Australian rainforests

Islands of green in a land of fire

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Introduction

The existence of patches of rainforest embedded in tracts of *Eucalyptus* forests have long perplexed and sometimes astonished field biologists. The abrupt rainforest boundaries often rise up like 'a dark wall' (Figure 1.1) in the relatively open *Eucalyptus* forest (Herbert 1932) and literally confront ecologists with the question 'what determines the position of the boundaries?' The floristic differences between rainforest and *Eucalyptus* forests can be 'so great as to suggest separate geographic and historical origins in spite of their growing side by side' (Herbert 1932). The purpose of this book is to investigate the deceptively simple question of why rainforests have such limited and fragmentary coverage in Australia (Figure 1.2). This basic geographic question raises other questions such as:

(i) Why should *Eucalyptus* and *Acacia* dominate the great bulk of Australian woody vegetation (Figure 1.3)?
(ii) How should rainforest be defined in Australia?
(iii) What environmental factors control the local extent of rainforest?

As will become apparent in this book, these questions are central issues in Australian vegetation science. The rainforest-boundary question occurs in nearly all the major arguments about Australian woody vegetation. Indeed, a number of important theories about the ecology of Australian woody vegetation have explicitly sought to resolve this problem of sharply contrasting forest types growing side by side. I recognise that the Australian rainforest boundary problem is a subset of the global biogeographic question concerning the cause of the differentiation between forest and savanna. The forest–savanna boundary is a problem of 'bewildering complexity' (Richards 1952) and has stimulated a

Figure 1.1
*Abrupt subtropical rainforest boundary in Cunningham Gap, southeast Queensland. Grasstrees (*Xanthorrhoea *sp.) dominate the savanna in the foreground. (© Murray Fagg, Australian National Botanical Gardens.)*

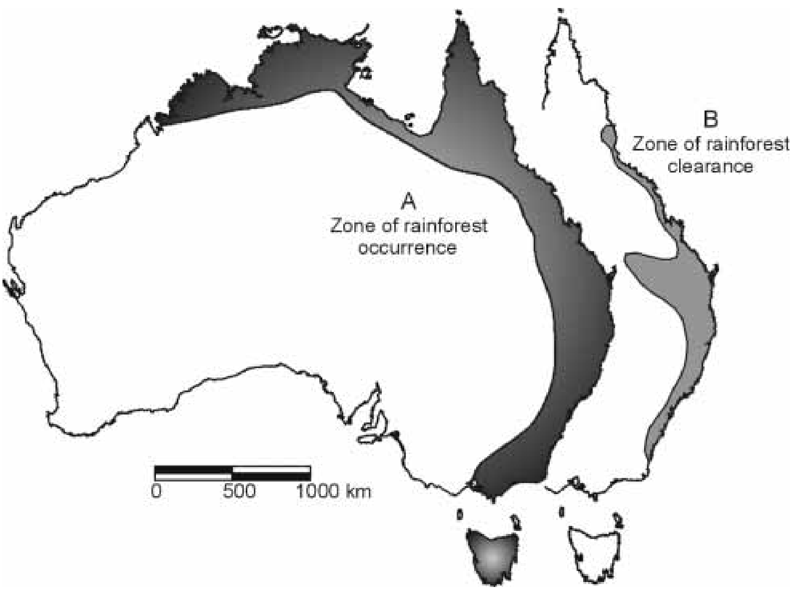


Figure 1.2
Original coverage of rainforest (closed forest and low closed forest) in Australia (A) and areas of rainforest clearance following European colonisation (B). Adapted from Anon. (1990) and Webb and Tracey (1981).

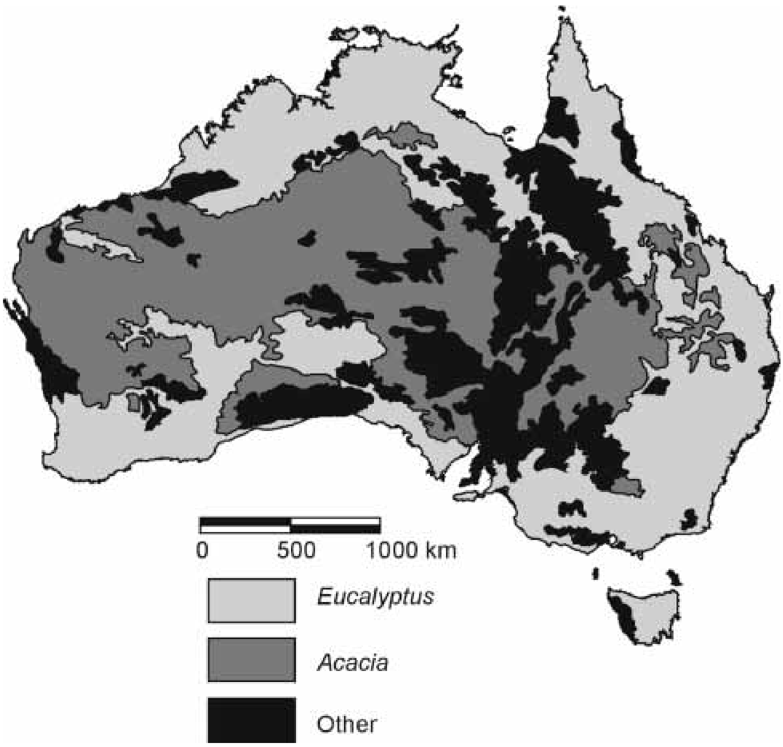


Figure 1.3
Australian vegetation dominated by Eucalyptus, Acacia *or other species. Adapted from Anon. (1990). This map is Copyright © Commonwealth of Australia, AUSLIG, Australia's national mapping agency. All rights reserved. Reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Industry, Science and Tourism, Canberra, ACT.*

sizeable literature and continuing debate as to what constitutes savanna and forest vegetation. It is outside the scope of this book to review this literature, and the reader is referred to the recent book edited by Furley *et al.* (1992). Similarly, it is not the aim of this book to provide a comprehensive overview of Australian rainforests which, in any case, is provided by the excellent book by Adam (1992). Rather, my aim is to summarise the voluminous literature about the factors controlling the distribution of rainforest in Australia and search for a general explanation of the puzzle of islands of rainforest in a sea of *Eucalyptus*-dominated vegetation.

A geographic sketch of Australia

Australia has been progressively isolated from Africa, Antarctica, India, and South America by continental drift. The southern super-continent Gondwana began to break up at the beginning of the Cretaceous Period some 150 million years (MY) before present (BP). India, South America, Africa and Australia migrated from high to low latitudes, whilst Antarctica remained in an approximately polar position (Wilford and Brown 1994). For the first half of the Tertiary Period (65 to 30 MY BP), the Australian continent lay close to Antarctica between latitudes 60 and 30 degrees south (Wilford and Brown 1994). This geographic position had a direct impact on the climate through massive annual variation in day length, with dark winters and long summer days. In the second half of the Tertiary (30 to 2 MY BP), the Australian plate moved northwards away from Antarctica at a rate of about 6 cm per year (Kershaw *et al.* 1994). During the Miocene epoch, it came into contact with the Sunda Plate (i.e. southeast Asia), and this collision resulted in mountain building on the leading edge of the Australian plate (i.e. the island of New Guinea). It also greatly increased the probability of exchanges between Australasian and Asian biotas (Raven and Axelrod 1972).

