1 Girt: A Continental Synthesis of Australian Vegetation

DAVID A. KEITH AND MARK G. TOZER

Australian vegetation, much like that on other continents, is characterised by evergreen forests in humid climates, savannas in the seasonal tropics, desert shrublands and grasslands in arid climates, and wetland vegetation where water accumulates. While continental plant diversity is intermediate on a global scale, Australian vegetation is characterised by high endemism at species and genus levels, a number of biodiversity hotspots and some structurally and physiognomically unique forms. We propose a continental model of vegetation assembly in which autochthonous and intrusive species pools are exposed to resource filters dominated by water and nutrients, other abiotic drivers such as temperature and disturbance regimes (particularly fire and floods), as well as local biotic filters, most notably competition and predation. We present a new high-level ecological typology of Australian vegetation and evaluate how ecological processes and legacies shape and differentiate major types of vegetation across the continent. Some key plant traits apparently enable persistence and turnover of species groups that characterise vegetation types inhabiting different environments. We conclude that Australian vegetation reflects a broad ensemble of evolutionary filters, varying combinations of which may come to the fore under particular conditions. Advances in Australian plant ecology over more than a century increasingly reflect the complex relationships between ecological legacy, directional selection by contrasting agents under varying environments, and stochasticity.

1.1 Introduction

The Australian continent and associated islands support a rich tapestry of vegetation composed of forests, woodlands, shrublands, grasslands and wetlands. In a broad sense, these patterns and the major processes that shape them are common features shared by other continents (Walter 1979). Like other continents, evergreen forests dominate Australia's high-rainfall regions, savannas dominate the seasonal tropics, desert shrublands and grasslands dominate the arid subtropics, and wetland vegetation is found where water accumulates (Beadle 1981). Even cursory examination, however, reveals unique compositional features and ecological behaviours.

Published estimates suggest more than 20 000 described vascular plant species are native to Australia, of which more than 90% are endemic (Chapman 2009). Although these are likely substantial underestimates due to ongoing discovery, high levels of endemism are unequivocal and hotspots of diversity occur in contrasting environments that span wet tropical and seasonal temperate climates, but largely exclude arid climates (Laffan and Crisp 2003).

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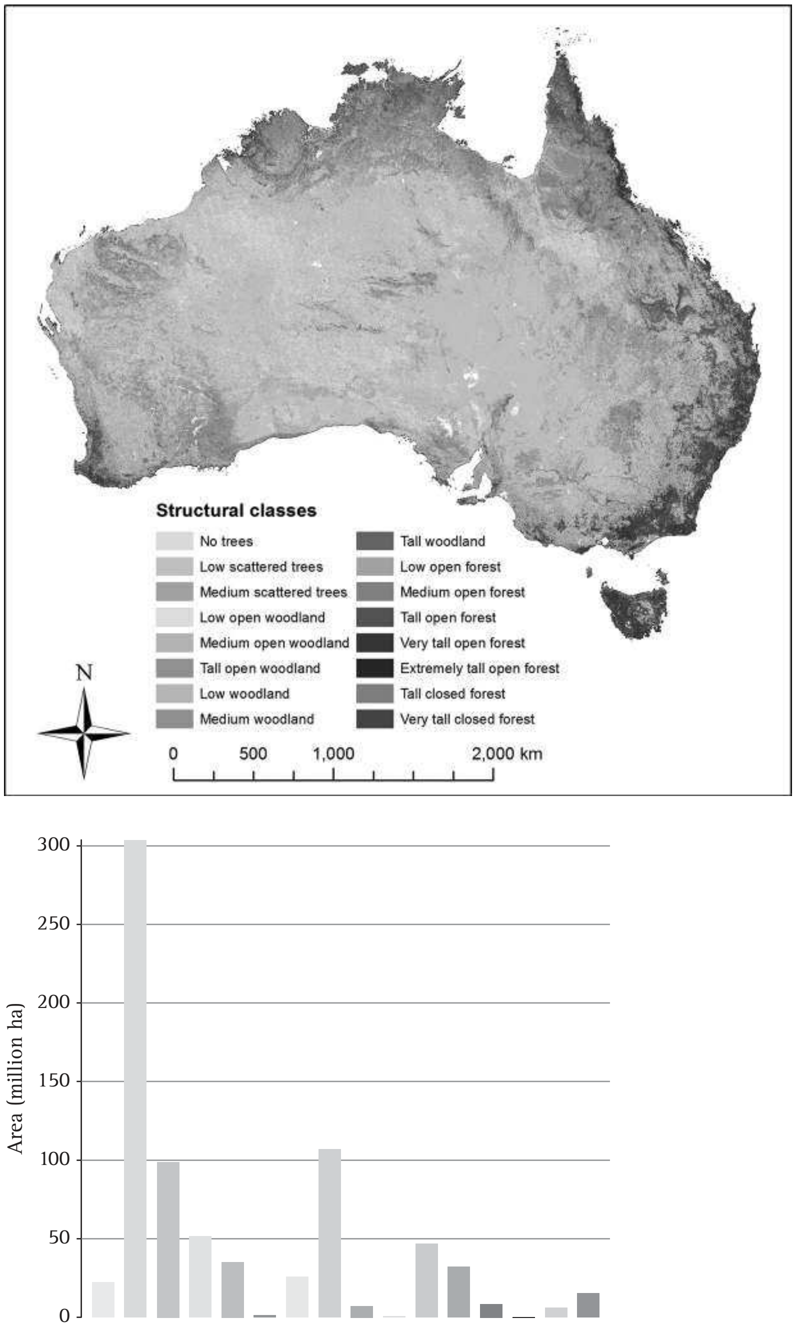

