

15 Quaternary vegetation

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The Quaternary is the period of modern life in which all the kinds of plants and animals still living have evolved, or have continued from the Tertiary unaffected by new environments. Technically, the beginning of the Quaternary has been defined as the last phase of the Matuyama reversed magnetism epoch after the Olduvai event, which finished at 1.62 million years (Ma). Others relate it to the first appearance of arctic marine faunas about 2.2 Ma in the mid-latitude North Atlantic (Bowen, 1978). The period therefore breaks with the definitions of older periods based on widespread evolutionary changes and instead uses climatic changes, such as the growth of icesheets and spread of cold surface water, to establish the chronology. Cores from the sea-floor show that parts of the tropical Pacific were little affected, but the lock up of snow in icecaps left the oceans enriched in the heavy isotope of oxygen (^{18}O), so that a record of ice on the earth is well preserved in marine sediments. This record shows a series of cyclic changes on time scales of about 100 ka, with phases of maximum and minimum ice extent (stadial and interglacial periods, respectively), each occurring for 10% of each cycle, the remainder being cool interstadials (Chappell & Shackleton, 1986). Over 20 of these alternations have been identified, showing that for the last 2.3 Ma the earth has been very sensitive to minor changes in thermal equilibria, forced, in part at least, by variations in the season and amount of solar radiation reaching the earth (Chappell & Grindrod, 1983).

There are only two divisions in the Quaternary: the Pleistocene from 2.2 (or 1.62) Ma to only 10 ka ago, and the Holocene, our present interglacial, which is the last 10 000 years. The Pleistocene represents the period of establishment of our present landscapes, climatic patterns and types of variability, and the adaptation of the Tertiary biota to these new environments. The term Holocene means life as at present and this is generally true in relation to evolution – the time has been far too short for major new species to appear. However, in terms of changes to populations and particularly to plant and animal communities, the Holocene has been far from stable, and presents us with some novel communities and others not seen since the last interglacial, 126 ka ago.

If we want to understand the modern vegetation of Australia, with its puzzles of distribution, floristic patterns and connections, we can look backwards from the present to ask about its continuity through time and sometimes the length of its occupation of the same place. Quaternary vegetation history differs from that of previous epochs in being concerned with comparing species still living, or which lived recently, with fossil flora. This provides a powerful tool, in that we can flesh out meagre fossil records by comparison with the richness of extant communities. However, it is also now realised that our Holocene is an interglacial that represents unusually warm conditions compared to those prevailing for 85% of the past million years or so. Interglacials take up only about 10–15% of the time of the Quaternary, so that

communities that form in them may be atypical, composed of species that have to survive much longer times of cool, dry conditions. Such species may have contributed to quite different communities during glacials and hence a fossil occurrence of a modern species need not imply the environmental niche presently occupied. For example, the koala fossils from semiarid Lake Mungo do not prove the existence of tall eucalypt forests near at hand 40 ka ago.

Biota of the Quaternary have had to adapt to some of the most radical changes since the evolution of the advanced groups in the Mesozoic. In general, it is assumed that migration of pre-adapted elements was minor, although Macphail *et al.* (Chapter 10, this volume) show that at least one alpine species (*Astelia alpina*) arrived here from New Zealand. By the start of the period, high levels of Poaceae, Asteraceae and Casuarinaceae pollen indicate that seasonally dry conditions with widespread droughts were well established inland, and eucalypt-dominated communities were to be found closer to the mountains. Semi-deciduous rainforests and noneucalypt savannas occupied the tropics and stretched across the Arafura Plain. Closed forests still persisted in New Guinea and on the Eastern Highlands down to Tasmania. At Lake George, New South Wales, in the most reliably dated site at the start of the Pleistocene, McEwen Mason (1991) found remarkably high levels of Asteraceae and Poaceae pollen replacing *Nothofagus* subgenus *Brassospora* forests in an environment that seems to have its closest analogy today in New Caledonia – subtropical, probably with moderate seasonal but reliable rainfall (Read *et al.*, 1990). Martin (1989) has already noted this change in central New South Wales, where eucalypts were already prominent in the Pliocene.

In Tasmania, Hill & Macphail (1985, 1994) commented on Early or mid-Pleistocene fossil plants from Macquarie Harbour. The pollen includes traces of *Eucalyptus*, Poaceae, Asteraceae and Chenopodiaceae but is dominated by *Allocasuarina*, which seems to have occupied the site with cool temperate *Lagarostrobos franklinii*–*Nothofagus* forest nearby. This is the earliest record of a modern type of Tasmanian rainforest

and it includes *Quintinia*, a genus now confined to more temperate montane rainforest in New South Wales, Queensland and New Guinea. Some sclerophyllous groups, such as two species of *Banksia* (now extinct; Jordan & Hill, 1991), and epacrids are present as well. The Pleistocene therefore continues a process of loss of diversity in the wet communities and reassortment in the sclerophyll that had commenced much earlier.

Faunas also demonstrate the continuing expansion into the Pleistocene of open conditions: the kangaroos, diprotodonts, short-faced kangaroos and open country flightless birds all actively radiated during the Pliocene and early Quaternary (Archer & Clayton, 1984). The newly arrived rodents have achieved their greatest diversity of new species in the arid zone, presumably because they had the opportunity to occupy the new niches of sandhills and gibber (rocks) that appeared in the Quaternary. Genera such as *Pseudomys* and *Rattus* have also adapted to the new (or certainly greatly expanded) cold mountain grasslands and shrublands.

The cycles of glacials and interglacials, with corresponding alternations in sea levels, rainfall, evaporation, temperature and possibly the frequencies of severe frost, drought, winds and storm events, imposed a new tempo of climatic variability on the Tertiary biota. The time scales, although involving tens of thousands of years, seem to have been short enough to discourage specialisation to stable niches. The Quaternary rewarded generalists such as *Eucalyptus* and species with the ability to migrate or disperse readily. The climatic changes caused major shifts in the boundaries of the major Australian biomes. For plants this meant widespread repeated annihilation of populations and complete ecosystems. This process caused extinction and range fragmentation, but it also may have provided opportunities for speciation by creating small, isolated populations often in areas with slightly different climates, geology and species associates. A response to such pressures is the rapid appearance of new groups able to evolve in small, isolated populations. The classic Australian example is *Acacia*, with over 640 species. These plastic groups

are extraordinarily well represented in Australia, where the climatic stresses seem not to have wiped out entire forest types, as occurred in Arctic regions. The migration of plants from outside Australia has been very limited, so it has been local genera that have diversified into many new niches.

The final major event for the Australian vegetation was the migration of humans, the ultimate Quaternary generalist species, around 50 ka ago. To what degree preindustrial humans in Australia and New Guinea had an impact on species and vegetation is an ongoing controversy, but for some regions at least it is clear that human-controlled burning created managed landscapes (Dodson, 1992). The extinction of all large browsers and most grazers and predators has occurred since the arrival of people and this must also have influenced vegetation structure (Flannery, 1990). Imposed on top of the extreme climatic change of the last glacial, human activities accelerated the rate of environmental change for biota.

The result of these processes is the present-day vegetation, which forms six distinctive areas or floristic provinces: Tumbuna, Papua, Torresia, Eremaea, southwest Australia and Bassiana (Figure 15.1). These correspond to the major modern climatic regions of Australia–New Guinea. If we analyse these provinces in terms of their vegetation histories, it is apparent that some have been much more affected by Quaternary change than others, and they differ in the age of their development as well. As might be expected, the less changed, more stable regions contain the greatest number of species that relate directly to Tertiary times (Melville, 1975), and may also contain newly evolved species (Hill & Read, 1987).