Australia is now the world's largest island. Compared to the other continents, it has the smallest land-mass (some 8×10^6 km^2), the least land above 1000 m and the most diminutive highest point (2228 m above sea level) (Jennings and Mabbutt 1986). In aggregate, Australia is the driest vegetated continent with 80% of the land area receiving less than a mean of 600 mm of rainfall per year. Nonetheless, areas with high rainfall occur in southwest Western Australia, western Tasmania and along the north and east coast of Australia (Figure 1.4). Seasonality of rainfall varies from winter rainfall in the southern part of the continent, erratic aseasonal rainfall in the centre of the continent and summer rain in the north (Figure 1.5). Extreme seasonality of rainfall occurs in the monsoon tropics, where summers are wet and winters are dry, and in southwest Western Australia where the opposite occurs. The cause of the contrasting rainfall patterns in northern and southern Australia is related to the continent's latitudinal position, lying as it does between 10° S and 44° S. In northern Australia the intertropical convergence zone is the major source of rainfall while in the south low pressure systems associated with the westerly stream are the primary source of precipitation. Mountain ranges on the east coast of Australia greatly enhance local rainfall due to orographic effects on moist air masses from the Pacific Ocean. Intense tropical low pressure systems, known in Australia as 'tropical cyclones', are an infrequent source of intense precipitation to the north

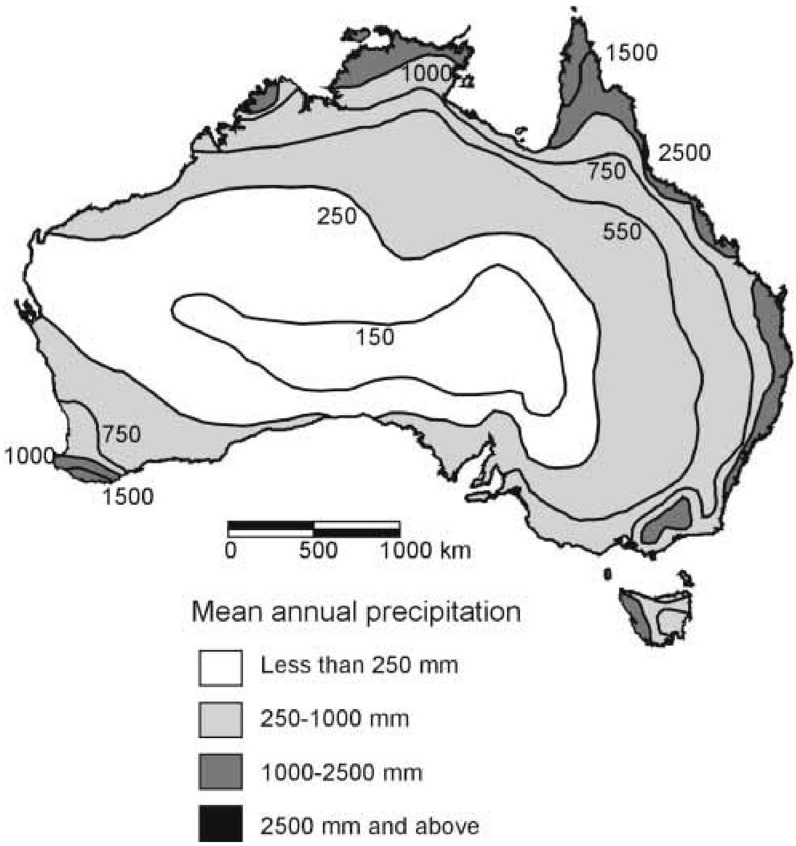


Figure 1.4
Mean annual precipitation in Australia. Adapted from Adam (1992).

of 30° S. Cyclones are an ecologically significant factor in coastal regions because of their enormously destructive winds.

The aridity of most of Australia is attributable to the belt of subtropical high-pressure systems that track across the centre of the continent during the winter and across southern Australia in the summer. These subtropical high-pressure systems produce cloudless skies and dry winds, and are responsible for the high air temperatures and great evaporative potential across much of Australia.

No month in northern Australia has an average air temperature below 18 °C. Only southeastern Australia including Tasmania, a narrow coastal belt in south-western Western Australia and a montane area in central New South Wales have

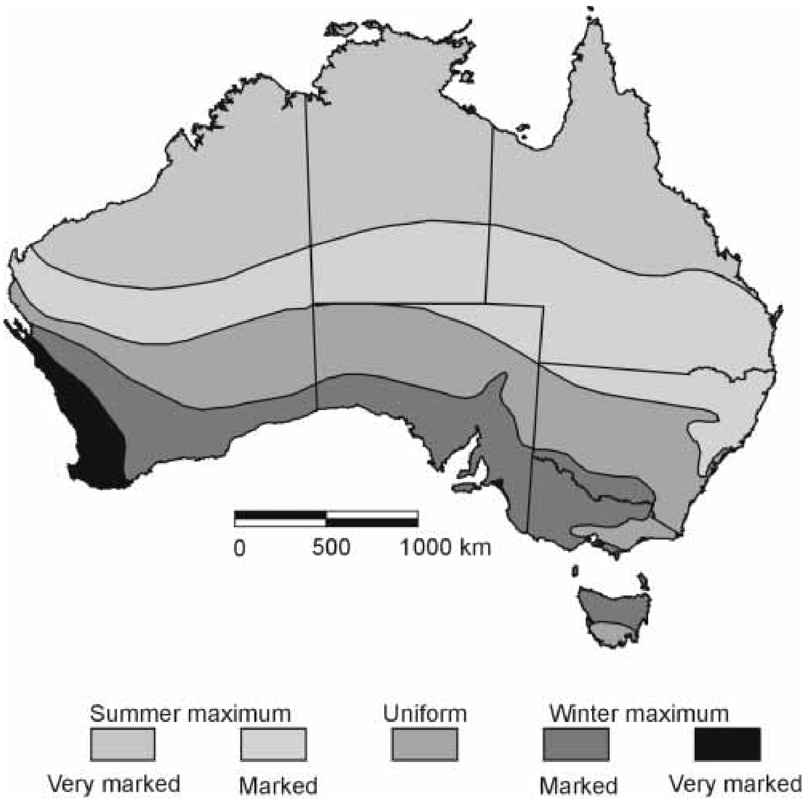


Figure 1.5
Seasonality of rainfall in Australia. The seasonality index is calculated from the ratio of median summer (November–April) and winter (May–October) rainfall. Very marked seasonality is where maximum seasonal (summer or winter) rainfall exceeds minimum seasonal rainfall by three times and marked seasonality is where maximum seasonal rainfall exceeds minimum seasonal by 1.3 times but less than 3 times. Adapted from Anon. (1986). This map is Copyright © Commonwealth of Australia, AUSLIG, Australia's national mapping agency. All rights reserved. Reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Industry, Science and Tourism, Canberra, ACT.

fewer than 3 months with mean air temperature greater than 18 °C (Figure 1.6). Nights with clear skies result in low nocturnal temperatures due to radiative cooling. Frosts are common in central and southern Australia, and can occur all year round in the eastern Australian mountain ranges and Tasmania (Figure 1.7).

