

CHAPTER 1

A separate creation: diversity, distinctiveness and conservation of Australian wildlife

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Summary

Australia is biologically diverse, with around 150 000 described species, representing perhaps 25% of the total number present. However, this biota is more notable for its endemism than its richness (e.g. 94% of Australian frog species are found nowhere else). Australia is distinctive, not only in terms of endemism, but also in terms of evolutionary adaptations (e.g. large hopping mammals) and ecological processes (e.g. nutrient cycling by fire). Distinctiveness is attributed to three principal factors: (1) a long period of geographic isolation; (2) the preponderance of ancient soils low in key nutrients; and (3) an increasingly arid and inherently unpredictable climate. Australia is also unfortunately distinctive in the scale of biodiversity loss since European settlement with 98 species and subspecies listed as extinct, and a further 1700 threatened with extinction. Both for historical extinctions and currently threatened species, habitat loss and introduced species are the key threats, while climate change is the emerging and possibly most significant threat of the twenty-first century. In the face of these perils, Australia's distinctive wildlife needs special attention because it makes such a large contribution to the biodiversity and cumulative evolutionary history of the planet.

1.1 Introduction

Australia is a biologically unusual continent. This is easily shown by a few examples such as the presence of large hopping marsupials, the prevalence of fire-adapted vegetation, and the sheer diversity of arid-zone lizards. Entire groups of organisms are found nowhere else. Many more are largely confined to the Australian continent, with only a

few representatives on nearby islands, such as New Guinea. While visiting Australia and pondering the unusual Australian animals, Charles Darwin wrote in his diary: “*An unbeliever in everything beyond his own reason, might exclaim ‘Surely two distinct creators must have been at work ...’*” (p. 402 of Darwin, 2001). The Australian fauna was so different from that found in Europe, Asia or the Americas, it was as though it was created completely separately from that elsewhere. Of course, Darwin was essentially correct in that Australian wildlife, to a large extent, have been ‘created’ separately. This separate-ness, however, was not the work of a separate supernatural entity, but rather the result of a long period of independent evolution on an isolated continent subjected to significant and unusual environmental change.

Precisely because of this distinctiveness, the conservation of Australian wildlife is essential to the conservation of global biodiversity. Loss of Australian species would result in the loss of large parts of the global tree of life, as many are both geographically and evolutionarily distinct. Unfortunately, many Australian species have already become extinct and more will likely follow in the coming decades. At the same time, many species that have evolved elsewhere have arrived, changing the structure and dynamics of Australian ecosystems, which, coupled with extinctions, has diminished the distinctiveness that the long years of separate evolution have wrought.

This chapter aims to provide a broad overview of Australian wildlife, focusing on diversity, distinctiveness and conservation of the biota. The term ‘wildlife’ is here used in the broad sense of naturally occurring, native populations (whether animals, plants or ‘other’) and should not be read as meaning terrestrial vertebrates in particular. Nevertheless, examples will often be drawn from terrestrial vertebrates. This is because data on vertebrates and terrestrial systems are more complete and more familiar to the author. When referring to ‘Australia’, this comprises the national territory of the Commonwealth of Australia (primarily the area of the Australian continental shelf including Tasmania but excluding New Guinea) rather than a discrete biogeographical or geological unit.

1.2 Australian biodiversity

1.2.1 Richness

The total number of species in Australia, or indeed any part of the world, is uncertain. The primary reason for this is that many species, especially in hyper-diverse groups such as the insects, remain undiscovered by science and thus undescribed (Purvis and Hector, 2000). This gulf between the known and unknown has been termed the *Linnean Shortfall* (Whittaker *et al.*, 2005). The sheer size of the biota will ensure that the shortfall will remain for some time to come. A recent global estimate (Mora *et al.*, 2011) suggests that there are 8.7 million species of eucaryotes, on land and at sea, of which approximately 1.2 million have been described, leaving more than 80% still to be given a scientific name.