Australia is so large and variable that we need the present variety of pattern and the persistence of small areas of vegetation out of balance with most of a region to remind us that past histories based on chance finds of fossils will conceal similar variability. The methods of studying vegetation history in the Quaternary use the same materials as the more distant past, that is micro- and macrofossil remains, but the existence of present-day stands of vegetation and of abundant sites of deposition allow the calibration of the microfossil

records so that vegetation structure can be inferred even though pollen is not usually identifiable to the species level. This means that Quaternary pollen analysis can be used to comment on the history and degree of stability of plant communities, as long as the link to modern ecology is retained. The location of sites is strongly biased to cool wet areas in the mountains of New Guinea, down the eastern coast and ranges, and in Tasmania, with a scatter of sites elsewhere (Figure 15.2). The voluminous literature on the Quaternary is available from a major database on Quaternary climates maintained by the Bureau of Mineral Resources, Canberra (Bleys *et al.*, 1991).

MAJOR CHANGES OF THE QUATERNARY

Cooler times: the mountains and the coast

The volume of ice in the earth's icecaps through time can be inferred from oxygen isotope analysis of deep-sea cores. Although cooling is apparent almost throughout the Tertiary, major variations in ice volumes are restricted to the Quaternary. So the major fluctuations in sea level are also Quaternary phenomena, reflecting the amount of land ice at any one time. The oceans were lowered by 120–140 m at times of maximum ice lock up and were 5–8 m higher than at present in the warmest interglacials. This has created a restricted but widespread new niche, the coastal zone, in which continuous change and seral responses are dominant. The other niche to appear and expand as a result of cold was the alpine (above treeline) niche, which fluctuated even more widely than the coastal. For the last glacial, some altitudinally limited vegetation boundaries descended more than 800 m in altitude, which was about the same as the lowering of the snowline (Galloway, 1986).

The present coastal zone has developed since the rise of the sea to its current level. The previous interglacial, at 126 ka ago, was the last time that the sea had reached this level, and surpassed it by a few metres. By 7 ka ago, the sea had flooded

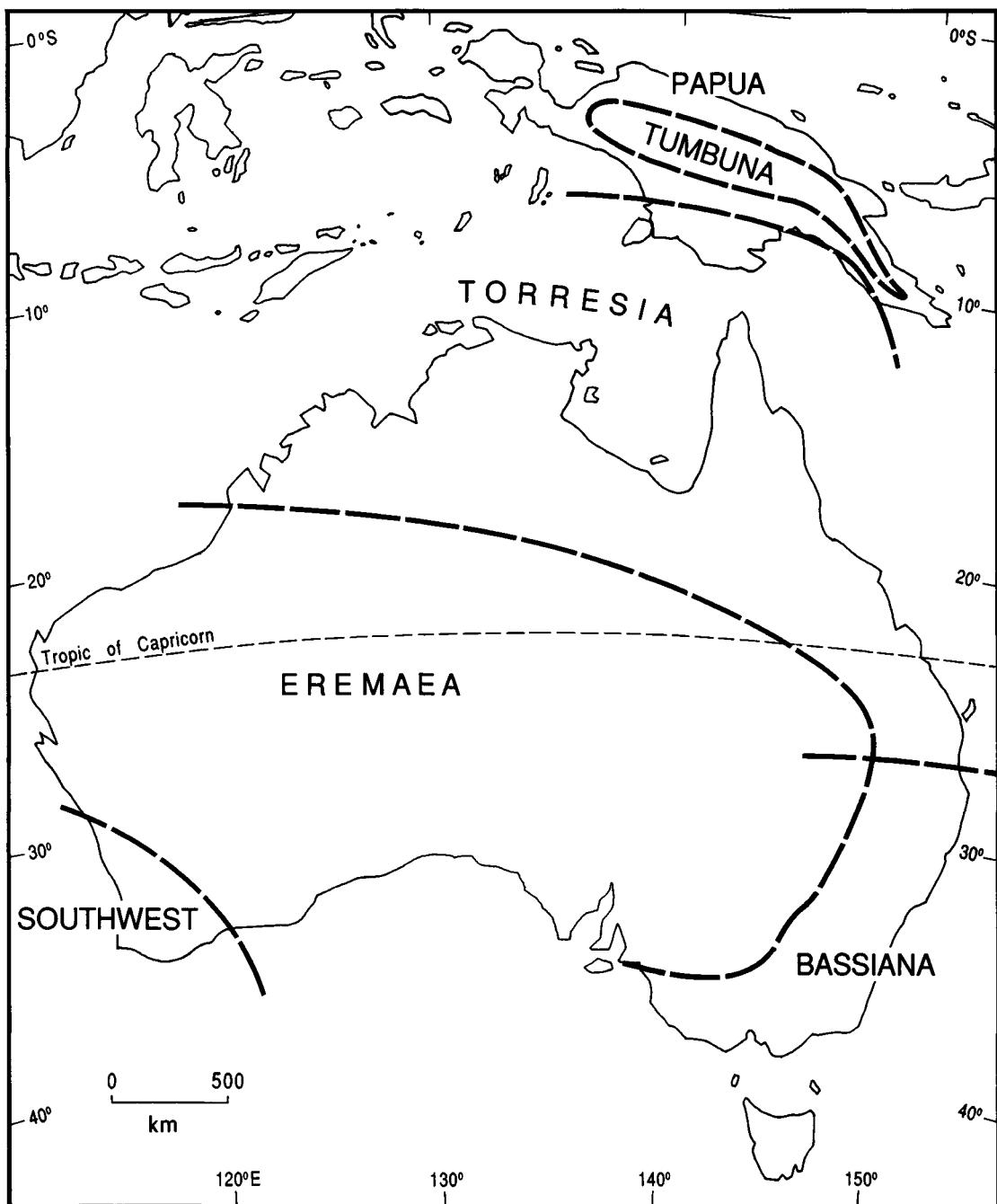


Figure 15.1 The biological provinces of the Australian region.

