

BIOGEOGRAPHY OF THE TERRESTRIAL FLORA

*M.D.Crisp*¹, *J.G.West*² & *H.P.Linder*³

Taxonomists usually map distributions of plants in their monographs and flora treatments, and they have always been intrigued by the resulting patterns. This has led them to pose questions such as 'Why do related taxa occur in widely disjunct areas while unrelated taxa share similar, endemic distributions?', and 'What were the geological, climatic and biological causes of such patterns?' Biogeography is the science of analysing and explaining biotic distributions. It is a 'big picture' science because it requires knowledge of taxonomy, evolution, ecology, palaeontology, geography, geology and climate. Or, as Croizat (1962) put it, biogeography is the integration of evolution through space, time and form.

Biogeographers look to the earth and its processes, such as plate tectonics and climate change, as the driving forces behind distributional patterns. Furthermore, many workers have been tempted to 'fit' biotic patterns to geological and climatic hypotheses. For example, the advent of continental drift theory stimulated research in biogeography (Raven & Axelrod, 1974; Axelrod & Raven, 1982; Briggs, 1987; Whitmore, 1987). However, there is no need to give primacy of explanation to earth processes (Ball, 1976). Biogeographic hypotheses can be formulated in the absence of any process explanation and moreover, they should be, to avoid circularity in later using biogeographic patterns to test process hypotheses. Indeed, the evidence of biotic distributions, past and present, strongly influenced geologists to accept the theory of continental drift (Tarling, 1980; White, 1986). This primacy of pattern over process is a general principle of comparative biology (Cracraft, 1989; Humphries, 1988; Eldredge & Cracraft, 1980; Sluys, 1994).

Description, narration and analysis

Ball (1976) suggested that all studies of historical biogeography pass through three phases: descriptive, narrative and analytical. The descriptive phase is the discovery of intriguing biotic distribution patterns as a result of routine taxonomic practice. It includes patterns of individual taxa and compilations of multiple taxa and whole biotas. The latter are expressed as maps of biotic regions which are characterised by high endemism. Such maps have been produced at various scales, e.g. the world (Wallace, 1876; Sclater & Sclater, 1899; Good, 1974; Takhtajan, 1986), regional (Van Steenis, 1963; Van Steenis & Van Balgooy, 1966; Van Balgooy, 1975, 1984, 1993) and national. National maps for Australia have been produced by, among others, Spencer (1896), Burbidge (1960) and Schodde (1989); see Figs 73 & 74.

Narrative biogeography attempts to explain the historical causes of observed distributions by constructing a scenario with a series of unique events that affected a particular taxon. For example, Schodde (1972) hypothesised that the angiosperm family Pittosporaceae originated in the Australian or Indian Ocean region, then migrated outwards to the Pacific, Africa and Asia as it diversified. Few biogeographic studies progress beyond this phase. While these scenarios may be valuable in ordering and collating information about the taxa on which they are based, narrative biogeography lacks predictive power and has little application to development of more general explanations of distribution (Ball, 1976).

The analytical phase of biogeography (Ball, 1976) formulates testable hypotheses. These are general explanations usually involving multiple taxa and so may be corroborated by new evidence from previously uninvestigated organisms or taxa. For example, Lyne (1993) made

¹Division of Botany & Zoology, Australian National University, Canberra, Australian Capital Territory 0200.

²Australian National Herbarium, Centre for Plant Biodiversity Research, CSIRO, GPO Box 1600, Canberra, Australian Capital Territory 2601.

³Bolus Herbarium, University of Cape Town, Rondebosch 7700, South Africa.

Biogeography of the terrestrial flora

a bioclimatic analysis of the rare species *Leptospermum namadgiensis* (Myrtaceae), which is restricted to the Australian Capital Territory/New South Wales border ranges. This analysis predicted new occurrences on mountain peaks not previously explored, and the species was subsequently found there. Analytical methods include the equilibrium theory of island biogeography (McArthur & Wilson, 1967), bioclimatic analysis (Nix, 1982), and cladistic biogeography (Nelson & Platnick, 1981; Humphries & Parenti, 1986). Croizat's panbiogeography (Croizat, 1952, 1958, 1962) falls somewhere between narrative and analytical methods (Ball, 1976; Craw & Weston, 1984).

Rosen (1988) argued that processes hypothesised to explain distributional patterns form a continuum over time and geographic scale. He organised these into three overlapping groups: *maintenance*, representing current or recent processes which maintain the presence of a taxon in a given area, and those processes that exclude it from other areas; *distributional change*, representing changing environments and responses by organisms such as adaptation, dispersal, range-contraction and range-expansion; and *origination*, being long-term evolutionary change such as speciation and extinction, often in relation to major earth events.