In the case of Australia, the Linnean Shortfall is likely especially pronounced. Although formal scientific description began shortly after the modern system of taxonomy was founded in 1758 (with the publication of the 10th edition of Linnaeus’ *Systema Naturae*), rates of description have been slower than many parts of the world (Plate 4). This is likely because of the large size of the continent, the small human population, and the concentration of available expertise in a few cities far from many of Australia’s biodiversity hotspots. Even for the well-known mammalian fauna, the rate of discovery more closely resembles that of Brazil than either the United States or Canada (Plate 4). Indeed the curve

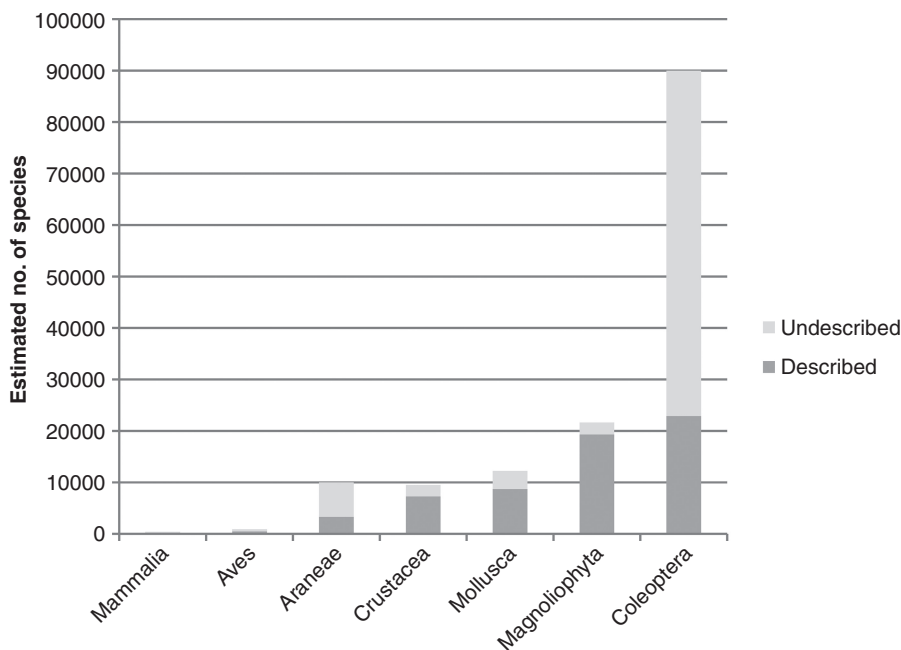


Figure 1.1 Estimated numbers of described and undescribed Australian native species for selected groups. Data taken from Chapman (2009).

may not have yet reached an asymptote, suggesting further new mammal species await discovery in the twenty-first century (Ceballos and Ehrlich, 2009). Of course, what applies to mammals applies much more so to insects and other less-studied taxa.

Considering all described taxa, Chapman (2009) estimates that Australia is home to 147 579 native species. Note that this is an estimate with an unknown margin of error because: (1) historically, species names have not been entered into a central repository but rather are scattered across numerous scientific journals (Minelli, 2003); (2) a large proportion of published names are now considered synonyms (Godfray, 2002); and (3) related to the last point, there is uncertainty and disagreements about species delination (Vane-Wright, 2003) and thus the number of valid species names. There has, however, been progress in the compilation of published species names in a central, publically available repository. At the time of writing, the Atlas of Living Australia (www.ala.org.au) has a national list of 152 080 accepted species names – quite similar to the estimate of Chapman (2009). Much more difficult, of course, is to estimate how many species remain to be described. Chapman (2009), by adding up individual estimates for all taxonomic groups, estimates that Australia is home to 556 398 species (described and undescribed). If this is a reasonable figure, then about three-quarters of Australia’s species await formal scientific recognition. However, the ratio of described to undescribed varies considerably among groups – mammals (Mammalia) are estimated to be 99% described while beetles (Coleoptera) may be only 25% (Figure 1.1).

The diversity of the Australian biota compared to the rest of the world can be assessed only for well-known groups such as birds and mammals. Overall, Australia appears neither especially species-rich nor particularly species-poor when compared to regions of similar area (Figure 1.2). A significant source of variation among countries is the