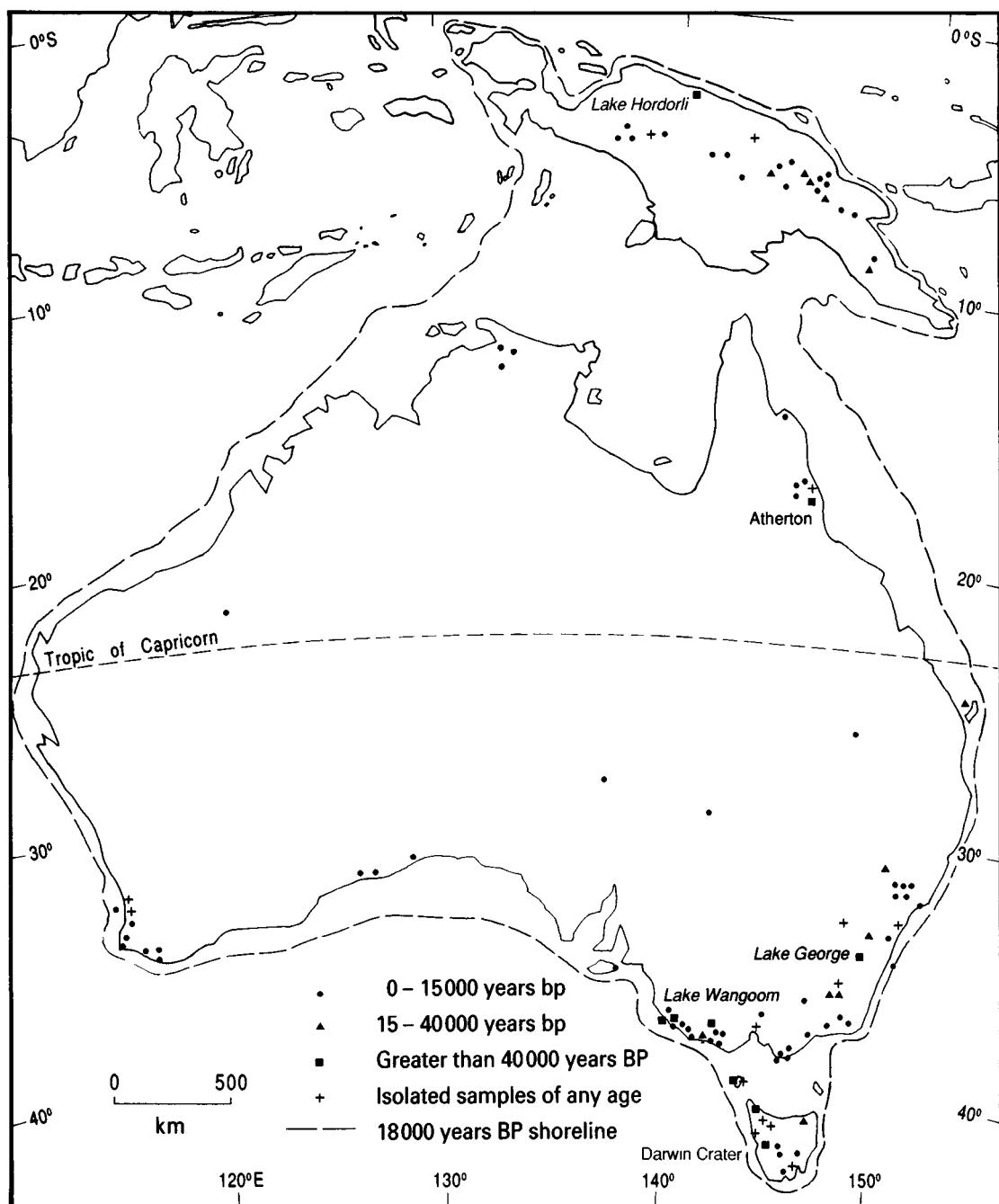


Figure 15.2 Sites of Quaternary palaeoecological investigation in Australia and New Guinea. (After Dodson, 1989.)

into every valley cut below its present level, and in most areas it is still infilling the valleys with swamps, lagoons and saltmarshes. Beach sand, brought onshore by the rising sea level, formed large dunes that were invaded and stabilised by plants once the sand supply diminished. Previous high sea levels have also left dunes and sandplains in many areas, and the long exposure to leaching has provided poor siliceous sands that support only specialised heaths or woodlands. The resultant mosaic of communities developing on cliffs, in marshes or on sand combines with a strong zonation in substrate stability and salt to provide very complex vegetation, with many locally endemic communities. The coastal flora is derived from pre-adapted genera of swamps, sand heaths and river edges. As is true of other new habitats, immigrant groups are well represented, because new environments provide vacant niches and unstable habitats reward migratory ability that will be a characteristic of immigrants. Migratory ability means that, in general, the least stable communities, such as strandline or saltmarsh, have the most widespread species. This contrasts with the more stable but isolated siliceous sand communities, which have many localised species.

Vegetation histories from coastal lagoons have been obtained in many localities, but are generally limited to the last 7 ka. Offshore cores from Narooma, on the south coast of New South Wales, go back to 14 ka, but are not very different from present-day samples (P. Roy personal communication). The lowest sections show mainly saltmarsh pollen with inputs from eucalypt forest. However Roy's analysis of foraminifera in this core suggests that sea temperatures could have been 2 deg.C warmer than at present, a most surprising result, given that the glacial maximum had only just passed, and land conditions were generally a lot cooler than at present. The answer may well lie in land-bridges that blocked off the Torres and Bass Straits at times of lower sea level. These barriers kept the eastern current flowing southwards close to the continent, resulting in a coastal strip of mild climate along the southern coast of present New South Wales, and the eastern coast of Victoria and Tasmania.

Similar results from coastal swamps and caves in Western Australia (Martin, 1973; Balme *et al.*, 1978) and the Northern Territory (Torgersen *et al.*, 1988; Shulmeister, 1991) show very little evidence for temperature change in the last glacial. In those areas there are clear indications of greater aridity at times of lower sea levels but these can be explained by the greater distance to the contemporaneous coast, which gave more inland characteristics.

Evidently the climates and arrangement of vegetation during glacial times in the Quaternary are not simply a shift downhill of those of the present day. If we needed any further reminders, then a consideration of the mountain biomes provides more examples. When it was realised that New Guinea, Tasmania and a tiny area of the Australian alps had experienced glaciation it was easy to calculate the mean lowering of the snowline required (Galloway, 1965). Varying estimates were obtained from different areas, because the snowline is a complex integration of temperature, snowfall, snow drift and exposure to melting. However the maximum figures indicate that the snowline was about 1000 m lower than at present, corresponding to temperatures approximately 6–7 deg.C cooler than present. In places such as Mt Kosciusko, smaller changes are apparent, suggesting that past conditions were drier as well as having depressed mean annual temperatures.

Many vegetation histories are now available from the mountains of Tasmania, Victoria and New South Wales (e.g. Kershaw *et al.*, 1986). These are mostly restricted to the last 12–15 ka or so and show that, at the peak of the last glacial 18 ka ago, there was aridity as well as cold. Treeless vegetation dominated by Asteraceae and Poaceae extended across most of southeastern Australia, down to sea level on the southern coast of Victoria (e.g. Hope, 1978; Dodson, 1989; Figure 15.3). Eucalypts were present but apparently scattered or restricted to sheltered positions. Faunal records from lowland areas contain more ecological groups of animals at a given locality than occur at any equivalent place today. For example, 16 ka ago on Kangaroo Island, South Australia, pygmy possums now restricted to



Figure 15.3 Composite shrubs in grasslands near Great Lake, Tasmania, provide an analogue of Late Pleistocene upland and Bassian shrub steppe.



Figure 15.4 Windswept coastal shrublands on the west coast of Tasmania provide a complex mosaic that may be structurally similar to larger areas of Southern Australia during the last glacial.

Tasmania occurred together with rodents found in red seif dune habitats today (Hope *et al.*, 1978). This mixed faunal ecology suggests a mosaic of vegetation types from dense scrubs to open shrub-

lands (Figure 15.4). Such a mosaic may have been a response to lowered precipitation and evaporation. The latter raised groundwater levels; perhaps ridges and dune crest habitats were desert

like, while swales supported lagoons and dense scrubs.

In southeastern Australia the long cores from Lake George, New South Wales (Singh & Geissler, 1985), Lake Wangoom, Victoria (Kershaw *et al.*, 1990), and Darwin Crater, Tasmania (Colhoun, 1988), provide records through more than one glacial–interglacial cycle. Well-wooded periods alternate with more open steppe, or grassland with increased alpine components. The alpine shrubs and herbs are also prominent in part of the wooded periods, often with cool temperate rainforest components. *Eucalyptus* dominated the vegetation on several occasions at all three sites. At Lake George and Lake Wangoom the past phases of *Eucalyptus* never match the dominance in the present interglacial, but at Darwin Crater parallels to the present vegetation arose several times.

