assessing overall genetic diversity across single species have detected significant north/south genetic disjunctions (*Fontainea australis* Jessup & Guymier, Rossetto et al. 2000; *Araucaria bidwillii* Hook., Pye & Gadek 2004; *Nothofagus moorei* (F.Muell.) Krasser, Taylor et al. 2005). A more recent study sampled the entire distribution of two related and co-distributed rainforest trees, documenting substantial discrepancies in genetic differentiation across biogeographic barriers such as the BMC (Rossetto et al. 2007). While *Elaeocarpus largiflorens* C.T.White revealed an abrupt genetic front between two morphologically distinct subspecies separated by the BMC, the same barrier was inconsequential to *E. angustifolius* Blume (which showed lower genetic differentiation across a much wider geographic gap). A broader study in progress is comparing genetic disjunctions across 11 tropical *Elaeocarpus* species representing a range of habitat preferences and life-history traits combinations. Interesting preliminary patterns include north/south genetic disjunctions for higher-altitude species (as previously shown in *E. largiflorens*), as well as an unexpected lack of impact of fruit type on genetic structure (Rossetto et al. in prep.).

Understanding evolutionary patterns at temporal and geographical scales is only the first step as it is essential to relate these patterns to causal factors. Simulations investigating the expansion potential of trees show that models that take into account life-history traits relating to dispersal and life-cycle are more realistic and more likely to provide the correct interpretation of molecular data (Austerlitz & Garnier-Gere 2003). Thus in order to discover the factors regulating landscape connectivity, it is important to develop more studies targeting range-wide sampling across related species representing diverse habitat preferences and life-history traits.

### **Evolutionary ecology: finding meaningful patterns**

Multi-species studies integrating ecological, molecular and environmental evidence can identify broad evolutionary patterns, and recognise the mechanisms that influence the survival of populations and species. Recent work is uncovering broad correlations between life-history traits and the distribution of taxa. For instance, a study comparing sexual systems across Australian tropical trees (1113 species from 83 families) found that the incidence of monoecy is significantly higher in Australia than in other tropical

floras (Gross 2005). Although phylogeny might be partly responsible for this (about 50% of the monoecious taxa are from two families), Gross (2005) suggested that the reliance on inefficient insect pollinators could have favoured the maintenance of monoecy. Another large-scale rainforest study including 258 species from the Nightcap Ranges (northern NSW), identified the life-history traits associated with persistence and dispersal as the most influential in describing the current distribution of locally rare trees (Rossetto & Kooyman 2005). The results suggest that major environmental changes have been important selective drivers on large-fruited species within these southern rainforests. It can be assumed that while large-seeded plants can establish more efficiently, lower seed production and the absence of dispersal organisms reduce expansion capability after a bottleneck. As a result, the large-fruited species that survived habitat contractions are likely to be the ones that could enhance their competitiveness through in-ground stem persistence. Fine-scale molecular studies on narrow endemic taxa are supporting this hypothesis (Rossetto et al. 2004a, Rossetto & Kooyman 2005, Rossetto et al. in prep.). For instance, the high levels of diversity within small, isolated populations of *Eidothea hardeniana* P.H. Weston and *Elaeocarpus sedentarius* could be symptomatic of a strategy involving the reliance on self-replacement of individuals through resprouting rather than recruitment. The lack of correlation between genetic and geographic disjunctions despite the presence of strong population-level genetic autocorrelation, also highlight the impact of limited dispersal.

### The persistence niche

The importance of persistence is often neglected while that of recruitment is emphasised, yet many ecosystems are dominated by resprouters (Bond & Midgley 2001). Vegetative reproduction provides a competitive edge by allowing the sharing of resources between connected ramets, and can be considered as an alternative lifecycle loop that allows persistence in species that are not able to complete a normal life-cycle. The persistence niche is suitable to a range of disturbance regimes, enables species to tolerate long periods without recruitment, allows regeneration in unsuitable conditions and can reduce the loss of population-level genetic diversity (Bond & Midgley 2001). This strategy can be particularly suitable to species constrained to less than ideal habitats, and Johnson and Lacey (1983) suggested that it might be an important long-term survival strategy for rainforest trees.

Resprouting is a relatively safe escape route under suboptimal conditions but prolonged clonal growth through environmental suppression of sexual reproduction can lead to monoclonal populations. There are some interesting examples of extreme clonality in the Australian flora. For example a range of molecular approaches could not identify any variation across individuals of *Wollemia nobilis* sampled from all known sites (Peakall et al. 2003). Similar circumstances were discovered for *Elaeocarpus williamsianus* Guymer, a tree restricted to a number of disjunct and mostly disturbed rainforest remnants in northern NSW. A genetic study found that all populations but one consisted of single clones and since this is a preferential outcrossing species, viable seed could not be set (Rossetto et al. 2004a). *E. williamsianus* is now locked into an evolutionary dead-end loop: long- and short-term disturbance events have favoured excessive clonality that prevents sexual reproduction and long distance dispersal. In turn, limited dispersal prevents range expansion and the potential gene flow which would re-establish a balance between vegetative and sexual reproduction.