The absence of great mountain ranges (Figure 1.8) and Australia's mid-latitudinal position permitted only localised glacial activity during the Quaternary Period (0–2 MY BP) and limits the extent of winter snow under the current

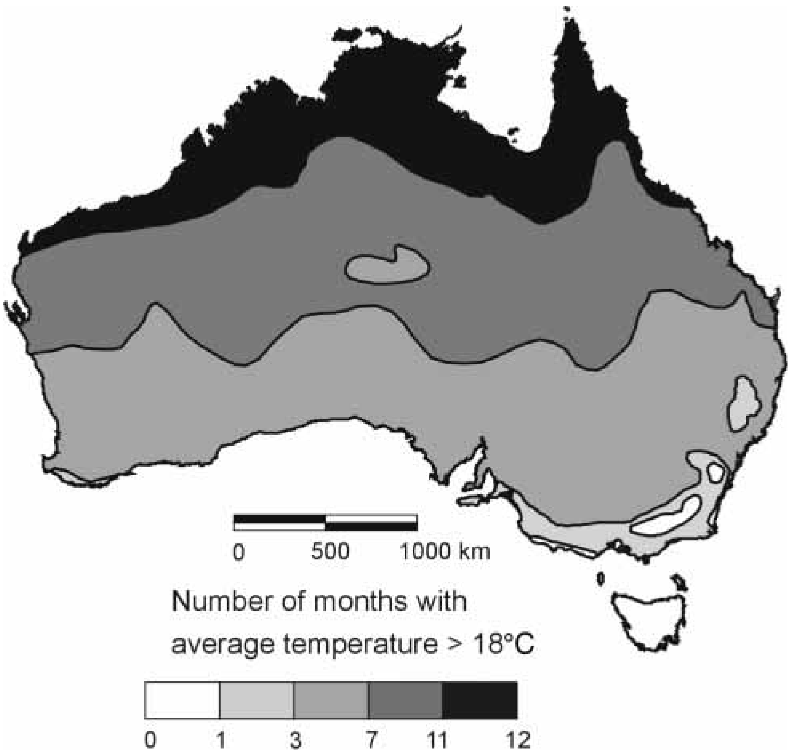


Figure 1.6
Number of months with mean air temperatures greater than 18 °C. Adapted from Anon. (1986). This map is Copyright © Commonwealth of Australia, AUSLIG, Australia's national mapping agency. All rights reserved. Reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Industry, Science and Tourism, Canberra, ACT.

climate. Extreme high or low temperatures are rare in Australia owing to the continent's small land mass and the moderating influence of the southern hemisphere oceans: northern hemisphere localities of similar latitude to those found in Australia experience greater temperature extremes.

Geologically, sedimentary rocks from the Precambrian Era (> 590 MY BP) and Palaeozoic Era (590–250 MY BP) dominate Australia although there are limited areas of basic igneous rocks, such as dolerite and basalt, scattered across the continent (Figure 1.9). Tertiary and Quaternary basaltic flows are restricted to the east coast where the Australian plate passed over a series of 'hotspots' (Quilty 1994). There is some evidence to suggest that the underlying geomorphology of Australian landscapes changed little during the Tertiary (Young and McDougall 1993; Nott 1995). For example, Nott (1995) suggested that many

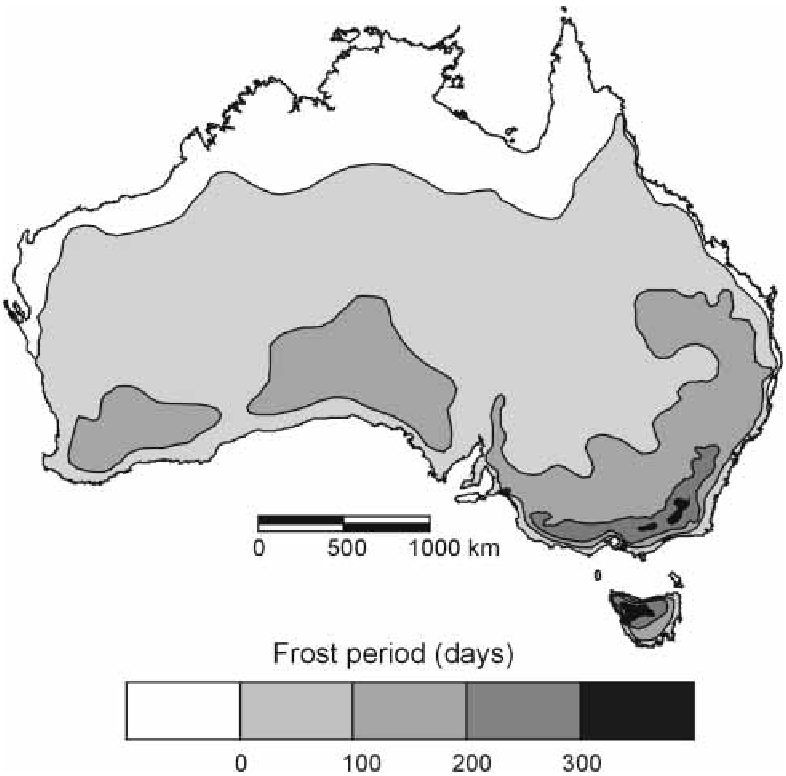


Figure 1.7
The median number of days per year when frosts are recorded. Adapted from Anon. (1986). This map is Copyright © Commonwealth of Australia, AUSLIG, Australia's national mapping agency. All rights reserved. Reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Industry, Science and Tourism, Canberra, ACT.

northern Australian landscapes, including 'ranges, plains and valleys', have changed little in the last 100 MY! The stability of the land surface allowed the production of very deeply weathered profiles (i.e. laterites to > 50 m) throughout Australia (including Tasmania, albeit where they are uncommon) (Taylor 1994). It is difficult to age lateritic surfaces, although isotopic dating of basalt flows in north-east Queensland enabled Coventry *et al.* (1985) to demonstrate that some lateritic profiles are 'considerably older than 6.3 MY'. Although it is widely assumed that deep weathering reflects hot, humid conditions, this may not be the case. Taylor (1994) noted that deep weathering might also occur under cold, humid conditions. The dominance of tectonically stable, ancient sedimentary rocks and very limited glaciation during the Mesozoic Era (250–65 MY BP) and Cainozoic Era (< 65 MY BP) have resulted in large areas of

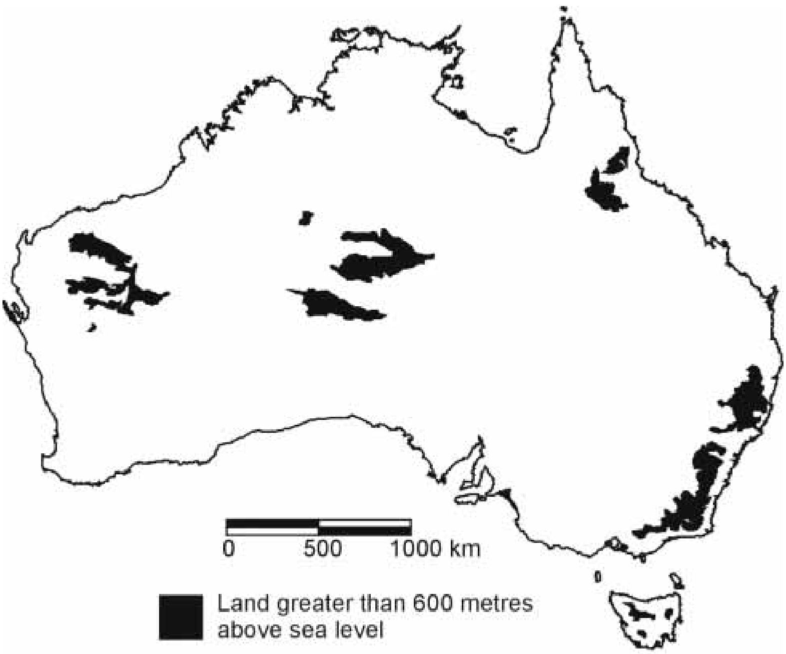


Figure 1.8
Areas greater than 600 m above sea level. Adapted from Taylor (1994) and reprinted with the permission of Cambridge University Press.