In New Guinea two major changes occurred: a depression of the treeline to below 2200 m (compared to 3900 m today) and an expansion of lowland grasslands and seasonally dry communities at the expense of lowland tropical rainforest. No very long cores have been collected to date from New Guinea, but the last 30 ka are well documented (Hope, 1986). The 1700 m depression in the treeline suggests that glacial-time conditions differed from the present in not allowing trees to form a closed forest as they do in the subalpine today. Periodic disturbance by drought or frost may have been a cause (Hope, 1989; Figure 15.5).

The records show that cold-adapted vegetation is restricted today, and in southeastern Australia generally occupies relatively wet mountain tops that favour dense sclerophyllous shrublands. This may explain the low endemism of this alpine flora, because many species may have been recruited from woodlands and forests. The formerly widespread alpine communities of glacial times are retained only on drier mountains and consist of mires and tussock grasslands with numerous composite herbs and shrubs and some seasonal species. Major elements of this cold steppe vegetation persist in lower altitude frost hollows such as the Central Plateau of Tasmania and the Monaro of New South Wales, and this leads to the impression of poor obligate alpine floras and



Figure 15.5 *Cyathea* tree fern-dominated grasslands above 3000 m in New Guinea are created by burning but seem to have recruited species that formerly made up natural above-treeline communities.

faunas. Occurrences of treeline species down to sea level are common in southeastern Australia, e.g. *Gentianella diemenensis*, *Eucalyptus pauciflora* or *Euphrasia* spp. while others display remarkably broad altitudinal ranges and ecological plasticity, e.g. *Allocasuarina verticillata*, *Acaena novae-zelandiae* or *Banksia marginata*. This evidence for widespread treelessness suggests that during the height of the glacial the treeline had virtually disappeared, allowing cold dry steppe to expand across a very large area, accompanied by unstable slopes and alluvial fan activity down to about

500 m above sea level (Barlow, 1986; Hope, 1989). Only in western Tasmania and the crest of the Great Eastern Scarp was there an alpine zonation like that of the present, with a largely woody vegetation changing in stature with altitude. Western Tasmania remained wet enough for the specialised subalpine gymnosperms and deciduous beech to survive to the present, although they were forced down to 200 m above sea level during both the last ice advance and the end of the previous interglacial (Colhoun, 1985).

The survival of a wide range of rainforests and tall eucalypt forests in southeastern Australia, differentiated north to south and altitudinally, shows the influence of the eastern fall of the coastal escarpment in providing reliable orographic rainfall and sheltered sites. At full glacial times there would have been an abrupt boundary from these forests to the treeless cold dry tablelands, exposed to the westerly winds. The period from 26 to about 12.5 ka was typical of these conditions in southern New South Wales.

However, not all of the last glacial penalised forests. *Nothofagus*, presumably *N. cunninghamii*, was living at an altitude of 1850 m on Mt Kosciusko 35 ka ago and survived through several early glacial phases near Lake George (Kershaw *et al.*, 1986). It had an expanded range in Victoria prior to the peak of the last glacial (M. Mackenzie, personal communication). Although beech has a discontinuous distribution in southeastern Australia today, there may even have been recent connections across the Bass Strait, for large *Nothofagus* logs have been found on King Island dated to 38 ka ago, and an expansion of wet forests compared to today is indicated at this time at Pulbeena Swamp in northwest Tasmania (Colhoun *et al.*, 1982). This suggests that the montane rainforests were well developed over a wide altitudinal range in southeastern Australia for lengthy periods between stadials (Hope & Kirkpatrick, 1989). A similar conclusion was reached for the mountains of northeast Queensland, where gymnosperm-rich forests containing *Araucaria*, *Agathis* and *Dacrydium* occur from the end of the last interglacial until about 38 ka ago (Kershaw, 1986). For this area Kershaw hypothesised that rainfall was less

than at present but that, none the less, expansion of rainforest occurred as a result of cooler conditions with less evaporation. Similarly the past wider extent of *Nothofagus* in southern Australia does not imply heightened rainfall but rather a more even rainfall, no substantial drought, and a reduced fire regime (Kershaw *et al.*, 1990).

There are no data about the warm rainforests of *Eugenia* and *Elaeocarpus* that today extend to the Bass Strait islands down the eastern coast of Australia in discontinuous patches (P. Cullen, personal communication). It is clear that these have not had a continuous distribution during the present interglacial, although they may have expanded when conditions seem to have been warmer and slightly wetter along the coast. In the Holocene the period from about 7000 to 4500 BP is notable for high levels of pollen of the under-storey shrub *Pomaderris*, which is even noticeable in New Zealand cores (Macphail, 1981). The last time when extensive connections may have existed may date back to the early Quaternary or even before that, but some expansion at least occurred during the last glacial, perhaps as a result of the strengthened warm current noted above. Evidence for this comes from Tasmania, where isolated Late Pleistocene fossils of macropods such as *Aepyprymnus rufescens*, now restricted to subtropical forests of New South Wales, have been found. Colhoun *et al.* (1982) noted that there were expanded wet forests along the northwest coast of Tasmania around 70–40 ka ago, suggesting more available moisture prior to the last glacial advance.

The Quaternary history of the eucalypt forests is also rather speculative. Many of the alpine communities and the montane tall wet forests of southeastern Australia are shared with Tasmania, for example alpine ash and mountain ash forests (Figure 15.6). Endemic eucalypts are concentrated in the drier southeast of Tasmania and in the alpine and escarpment crest of the mainland. Pollen diagrams are not helpful in defining the kinds of eucalypt present, although the associated species show that dense eucalypt forests have probably always been retained on the eastern coast of Wilson's Promontory (Ladd, 1979). It is currently assumed that the Bassian disjunctions of



Figure 15.6 The *Eucalyptus regnans* forests of central Tasmania are disjunct from mainland examples in Victoria. They possibly represent an early stage in the development of eucalypt communities as they are killed by frequent fires but flourish when rare fires open up a rainforest canopy.

the ash forests occurred by Early to mid-Pleistocene times, since they support some locally endemic species, including arboreal mammals such as Leadbeater's possum (*Gymnobelideus leadbeateri*). However, the forests would have been favoured by the same conditions that permitted the spread of rainforests in the earlier part of the last glacial. At Darwin Crater in Western Tasmania, there are at least four phases of tall eucalypt forest dominance within the Late Pleistocene (Colhoun, 1988). These forests have presumably survived in the region and expanded out periodically whenever conditions have been warm enough and dry enough to encourage fires at infrequent intervals. It is possible that rainforest retreated and was replaced by ash forests about 4 ka ago in central Tasmania because of an increase in fire frequency (Macphail, 1979).

The pollen diagrams from Victoria and Lake

George, combined with modern eucalypt distributions, show that open eucalypt woodlands were very widespread across the Bassian Plain and along the Western Slopes as far as Queensland. Direct evidence is scanty, but some of these woodlands supported cold-tolerant species such as the *Pimelea pauciflora* found in Late Pleistocene clays at Spring Creek in western Victoria (Flannery & Gott, 1984) and possibly *Astelia* and *Plantago*. In the Coorong of southeastern South Australia, snow gum (*E. pauciflora*) was apparently widespread before 10 ka ago (Dodson, 1975).