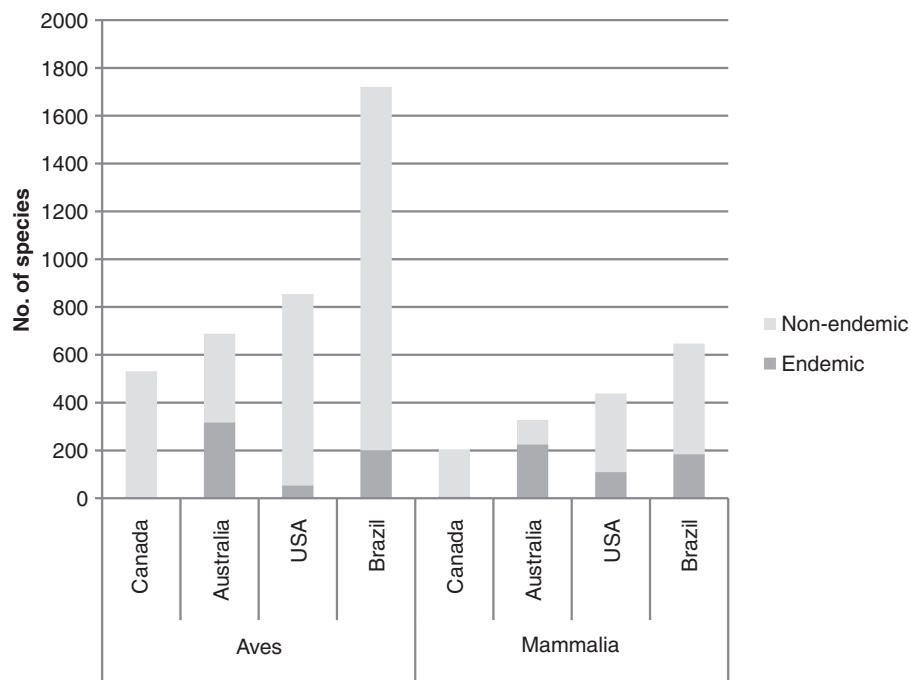


Figure 1.2 Species richness and endemism of extant birds (Aves) and mammals (Mammalia) in Australia compared to other countries of similar area. Data sourced from IUCN Red List (www.iucnredlist.org) for mammals and BirdLife International (www.birdlife.org) for birds.

latitudinal gradient they encompass as species richness is highest at the tropics, due at least in part to higher primary productivity (Gaston, 2000). However, the United States has more mammal and bird species than Australia despite being further from the equator. Clearly other factors are also important, such as Australia’s geographic isolation, low topographic relief, extensive aridity and low soil fertility (discussed further below).

1.2.2 Endemism

While Australia may not be exceptional in terms of species richness, this is not the case when it comes to endemism. When compared to other countries of similar area, Australia has proportionally many more endemic species (i.e. species found nowhere else) of birds (46%) and mammals (69% including marine species) (Figure 1.2). High levels of endemism are found throughout the biota. Chapman (2009) estimates that 94% of species of amphibians, 93% of flowering plants, and 93% of reptiles are endemic to Australia. In the case of arthropods, endemic species are likely to makeup about 90% of the fauna, with specific groups, such as cicadas (Cicadoidea), being even higher (Raven and Yeates, 2007). Of those species native to, but not strictly endemic to, Australia, many are found only in areas in the immediate vicinity such as New Guinea.

Endemism can be thought of in a temporal as well as a spatial sense – the length of time a particular lineage has been restricted to an area contributes to the degree of endemism. This can be assessed by noting endemic higher taxa such as genera, tribes, subfamilies and families (Table 1.1). In general, these taxa can be described as *palaeoendemics* as they each represent ancient lineages with a long period of association with the Australian

Table 1.1 Examples of Australian palaeoendemics. Those taxa marked with an asterisk are monotypic (represented by a single species).

Taxon	Taxonomic rank
<i>Wollemia</i> (Wollemi Pine)*	Genus
Austrobaileyaceae (Flowering plant)*	Family
Xanthorrhoeoideae (Grass-trees)	Subfamily
<i>Euastacus</i> (Spiny Crayfish)	Genus
Hemiphysalidae (Ancient Greenling – Damselfly)*	Family
Lamingtoniidae (Beetle)*	Family
Myrabolidae (Beetles)	Family
Tettigarctidae (Hairy Cicadas)	Family
Hypertrophidae (Moths)	Family
Ceratodontidae (Queensland Lungfish)*	Family
<i>Pseudemydura</i> (Western Swamp Turtle)*	Genus
Carphodactylidae (Geckoes)	Family
Ornithorhynchidae (Platypus)*	Family
Potoroidae (Potoroos and Bettongs)	Family
Atrichornithidae (Scrub-birds)	Family
Pardalotidae (Pardalotes)	Family

continent. Many are relictual, with one or a few surviving species (e.g. Wollemi Pine), while others represent substantial indigenous radiations (e.g. Spiny Crayfish).