Australia having extremely old and infertile soils. Significant exceptions are fertile soils developed on basalt flows and alluvial plains.

During the Quaternary ice ages, lower sea levels exposed a vast continental shelf which increased Australia's land mass by more than 40% and united the mainland with the islands of Tasmania to the south and New Guinea to the north. These allowed the ancestors of the modern Aborigines to colonise the continent from southeast Asia about 50 000 years BP. Remarkably little is known about these ice-age Australians, indeed there is considerable debate as to the exact timing of their colonisation. Although variable across the continent, Aboriginal cultures were characteristically nomadic, tracking seasonal resource availability: no group of Aborigines practised agriculture. European colonisation occurred following the first settlements in 1788. Europeans have greatly transformed the Australian continent through intentional and unintentional introduction of numerous plants, animals and diseases, large scale clearance of native vegetation (Figures 1.2 and 1.10) and by draining wetlands, damming rivers and increasing local supplies of water by irrigation and tapping aquifers. Kirkpatrick (1994) has concisely summarised many of these profound ecological

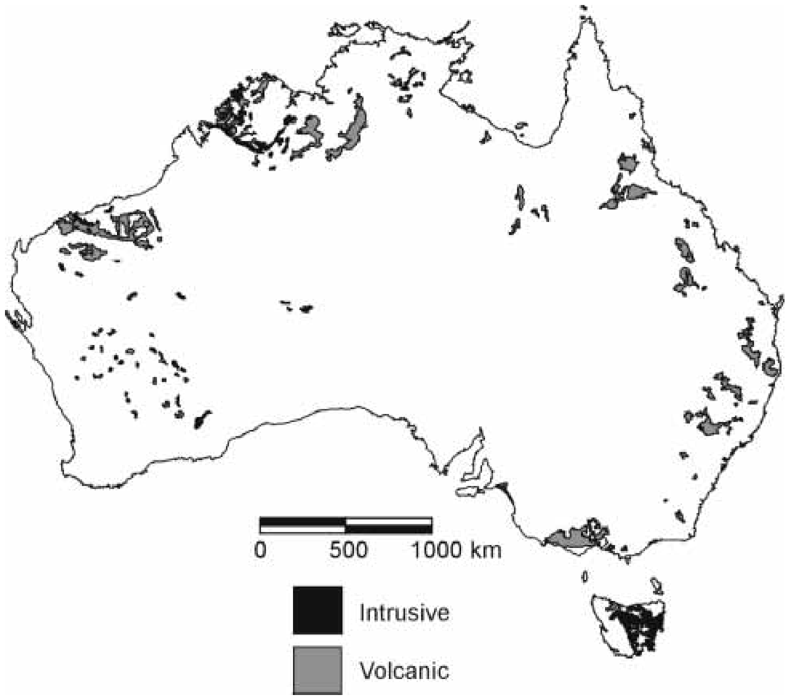


Figure 1.9
Area of basic to ultrabasic volcanic rocks (i.e. basalt, minor agglomerate, tuff) and basic to ultrabasic intrusive (dolerite, serpentine, minor norite, gabbro) in Australia, regardless of geological age. Adapted from Anon. (1988). This map is Copyright © Commonwealth of Australia, AUSLIG, Australia's national mapping agency. All rights reserved. Reproduced by permission of the General Manager, Australian Surveying and Land Information Group, Department of Industry, Science and Tourism, Canberra, ACT.

transformations. These changes are ongoing, but have had little direct effect on large areas of northern Australia. There European population densities remain very low and Aboriginal populations are relatively high. Nonetheless, the breakdown of Aboriginal fire-management practices, weed invasion, decline of some mammal and bird species and damage by feral and domesticated stock suggest that the apparently intact north Australian ecosystems have been degraded since European colonisation.

Geographic pattern of Australian rainforest

Putting aside the vexatious issue of rainforest definition for the moment, I shall briefly describe the distribution patterns of Australian rainforest at the continental, regional and local scales. Australian rainforests have a fragmentary distribu-

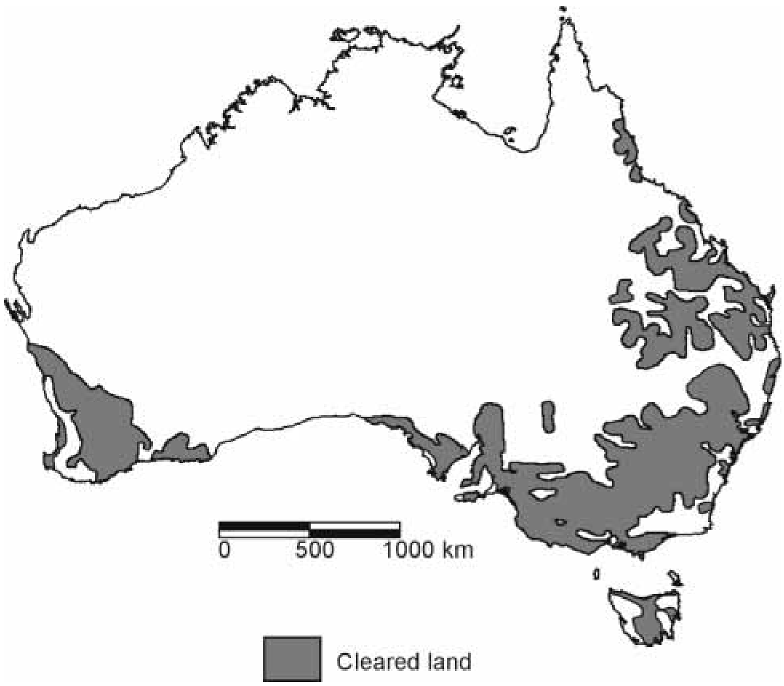
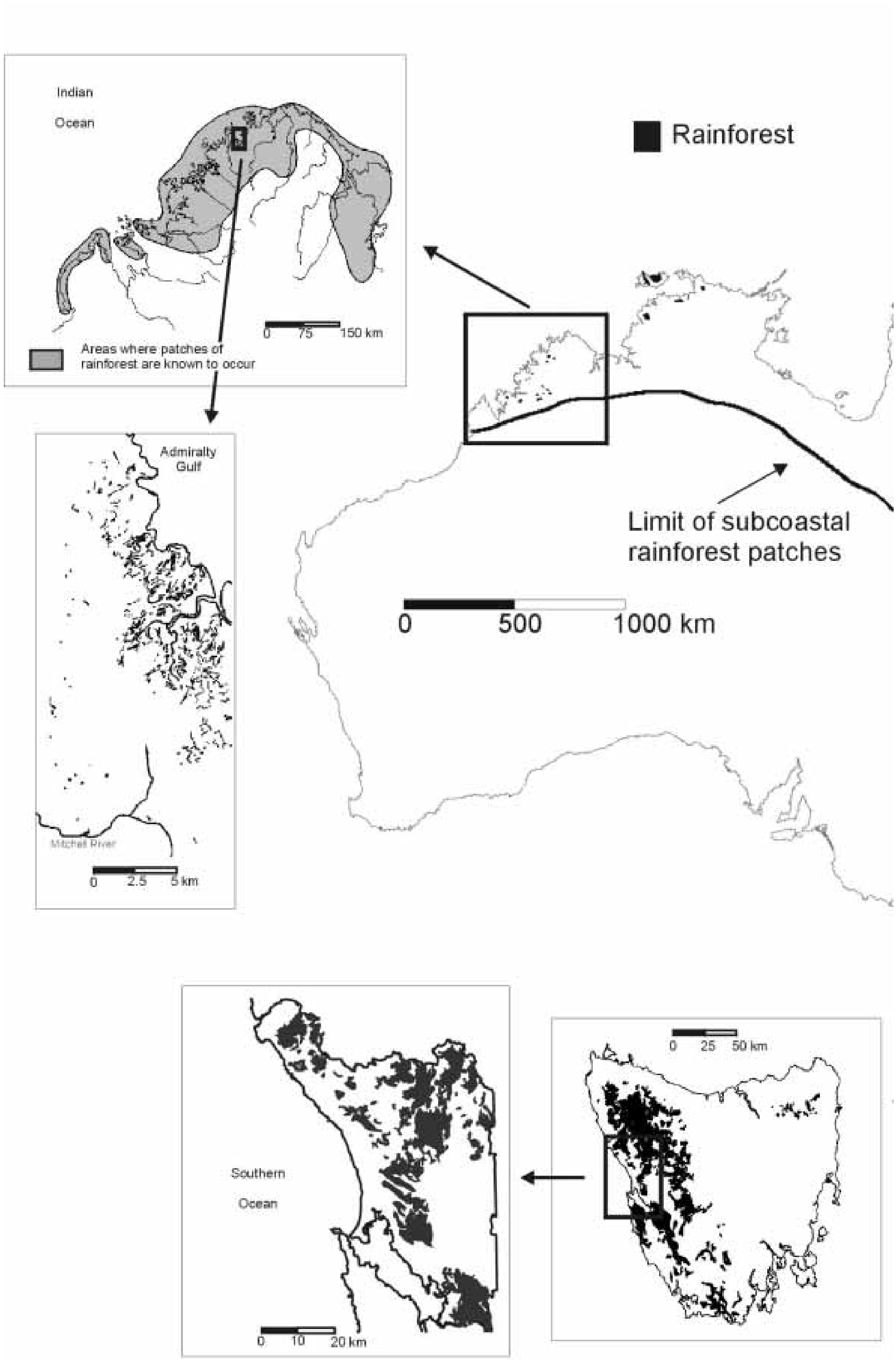