Research programs of ecological and historical biogeography may be differentiated in relation to Rosen's classification. Maintenance is concerned with short-term processes operating on a scale of thousands of years and is the sole domain of ecological biogeography. Origination concerns very long time scales of millions of years, and is the sole domain of historical biogeography. Both programs overlap in the middle of the scale (distributional change). For example, analyses of the monsoon tropical flora of northern Australia and New Guinea by Nix & Kalma (1972) and Crisp *et al.* (1995) both made predictive inferences about the causes of the floristic similarity of these areas. However, Nix's method was concerned with climate and belongs to the domain of ecological biogeography, whereas Crisp *et al.* were concerned with cladistic methods from the domain of historical biogeography.

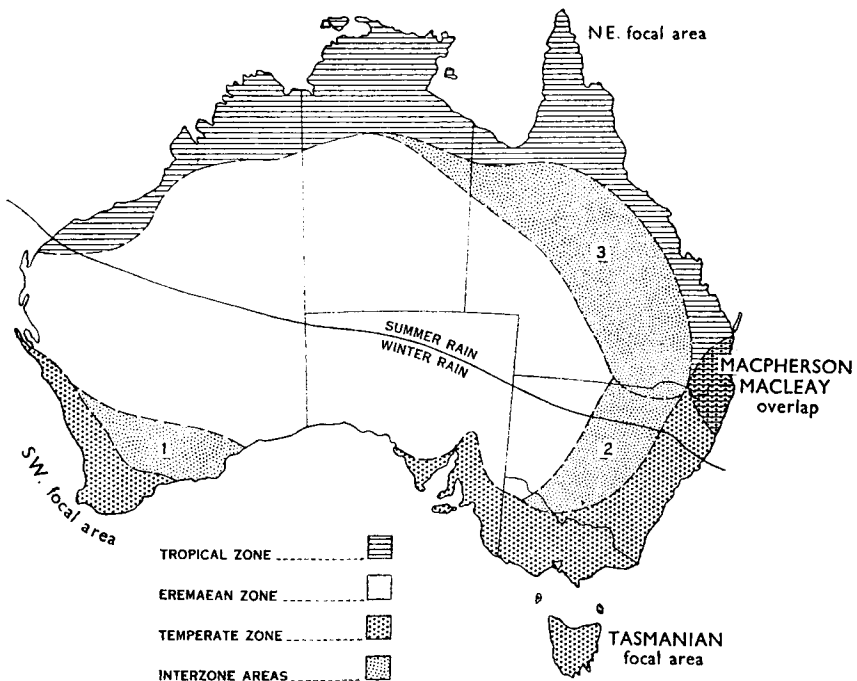


Figure 73. Map of floristic zones (equivalent to biotic regions or elements) in Australia. Reproduced from N.Burbidge, *Austral. J. Bot.* 8: 79 (1960) with permission.