Figure 1.1 Map of vegetation structure of Australia derived from ALOS-1 PALSAR, ICESat/GLAS and Landsat imagery time series for 2003–2009. Histogram shows areas of structural types with a vast core of low open woodland and scattered trees, girt by a semi-continuous band of medium woodland and narrow coastal fringe of forest.
Data from Auscover (2016). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

Australia also includes structurally unique forms of vegetation including open-canopy (eucalypt) forests and woodlands, and hummock grasslands. The forests and woodlands of more humid climes fringe an extensive arid biome of low open vegetation that extends to the west coast (Figure 1.1). Relative to other land masses, Australia has an overrepresentation of sclerophylly and underrepresentation of succulence, while cold deciduous forests and exclusively coniferous forests are virtually absent (Box 1996; Orians and Milewski 2007).

In explaining the uniqueness and analogues of Australian vegetation, researchers have pointed to the biogeographical legacies of long isolation and intermittent long-distance dispersal (Barlow 1994; Crisp and Cook 2013; Weston and Jordan, Chapter 2, this volume); the widespread pressures of seasonal and extended droughts and temperature extremes (Nix 1982; Byrne *et al.* 2008); landscape age and climatic stability (Hopper 2009; Mucina and Wardell-Johnson 2011); nutritional poverty of soils (Lambers *et al.* 2010); and the pervasive influence of wildland fires (Bond *et al.* 2005; Bradstock 2010). The chapters in Part I of this book examine some of the most important ecological processes that shape Australian vegetation in both historical and contemporary time frames. A continental synthesis is needed to explain and predict where particular processes have strong influences on vegetation, where they do not, and why. Such a synthesis requires: (i) a conceptual model that provides a theoretical basis for explanation and prediction; and (ii) a descriptive framework for comparative analysis and expression of ecological relationships.

In this chapter, we first build on community assembly theory (Keddy 1992) to develop a generic conceptual model for understanding how ecological processes shape vegetation at a continental scale. The model emphasises, on one hand, species pools and the selection pressures to which they are exposed and, on the other hand, the resulting expressions of ecological traits, processes and ecosystem behaviour. Second, we propose a general ecological typology of Australian vegetation, defining the units in a way that is spatially explicit at continental scale and reflects the ecological traits of their component species. We briefly review and build on previous descriptive work in this area. We then use the conceptual model and typology to discuss how legacies and ecological processes differentiate major types of vegetation across the continent, focussing on some key plant traits that enable persistence and turnover of component species groups. In doing so, we orientate our interpretations to existing theories on the distribution and character of vegetation at global and continental scales. We conclude by reflecting on the progressive development of continental-scale ecology of Australian vegetation.