Figure 1.10
Areas of native vegetation cleared between 1788 and 1980. Adapted from Lowe (1996), Commonwealth of Australia copyright reproduced by permission.

tion across a coastal arc of some 6000 km from the Kimberley in Western Australia to southwest Tasmania (Figure 1.2). The inland limit of rainforest occurs at approximately the 600 mm isohyet. Curiously, the high rainfall region of southwestern Western Australia does not support any rainforest vegetation. Continental and regional scale maps of rainforest mask the high degree of rainforest fragmentation, which is more accurately illustrated by detailed vegetation maps of four regions across the geographic range of Australian rainforest (Figure 1.11).

On the east coast, some large tracts of rainforest are associated with fertile soils derived from basalt flows, although there is by no means a perfect correlation between soil fertility and rainforest distribution (Figures 1.2 and 1.9). For example, large tracts of rainforest occur in southwestern Tasmania and Cape York Peninsula on infertile soils derived from quartzite rocks and granites respectively.

Not only does Australian rainforest have a wide latitudinal range from southern Tasmania to northern Australia; it also has a very wide altitudinal range.


Indian
Ocean
Rainforest
Areas where patches of rainforest are known to occur
0 75 150 km
Admiralty Gulf
Mitchell River
0 2.5 5 km
Limit of subcoastal rainforest patches
0 500 1000 km
Southern
Ocean
0 10 20 km
0 25 50 km

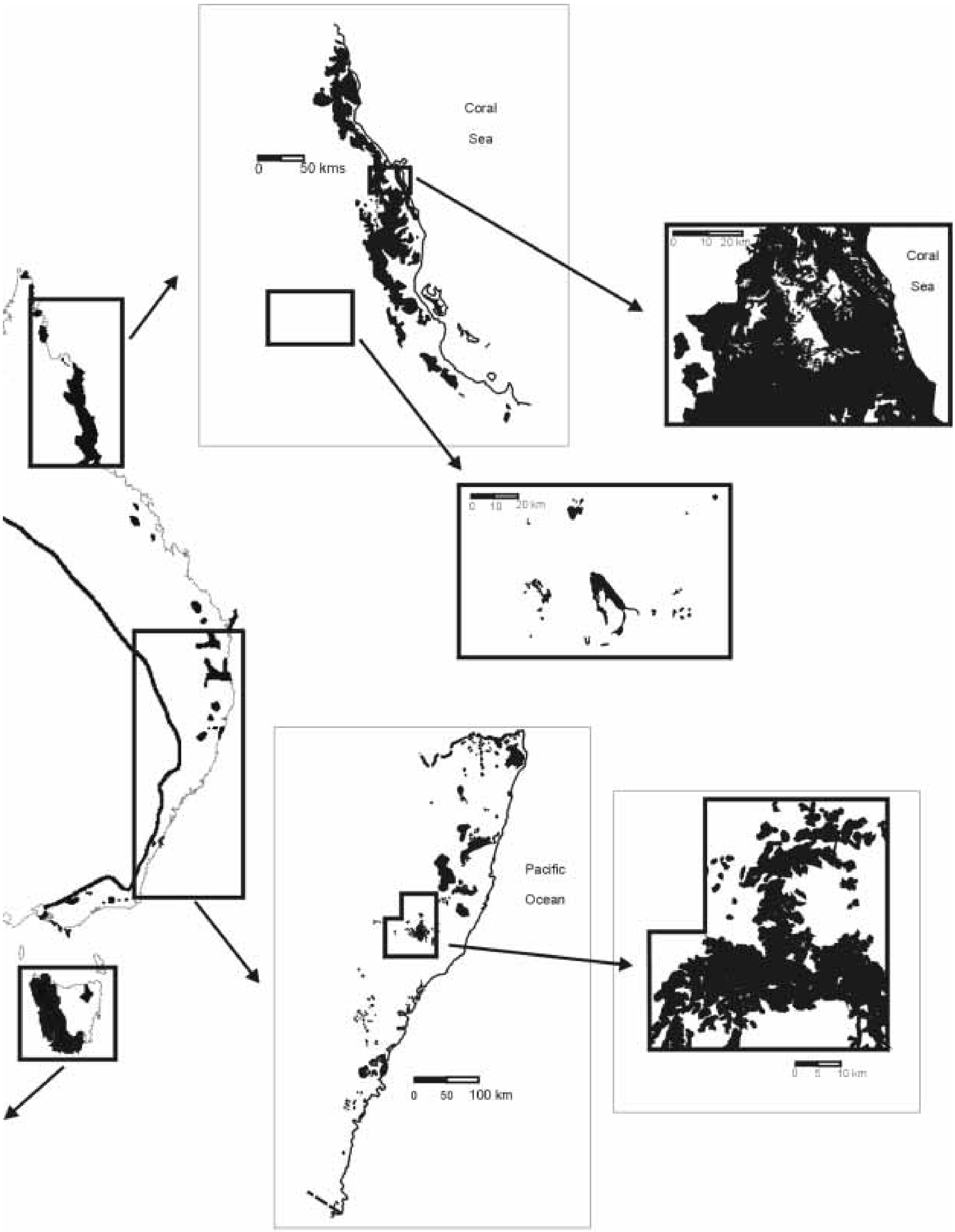


Figure 1.11
Maps showing the effect of spatial scale on the distribution of rainforest in four regions across the arc of rainforest in Australia. Adapted from Adam (1992), Kirkpatrick (1977), Dodson and Myers (1986), Ash (1988), and Clayton-Greene and Beard (1985).