Because of the many palaeoendemics, Australia has a biota that is evolutionarily distinct (see Box 1.1). Whole groups of organisms are found nowhere else (Table 1.1), while others, such as the Eucalypts (Eucalyptae) are very much centred on the Australian continent. The cause of this distinctiveness, is of course, a long period of independent evolution due to isolation but environmental factors may have also played a role. From a conservation perspective, high distinctiveness means high complementarity (Margules and Pressey, 2000), with Australian sites making large and unique contributions to global biodiversity (Box 1.1).

1.2.3 Provincialism

Starting with Buffon (1761), it has long been noted that the ranges of organisms are not distributed randomly across the globe but are spatially clustered, producing distinctive regions, often with relatively sharp boundaries (Lomolino *et al.*, 2010). Consequently, numerous schemes have been proposed to divide the Earth’s terrestrial surface into biogeographically distinct regions or provinces based on the distributions of various taxa (Sclater, 1858; Wallace, 1876; Udvardy, 1975; Holt *et al.*, 2013). Almost invariably, the Australian continent, including Tasmania, is seen as a discrete biogeographic unit, with affinity with the nearby landmasses of New Guinea, Eastern Indonesia, Melanesia and New Zealand. In the still commonly used classification of Wallace (1876), Australia plus the above-mentioned regions form the Australian (or Australasian) Realm, with its north-western boundary marked by Wallace’s Line (Plate 1). Marine biogeographic

Box 1.1 Evolutionary distinctiveness of mammalian faunas

The distinctiveness of the Australian biota has long been recognised but rarely quantified (Westoby, 1993). The idea of distinctiveness is related to endemism because a biota with many endemic taxa is clearly distinctive by any reasonable measure. Distinctiveness also implies a temporal (evolutionary) component in that the proportion of palaeoendemics should contribute more heavily to distinctiveness than more recent arrivals (neoendemics). Distinctiveness is important because it indicates the *complementarity* of Australia to the rest of the world as a conservation hotspot. Complementarity is a measure of the contribution of a location to overall biodiversity (Margules and Pressey, 2000) and, conversely, the extent of the loss to biodiversity should that location be lost to conservation.

Plate 2 is an attempt to map evolutionary distinctiveness for mammals for the world's terrestrial ecoregions. Distinctiveness was measured as the average dissimilarity in Phylogenetic Diversity (PD-dissimilarity) between each ecoregion and all other ecoregions. PD-dissimilarity measures the extent to which the branches in a phylogenetic tree are *not* shared between a pair of regions (Nipperess *et al.*, 2010). The Simpson variant of PD-dissimilarity was used, which ignores differences in species richness (Leprieur *et al.*, 2012), and has the following formula:

$$\text{dissimilarity} = \frac{\min\{b, c\}}{a + \min\{b, c\}},$$

where a is the total branch length of a phylogenetic tree that is shared between two ecoregions, b is the total branch length occurring in the first ecoregion but not the second, and c is the total branch length occurring in the second ecoregion but not the first. The phylogenetic tree used was the supertree of mammals published by Fritz *et al.* (2009).

It is clear that Australia, and the southern continents generally, make substantial contributions to global mammalian phylogenetic diversity. New Zealand, with only two living species of terrestrial mammal, is much less distinct, although one of those two species, the endemic Lesser Short-tailed Bat (*Mystacina tuberculata*), is the only surviving member of its family (Mystacinidae). A long period of geographic isolation, both from the northern continents and from each other, has engendered significant indigenous radiations of mammals in South America, Africa, Madagascar and Australia (Meredith *et al.*, 2011). In contrast, North America and Eurasia, have had intermittent land connections since the breakup of Pangaea in the mid Jurassic (~180 Ma), allowing greater dispersal and thus less evolutionary distinctiveness (Lomolino *et al.*, 2010). The pattern shown here for mammals is also seen in other vertebrate groups (Holt *et al.*, 2013), indicating that the geological history of land connections is a fundamental factor contributing to the evolutionary distinctiveness, and thus the complementarity, of continental biotas.

classifications are less common because distributional data have historically been sparse, and many marine taxa have large distributions making boundaries less distinct. However, in a recent and comprehensive classification of the world's coastal waters (Spalding *et al.*, 2007), Australian national territory largely spans two marine realms

(Central Indo-Pacific, Temperate Australasia), with Australia's sub-Antarctic territories (e.g. Macquarie Island) falling within the Southern Ocean realm (Plate 1).