We should be cautious in assuming that some novel kind of subalpine woodland had displaced all other eucalypt communities from the area. Many probably persisted in sheltered sites. Today the most widespread eucalypt communities are the savanna box woodlands and their associated grasslands. These communities have presumably

advanced to higher altitudes in the Holocene, probably by a process of tree invasion and range retreat by shade-intolerant steppe species (Hope & Kirkpatrick, 1989). The ranges of a number of herbs and low shrubs became disjunct and some extinction may have occurred in seasonal geophytes. Examples include species of *Swainsona*, *Leptorhynchos*, and other Asteraceae, *Bulbine*, *Discaria*, *Scleranthus* and *Hymenanthera*. Some species of Chenopodiaceae and Asteraceae seem to have become extinct in this process, and many of the herb species are now rare and endangered.

We can therefore reconstruct full glacial conditions of southeastern Australia as consisting of very open steppe grasslands with annuals and perennial geophytes and drought-deciduous shrubs. Some of these plants are now restricted to the alpine zone, but most are preserved in frost and drought-prone montane grasslands of rain-shadows, such as the Monaro of New South Wales and the Midlands and Central Plateau of Tasmania. These communities were presumably also extensive at times of rainforest expansion, but excluded by forests or shrublands from the wetter mountains (Macphail, 1986). The dense *Allocasuarina nana* heaths of the eastern scarp must have been more extensive under harsh and windy conditions. Many of the present open forests, for example gum-stringy bark (e.g. *Eucalyptus mannifera*, *E. macrorhyncha*), ironbark (*E. sideroxylon*) and mountain gum (*E. dalrympleana*) forests, were presumably favoured by wet glacial conditions, but reduced in area during the cold dry maxima.

It is clear that at least one major woodland became restricted in southern Australia during the last glacial maximum. This is the riparian forests of river red gum along the Murray and its tributaries. *Eucalyptus camaldulensis* is the most widespread eucalypt in Australia but occurs in several forms. The occurrence of widespread source-bordering dunes and lunettes on streams and lakes after 30 ka ago and a changed river regime prior to the Holocene suggests that the bank stability provided by riparian trees was absent. *Eucalyptus camaldulensis* is derived from the tropical red gum group and its southern form is less tolerant of very high temperatures than the northern form,

but also is frost tender. It may be an example of a species that has adapted to Pleistocene change but which has been unable to exploit a cold riparian niche. However, the role of raised water tables and consequent high soil salinity in the Murray Basin may be contributory. It is curious that late glacial wood of river red gum was recovered from the channel sediments of the Yarra River in Melbourne, and that it was associated with fossils of *Sphagnum* (Duigan & Cookson, 1956).

Nix (1982) has pointed out that a cold-limited growing season changes the favoured strategies for exploiting moisture. In water-limited vegetation, tall grasses (usually C₄) will be favoured in tropical regions because they can respond quickly to favourable moisture conditions. In cold areas with winter rains, however, the dormant vegetation cannot intercept the water, which infiltrates to greater depth and favours perennial shrubs and trees with well-established root systems. Colder conditions of glacial times might therefore be anticipated to cause a substantial advance of southern shrub steppe at the expense of tropical grassland formations (Singh & Luly, 1991).

DRIER TIMES AND AUSTRALIAN DESERT BIOMES

The evidence for substantial changes due to cold are restricted to upland southeastern Australia, but the modern biota, landforms and fossil evidence show that change was widespread across the whole continent in the Pleistocene. This change towards aridity was well advanced by the start of the Quaternary, as shown by the evolution of central Australian large browsers and grazers, but further faunal development took place in the Pleistocene, resulting in specialised genera such as *Diprotodon*, with some species adapted to the shrub steppe and others to desert.

The biogeography of Eremaea presents several puzzles. A few genera and families are very large, with local endemism evident, e.g. *Eremophila*, *Cassia*, *Acacia*, some Chenopodiaceae and Amaranthaceae. Specialised grasses such as the hummock grasses (*Triodia*) and cane grass (*Zyg-*

ochloa paradoxa) fill the small shrub niche across the continent. Several communities are dominant over large areas but absent from apparently suitable habitats. An example of disjunction is *Acacia peuce*, which occurs only in three widely separated stands around the northern Simpson Desert. These are the symptoms of a very young habitat that has been stressed or partitioned (Barker & Green-slade, 1982). Few physical barriers exist, other than the vast size of the area. However, soils are quite variable, including calcareous, gypsiferous and sandy clay soils, and the shield area ironstone laterites. The pattern of seif dunes is generally relict at present, with well-developed soils and orientation often not in balance with modern sand-moving winds. The pattern of dunes became finally established within the last 500 ka. This is indicated by dunefields overrunning lake beds that contain the palaeomagnetic reversal dated at approximately 700 ka, thermoluminescence dates of 290 ka for sand burial and an evident increase in aeolian dust accession on the northwest shelf after 500 ka (Wasson, 1986). The dunes are partially reactivated at times during the glacial, as shown by seif dunes that extend below present sea level in northwest Australia, and by records of aeolian dust dated to 18 ka in New South Wales, Victoria and the Tasman Sea.

It therefore seems that the Pleistocene continues a trend towards aridity in Australia, with enlargement of the dunefield on several occasions within the Pleistocene and the loss of the large Tertiary lakes. Some species are older than these events and are now relictual. The best-known examples are the oasis species such as the palm *Livistona mariae*. The distribution of *Acacia peuce* correlates with noncalcareous soils and this species presumably pre-dates the drying and deflation of the lakes of the Lake Eyre Basin. Many plants in these categories have growth related to summer rainfall regimes. We can thus speculate that the flora of arid Australia is derived partly from immigrants, such as the daisies, salt bush and grasses, and partly by adaptation of seasonal tropical forest (dry scrub) taxa to a regime of long droughts. Families contributing to the arid shrub and tree floras are often also promi-

nent in rainforests, e.g. Pittosporaceae, Rutaceae, Sapindaceae, Sterculiaceae, Bombacaceae, Meliaceae, Cupressaceae, Casuarinaceae, Malvaceae, Papilionaceae and Mimosaceae (Figure 15.7). Many of these species are not cold tolerant, and the southern arid lands instead are dominated by specialised shrub eucalypts with lignotubers, the mallees. This adaptation is also common in cold moist mountain summits, reflecting a common strategy to enhance regeneration and survival in growth-limited areas.

Quaternary plant fossils are uncommon in the semiarid regions of Australia, and pollen is of limited use because the desert plants respond to dry conditions by ceasing to flower and reducing density rather than replacement by other species. In addition ephemerals or drought evaders are important there, and so it is difficult to identify climatic change in the core of the desert. Singh has argued for change in the balances between summer and winter rainfall reaching Lake Frome, with a general retreat of summer flowering grasses during dry or cold times. This is held to reflect a failure of the monsoon and favours perennial shrublands of Asteraceae and Chenopodiaceae that are adapted to winter rainfall and cold conditions (Singh & Luly, 1991). Martin (1973) suggested that on the Nullarbor the coastal zones migrated southwards as sea level fell, causing localities to become more open at 20 ka ago.