Throughout its range, rainforest occurs from sea level to the altitudinal limit of woody vegetation; indeed some types of rainforest are restricted to high elevation sites (e.g. montane tropical rainforests, and alpine rainforests in Tasmania).

Webb *et al.* (1984) undertook a numeric biogeographical analysis of Australian rainforests based on floristic lists collected across the geographic range of the vegetation. They identified three broad classificatory groups of rainforest that correspond to climatic zones which they described as 'ecofloristic regions': their 'Group A' was mainly temperate but includes some areas in the humid subtropics; 'Group B' was characterised by tropical forests; and 'Group C' was characterised by rainforests in the subtropics. However, within these three broad groups Webb *et al.* (1984) identified a total of eight further subdivisions which they described as 'ecofloristic provinces' (see Table 1.1 and Figure 1.12). Only three (A_3; B_3; C_2) of these eight groups were geographically distinct (Figures 1.13 and 1.14). The other groups, which all occur on the east coast, overlap to greater or less amounts (Figure 1.15). They explained the overlap between the various 'ecofloristic provinces' as being a consequence of habitat heterogeneity in eastern Australia associated with steep altitudinal and rainfall gradients and the juxtaposition of sites with contrasting geology and hence soil fertility. They also suggested that some of the overlaps might be explained as the result of long-term climatic changes that have resulted in 'relictual' or environmentally-discordant distributions of some rainforest types. Clearly, the complex distribution patterns of rainforest types prohibit the rigid application of simple climatic classifications such as tropical and subtropical rainforest. In any case, Webb *et al.* (1984) demonstrated that Australian rainforests can legitimately be seen as a floristic continuum with a considerable number of species and genera co-occurring between 'ecofloristic regions' (Figure 1.16). For example, about 13% of the rainforest tree species occur in all three 'ecofloristic regions'. Thus any biogeographic classification of Australian rainforests is necessarily imperfect, and definitions of regions ultimately include an arbitrary component. In this book, I have occasionally broken up the huge continuum of Australian rainforests into four geographic zones: monsoon tropics, humid tropics, subtropics and temperate. I acknowledge that this division ignores the complexity of altitudinal effects on climate and edaphic influences on rainforest vegetation. I have pursued this classification because it is a convenient method of relating studies that have been conducted in the same geographic zone, and in some cases, the same landscape.

The transition between rainforest and the surrounding non-rainforest vegetation is typically abrupt for monsoon and tropical rainforests (Figure 1.17). However, in some situations rainforest invades the surrounding *Eucalyptus*

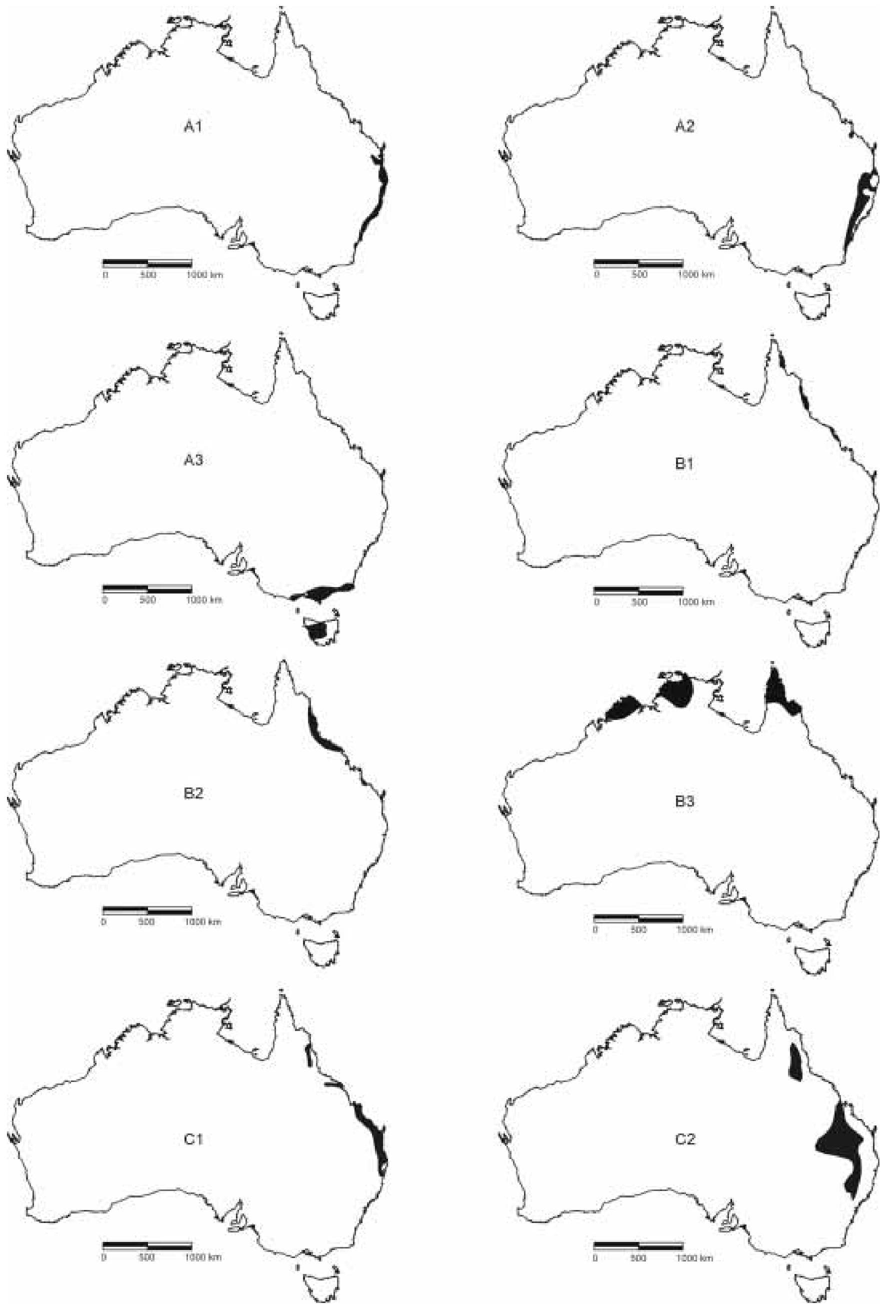


Figure 1.12
Boundaries of 'ecofloristic provinces' defined by Webb et al. *(1984).*

TABLE 1.1. Climatic variables for characteristic meteorological stations for eight major rainforest 'ecofloristic provinces' in Australia