Provincialism, the clustering of species distributions, is the result of two principal factors: limits to dispersal and environmental gradients (Lomolino *et al.*, 2010). Dispersal barriers are obviously important in explaining the general distinctiveness of the Australian continent compared to surrounding areas due to the intervening ocean. Within the continent, there is limited relief and thus few effective topographic barriers to dispersal compared to other continents. However, Australia experiences substantial environmental gradients. Mean annual temperatures range from less than 6 °C in upland Tasmania to more than 28 °C in parts of the Northern Territory and Western Australia, while mean annual rainfall varies from less than 200 mm in central Australia to over 3000 mm in Far North Queensland (data from Bureau of Meteorology, Australian Government). There is also a significant gradient in the seasonality of rainfall, with strong monsoonal summer rainfall in the north and winter rainfall in the south.

Australia has several distinct terrestrial biomes, each characterised by a particular vegetation structure, and corresponding to major climatic zones of temperature and rainfall (Plate 1). The scheme followed here is that of Olson *et al.* (2001) but many others have been suggested – see Archer and Fox (1984) for a dated but still relevant review. All classifications agree on the fundamental distinction between the arid centre, dominated by grasslands and Acacia shrublands, and the wetter (mesic) fringe, dominated by Eucalypt woodlands and open forests (Augee and Fox, 2000). Within the mesic fringe, there is a key division between the tropical north, with strongly seasonal summer rainfall, and the temperate south, with less seasonal winter rainfall (Bowman *et al.*, 2010; Byrne *et al.*, 2011). This north–south division is also reflected in the marine realms of Spalding *et al.* (2007). Because it is relatively flat, Australia has a very small montane biome in the Australian Alps. Rainforest is restricted to isolated pockets along the east coast with the largest extent occurring in Far North Queensland (classified as moist broadleaf forest in Olson *et al.*, 2001). Yet finer biogeographical divisions can be made. Olson *et al.* (2001) recognises 37 distinct terrestrial ecoregions on the Australian continent and Tasmania, and Spalding *et al.* (2007) describes an additional 17 marine ecoregions along the coast (Plate 1). These units reflect variation in climate and topography and consequently show significant turnover in species composition.

1.3 Key factors shaping the Australian biota

1.3.1 Isolation

Splendid isolation (to misappropriate a phrase) is the principal defining characteristic of Australian wildlife. Geographic isolation is not a recent phenomenon but extends deep into the past and has had a profound effect upon the composition and evolution of Australia's biota. So sudden is the change in the terrestrial fauna, as one passes from west to east through the Indo-Malayan archipelago, that it motivated Wallace (1860) to draw a line to mark where the recognisably Asian fauna ended and the distinctly and peculiarly Australasian fauna began (Plate 1). Unknown to Wallace, his line corresponded almost exactly to the Asian continental shelf and thus to the limit of historical land connections between the islands of the archipelago and the Asian mainland.

The relative proximity of Australia to Asia is, geologically speaking, a recent phenomenon. In the early Cretaceous (97–140 Ma), Australia was part of the supercontinent of

Gondwana (also including Africa, Arabia, South America, India, Madagascar, Antarctica, New Zealand and some smaller fragments). Australia was located at high latitudes, straddling 60° S at the centre, and experienced a generally cool, wet climate (Rich *et al.*, 1988; White, 2006). Gondwana had already begun to break up by this time (see the review by Upchurch, 2008), although the Australian plate would not separate from Antarctica until the Eocene (about 45 Ma) (White, 2006). By the Oligocene (23–33 Ma), Australia was completely isolated from other landmasses, floating northwards on the convection currents of the Earth’s mantle. As Australia drifted, the islands to the north, up to Wallace’s Line, were formed from a complex amalgam of Gondwanan microcontinental fragments and new land driven up from the seafloor as the northern edge of the Australian plate collided with Asia (Michaux, 2010).