1.2 A model of vegetation assembly

Ecological communities are shaped by their natural capital of biological variation and the selective forces that act upon it. The outcomes of this filtering process are reflected in the spectra of ecological traits exhibited by the suite of component species that characterise a given assemblage (Keddy 1992; Grime 2001; Shipley *et al.* 2006; Craine *et al.* 2012). Hence the observed properties of any two assemblages may differ because: (i) selective forces on a common species pool differ in type, direction or relative strength; (ii) a similar suite of selective forces act upon different species pools; or (iii) both species pools and selective forces differ. Neutral processes, such as stochastic arrivals and extinctions (Crisp and Cook 2013), stochastic variation in the filtering process and equivalence of competitive abilities may also play a role in differentiating ecological assemblages, even where species pools, traits and selection pressures are similar (Hubbell 2005; Chase 2010).

The relative influence of niche differentiation and neutral processes in structuring local communities depends on the balance between environmental variation (both spatial and temporal) and fitness differences (Adler *et al.* 2007), as well as the degree of resource partitioning and effects of natural enemies (Adler *et al.* 2013). All of these elements vary with spatial scale, with different suites of selective forces and neutral processes shaping biomes at continental and global scales (Box 1995) and ecological communities at local scales (Keddy 1992). In this chapter, we focus on continental-scale vegetation types, and propose a conceptual model to represent key elements and processes involved in their assembly (Figure 1.2).

The species pool is central to biome assembly (Figure 1.2), as it defines the evolutionary capital on which filters, stabilising mechanisms and neutral processes operate. It reflects legacies of historical biogeography (Crisp and Cook 2013; Weston and Jordan, Chapter 2, this volume) as well as antecedent filtering and stochastic events. Four main groups of drivers operate on traits represented within the species pool to shape the assemblage in a particular area at a particular time. We separate the supply of primary resources (Craine *et al.* 2012) from other abiotic drivers that influence their availability or the ability to acquire them (Figure 1.2). The latter include ambient factors such as temperature and salinity, as well as naturally occurring toxins such as aluminium (an inhibitor of root growth) and heavy metals. Another group of environmental filters includes disturbance regimes, notably sequences of fire, flood and storm events, which interrupt resource acquisition and indeed liberate resources from existing biota or

