Prologue

"Knowledge of the plant life of Western Australia was very limited at the time of my visit. While the floral elements were well known, no studies had been made on their inter-relationships in the field....little was known about the conditions that determined the inner relationships of the endemic flora. These aspects were considered as being fundamentally important...

...Also the country's unrivalled richness in species could be expected to prove rewarding to those who studied its vegetation".

Ludwig Diels (1906)

Extract from a translation of the book "Die Planzenwelt von West-Australien südlich des Wendekreises"

In 1906, Dr Friedrich Ludwig Diels (1874–1945), Director of the Munich Botanic Gardens, published his book *Die Planzenwelt von West-Australien südlich des Wendekreises*, translated meaning *Plant Life of Western Australia South of the Tropics,* based on his 1900-1902 travels with fellow botanist, Dr Ernst Pritzel. The uniqueness of the Western Australia flora was already recognized prior to this book's publication but Diels' work is considered seminal to our current understanding of the distribution and general composition of the flora; however, his work has not been easily accessible, as a translated version only became available in 2007.

P.1 Southwestern Australia and its Functional Biodiversity

Southwestern Australia (hereafter referred to as the 'SouthWest') — defined as the area south of a line from Shark Bay in the north to Eyre in the south-east — is unique among Australia's bioregions because of its high species richness and levels of endemism and exceptional functional diversity. The SouthWest is Australia's only recognized biodiversity hotspot among 25 regions world wide (Myers *et al.*, 2000). The SouthWest is also special in that it is one of only five regions that experiences a mediterraean-type climate characterised by cool, wet winters and summers that are hot, dry and prolonged.

Biodiversity can be defined as the level of variability present among organisms and their life processes within a reference area, and includes composition, structure and function at the scales of genes, species, communities and ecosystems (Noss, 1990; Lamont, 1995). The functional component of biodiversity in the SouthWest flora relates directly to trait diversity resulting from macro- and micro-evolutionary trade-offs between form (e.g. morphology, structure) and function (e.g. physiology,

protection) shaped by climatic, edaphic, pyric, hydrological, geological and biotic pressures that began over 100 million years ago and intensified over time.

Thus, it is not just the number of plant taxa, diversity of habitat types and ancient, weathered landscapes that sets the SouthWest apart from other Australian bioregions. The flora also exhibits a diverse range of morphological and physiological adaptations that aid its survival in extremely nutrient-impoverished, drought- and fire-prone environments and subject to intense herbivory and granivory by such unique animals as strong-billed black cockatoos. It also lacks the long-tongued social bees and humming birds that are such efficient pollinators in other continents but has instead solitary bees and unrelated nectar-feeding birds and small marsupials that can take over the task. Emus and kangaroos are not only voracious plant feeders to which the flora must adapt but these animals can also be utilized for long-distance transport of seeds. The SouthWest flora is characterized by tough, prickly-leaved species that have a persistent seed bank stored either on the plant or in the soil, have modified roots or symbiotic relationships with microorganisms that enhance soil nutrient and water uptake, and a general reliance on fire for long-term survival. These adaptations are not necessarily confined to the SouthWest, they are just exceptionally well developed here.

P.2 Environmental and Biotic Constraints

Our book recognizes that the major environmental constraints to which species in the SouthWest flora have had to adapt can be grouped into three *abiotic factors*: 1) the nutrient-impoverished soils, 2) seasonal drought and heat, and 3) recurrent crown fires, and two *biotic factors*: 1) absence of highly efficient pollinators and dispersal agents, but 2) presence of highly efficient herbivores and granivores (Fig. P.1). Our emphasis is on environmental factors that constrain growth and reproduction and to which species have had to adapt through the processes of genotypic variation and directional selection if they are going to survive, followed by stabilizing selection among the adapted core of survivors. Few taxa were able to adapt to such severe constraints but those that did underwent exceptional rates of speciation with remarkable proliferation of their adapted traits leading to a limited number of clades at the levels of widespread genera and families but remarkably high numbers of endemic taxa at the species level (Hopper & Gioia, 2004).

Thus, the family Proteaceae, with a 115-million-year history, is distributed throughout Australia, Africa, South America, New Zealand, Asia, New Guinea and New Caledonia but 800 of the 1,400 species in the family occur in the SouthWest with over 95% confined here (Cowling & Lamont, 1998). It is no accident that >90% of these species have novel dispersal agents (ants, emus, willy-willies, Chapter 10), fire-responsive seed storage and release (with a 90-million-year history, Chapters 1, 10, 11), life cycles adapted to recurrent crown fire (Chapter 2), specialised root clusters for

enhancing nutrient uptake (with a 90-million-year history, Chapter 6), a wide range of pollinators, including the novel use of bees, marsupials and birds (Chapter 8), and unusual breeding systems including protandry and flower colour change (Chapter 7), among the world's most scleromorphic, long-lived and spinescent leaves as a response to impoverished soils (with a 100-million-year history), and later exposure to recurrent drought and strong light (with a 15-million-year history, Chapters 3, 9), and novel granivores such as moths and cockatoos that have involved innovative solutions such as crypsis and woody fruits (with a 20-million-year history, Chapter 9). Paradoxically, the seeds of SouthWest Proteaceae store among the highest levels of N and P in their seeds of any worldwide but are accumulated from foliage and soils whose levels of these nutrients are among the lowest in the world (Hocking, 1981; Kuo *et al.*, 1982; Hocking, 1986; Pate *et al.*, 1986; Groom & Lamont, 2010).