Because of this geological history, Australia’s wildlife can be divided into a Gondwanan component (Table 1.2), reflecting ancient (>45 Ma) dispersal routes among the southern continents, and a post-Gondwanan component, reflecting more recent (<45 Ma) dispersals, especially from Asia. The Gondwanan component has, of course, a long period of association with the continent and includes all the palaeoendemic taxa (Table 1.1). Gondwanan taxa often have disjunct distributions (Table 1.2), being found on two or more southern continents, now widely separated, and their evolutionary relationships generally reflect this by having major branching events that correspond to ancient tectonic rifts (Upchurch, 2008). However, not all taxa with Gondwanan origins have remained restricted to these landmasses. Possibly the most spectacular example is the passerine birds (Passeriformes). Phylogenetic and fossil evidence point to the origin of the group in East Gondwana in the late Cretaceous (~80 Ma), a subsequent radiation in Australia, followed by dispersal to the rest of the world, where they now comprise around half of all bird species (Edwards and Boles, 2002).

Table 1.2 Examples of Gondwanan taxa occurring in Australia with disjunct distributions on other southern continents. Key: + = taxon is currently present; * = taxon was recently (<10 ka) present; SA = South America; NZ = New Zealand; NC = New Caledonia; In = India; Ma = Madagascar; Af = Africa.

Taxon	SA	NZ	NC	In	Ma	Af
Podocarpaceae (Podocarp Conifers)	+	+	+	+	+	+
Proteaceae (Proteas)	+	+	+	+	+	+
Nothofagaceae (Southern Beech)	+	+	+			
Rytididae (Land Snails)	+	+			+	+
Peripatidae (Velvet Worms)	+	+				+
Peloriidiidae (Moss Bugs)	+	+	+			
Palaephatidae (Gondwanaland Moths)	+					+
Galaxiidae (Galaxiid Fish)	+	+	+			+
Dipnoi (Lungfish)	+					+
Australobatrachia (Frogs)	+					
Pleurodira (Side-necked Turtles)	+				+	+
Diplodactyloidea (Geckoes)		+	+			
Marsupialia (Marsupials)	+					
Palaeognathae (Ratites)	+	+			*	+
Psittaciformes (Parrots)	+	+	+	+	+	+

Beginning at least as early as the Oligocene (23–33 Ma), Australia has received immigrants along non-Gondwanan dispersal routes. These dispersals have mostly been from the north but long-distance oceanic dispersals have also occurred (Schwarz *et al.*, 2006). The influence of northern dispersal has of course become stronger over time. As a result, the proportion of endemic genera of plants is considerably less in the tropical north (14%) compared to the temperate south (47%) (Augee and Fox, 2000). Interestingly, much of Australia's diverse reptile fauna has been founded from post-Gondwanan immigrants (Hugall *et al.*, 2008; Sanders *et al.*, 2008; Vidal *et al.*, 2012), with perhaps the most intriguing example being that of the Elapid snakes (Elapidae). Australian Elapids share a common ancestor with the sea snakes (Hydrophiinae), suggesting a marine origin, and despite their current diversity, probably entered Australia only in the last ten million years (Sanders *et al.*, 2008). Despite Australia's reputation as a marsupial haven, native placental mammals currently make up almost 47% of terrestrial mammal species (Van Dyck and Strahan, 2008), all of these being either bats (Chiroptera) or Old World Rats and Mice (Murinae). Bats have a long association with the continent (ancestors of the modern bat fauna were already present around 25 Ma; Hand, 2006) while Murines arrived much more recently (probably 5 Ma; Aplin, 2006) but have since become a numerically and ecologically important group.

Isolation has created a great natural experiment in that Australian wildlife has evolved separately from the rest of the world. We see many instances of convergence of ecological roles between Australian and non-Australian taxa, despite considerable phylogenetic divergences, indicating that common evolutionary pressures can lead to similar, independently derived solutions. Probably the most frequently cited examples are comparisons between North American placental mammals and Australian marsupials, such as the Thylacine (*Thylacinus cynocephalus*) and the Wolf (*Canis lupus*). These comparisons should not be taken too literally as there are definite differences in form and function – thylacines were both less agile and less social than wolves (Van Dyck and Strahan, 2008). More convincing examples can be found in Australian deserts. Marsupial Moles (*Notoryctes* spp.) bear an incredible likeness to the Golden Moles (Chrysochloridae) of southern Africa, including the unusual dentition (Archer *et al.*, 2011). Hopping Mice (*Notomys* spp.) have evolved the same set of morphological, ecological, physiological and behavioural characteristics as other unrelated hopping rodents found in the arid zones of Africa, central Asia and North America (Mares, 1993).