More dramatic changes have occurred around the margins of the desert lands. The widespread treelessness of southeastern Australia, which reflects drought and raised saline watertables as well as cold, has already been described. Modern disjunctions, such as isolated stands of arid hummock grasses along the Glenelg River (near Portland, Victoria), white box (*Eucalyptus alba*) and *Callitris glauca* in the Snowy and upper Hunter river valleys, and a patch of mallee in well-watered southern Victoria, suggest that at times the semiarid zone has been very extensive. From the Glenelg River, fossil desert animals have been recovered from cave sediments dating from 30 to 12 ka (Hope, 1983), and seif dunes cross Kangaroo Island in South Australia (Bowler & Wasson, 1984). A retreat of moist forests is also marked



Figure 15.7 Arid zone woodlands are dominated by species derived from rainforest families. *Atalaya hemiglaauca* (Sapindaceae)–*Pittosporum philliraeoides* (Pittosporaceae) woodland, Strezlecki Desert, eastern South Australia.

at the Atherton Tablelands after 35 ka ago, and Kershaw (1986) estimated a drop in precipitation to 30% of present at that time. This requires a shift of vegetation boundaries eastwards of only 30 km at this locality, but much more extensive adjustments to vegetation zones seem to have occurred across the plains of Northern Australia at this time. Cores from Lake Carpentaria suggest only open grassland at 20 ka ago (Torgersen *et al.*, 1988). Marine cores taken by the Snellius expedition from the Timor Sea show an increase in Chenopodiaceae, Asteraceae and a decline in *Eucalyptus* after 40 ka ago until the Holocene (van der Kaars, 1989). This supports the model of vegetation change suggested by Nix & Kalma (1972) for an advance of non-eucalypt arid communities almost to the Arafura shelf, representing migration of about 400 km northwards. At this

time monsoon forests would have been quite restricted, although Arnhem Land obviously acted as a major refuge. We do not yet know what the vegetation response to early glacial conditions may have been, although higher sea levels and lower temperatures may have contributed to rainfall and available moisture.

Periods of heightened aridity and possibly stronger winds have thus been important in stressing Eremaea and may be one of the causes of the patchiness of community growth across the area. Fossil soils and some dating of dunes show repeated episodes of sand dune activity in the past (Wasson, 1986). Development towards withstanding both short- and long-term change is characteristic of evolution in the arid areas.

ARRIVAL OF HUMANS AND VEGETATION CHANGE

It is not excessively anthropocentric to claim that the most significant Cenozoic migration event for the Australian vegetation was the arrival of people more than 40 ka ago. We were preceded here in the Miocene by well-dispersed placental mammals such as whales and bats, in the Pliocene by the murid rodents, and we ran a close race with stegodonts in the late Quaternary, which we probably won by cheating (we ate them). Nevertheless, human activity has caused massive changes to floristics and structure through fire, faunal change and plant introductions. Of course it can be argued that the arrival of the advanced plant families and genera such as grass, daisies, saltbush and possibly *Acacia* were events of greater magnitude, but the significant species are autochthonous species that have evolved following the establishment of aliens. Humans had occupied all available niches by 35 ka ago, including New Guinea, montane Tasmania and the arid zone (Dodson, 1992). The limitations of radiocarbon dating make an assessment of earlier occupation rather hazardous. It seems clear, however, from thermoluminescence and uranium series dates at selected localities, that coastal New Guinea and Australia had scattered occupation by 50 ka ago and some claims for earlier dates have been made.

The effect of occupation on vegetation structure and plant community formation is currently being argued. With the exception of closed non-seasonal rainforests such as those of New Guinea, the Queensland mountains and Tasmania, all Australian vegetation tolerates fire, and some communities are adapted to particular fire regimes. Perhaps early sparse settlement had little effect on the environment, since deliberately lit fires would not have made much difference. However, the change to vegetational structure when Aboriginal firing was changed after European contact is well documented in many localities, such as northwestern Tasmania, the Brigalow scrub and Kakadu. In terms of fossil evidence, some of the best comes from large offshore islands

that were not occupied at the time of European arrival. Clark (1983) examined a 7000 year lagoon record on the eastern end of Kangaroo Island, only 14 km from mainland South Australia. She showed that a significant change in fire regime occurred after 2.6 ka ago when occasional fires yielding large amounts of charcoal and soil erosion started to occur. Prior to this, the fires seemed to have been frequent, but yielded only minor amounts of charcoal and no significant erosion products. Clark proposed that the island was abandoned 2500 years ago for unknown reasons. The result of the 'natural' fire regime was to allow a dense eucalypt forest to occupy all sites. Meanwhile, on the mainland, open savanna woodlands of fire-tolerant box species above grassland had developed, and this difference seems to have been the result of a continuing firing on the mainland. Traditional Aboriginal groups of central and northern Australia are quite clear that management of land involves careful burning, and the staggering area of hummock grass in central areas may be the result of mosaic burning. In Kakadu, the difference between hot wildfires, which tend to occur at the end of the dry season in November, and human-lit patch fires, which burn the tall moist grass at the start of the dry season in May, is acknowledged (e.g. Gill *et al.*, 1981). In subtropical climates in Fiji and New Caledonia equivalent to coastal Queensland, people arrived later, at about 3 ka ago, and caused a dramatic shift from closed forest to open savanna (G. S. Hope, unpublished data). The seasonally dry subtropics have enough moisture to allow trees to flourish, but the dry season also provides a period of vulnerability to fire. Clearly the balance throughout most of Australia is in favour of open vegetation, reflecting a high frequency fire regime; how far this is a human artefact is debatable.

At the time of human arrival, Australia supported large browsing and grazing animals in the now extinct families Diprotodontidae, Palorchestidae and the subfamily Sthenuridae. Kangaroos larger than any presently known in the genera *Macropus* and *Protemnodon* were also present. The niches occupied by these animals were in general

the open communities from central Australia to the alpine steppes of Tasmania, although some species occupied forests in New Guinea. The causes of the almost complete loss of the large browsing niche are also debated, but the timing of the extinctions appears to be drawn out from perhaps 50 to 30 ka ago for the largest species, and continuing to the end of the Pleistocene for the smaller. Although the process by which extinction took place is unknown, the effects on the vegetation would have been dramatic (Flannery, 1990). Large open areas in the semiarid and subalpine regions may have been controlled by grazing, as the African tropical plains are supposed to be today. The chief effect is to reduce tree and shrub growth to a few lucky survivors, widely separated by grasslands. Although Flannery has argued that Australia has always been depauperate in vertebrate faunas due to intrinsic habitat poverty, this is contradicted by the dramatic success of introduced grazers and browsers, such as goats, horses and camels, that have invaded the Australian deserts and subalpine woodlands. The rapid evolution of mammals and birds from the Pliocene onwards also argues for significant opportunities for specialisation in these niches. The loss of the animals may have encouraged more perennial shrubs and trees to survive and compete for water, with the reduction in ephemerals and shallow-rooted plants. This trend might have encouraged fire and the growth of fire-tolerant or evading groups such as the mallee eucalypts at the expense of taxa such as *Callitris*. Our impressions of the semiarid shrublands of *Acacia*-rich formations as natural may therefore have to be amended because other potential dominants have been forced out by insufficient competitive ability or fire tolerance. The spread of woody weeds in western New South Wales after overgrazing of palatable shrubs by sheep provides another possibility in that our precontact semiarid vegetation may be relatively palatable. The abrupt shift in saltbush dominance from palatable to noxious species in the semiarid and from species-rich herbfields towards coarse tussock in subalpine areas occurred very quickly following stock (and rabbit) introduction. These changes indicate how

sensitive the vegetation is to increases in grazing pressures.