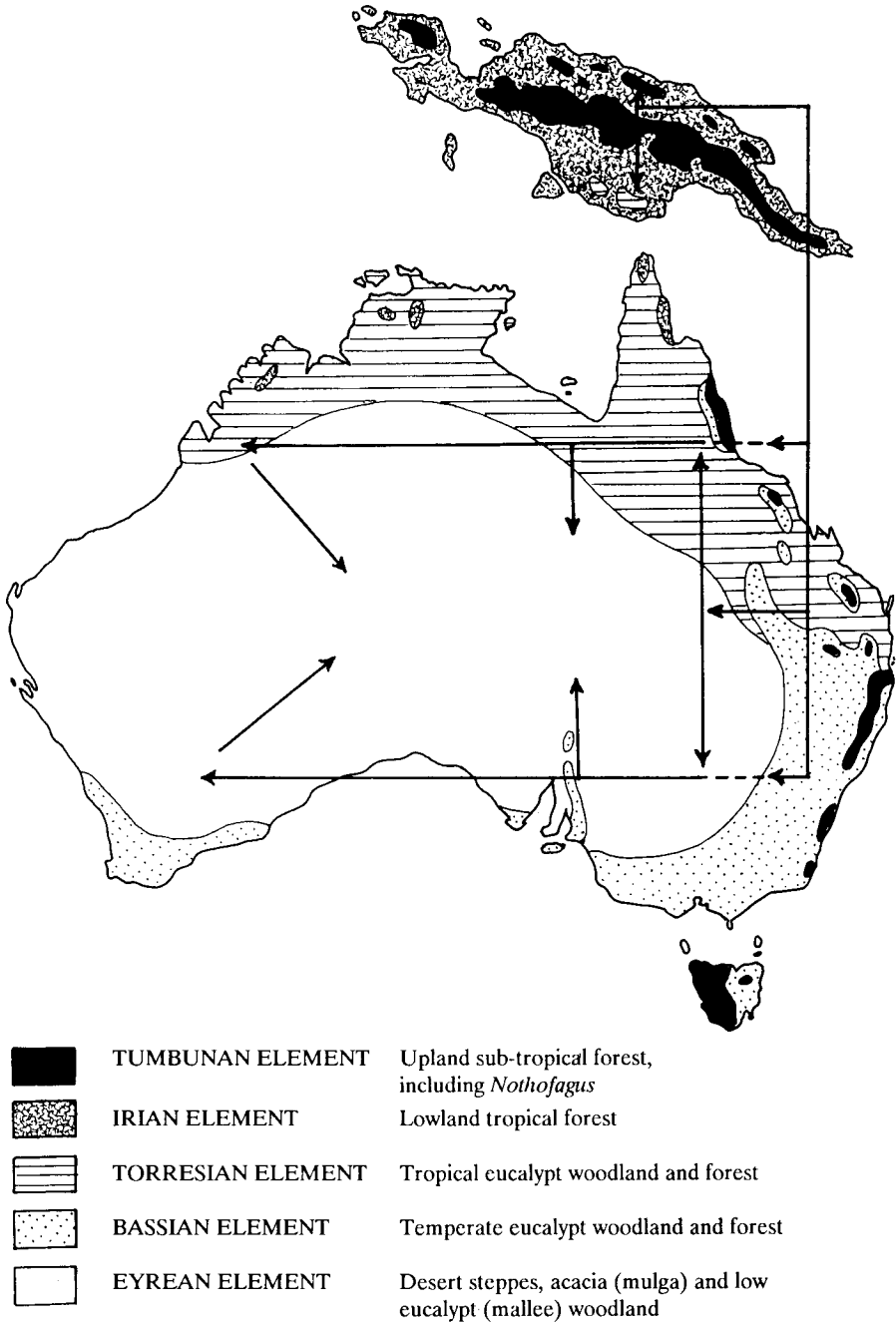


Figure 74. Map of biotic elements in Australia and New Guinea. This map is based on that of Burbidge (Fig. 73), but recognises additionally the Tumbunan and Irian elements. Arrows indicate putative pathways of migration and radiation. Reproduced from R.Schodde, Origins radiations and sifting in the Australasian biota - changing concepts from new data and old, *Austral. Syst. Bot. Soc. Newsletter* 60: 10 (1989) with permission.

Furthermore, different elements of the same biota may have different histories which are the outcomes of different processes. Thus, a *Livistona* fan palm which is endemic to a central Australian gorge might be growing next to a cosmopolitan *Phragmites* reed. The nearest relative of the fan palm may be a species occurring in distant gorges of the Great Dividing Range in eastern Queensland. These two species of *Livistona* may be descended from a common ancestor dating back to the Miocene, when perennial rivers and freshwater lakes made a continuous link from central Australia to eastern Queensland. The ancestor may have spread widely across this river system, rather as the more hardy river red gum does today over these same but now intermittent watercourses. As aridity set in through the Pliocene, the rivers and lakes dried up, and the distribution of the ancestral fan palm shrank to refuges along perennial billabongs in the central Australian ranges and the Great Dividing Range. With a vast distance separating them, these now vicariant populations could have evolved into distinct species. This history of ancient speciation by vicariance (splitting of an ancestral range) can be reconstructed today by overlaying a phylogeny of *Livistona* on a map of the distributions of the species. If other taxa endemic in the same areas, such as *Macrozamia* cycads, show the same phylogenetic relationship between areas, then the hypothesis of vicariance is corroborated.

On the other hand, the *Phragmites* is a single species spread widely in wetlands throughout Australia and beyond, even as far away as Africa. Unsuitable desert habitats and even oceans seem to provide no barrier to the dispersal of its seeds, which are easily blown on the wind. This may be a 'young' species that has spread quickly around the world. Thus vicariance may not affect it, and its distribution would be best explained by climatic or ecological modelling, assuming that its dispersal has not been historically limited. Further research is needed before we understand the limits of applicability of ecological and phylogenetic methods, especially for events of intermediate age, e.g. Pleistocene.

Hereafter this chapter is concerned primarily with historical biogeography, that is ancient patterns of the kind shown by *Livistona*. Australian ecological biogeography is discussed further in the present volume by Groves (*q.v.*).

History of biogeographic studies on the Australian flora

J.D. Hooker and his legacy

Study of the phytogeography of the Southern Hemisphere, including Australia, effectively began with Joseph Hooker (Brundin, 1966). His was the earliest attempt at a consolidated description of the composition and affinities of the Australian flora. Hooker visited Australia, New Zealand, Patagonia and various sub-Antarctic islands during 1839–1843 as Assistant Surgeon with James Clark Ross' *Erebus* and *Terror* expedition. During and shortly after this voyage, Hooker was struck by the close affinities, especially at generic level, between the southern lands, despite their separation by vast tracts of ocean. He came to the conclusion that he had discovered a circumpolar Antarctic flora, and that the present-day floras had evolved, at least in part, by the development of physical and climatic barriers between formerly contiguous areas (letter to Darwin of 1 September 1845, cited in Anonymous, 1997). In *Flora Novae-Zelandiae* (Hooker, 1853) he stated:

'Enough is here given to show that many of the peculiarities of each of the three great areas of land in the southern latitudes are representative ones, effecting a botanical relationship as strong as that which prevails throughout the lands within the Arctic and Northern Temperate zones, and which is not to be accounted for by any theory of transport or variation, but which is agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic causes.' (see also quotes cited by Brundin, 1966).