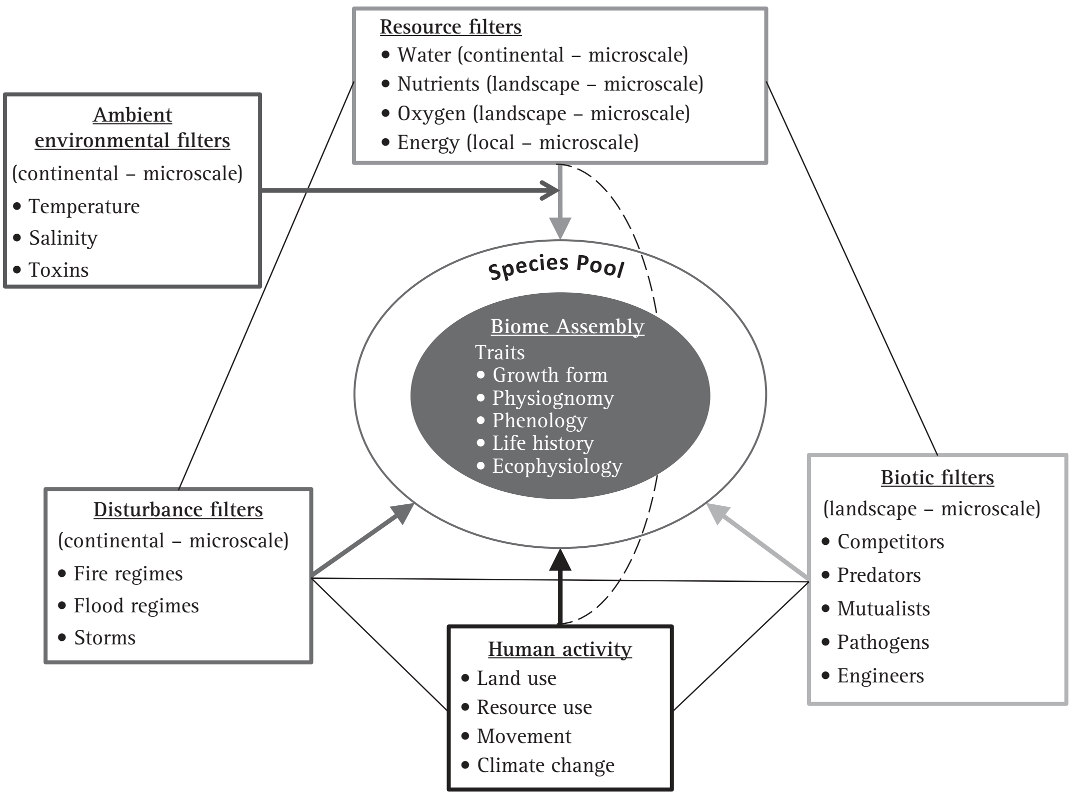

Figure 1.2 Conceptual model of vegetation assembly showing influence of, and interactions between, the main groups of ecosystem drivers and the spatial scales over which they vary (see text for details).
Note: Interactions between human activity and resource drivers are present but not shown in graphic display. Ambient environmental filters also influence biotic processes, disturbance and human activity (arrows not shown).

other sources. The biotic drivers include filters, such as interspecific competition and pathogens, as well as a range of stabilising or compensatory mechanisms that may promote coexistence (Figure 1.2). We distinguish human activity from other biotic drivers to emphasise its influence on biome assembly through exploitation of resources (including biota), movement of biota and modification of global circulation systems.

Spatial and temporal heterogeneity regulate the influence of the four main groups of drivers on biome assembly. Spatial heterogeneity is critical to niche partitioning, with different elements of each driver varying at a range of spatial scales. For example, the availability of water varies with climate at global scales and also with variations in microtopography. Other drivers vary over a narrower range of scales, such as nutrient availability, which is strongly influenced by substrate distributions and topography at landscape scales. Temporal variability in biome drivers is also critical to coexistence by disrupting competitive elimination (Tilman 1988; Keddy 1989) or through mechanisms such as storage effects (Chesson 2000). Some elements, such as water availability, vary over a broad range of temporal scales from days to decades, while others, such as energy influx, vary on a daily and seasonal basis. Disturbance, by definition, involves temporal variation expressed through the duration of events and intervals between them (e.g. Bunn *et al.* 2006).

Finally, interactions among drivers may inflate or moderate their influences on biome assembly (Figure 1.2). For example, an overabundance of water may generate anoxia in plant substrates (Vartapetian and Jackson 1997). Herbivore activity may influence fire regimes through their effects on available fine fuels (Keeley *et al.* 2012). Human activities may be major mediators of other drivers. Water extraction and storage on industrial scales, for example, limit availability of a key resource and transform hydrological flows and flood regimes critical to the persistence of some biota (Bunn and Arthington 2002).

1.3 An ecological typology of Australian vegetation

The direct outcomes of assembly processes are expressed in the composition and trait spectra of ecological communities. Ecological classifications are abstract descriptive tools for summarising patterns in these essentially continuous outcomes and for projecting them collectively across real landscapes (Whittaker 1975). We propose a new typology of Australian vegetation that enables an ecological interpretation of vegetation assembly across the continent and associated islands. Our aim is to build on existing, primarily descriptive typologies to produce a framework that not only represents spatial patterns in species pools, but also reflects similarities and contrasts among plant traits represented in different assemblages and characterises ecological drivers that shape and sustain the biota (Figure 1.2). The framework is hierarchical to enable representation of ecological and evolutionary relationships at different scales. While finer levels of the typology are under development (Keith and Pellow 2015), here, we present the upper level of the hierarchy comprising 16 'vegetation formations' (Table 1.1) based largely on growth form and physiognomic traits that are interpreted as outcomes of ecological drivers and selection processes. There are also strong patterns in floristic and structural features that help identify the units (Table 1.1), although these properties are not the primary basis for classification at the formation level.

