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A riparian perspective on species ecology and evolution:
Melaleuca leucadendra (Myrtaceae)

Thesis submitted by

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Supervision

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Abstract

This thesis investigates structure and survivorship in vegetation that inhabits disturbance-driven riparian environments. The outcomes of this thesis contribute to developing a framework to test predictions of scale-dependent variation in genetic structure and functional traits in woody species in relation to patterns of disturbance. I use as a model species *Melaleuca leucadendra* (Myrtaceae)—the paperbark tree that inhabits river systems across northern Australia. These environments are sub-humid and seasonally arid, typical of dry southern hemisphere subtropical biomes, and are among the most hydrologically variable systems on a global scale. In these river systems, the flow regime features stochastic high-energy floods and seasonal drought. The genus *Melaleuca* is a major group in the family Myrtaceae and is dominant in riparian habitats. *Melaleuca* displays diverse phenotypes and unclear taxonomic boundaries. I aim to improve our understanding of how members of this genus persist and the influence of the environment on genetic processes within this lineage. This will contribute to a broader understanding of the interaction between plant ecological strategies and drivers of evolutionary change, with special relevance to questions related to species persistence in disturbance-driven ecosystems.

I demonstrated high capacity for stem resprouting in *Melaleuca leucadendra* throughout the seedling life stage and strong spatial aggregation of stems relating to clonal genotypic structure in the mature life stage. These results agree with the theory that resprouting, as a clonal growth mechanism, confers advantages for survival against physical disturbance. It also demonstrates that environmental pressures can influence above-ground spatial genetic structure of ramets through increased spatial aggregation of stems. In *M. leucadendra* and *Eucalyptus camaldulensis*, two conspicuous species that occupy niches with elevated hydrological stress, the physiological capacity to resprout is independent of seed size and relative growth rate, is acquired very early in ontogeny and is maintained during seedling growth. Thus conventional explanations for resprouting as a resource-constrained trait do not account for this pattern. Resprouting more plausibly reflects a biological solution for generalised physiological tolerance across individual life spans. Spatial genetic analyses conducted on adult-stage *M. leucadendra* provided evidence of selection for resprouting. The probability of detecting clonal ramets was far greater at three mainstream locations than at a headwater location differentiated by hydrological energy. Clonality was detected in 42 genotypes (30% of mainstream samples) in the range 0.12–17 m, corresponding to clumps of stems within groves. In contrast, there was no evidence that clonal growth extends genetic structure beyond 20 m, or at any scale at the headwater location (all 90 genotypes unique).

Data from these studies support clonal growth as a principal mechanism defining survival and dominance in river environments subject to unpredictable and severe

fluvial disturbance. In addition, non-clonal dispersal via the river system appears to constrain population connectivity. No relationship was detected between spatial proximity and genetic relatedness among individuals within sampled populations (here 600 m channel lengths) whereas a pool of common genotypes was detected over distances greater than 100 km in the river system. In addition, mainstream and headwater locations are differentiated by an order of magnitude difference in disturbance as assessed using stream-power distributions and flood extreme event analysis. These stream types (mainstream and headwater) feature strong population structure and genetic differentiation mechanisms with low probabilities of allelic exchange. This suggests a process hierarchy whereby (i) resprouting in response to disturbance promotes individual survival (i.e. clonality); (ii) fluvial action, including floods and channel re-structuring, causes stochastic changes in demography and genetic connectivity; (iii) periods of genetic and fluvial connectivity result in admixture among mainstream locations forming a common genotype pool; (iv) selection occurs for phenotypic tolerance to variable environmental stresses enabling niche persistence.

In this thesis I have demonstrated that a hierarchy of scales is a useful construct to examine organismal life-history strategies. Valuable insights may be gained from extension beyond conventional concepts of biological units as individuals, populations and species. *Melaleuca leucadendra*, the focus of this thesis, represents an example of how individuals, populations and species are interlinked by genetic exchange. In addition, feed-back with abiotic processes such as natural disturbance provides both a driver of, and a barrier to, evolutionary change (speciation). The phenotypic variability observed in this group across all levels represents both an expression of (selection for adaptability) and a solution to (environmental stochasticity) evolutionary drivers acting at different spatial and temporal scales. This warrants further investigation in the context of the poorly-studied arid and sub-humid Australian flora. Adaptability in phenotypic and evolutionary responses may be common in taxonomic groups that do not exhibit rapid radiations under variable environmental conditions.

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