Hooker was proposing vicariance as a mechanism for the differentiation of a widespread ancestral flora. This idea lapsed and was not revived until the next century (Herbert, 1935, 1950; Croizat, 1952, 1958), and only became generally accepted even later (Nelson & Rosen,

1981). Darwin did not accept Hooker's views on this, and in *Origin of Species* (Darwin, 1859), following the ideas espoused by Lyell (1837), invoked long distance dispersal as the mechanism for generation of similarities in Southern Hemisphere floras:

'...I am inclined to look in the southern, as in the northern hemisphere, to a former and warmer period, before the commencement of the Glacial period, when the antarctic lands, now covered with ice, supported a highly peculiar and isolated flora. I suspect that before this flora was exterminated by the Glacial epoch, a few forms were widely dispersed to various points of the southern hemisphere by occasional means of transport, and by the aid, as halting places, of existing and now sunken islands, and perhaps at the commencement of the Glacial period by icebergs. By these means, as I believe, the southern shores of America, Australia, New Zealand have become slightly tinted by the same peculiar forms of vegetable life.'

Hooker (1860: xvi) was skeptical of Darwin's hypothesis:

'...the general distribution of species cannot be wholly accounted for by the supposition that natural causes have dispersed them over such existing obstacles as seas, deserts, and mountain chains...'

However, Hooker was equivocal about the processes underlying the differentiation and dispersal of floras around the globe. There was no contemporary theory such as plate tectonics to support his embryonic notion of vicariance as an explanation for distant affinities between floras. He speculated about climatic change and movements of land-masses, both horizontally and vertically, as mechanisms driving migration, extinction and differentiation of floras.

Nevertheless, on his main point Hooker was consistent (Hooker, 1853, 1860, 1867: 25–26). Observing that trans-oceanic affinity among floras was a global phenomenon, he hypothesised that this pattern was an ancient one, and was the historical relic of a widespread, ancient flora that had evolved under different climates and configurations of land masses than prevail in the present. His primary interest, then, lay in understanding the evident pattern, and not in a fruitless search for unobservable past causes.

Hooker's (1860) major treatise on Australian biogeography in *Flora Tasmaniae* appears to have been misunderstood or misrepresented by some later authors. After careful analysis of the familial and generic makeup of the Australian flora, and comparison with that of other areas, he identified several 'elements' that he named according to their affinities: Indian, Australian, New Zealand and Polynesian, Antarctic, South African and European.

Later authors emphasised only three of these:

- (1) an 'autochthonous' (= Hooker's 'Australian') group of mainly endemic taxa with distinct scleromorphic features and occupying temperate open communities,
- (2) an 'Indo-Malayan' (= Hooker's 'Indian') element dominated by plants in tropical and subtropical rainforest and monsoonal habitats, and
- (3) an 'Antarctic' element dominated by temperate rainforest taxa such as *Nothofagus*,

and attributed to Hooker the hypothesis that they migrated to Australia from elsewhere.

Barlow (1981) terms this the 'invasion theory', and provides an excellent review of its history. It was based on the assumption that the angiosperms did not evolve in Australia, but invaded the continent in three waves via various postulated 'land-bridges' (Van Steenis, 1962) from neighbouring regions that today support similar stocks of angiosperms. The first wave, via landbridges from the north, established the autochthonous group, which spread with little competition to occupy an empty continent and then diversified *in situ*. The second wave, from the south, contributed the Antarctic element, and later a third wave from the north contributed the Indo-Malayan element. The second and third waves, encountering already-adapted taxa, spread much more slowly and were only able to colonise those regions for which they were already pre-adapted. Hence, the Indo-Malayan flora remained confined to the tropical mesic and monsoon habitats of the north and east and the Antarctic element to the cool temperate and alpine regions of south-eastern Australia. For most of the next

century, the invasion theory, with variations, formed the basis for discussions of Australian biogeography.

However, Hooker (1860) himself was very careful to avoid any suggestion of an invasion theory:

'In discussing the Antarctic vegetation of Australia, I shall have to adopt a style that appears to indicate that this flora is an immigrant, whereas it may, to a considerable extent, both in Australia and elsewhere, consist of altered forms of the plants of that continent, which have migrated from it to the Antarctic region.' (p. xxxix)

and

'According to the hitherto prevailing theory of the distribution of plants, this presence of so many Indian species in tropical Australia would be accounted for by trans-oceanic migration, but this theory offers no explanation of the total absence of Australian species and typical genera in the tropical parts of India' (p. 1).

Throughout the essay, he states repeatedly that insofar as migration of flora may have occurred, he cannot identify the source or direction. In other words, he identified and named his elements only according to their affinities. He seems to have used the word 'migration' as a metaphor for affinity, not intending it to be taken literally.