1.3.2 Nutrient poverty

Unlike New Zealand, Australia has experienced very little orogeny (mountain-building), glaciation or volcanism since separating from Gondwana (White, 2006). This has resulted in a land surface that is generally very old and a topography that is mostly flat. Except for alluvial systems and a few sites in Eastern Australia affected by hotspot volcanism, soils are ancient and largely leached of nutrients (oligotrophic) due to an extended period of weathering with little opportunity for replenishment (Augee and Fox, 2000). This nutrient poverty has been a huge challenge for Australian wildlife and has played a substantive role in determining the form and function of species and ecosystems.

Australian vegetation exhibits an unusual combination of features related to nutrient poverty. Sclerophylly (the characteristic of having long-lived, hardened leaves) is

associated worldwide with Mediterranean climates (Beadle, 1966) but, in Australia, it is common in all biomes except rainforest. Although often considered an adaptation to drought, the occurrence of sclerophylly seems most reliably correlated with nutrient limitation (Beadle, 1966; Westoby, 1993). Sclerophyllous leaves are generally resistant to damage, well-protected by chemical defences, and low in the essential nutrients nitrogen and phosphorous (Orians and Milewski, 2007; Morton *et al.*, 2011). Nitrogen-fixing species, such as Wattles (*Acacia*), are common, ensuring that phosphorous is the key limiting nutrient in Australian ecosystems (Augee and Fox, 2000; Orians and Milewski, 2007). High light availability means that Australian plants can generally photosynthesise year-round, producing large amounts of carbon-rich, but nutrient-poor, tissues such as wood, oils, exudates and nectar (Orians and Milewski, 2007; Morton *et al.*, 2011).

The unusual features of the Australian flora have direct effects on the ecology of the fauna. The generally low quality of plant production has likely constrained the diversity and dietary habits of herbivores (Orians and Milewski, 2007). For example, despite being much smaller in area, New Guinea has nearly twice the number of arboreal mammalian herbivores (Flannery, 1995), with Australian species being generally less specialised for folivory (the Koala, *Phascolarctos cinereus*, is an obvious exception). Feeding on nectar and other plant exudates is, in contrast to folivory, a relatively common adaptation. Australia has a large radiation of nectar-feeding birds (mostly in the family Meliphagidae), which attain a large average body size compared to avian nectarivores elsewhere (Orians and Milewski, 2007). The Honey Possum (*Tarsipes rostratus*) is the only mammal in the world to subsist exclusively on nectar and pollen (Van Dyck and Strahan, 2008). Australia has a large diversity of sap-sucking insects with the plant lice (Psylloidea) representing more than 10% of the world's species (Austin *et al.*, 2004). Low-quality plant production, coupled with aridity, is also thought to constrain the activity of detritivores (Morton *et al.*, 2011). The likely exception are termites (Termitoidae), which can occur at high densities in Australia, and are uniquely adapted to deal with the breakdown of nutrient-poor woody plant material (Orians and Milewski, 2007).

Nutrient poverty is thought to be the principal reason for the importance of fire in Australian ecosystems. Constraints on herbivory and detritivory allow a build-up of carbon-rich plant material, which, when combined with hot, dry conditions, leads to fire. In effect, fire largely replaces detritivore and generalised herbivore activity as a recycler of nutrients in Australian ecosystems (Morton *et al.*, 2011). As a result, Australian plants have evolved a remarkable array of adaptations to survive fire or to exploit conditions after fire. Many species can resprout after fire from lignotubers or epicormic buds, while others re-establish from seed that can germinate only when exposed to fire (Augee and Fox, 2000). Interestingly, resprouting from epicormic buds may have arisen in Eucalypts (Eucalypteae) around 60 Ma, suggesting that fire has long been a feature of Australian ecosystems (Crisp *et al.*, 2011).

1.3.3 Aridity and climatic variability

Since the early Cretaceous, Australia has drifted more than 30 degrees of latitude resulting in profound climate change (White, 2006). Moving towards the equator has of course increased temperatures, but only relative to global averages for the time, which have generally been decreasing for the past 50 Ma (Zachos *et al.*, 2008). Probably more important has been increased insolation and decreased seasonality, allowing for