We developed a continental view of spatial vegetation patterns at the formation level (Figure 1.3) by re-interpreting national and regional mapping (Department of the Environment and Water Resources 2007). Such mapping is enabled in part by distinctive remote sensing signatures that represent combinations of physiognomic, energetic and structural features of vegetation (Keith 2004). As well, relatively strong environmental relationships among the formations enable their environmental niches to be characterised (Table 1.1; Figure 1.3)

Table 1.1 **Characteristics of Australian vegetation formations and their relationships to other national and international vegetation typologies.**

Australian vegetation formations	Description	Environmental niches	Distribution
Rainforests (Chapter 11)	Closed-canopy non-eucalypt forests, vine scrubs and monsoon forests	Humid–semi-humid, tropical–cool temperate macroclimates and mesoclimates, eutrophic–mesotrophic substrates, rarely fire-prone	Tropics, east coast lowlands and ranges
Wet sclerophyll forests (Chapter 12)	Tall eucalypt forests over mesomorphic shrubs, ferns or herbs	Humid, subtropical–cool temperate macro and mesoclimates, mesotrophic substrates, prone to warm-season century-scale crown fires	East coast lowlands, ranges, far south-west outlier
Dry sclerophyll forests and woodlands (Chapter 13)	Eucalypt forests and woodlands over scleromorphic shrub understories	Humid–semi-humid, aseasonal subtropical–cool temperate macroclimates, mesotrophic–oligotrophic substrates, prone to warm-season decadal fires	East coast lowlands, ranges and slopes, south-west outlier
Heathlands (Chapter 14)	Closed–open scleromorphic shrublands, some with emergent eucalypts	Humid–semi-humid, tropical–cool temperate macroclimates, oligotrophic substrates, prone to warm-season decadal fires	South-west and east coast lowlands and ranges, southern sandplains, tropical plateaus and sandplains
Savanna (Chapters 15, 16)	Eucalypt and other tree genera over C_4 grasses and scattered shrubs	Winter – dry, humid tropical–subtropical macroclimates, eutrophic–mesotrophic substrates, prone to cool-season subdecadal fires	Tropics, eastern subtropics
Temperate sub-humid woodlands (Chapter 17)	Eucalypt woodland over mixed C_3/C_4 grasses and forbs with variable shrub cover	Winter – wet or aseasonal, humid–subhumid temperate macroclimates, eutrophic–mesotrophic substrates, prone to warm-season decadal surface fires	South-west hinterlands, south-east coastal valleys, tablelands and western slopes
Tussock grasslands (Chapter 18)	Perennial tussock grasses with interstitial herbs and few or no woody plants	Humid–semi-arid, tropical–temperate macroclimates, eutrophic–mesotrophic periodically damp clay substrates, prone to decadal–subdecadal surface fires	Tropical and arid plains, south-east hinterlands and plateaus, coast and offshore islands