Tate (1888) used Hooker's floristic elements in an analysis of the arid zone flora. Spencer (1896) used faunal groupings to divide Australia into three subregions, Torresian, Bassian and Eyrean, which have been accepted by most subsequent authors, with variations, for both flora and fauna. He recognised linkages of the Torresian subregion with northern Papuan biota, and linkages of the Bassian subregion with an Antarctic land.

Barlow (1981) discussed the views of others, such as Andrews (1916), Schwarz (1928) and Crocker & Wood (1947) who built on Hooker's ideas. Diels (1906), who concentrated his botanical forays in the south-west of Western Australia, hypothesised that this region was the centre of origin of the Australian (autochthonous) element of the flora. The high diversity of the south-western flora probably misled Diels as well as some other workers in their biogeographic interpretations. Hooker had speculated upon, but dismissed this possibility, again refusing to identify a centre of origin or direction of migration.

The invasion hypothesis reached its most detailed development in Burbidge's (1960) floristic analysis of the vegetation of Australia. She concluded that there were distinct elements in the flora, recognising three main phytogeographic zones: Tropical, Temperate and Eremaean (Fig. 73). These equated well with Spencer's (1896) faunal regions (respectively Torresian, Bassian and Eyrean). Burbidge also identified three smaller 'focal areas' (exhibiting high endemism or diversity), in northern Queensland, south-western Australia and Tasmania, as well as the 'McPherson-Macleay overlap', whose high regional diversity was attributed to an overlap between the Tropical and Temperate zones. Although Burbidge espoused the idea that the present Australian flora was the result of evolutionary processes acting on immigrant floras, she also suggested that the autochthonous element might have been derived from some early Cretaceous element, echoing Hooker's original hypothesis. Karyological work by Smith-White (1954, 1959, and other papers, summarised in Barlow 1981) was seen to support this theory.

Perhaps Burbidge's most original contribution was to suggest that the arid-zone flora (especially those genera with warm-temperate links to the Northern Hemisphere) radiated from ancestors with cosmopolitan distributions on Cretaceous coastlines. These include endemic genera and species groups in the Aizoaceae *s. lat.*, Amaranthaceae, Asteraceae, Brassicaceae, Chenopodiaceae, and possibly others such as Convolvulaceae, Frankeniaceae and Portulacaceae. Burbidge considered that their habitat on coastal dunes and saline tidal flats pre-adapted them to the arid climate which set in during the Pleistocene (actually earlier, during the Pliocene). This suggestion has been adopted by subsequent authors such as Schodde (1989, see below).

Two major schools developed to explain the arrival of the different elements in the Australian flora, the so-called 'land-bridge theories' (Burbidge, 1960; Van Steenis, 1962 and

references therein; Takhtajan, 1969) and the 'long-distance dispersal theories', originating with Darwin (1855, 1859) and furthered by, among others, Darlington (1965). Both of these schools had in common the twin ideas that the present exposed land areas were more or less fixed, apart from fluctuations of sea level, rise and erosion of island chains, and minor accretion and erosion of continental margins (although Darlington touched on the possibility of continental drift), and that the centre of origin of the Australian flora was outside the continent. They differed in the mechanisms proposed for migration of the flora, or its precursors, into Australia.

A third view was espoused by Herbert (1932, 1935, 1950, 1960, 1964, 1967). As Hooker (1860) had done before him, he believed that the Australian flora was derived from an ancient palaeotropical flora, which had existed on the continent since at least the early Mesozoic. He thought that the 'immigrant' elements hypothesised by other biogeographers such as Burbidge, were nothing more than the result of ecological and climatic sorting of an ancestral flora. He rejected migration via landbridges, pointing out they themselves would provide a sifting effect on communities.

Continental drift: a new paradigm

In 1915 Wegener presented his theory of continental drift, in which the continents were not fixed in place, but moved over time, splitting and uniting (Wegener, 1915). While geomorphologists were slow to accept Wegener's theory, mainly because a motive force for the continents was lacking, some biologists seized upon it as an explanation for observed biological distribution patterns. The idea that whole floras and faunas could be rafted about the surface of the globe on continent-size land masses, with all that that implied in terms of maintaining ecosystems more or less intact, of moving a range of habitats across climatic zones, and of moving organisms with little inherent vagility across vast distances over time, provided new possibilities for explaining biogeographic patterns. Several influential plant geographers, including Cain (1944) and Good (1947), clearly favoured continental drift as the major mechanism for movement of plants and floras, as opposed to long distance dispersal, although even as late as the mid-1960s there was no clear geophysical mechanism to explain the continental movement (Good, 1964). However, with geophysical research of the 1970s and 1980s revealing discoveries of mid-ocean ridges, sea-floor spreading and palaeomagnetism, geomorphology provided confirmation of Wegener's broad principles, and geomorphology and biogeography began to develop a strong feed-back loop, each supporting the other (Raven & Axelrod, 1974; Thorne, 1978; Coleman, 1980; Tarling, 1980; Beadle, 1981; Cocks, 1981; Whitmore, 1981; Axelrod & Raven, 1982; Raven, 1983; Briggs, 1987).