THE ADAPTATIONS OF THE QUATERNARY

Unravelling the skein

The problem of assessing the responses of vegetation to climatic change, humans, fire and faunal loss is that they are all compounded. The vegetation histories that cover the last 40 ka demonstrate the frequent presence of fire. At Lake George this increases markedly in the Holocene to levels not apparent in the previous records. At Lynch's Crater on the Atherton Tableland of North Queensland, on the other hand, burning was apparent after 38 ka ago, but diminished in the Holocene as wet vegetation reinvaded the area. Bass Strait shows abundant evidence for fire in a grassy steppe 25 ka ago (Hope, 1978), but a similar vegetation on the Central Plateau of Tasmania in the Holocene does not seem to undergo burning, although a grassy cover is maintained (Thomas & Hope, 1994). Some fires are evident over the several glacial/interglacial cycles recorded at Darwin Crater, and there is no marked increase in the last 50 ka (Colhoun, 1988). This matches a preliminary analysis of a deep-sea core from the Tasman Sea that shows only a minor increase in carbonised particles over the past 150 ka (G. S. Hope, unpublished; see p. 389).

The obvious solution to discriminating the effects of human arrival from climatic change is to compare the Holocene with the last interglacial, 129 ka ago, and the penultimate glacial maximum, at around 135 ka ago, with the well-understood changes of 25 to 12 ka ago. Sea level records, and the occurrence of corals as far south as Newcastle, hint that the peak of the last interglacial was slightly warmer than at any time in the Holocene (Roy & Thom, 1981). However, there are few useful last interglacial records. On the Atherton Tablelands, and at Darwin Crater, vegetation cover seems fairly equivalent to that of the Holocene. Some gymnosperm species that subsequently became extinct were present at Ather-

ton (Dodson, 1992). Both these sites are wet forests that seem to have been unaffected by humans in the Holocene. The grassland-woodland sites of Lake George and Lake Wangoom show a similar pattern, but there are some distinctions between the interglacials (Kershaw *et al.*, 1990). At Lake George the supposed last interglacial is marked by declines in Casuarinaceae and an increase in *Eucalyptus* and grass, as well as the appearance of carbonised particles (fine charcoal from fires). By the present interglacial, one type of Casuarinaceae appears to be extinct and carbonised particles reach historical high levels. Singh & Geissler (1985) have suggested that these changes were caused by an increase in fire consistent with human occupation. However, there are significant peaks of carbonised particles further back in the Lake George record, but the sequence is not well dated and seems to contain significant gaps. Wright (1986) has pointed out that the pollen and charcoal do not yet provide good evidence for very early occupation and no direct occupation traces have been located. Lake Wangoom does not change greatly in vegetation structure between interglacials, but Edney *et al.* (1990) have pointed out that Asteraceae become less important and Poaceae more so, which may be consistent with an increase in fire frequencies.

Clearly many more interglacial records must be found and interrogated before we can assess our own period with any confidence. Although the data are still contradictory, there is the possibility that sclerophyllous forests are now more fire adapted and dominated by eucalypts than was previously the case. This is a possible explanation for the manifest rapid differentiation occurring in *Eucalyptus* at the present time. But it is still impossible to say that this commenced with the advent of humans, and for some communities it has probably been developing over the last million years, as climates have dried, soil mulches been destroyed and nutrients flushed away.

Similarly it is difficult to assess whether plant extinction has been more marked during the last glacial cycle than occurred previously. Kershaw (1984) has reviewed plant extinctions and range

retreats and noted some clear losses such as *Dacrydium*, large-grain Casuarinaceae, a small spine alpine Asteraceae, and possible shrub steppe Chenopodiaceae in Tasmania. Range retreats, such as *Phyllocladus* being lost from Victoria (Churchill & Dodson, 1980), *Cordyline* from the Atherton Tableland (Kershaw, 1985) and *Nothofagus* from southern New South Wales (Kershaw *et al.*, 1986), also occur with the onset of the last glacial peak about 30 ka ago, or in the rapid warming approaching the start of the Holocene. These are palynologically obvious taxa, and the vast majority of extinctions probably will never be known. Extinctions do appear to be marked in the last glacial compared to earlier times, but this conclusion may be shown to be incorrect when we learn more about the past. It is certain that many rainforest communities had all but disappeared by the time the late Quaternary record commenced. Lake George, one site that traverses the entire Quaternary, is silent for over one million years due to the fact that the lake sediments have been oxidised and reddened by long periods of soil formation. If seasonal, relatively subtropical, conditions are assumed for periods in the early and mid-Quaternary, this must have been the time when drought first became characteristic (McEwen Mason, 1991; Martin, 1989). Some of these early droughts may have resulted in wide-scale devastation to plant ranges, with consequent extinctions. This possibility is speculative so far.

The last glacial maximum

In Australia, the Holocene/Pleistocene boundary is generally very clearly marked. Most upland sites do not extend back beyond 11 ka, due to gravels or soils underlying swamp and lake sediments. In fact the last glacial, 26 to *ca* 12.5 ka, stands out as the most extreme time visible in the palynological and limnological record (De Deckker, 1986). This is surprising, given that the episode is not particularly distinctive in the deep-sea cores, compared to previous periods of ice lock-up. Colhoun (1991) believed that ice extent in Tasmania around 85 ka ago (and also in earlier glaciations) probably exceeded that of the last glacial

maximum. Contrasting to this is the fact that the fossil lakes of western New South Wales are mostly less than 120 ka old and appear to be a new landscape response to river and groundwater changes (Bowler, 1980). Taken together, the vegetational response seems to reflect colder but drier times than ever before experienced. This may indicate a relatively recent expansion of the range of the Poaceae and Asteraceae flora that today characterises the dry uplands of southeastern Australia. Similarly, the peak of the last glacial may represent the first time that montane rainforest has become so disjunct and also may mark the retreat of monsoon jungle and the deciduous scrubs of Northern Australia to restricted refuges (Russell-Smith *et al.*, 1992).

Directions in Quaternary evolution

It is apparent that the question of how the Quaternary vegetation developed has a multiplicity of answers, depending on the history of the site and its access to preadapted biota. Judged by the floras of the present day, the six biogeographical provinces all experienced some degree of increased change. Tumbuna, Papua and southwestern Australia were probably the least stressed provinces and their overall diversity probably continued to increase throughout the Quaternary. Not only would extinction rates have been low in these provinces, but, as Walker (1982) has pointed out for the north and Hopper (1979) for the southwest, mild climatic changes caused opportunities for both migration and allopatric speciation due to isolation. A powerful impetus for local speciation is the gentle change to local habitat, which provides sites for natural experiments in migration and variation in populations. Thus, Hopper explained the very high diversity of the central zone of southwestern Australian heaths by considering that this zone has fluctuated sufficiently to encourage speciation. The driest and wettest areas would also vary, but not sufficiently to isolate populations and encourage novelty. In New Guinea, continuing dramatic landscape change and alternations in temperature seem to have led

to rapid local speciation in at least some genera and families (Walker & Hope, 1982).