Beadle and Costin (1952); Specht and Specht (2001)	Whittaker (1975)	Faber-Langendoen *et al.* (2014)
Rainforest (temperate, subtropical, tropical and monsoon)	1 Tropical rainforest, 3 Temperate rainforest, 5a Temperate evergreen forest–broadleaf	1.A.2 Tropical lowland humid forest, 1.A.3 Tropical montane humid forest, 1.B.1 Warm temperate forest and Woodland, 1.B.2 Cool Temperate Forest and Woodland
Sclerophyll forest (wet)	5c Temperate evergreen forest–sclerophyll [Mediterranean]	1.B.1 Warm temperate forest and woodland, 1.B.2 Cool temperate forest and woodland
Sclerophyll forest (dry)	5c Temperate evergreen forest–sclerophyll [Mediterranean], 10b Temperate woodland–sclerophyll	1.B.1 Warm temperate forest and woodland, 1.B.2 Cool temperate forest and woodland
Heath, mallee (wet), scrub (wet)	11b Temperate shrubland–heath, 11c Temperate shrubland–sclerophyll [Mediterranean], 29 Marine rocky shores	2.A.3 Tropical scrub and herb coastal vegetation, 2.B.1 Mediterranean scrub and grassland, 2.B.2 Temperate grassland and shrubland, 6.A.1 Tropical cliff, scree and other rock vegetation, 6.B.1 Temperate and boreal cliff, Scree and other rock vegetation
Savannah (shrub, tree, mallee)	2 Tropical seasonal forest, 8 Tropical broadleaf woodland	1.A.1 Tropical dry forest and woodland, 2.A.1 Tropical lowland grassland, savanna and shrubland
Woodland (savannah and sub-alpine)	5c Temperate evergreen forest–sclerophyll [Mediterranean], 10b Temperate woodland–sclerophyll	1.B.1 Warm temperate forest and woodland, 1.B.2 Cool temperate forest and woodland
Grassland (dry and wet tussock)	12 Savanna [tropical grassland], 13 Temperate grassland, 30 Marine sandy beaches	2.A.1 Tropical lowland grassland, savanna and shrubland, 2.B.2 Temperate grassland and shrubland, 3.A.2 Warm desert and semi-desert scrub and grassland

Table 1.1 (cont.)

Australian vegetation formations	Description	Environmental niches	Distribution
Alpine (cryophilic) herbfields and shrublands (Chapter 19)	Alpine forbs and grasses with or without low shrubs tolerant of snow burial	Humid, alpine–subpolar macroclimates with seasonal snow cover, eutrophic–mesotrophic periodically damp substrates, prone to century-scale surface fires	South-east mountains, sub-Antarctic islands
Freshwater wetlands (Chapter 20)	Perennial and ephemeral wetlands with helophytic shrubs, forbs and/or graminoids	Diverse macroclimates on depositional fluvial or groundwater-influenced landforms with mesotrophic–eutrophic substrates, periodically inundated by streams, overland flows or rising groundwater	Throughout tropical and temperate regions
Floodplain (hydrogenic) forests, woodlands and shrublands (Chapter 21)	Riparian and flood-prone forests, woodlands and thickets of *Eucalyptus*, *Melaleuca* or *Casuarina* with helophytic understorey	Diverse macroclimates on depositional fluvial landforms with mesotrophic–eutrophic substrates, periodically inundated by perennial or ephemeral streams or overland flows	Tropical, temperate and semi-arid floodplains and rivers
Saline wetlands (Chapter 22)	Halophytic forests, scrubs, succulent forblands or grasslands	Diverse macroclimates on depositional flats in coastal estuaries or drainage pans with saline substrates, periodically inundated by tides, overland flows or rising groundwater	Tropical and temperate tidal coasts, arid inland depressions
Semi-arid acacia/casuarina woodlands (Chapter 16, 25)	Woodlands of *Acacia*, *Casuarina* or *Callitris* with reduced leaves (leaf blades absent) and mixed perennial/ephemeral ground layer	Semi-arid–arid aseasonal tropical–temperate macroclimates, mesotrophic–eutrophic fine–medium-textured substrates, mostly depositional landforms, rarely fire-prone	Subtropical and temperate semi-arid inland
Semi-arid eucalypt woodlands (Chapter 23)	Eucalypt woodlands including mallee, with xerophytic shrubs and mixed perennial/ephemeral ground layer	Semi-arid–arid aseasonal subtropical–temperate macroclimates on mostly oligotrophic coarse-textured substrates on erosional landforms, occasionally fire-prone	Subtropical and temperate semi-arid inland plains and ranges