Here, then, was a paradigm shift (Cranston & Naumann, 1993). Under the old paradigm, the aim of biogeographic research was to identify the overseas centres of angiosperm origins and to trace the dispersal routes by which Australia received its stocks. This long-standing approach to biogeography attempts to explain the distribution of each taxon individually. It usually involves assuming a centre of origin from which some of the taxon's species either migrated or were displaced outwards. Criteria used to identify a centre of origin include a search for the most 'primitive' (hence oldest) living representatives, oldest fossils, and maximum diversity. An example here is the case of *Nothofagus* (Truswell *et al.*, 1987; Hill, 1994a, 1996). Conversely, Darlington (1957, 1965) considered that the more advanced members of a taxon occupy the centre of origin, because being competitively superior, they force the primitive, less competitive members outwards or to extinction. Other authors (Hennig, 1966; Nelson & Platnick, 1984; Brundin, 1988) proposed the 'progression rule', whereby speciation, and the evolution of novel features, occur only following dispersal out of the centre of origin. This would give the opposite pattern from that of Darlington. Authors proposing dispersal of a taxon consider modes of transport (whether active or passive), barriers against dispersal such as oceans, mountains or any unsuitable habitat, and ecological limitations on establishment in the new, distant habitat, which may be already occupied by functionally similar organisms (e.g. Darwin, 1855).

Reconstructing the history of an individual taxon in this way usually means proposing *ad hoc* hypotheses that cannot be corroborated, very often involving highly unlikely events with inestimable probability, such as a chance dispersal across an ocean. Such a hypothesis cannot be corroborated because unique past events cannot be observed directly, and because it makes no testable predictions.

The new paradigm involved evidence derived from palaeoclimatic and palaeontological studies and required a major change in thinking (Schodde, 1989):

'Whatever biotic elements Australia received before its break from Antarctica in the early Tertiary it inherited from Gondwana. If angiosperms did come into the region from the north in the Cretaceous, they came to Gondwana, perhaps even the Australian-sector of Gondwana; but not to Australia as such.'

Thus with the acceptance of plate tectonic theory, it has been realised generally that it may not be productive to search for a point of origin of the angiosperm flora, and its migration paths. Although Raven & Axelrod (1974) still postulated an area of origin (in their case, 'Western Gondwana', which equates to Africa and South America), with subsequent migrations or transportations to their present distributions, this approach was rapidly becoming outdated. Instead, the evolution of the flora was interpreted as the gradual specialisation of a once more generally distributed biota (Barlow, 1981; Thorne, 1986; Webb *et al.*, 1986; Schodde, 1989). The existence of migration, or long-distance dispersal, is not necessarily discounted, but it no longer forms the generally accepted model for the origin of the majority of the Australian flora.

A diversification of approaches

From the late 1970s there has been an upsurge of interest in biogeographic studies of Australian biota, partly stimulated by the new theories of continental drift and cladistic biogeography, but also as a result of the establishment of the Australian Biological Resources Study, and consequent increase in taxonomic research.

Cladistic biogeography

Cladistic biogeography combines the power of cladistics to generate hypotheses about phylogeny and hence speciation with the notion that, if there is a congruent area pattern among many taxa, then one may postulate a single cause (Rosen, 1978; Nelson & Platnick, 1981; Page 1993b, 1994a, 1994b). Its development was heavily influenced by Croizat's notion of vicariance. Recognising that many related taxa were widely separated in different areas of endemism, Croizat (1952, 1958, 1962) had drawn lines on maps connecting such areas; these he called tracks. Where several tracks coincided he drew general tracks (Fig. 75), which he said represented vicariance events, that is historical splits between previously contiguous areas, causing isolation and speciation in their biotas. On a global scale, many general tracks cross oceans, and these have been interpreted as the legacy of splitting continents caused by plate tectonics (Rosen, 1978; Humphries & Parenti, 1986; Briggs, 1987). However, the primary purpose of general tracks is to indicate relationships between areas; they are not explanations in themselves.

Moreover, congruent patterns may have any common cause, such as concerted dispersal, and not necessarily vicariance. The exact cause does not matter as much as the question of whether there *is* congruent pattern. An hypothesis of congruence is testable and corroborable. If no general pattern emerges, then no general causes can be postulated.