Ecofloristic province	Climate type	Latitude and longitude	Altitude	Mean annual rainfall (mm)	Mean annual rain days	Mean rainfall in driest 6 consecutive months (mm)	Mean annual air temperature (°C)	Mean minimum temperature of coldest month (°C)
A_1	aseasonal humid warm	28° 19' S 153° 26' E	5	1722	142	550	19.3	5.8
	subtropical	30° 19' S 153° 07' E	3	1759	147	569	18.3	6.6
	aseasonal humid cool	28° 36' S 153° 23' E	381	2388	147	762	16.6	5.8
	subtropical	31° 23' S 152° 15' E	146	1603	159	499	17.3	3.8
A_2	aseasonal humid	33° 42' S 150° 22' E	883	1374	149	406	12.3	1.5
	montane subtropical	30° 37' S 152° 11' E	1036	1516	130	444	13.1	2.8
	aseasonal humid warm temperate	37° 32' S 149° 09' E	88	1004	146	448	14.1	2.0

A_3	aseasonal humid cool temperate	41° 26' S 145° 31' E	624	2201	252	820	8.3	1.6
		41° 38' S 145° 57' E	915	2774	237	1066	6.7	0.0
B_1	seasonal humid tropical	12° 26' S 130° 52' E	29	1594	109	110	27.5	18.9
		12° 31' S 138° 03' E	7	1360	92	51	27.8	17.9
		12° 47' S 143° 18' E	19	2049	202	215	25.4	18.4
		12° 27' S 142° 38' E	39	1362	102	66	26.2	17.0
B_2	aseasonal humid tropical	17° 32' S 145° 58' E	40	3644	155	760	23.5	15.1
		18° 16' S 146° 02' E	5	2127	122	289	24.1	13.3
		17° 12' S 145° 34' E	715	1260	113	189	20.2	10.8
B_3	seasonal subhumid tropical	13° 57' S 143° 12' E	193	1146	86	44	25.4	16.7
		15° 28' S 141° 25' E	13	1222	71	36	26.9	14.8
		14° 28' S 132° 16' E	107	952	62	46	27.2	12.9

TABLE 1.1. (*continued*)

Ecofloristic province	Climate type	Latitude and longitude	Altitude	Mean annual rainfall (mm)	Mean annual rain days	Mean rainfall in driest 6 consecutive months (mm)	Mean annual air temperature (°C)	Mean minimum temperature of coldest month (°C)
C_1	seasonal humid warm subtropical	27° 28' S 153° 02' E	38	1146	123	366	20.7	9.8
		26° 11' S 152° 40' E	94	1161	117	354	20.4	6.0
		24° 42' S 151° 18' E	339	905	89	245	18.7	3.7
C_2	seasonal subhumid warm subtropical	24° 24' S 150° 30' E	173	699	75	187	20.7	5.1
		18° 09' S 144° 19' E	453	799	57	67	23.8	9.5
		26° 30' S 147° 59' E	335	575	61	188	19.8	3.3

Adapted from Webb *et al*. (1984).

Figure 1.13
Interior of a Nothofagus cunninghamii *rainforest on fertile soil in northwestern Tasmania. This forest type is typical of the rainforests in the* A_3 *ecofloristic province (Webb* et al. *1984). (Photograph: David Bowman.)*

Figure 1.14
Boundary of a monsoon vine-thicket rainforest on basalt soils in northeastern Queensland. This forest type is typical of rainforest in the B_3 *ecofloristic province (Webb* et al. *1984). (Photograph: David Bowman.)*

Figure 1.15
Profile of humid tropical rainforest near Cape Tribulation in northeastern Queensland. This forest type is typical of rainforest in the B_1 ecofloristic province (Webb et al. *1984). (© Murray Fagg, Australian National Botanical Gardens.)*

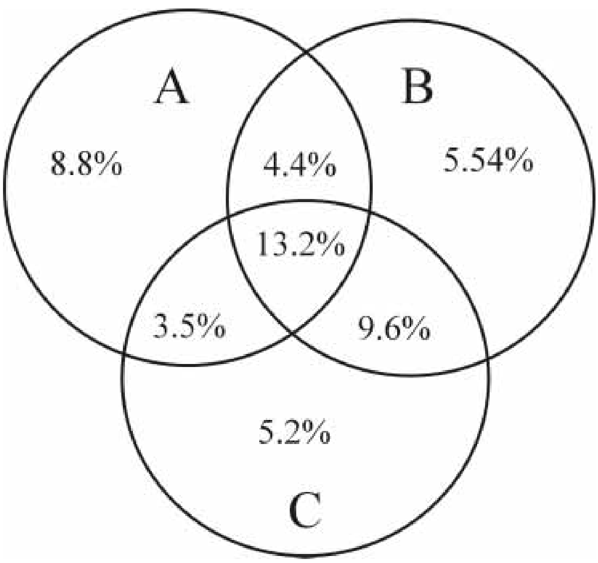


Figure 1.16
Percentage of rainforest species from a sample of 1316 tree species that occur in the three 'ecofloristic regions' that divide up the geographic range of Australian rainforest. Adapted from Webb et al. *(1984).*

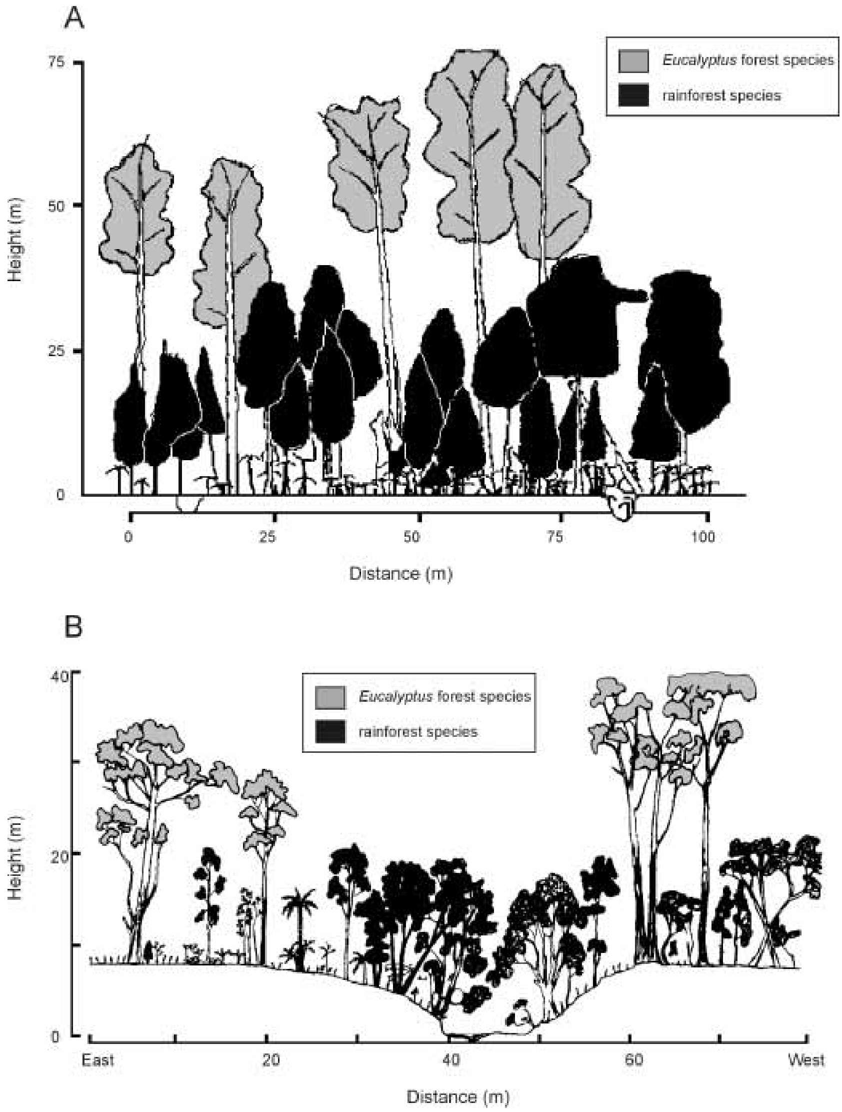


Figure 1.17
Profile diagrams of rainforest boundaries from four regions in Australia.
A. Mixed Eucalyptus–Nothofagus cunninghamii *rainforest in Tasmania (adapted from Gilbert 1959). B. Riverine rainforest dominated by* Acmena smithii *and* Tristaniopsis laurina *within a* Eucalyptus *forest in Victoria (adapted from Melick and Ashton 1991). C. Humid tropical rainforest boundary on the Atherton Tablelands in northeastern Queensland (adapted from Unwin 1989). D. Monsoon rainforest–*Eucalyptus *savanna boundary on Groote Eylandt, Northern Territory (adapted from Langkamp* et al. *1981, with kind permission from Kluwer Academic Publishers).*