### **The importance of dispersal**

There is increasing evidence that expansion mechanism and habitat preference are among the main factors affecting the temporal distribution and the diversification potential of plant species (Pearson 2006). Dispersal of propagules enables genetic exchange (thus reducing vicariant divergence and inbreeding), as well as expansion to newly available habitat and recovery after unfavourable circumstances. For instance, rainforest trees that produce fleshy, highly dispersible fruits can be expected to have lower levels of between-population genetic differentiation than species with less palatable fruits (Shapcott 2000). Thus fruit morphology can affect current distribution patterns, and mal-adaptation through lack of dispersers can explain rarity in the vertebrate-poor rainforests of northern NSW (Rossetto et al. 2004a, Rossetto & Kooyman 2005, Rossetto et al. submitted), although it does not imply short-term extinction (as previously suggested; Archer et al. 1994). It is important to remember that inference of expansion potential from fruit morphology alone can be unsatisfactory, as capacity for dispersal is not necessarily synonymous with effective dispersal (i.e. including establishment). Unfortunately, information on dispersal efficiency of the Australian rainforest flora is still limited although an increasing number of recent studies are measuring active fruit dispersal by Wet Tropic frugivores (Westcott & Graham 2000, Westcott et al. 2005). The tension between persistence and dispersal is likely to be an important mechanism contributing to the current distribution of many rainforest species, but clearly there are other factors that also need to be investigated.

These early studies are showing that paleo-endemic species can survive for a long time within small populations (Rossetto et al. 2000, Rossetto et al. 2004a, Rossetto & Kooyman 2005). This suggests that single populations, or even whole new species (Weston & Kooyman 2002), can still be found within moderately-sized vegetation remnants, and that small populations are not doomed as they can persist and maintain potential for future expansion (if and when suitable conditions arise). However, it is important to stress that this apparent resilience does not make restricted populations less vulnerable to stochastic events and anthropogenic disturbance.

### **Reacting to the biodiversity crisis**

During the last 150 years the impact of logging, clearing and urbanisation has further reduced the extent of rainforest vegetation in Australia (Connelly & Specht 1988). This is particularly true for the Big Scrub of northern NSW (which covered an area of over 70 000 ha prior to European settlement) where widespread clearing has restricted rainforest vegetation to approximately 1% of its original distribution (Lott & Duggin 1993). Rainforests worldwide are subject to increasing external pressures and degradation that dissect continuous species distributions into isolated fragments (Whitmore 1997, Arnold & Rossetto 2002, Rossetto et al. 2004b) and despite recent controversy on the true extent of the global rainforest biodiversity crisis (Wright & Muller-Landau 2006; but see Laurence 2006), we now recognise that drastic environmental modifications linked to impending climate change threaten the integrity and long-term sustainability of rainforest ecosystems. For instance, in the Wet Tropics where the altitudinal gradient is the most significant factor explaining fauna compositional patterns (Williams et al. 2003), climate change scenarios (with temperature increasing up to 5°C in the short term) predict a significant reduction in suitable upland conditions and the potential disappearance of entire habitat types. Consequently, rainforest conservation and

management faces challenges at two temporal levels: the contemporary, dealing with current threatened species lists and habitat fragmentation, and the future, dealing with the predicted decline of already small habitat remnants.

Understanding likely responses to future threats is crucial to conservation planning, and one of the main challenges for conservation biology will be to anticipate environmental change and adjust management approaches accordingly. By appreciating how past climatic cycles have affected selective biotic and abiotic pressures and consequently the survival and distribution of species and ecological communities, we will be able to develop predictive models that determine vulnerability to future change. An increasingly common response to the problem is the development of multi-species recovery plans, which hopefully will be followed by multi-species implementation projects. Biologically meaningful multi-species approaches are being explored, such as the one based on trait-based functional groups currently being developed for the threatened flora of the Border Ranges (Kooyman & Rossetto in prep.). In the long-term, a focused approach involving integrative research will facilitate the management of threats and risks at the species, multi-species and the ecosystem levels.

### **Conclusion: where to from here?**

Fossil evidence shows a considerable level of conservatism in the Australian rainforest flora despite gradual long-term and intensive short-term environmental change. This suggests the presence of localised environmental stability, but also points to the adaptive potential of some lineages that have survived the evolutionary sifting of severe climatic cycles. It can be expected that a range of key biological (evolutionary) factors played an important role in the endurance of the remaining rainforest flora. To better understand the factors influencing evolutionary processes, future research should include:

- 1) Phylogenetically structured multi-species molecular ecology studies targeting important biogeographic barriers and selected functional groups. The discovery of repeated patterns of genetic divergence will identify landscape features of evolutionary significance and selectively important life-history traits. The availability of relevant paleo-ecological data would also enable the accurate dating of these events.
- 2) Evaluations of multiple associative patterns among selected life-history traits and the distribution of species (and/or genes). This will contribute to the identification of the major factors likely to affect the evolutionary response to changing environmental circumstances.
- 3) The development of models (based on appropriate levels of ground-truthing and in-situ data gathering) that can differentiate between potential and realised niches for species and ecological communities. This will improve our understanding of the level of tolerance of species and communities, and enable us to predict the impact of future environmental and climatic change.

On their own, these are important areas of research but the greatest scientific benefit will arise from developing experimental designs that combine them all. The Australian rainforest flora provides a unique evolutionary scenario for this type of research; however these approaches are suitable and relevant to a broad range of vegetation types.

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