Croizat's ideas strongly influenced the development of two disciplines: cladistic biogeography and panbiogeography (Croizat, 1958; Croizat *et al.*, 1974). Panbiogeography developed mainly in New Zealand, where its proponents attempted to develop quantitative methods for deriving general tracks from many partially coincident individual tracks (Craw & Weston, 1984; Page, 1987; Craw, 1989a, 1989b; Heads, 1989; Michaux, 1989; Grehan,

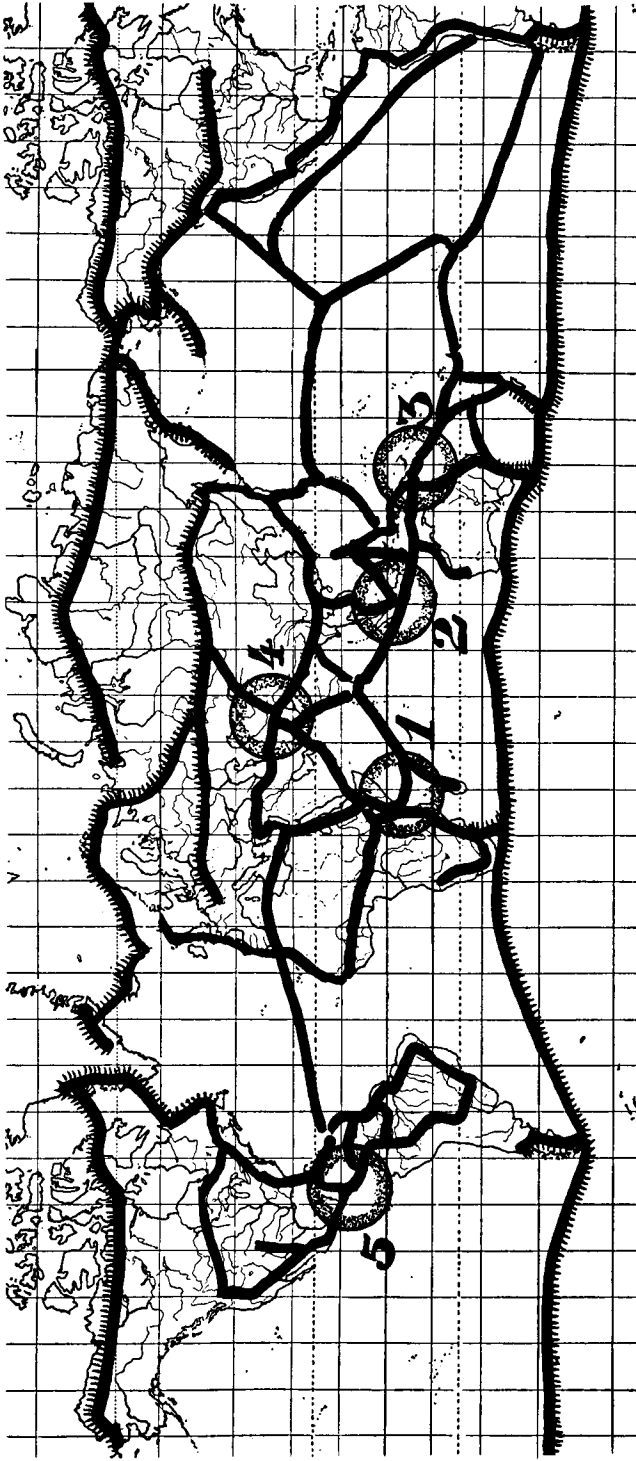


Figure 75. Leon Croizat's (1958) main *general tracks* of the world. These trace lines of affinity in the distributions of plant and animal taxa on an intercontinental scale. Each general track represents congruence of many tracks of individual taxa. The hatched tracks are those considered *boreal* (Arctic) and *austral* (Antarctic). The numbered circles are *nodes*, or crossing points of multiple general tracks.

1990; Michaux, 1994). This research program has been criticised (Seberg, 1986; Platnick & Nelson, 1988; Humphries & Seberg, 1989; Mayden, 1991) and largely abandoned in favour of cladistic biogeography, which explicitly addresses history by using phylogenies.

Several cladistic methods have been used, reviewed by Morrone & Crisci (1995). A more recently developed method using paralogy-free subtrees (Nelson & Ladiges, 1996) extracts only the biogeographically relevant information from input cladograms, and at the same time eliminates most sources of error. It also has the considerable advantage of simplicity in concept and application.