Some vegetation types in Torresia have been greatly stressed, while others have been fairly stable. The evidence for open woodland and retreat of wet forests on the Atherton Tableland demonstrates that massive migrations have occurred. The disjunctions in the range of depauperate evergreen rainforests, including the dry types, indicates that little speciation has occurred under the late Quaternary regime. But some dry forests and coastal scrubs display some local endemism. These communities have managed to recolonise burnt and dry niches very successfully, although they are now impeded by the arrival of placental grazers. Some communities, e.g. Brigalow and *Callitris intratropica*, are disjunct at present, but able to dominate large areas, and presumably are well adapted to the stresses of aridity. The absence of many physical or thermal barriers in this province means that the main stress has been changing aridity. This stress is usually modified by local conditions so that refugia persist on sites with permanent groundwater.

Eremaea and Bassiana have been influenced by cold as well as aridity, and some areas so altered that complete changes of plant formation have been effected. These regions generally experienced levels of stress that exceeded the modest change that can be a cause of increased diversity. Presumably extinction rates have exceeded speciation rates in these cases. The diverse pattern of microendemism along the eastern scarp of the continent is an exception to this, and may be evidence for a gradient in stability from the moist slopes to the open cold dry steppes of the tablelands. In the southeastern mountains above 500 m altitude, the complex alternations of cold moist, cold dry and warm moist (but drought prone) conditions would have prevented almost any vegetation community from enjoying a long tenure on a given site. Plants in this zone show considerable plasticity and it is possible that in many cases species have been capable of contributing to several vegetation formations that thus varied in structure and dominance even though retaining a

range of species in common. Hope & Kirkpatrick (1989) have suggested that snowgum (*E. pauciflora*) woodlands and subalpine grasslands are examples of this.

Australia does not seem to have been stressed to the point of massive extinction in the Quaternary in the way that the Arctic or Boreal regions have, with consequent simple communities of generalists. Australian ecosystems perhaps retain or exceed the levels of community diversity developed in the Tertiary, despite the new climates and instability.

The Holocene

The last 10 ka seems curiously undramatic and familiar. Alpine studies in New Guinea, Mt Kosciusko and Tasmania (Macphail, 1979; Hope, 1986; Kershaw *et al.*, 1986; Markgraf *et al.*, 1986; Kershaw & Strickland, 1990) indicate warming conditions and invasion of the alpine tundra by herbfields after 13–14 ka ago, and temperatures equivalent to those of the present occur by 9.5 ka ago. The delay in the arrival of sea levels to about their present position for another 2500 years influences coastal rainfall in some sites, such as the Nullarbor. Adjustment by vegetation to interglacial climates takes varying amounts of time. As argued for Kangaroo Island earlier, in some cases the adjustment has been hindered by fire. However, in western Tasmania the paradox exists that the amelioration of the climate led to the exclusion of humans from large areas, as closed forests and scrubs invaded former open alpine communities (Cosgrove *et al.*, 1990). The same process may have occurred in New Guinea as well (Hope, 1986). For burnable areas, the expansion of forest has been hindered or even halted, and it is in a state of dynamic equilibrium or even gradual adjustment. For example, an area such as the Monaro is capable of supporting eucalypt open forest, and in fact does so on favourable sites. But thin soils and the effects of cold, drought and fires has resulted in widespread grasslands with miserable tortured specimens of *Eucalyptus rubida* and *E. pauciflora* scattered about, perhaps the van-

guard of an advancing treeline for which ten millennia have still not provided enough time. Many pollen diagrams from the Holocene establish the continuity of Pleistocene vegetation to the present, such as some of the western Victorian lakes studied by, for example, Dodson (1975, 1979), D'Costa *et al.* (1989), and Edney *et al.* (1990). Singh & Luly (1991) studied Lake Frome, a desert playa lake, and found relatively undramatic changes other than supposed increased densities of desert species, and possible shifts in the balances between grassland and shrubland. These occur through the Holocene, and remind us that the adjustment by the arid vegetation to warmer conditions was probably quite quick, since outlier populations probably survived in the southern deserts throughout the glacial.

The final event of the Quaternary was the arrival of agriculture and direct disturbance of the ground by ploughing and overgrazing. Agriculture (and even commercial forestry) is an attempt to manipulate ecosystems to favour short-lived species for their fruits, leaves or wood. The species selected are usually aggressive colonisers and they came complete with a suite of their competitors, defined as weeds because of their success in the same environment as wanted plants. With the exception of the poorest habitats, weed invasion of Australia has been dramatic, though less so in New Guinea. But the experience of the Quaternary, with its gradually increasing tempo of change, has produced native species that are well adapted to stress, and which survive well in competition with introductions. The grazed rangelands of Australia may in some ways resemble the Pleistocene shrub steppe communities. The current remobilisation of the desert dunefields by feral grazers and browsers seems to demonstrate that pre-extinction Pleistocene steppe could also have been influenced by mammal utilisation. Clearing, firing and grazing of *Eucalyptus* woodlands may tend to recreate types of savanna or shrublands that existed in the past. In that sense the last part of the Holocene has continued to be a major laboratory of evolution of adaptation to disturbance.

CONCLUSIONS

The boundary of the Quaternary is probably not especially dramatic in Australia, where the long-term evolution of the climate towards more arid environments had been proceeding for the previous ten million years, and there was no sudden onset of glaciation. The continent is large enough to cover a wide range of climates, so that habitats were preserved for species capable of migration. The eastern ranges and Tasmanian west coast remained wet and preserved rainforests reasonably intact. The most dramatic event was the expansion of the longitudinal dunefields, indicating a vegetational cover of less than 10% and strong winds, probably about 700 ka ago. Subsequent development of the arid-adapted vegetation perhaps means that cover will not drop as low again. The biota have become adapted to relatively slow but complex cycles of climatic change and to the appearance of short growing seasons in the south.

At least some species have acquired ecological (and probable genetic) plasticity and have the ability to contribute to different kinds of vegetation at various levels of dominance. These strategies have been encouraged by the intrinsic variability of many Australian environments, leading to such characteristic innovations as mallee (lignotuberous) shrubs and trees and hummock grasses. Many of the semiarid and woodland communities have relatively simple floristics, and this may reflect widespread, highly stressed environments in the past. Other communities with a high level of local species are more likely to have survived in intact stands but have probably been isolated for long periods. Where endemic species from isolated taxonomic groups (palaeoendemics) are important, the vegetation will in many cases be relictual and occupy habitats that have had stable cores throughout the Quaternary.

The effect of humans on the environment has been to favour species that have become well adapted to Pleistocene variability by developing the mechanisms of fire tolerance or avoidance and migratory ability. Human disturbance may have favoured *Eucalyptus* over some other taxa in wood-

lands and open forest. The removal of many large grazers and browsers and all large predators may have swung some areas towards shrubland growth and stabilised some landscapes. This interference has now been reversed by the introduction of a complete range of placental species (excepting large carnivores). A fundamental shift in vegetation cover towards ephemeral species and lower cover is currently taking place.

I am grateful to Jon Luly, Bob Hill, Greg Jordan, Bren Weatherstone and Peter Kershaw for their cruel but justified trashing of early drafts of this chapter. I also owe a debt to Jim Bowler, Eric Colhoun, John Dodson, Dave Gillieson, Jamie Kirkpatrick, Brian Lees, Mick MacPhail, Gus van de Geer and Peter White for their various works in the Quaternary. I defy anyone to singlehandedly write the story of the Australian Quaternary and really appreciate all the insights derived from geomorphologists, biologists, ecologists, prehistorians and oceanographers too numerous to mention.

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Note added in proof

Kershaw *et al.* (1993) note a dramatic increase in black material after 160 ka in a core from the continental slope. They suggest that a fundamental shift in burning regime occurred at that time.

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