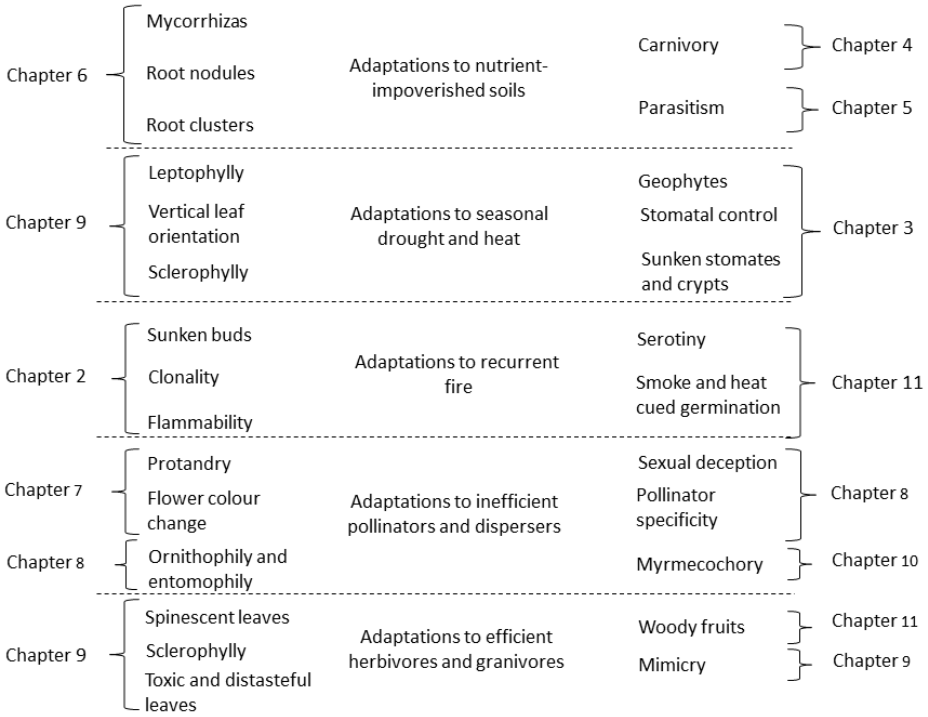

Fig. P.1: Adaptive responses to the major constraints on survival, growth and reproduction of SouthWest plant taxa, as they relate to chapters within this book.

Both the large seeds and scleromorphic leaves share the constraint sequence through time of nutrient impoverishment beginning in the high rainfall climates of the

Upper Cretaceous followed by increasing drought and seasonality in the Miocene with fire a pervasive but increasingly restrictive selective agent throughout. While climates in the Paleogene are considered to have been even wetter than the Cretaceous, it is clear that the climate was seasonal and still fire-prone at this time (Lamont & He, 2012). These same climatic effects oscillated at about 100,000-year intervals throughout the 2.6-million-long Quaternary (Rognon & Williams, 1977; Byrne, 2008) and hastened the extinction-adaptation cycle to produce the unique SouthWest flora we see today. Thus, while we accept the importance of poor soils (Hopper, 2009) and fire (Mucina & Wardell-Johnson, 2011) of previous models in shaping this flora, we cannot accept that climatic stability has had a key role as proposed by Hopper (2009). Increasing and fluctuating seasonality and aridity over time have had a major impact on plant traits (Lamont *et al*., 2002) but also on the other two constraints, especially the formation and distribution of the nutrient-impoverished laterite and sands and exposure of the parent granite so characteristic of the SouthWest (Glassford & Semeniuk, 1995), and the intensity and frequency of fire (Pausas & Keeley, 2009).

P.3 Our Book

The Western Australian Herbarium has adopted a systematic approach to the classification of vascular plants, based on current research conducted by the Angiosperm Phylogeny Group, a global partnership among plant scientists interested in understanding the relationships between plant families and orders. This revision, known as APG III (The Angiosperm Phylogeny Group, 2009), involves some family-level changes. To maintain consistency with the Herbarium's move towards the APG III's taxonomic classification, this book also follows this system. We have also endeavored to provide current species and plant family names according to *Florabase*, the Western Australian Herbarium's authoritative online species database. Several myrtaceous genera have now been merged into *Melaleuca* (Craven *et al*., 2014), including *Beaufortia, Calothamnus* and *Eremaea*, all endemic to the SouthWest. We have elected to maintain these genera because of ecological differences between and within these genera and *Melaleuca sensu stricto*, and also readers may be unfamiliar with the new nomenclature resulting from these recent combinations.

The title of our book—*Plant Life of Southwestern Australia*—is in part a tribute to Diels' monograph. Whereas Diels' book focused on describing Western Australia's temperate and semi-arid flora according to its composition, distribution, and structure, our book is about the flora's adaptations, hence the subtitle *Adaptations for Survival*. Our book begins with a general introduction to the evolution and diversity of the flora, then details adaptations that are in response to nutrient-impoverished soils, recurrent fires and summer drought. Finally, strategies or morphologies designed to maintain or ensure species survival that relate to pollination, plant leaves and seeds

are discussed. While compiling this book, we re-examined the available literature to provide a comprehensive up-to-date overview of the topics discussed.

Just like Ludwig Diels' book, we hope that our book will "*prove rewarding*" to those who have an interest in southwestern Australia's unique flora, as well as providing insights into the adaptations that the native flora has developed to survive what can be a persistently harsh environment.