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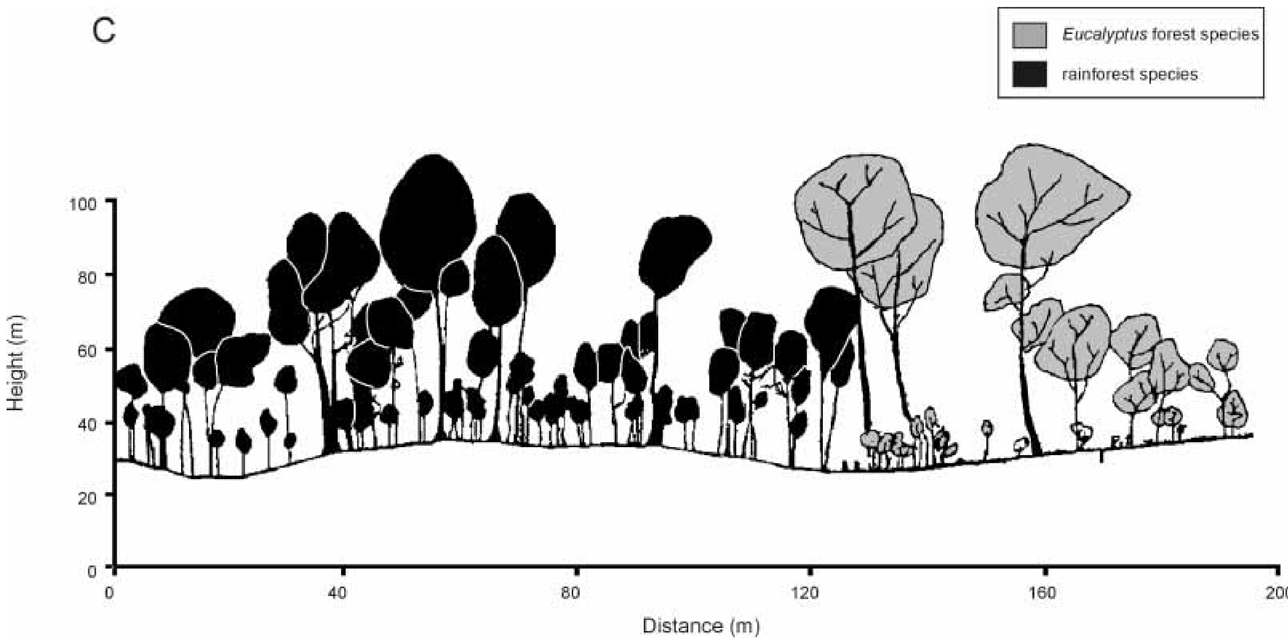
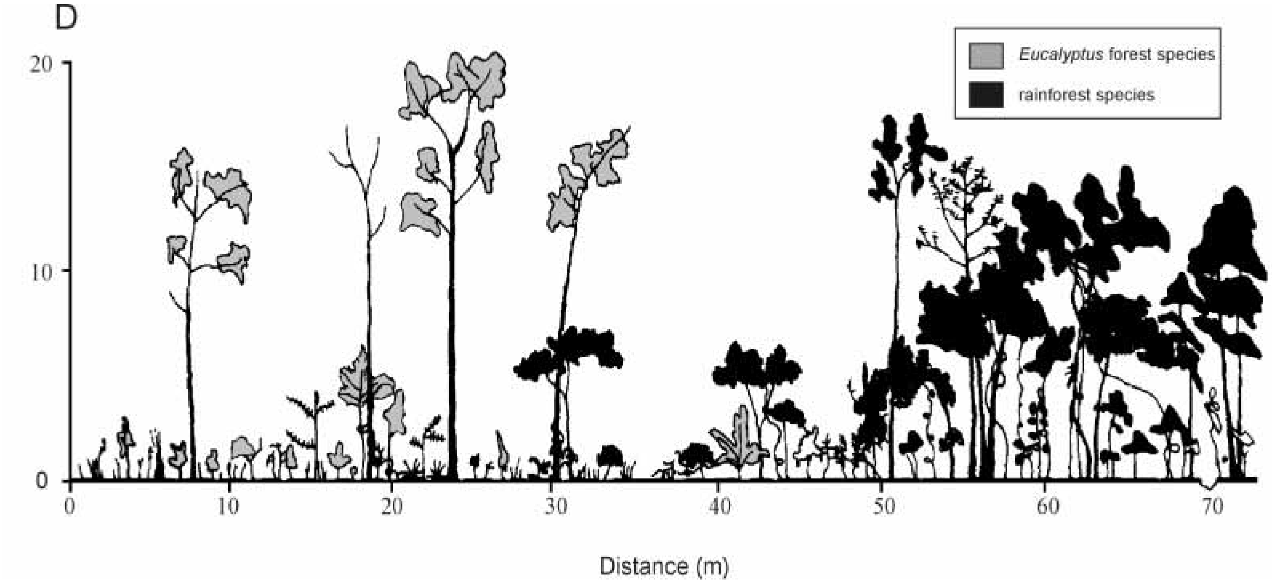

C
Eucalyptus forest species
rainforest species
Height (m)
100
80
60
40
20
0
0
40
80
120
160
200
Distance (m)



D
Eucalyptus forest species
rainforest species
20
10
0
0
10
20
30
40
50
60
70
Distance (m)

forests (Figure 1.17). The width of these rainforest ecotones is highly variable but typically less than one km. The boundary of temperate rainforests can be either abrupt or extremely gradual. Wide ecotones are often recognised as a distinct community known as 'mixed forests' (Figure 1.17), and in Tasmania there are large tracts of these mixed forests. The mixture of rainforest and *Eucalyptus* forest has bedevilled neat definitions of 'rainforest' in Australia. The definition of rainforest in Australia is the subject of the following two chapters. The remainder of the book seeks to explain why Australian rainforests have a fragmentary distribution.

Fire, air, earth and water

A number of theories have been advanced to explain the control of rainforest in Australia. Some of these theories have been concealed, Trojan-horse-like, within definitions of 'rainforest'. Other theories are explicit and typically have championed the primacy of single environmental contingencies such as fire history, environmental changes, soil fertility, or water stress. Some theories are so broad in scope that they cover all bases by acknowledging the importance of many factors and their complex interactions. Clearly, the various theories are competing for the same intellectual space. The aim of this book is to subject them to critical analysis to determine if there is a general explanation for the continent-wide fragmentary distribution of Australian rainforest.