	Beadle and Costin (1952); Specht and Specht (2001)	Whittaker (1975)	Faber-Langendoen *et al.* (2014)
	Alpine herbfield (tall and short), grassland (sod), Fjeldmark	11d Temperate shrubland–sub-alpine, needleleaf, 11e Temperate shrubland–sub-alpine, broadleaf, 14 Alpine shrubland, 15 Alpine grassland	4.B.1 Temperate and boreal alpine dwarf-shrub and grassland
	Fen, bog (valley and raised bog)	22 Cool temperate bog	2.C.2 Temperate to polar bog and fen, 2.C.3 Tropical freshwater marsh, wet meadow and shrubland, 2.C.4 Temperate to polar freshwater marsh, wet meadow and shrubland, 5.B.1 Tropical freshwater aquatic vegetation, 5.B.2 Temperate to polar freshwater aquatic vegetation
	Sclerophyll forest (swamp), woodland (tall and swamp)	24 Temperate freshwater swamp forest, 23 Tropical freshwater swamp forest	1.A.4 Tropical flooded and swamp forest, 1.B.3 Temperate flooded and swamp forest
	Scrub (mangrove)	25 Mangrove swamp, 25 Saltmarsh, 26, 27, 29, 31 Marine mudflats	1.A.5 Mangrove, 2.C.5 Salt marsh, 5.A.1 Floating and suspended macroalgae saltwater vegetation, 5.A.2 Benthic macroalgae saltwater vegetation, 5.A.3 Benthic vascular saltwater vegetation
	Woodland (shrub)		
	Mallee (dry), woodland (shrub)		

Table 1.1 (cont.)

Australian vegetation formations	Description	Environmental niches	Distribution
Arid subsucculent chenopod shrublands (Chapter 24)	Chenopod shrublands of *Atriplex*, *Maireana* or *Sclerolaena* with tussock grasses	Arid – semi-arid aseasonal temperate macroclimates with eutrophic–mesotrophic fine-textured substrates, rarely fire-prone	Temperate arid inland
Arid sclerophyll shrublands (Chapter 25)	*Acacia* and other xeromorphic shrublands with ephemeral forbs and grasses	Arid–semi-arid aseasonal subtropical–temperate macroclimates with mesotrophic–oligotrophic coarse-textured substrates, prone to occasional fire	Subtropical and temperate arid inland
Hummock grasslands (Chapter 26)	Deserts dominated by hummock *Triodia* with scattered shrubs and ephemeral forbs	Arid aseasonal subtropical–temperate macroclimates with oligotrophic substrates, prone to occasional fire	Subtropical and warm temperate arid inland

Global formations not represented within Australia. Whittaker (1975): 4 Temperate deciduous forest; 5b Temperate evergreen forest–needleleaf; 6 Taiga and subarctic–sub-alpine needle-leaved forest; 7 Elfin woodland; 9a Thornwood–woodland; 9b Thornwood–scrub; 10a Temperate woodland–needleleaf; 10c Temperate woodland–deciduous broadleaf; 11a Temperate shrubland–deciduous; 16 Tundra; 18a Cool semi-desert–open scrub; 18b Cool semi-desert–dry grassland; 19 Arctic–alpine semi-desert; 20 True desert; 21 Arctic–alpine desert (Note: 16, 19 and 21 on sub-Antarctic islands).

and their distributions to be spatially modelled and temporally projected (Prober *et al.* 2012; Keith *et al.* 2014). Part II of this book (Chapters 11–26 of this book; cross-referenced in Table 1.1) elaborate on floristic, structural and ecological features of the formations and their variation across the continent.

1.3.1 Historical context and relationships to other classifications

The first significant typological synthesis of Australia's vegetation (Diels 1906) recognised elements with major physiognomic contrasts such as rainforest, savanna, sclerophyll forest, brigalow, mallee and desert, but there are a number of omissions and anomalies in the broad typology and accompanying map (Beard 2001). Beadle and Costin (1952) advanced a more comprehensive typology of physiognomic formations and subformations. Many of these correspond well with units of our proposed typology (Table 1.1). Beadle (1981) later elaborated on continental-scale floristic variation at the alliance level and provided a generalised continental map. This filled many of the gaps in his formation-level typology, but did not explicitly relate alliances to formations.

More recent typologies of Australian vegetation focus on structural and taxonomic attributes of vegetation. Specht (1970) proposed a factorial classification based on growth form, height and cover of the tallest vegetation stratum, and later revised it and developed a detailed classification of floristic associations (Specht *et al.* 1995). A scheme that defined dominant plant taxa based on cover, irrespective of their vertical stratum, was first applied in Western Australia (Beard and Webb 1974) and adapted in a spatially explicit continental synthesis