There has been rapid growth in the use of DNA sequences to reconstruct phylogenies and these data are becoming a powerful tool in cladistic biogeography. While the sequence of branch-points in an area-cladogram shows the relative age of speciation events, independent information is needed to date these absolutely. The fossil record is one such source, and knowledge of this in Australia has progressed enormously in recent years (Hill 1994b; Hill *et al.*, this volume). However, given the gaps and uncertainties, such data will always be very approximate (Easteal *et al.*, 1995). The 'molecular clock' (rate of evolution as measured along the branches of a molecular phylogeny) has great potential as an alternative to fossils in dating ages of taxa (Parks & Wendel, 1990; Easteal, 1991; Harrison, 1991; Wendel & Albert, 1992; Thorpe *et al.*, 1994; Harvey *et al.*, 1995; Juan *et al.*, 1995). A confounding problem is that the molecular clock does not tick at a uniform rate – it varies both among taxa and between parts of the genome (Li & Tanimura, 1987; Penny *et al.*, 1987; Barinaga, 1992). Thus, to estimate age by a molecular clock it is necessary to understand the constraints of molecular and genome evolution, and there is a statistical problem: how to estimate the probability of being accurate (Albert *et al.*, 1994; Easteal *et al.*, 1995; Steel *et al.*, 1996). Biogeographic congruence in itself can be used to calibrate the molecular clock, because if many taxa are shown by cladistic biogeography to have speciated at the same time in response to the same causal event, then a molecular phylogeny of each taxon gives an independent estimate of the date of that event (Martin & Dowd, 1988; Page, 1990; Martin & Dowd, 1991). Moreover, the molecular clock has the potential to distinguish between vicariance, which causes simultaneous speciation in many taxa, and concerted dispersal, in which speciation events should not be contemporaneous (Page, 1990; Linder & Crisp, 1995).

Symposia

During the last 20 years, major symposia and multi-authored books have brought together the common threads in floral and faunal biogeography of Australia. These vary in geographic focus from regions within Australia to the whole Southern Hemisphere, e.g. the arid zone (Barker & Greenslade, 1981), Australia and New Guinea (Keast, 1981), the alpine region (Barlow 1986), the wet tropics (Kitching, 1988), the Southern Hemisphere (Ladiges & Humphries, 1991; Hill, 1993), the monsoon tropics (papers in *Aust. Syst. Bot.* 9(2), 1996) and the Pacific (Keast & Miller, 1996). A diversity of approaches is seen in these and other recent literature.

Descriptive and narrative studies

Concurrently with the development of an analytical approach to biogeography based on the theories of cladistic analysis and plate tectonics, descriptive and narrative studies on Australian biogeography have continued. Many have presented scenarios for taxa originating in one region and dispersing to others, e.g. angiosperms in general (Raven & Axelrod, 1974), the Australian flora in general (Beadle, 1981), plant taxa in the Malesian-Pacific region (van Steenis, 1963; van Steenis & van Balgooy, 1966; van Balgooy, 1975, 1984, 1993), Proteaceae (Johnson & Briggs, 1975), Proteaceae, Restionaceae and Myrtaceae (Johnson & Briggs, 1981), *Eucalyptus* (Pryor & Johnson, 1981), *Euphrasia* (Barker, 1986), *Acacia* (Maslin & Hopper, 1982). In general the palaeobotanical community has continued to use this approach (Truswell *et al.*, 1987; Hill, 1994b; Pole, 1994), although the role of vicariance too is sometimes acknowledged (Hill *et al.*, this volume).

As part of a work dividing the world into 35 floristic regions, Takhtajan (1986) treated continental Australia as three regions: Northeast, Southwest, and the Central, or Eremaean Region. These regions were further divided into provinces. A new and much more useful classification of Australasian biotic regions was published by Schodde (1989), integrating flora and fauna into five mapped elements (Fig. 74) and accounting for their origins by a combination of plate tectonics, climate change, radiation and extinction. This scheme is discussed in detail below.

Studies on individual taxa

Many researchers have investigated the phylogeography of individual groups, as a spin-off from taxonomic revisions. Initially these tended to be descriptive treatments with narrative analyses of the historical causes of the observed distribution patterns (e.g. most papers in Barker & Greenslade, 1981). Increasingly, such studies have been based on phylogenetic reconstructions, although they have mostly focussed only on the history of the individual group: where it originated and the taxon-specific sequence of events (vicariance, dispersal and extinction).

Australian studies on individual taxa include eucalypts (Myrtaceae) in eastern, southern and south-western Australia (Ladiges *et al.*, 1983; Ladiges *et al.*, 1984; Ladiges & Humphries, 1986; Ladiges *et al.*, 1987; Humphries *et al.*, 1988; Thiele & Ladiges, 1988; Ladiges *et al.*, 1989; Ladiges *et al.*, 1992; Wardell-Johnson *et al.*, 1997); Sapindaceae along a track from eastern Australia to Malesia and the Pacific (Turner, 1995, 1996); *Euphrasia* in temperate Australia (Barker, 1986); *Boronia* sect. *Valvatae* (Rutaceae) throughout non-arid Australia (Duretto, 1995); Embotriaceae (Proteaceae) in eastern Australia, New Guinea and South America (Weston & Crisp, 1994); *Lechenaultia* sect. *Latouria* (Goodeniaceae) (Morrison, 1987) and *Leptosema* (Fabaceae) (Crisp, 1982) in the south-west, centre, north and north-east of Australia; *Gossypium* (Malvaceae) in northern and central Australia (Wendel & Albert, 1992); *Oreobolus* (Cyperaceae) in Australia and the Pacific (Seberg, 1988); and *Guioa* (Sapindaceae) in Malesia and Australia (Van Welzen, 1989).

A recent approach seeks to identify ancestral areas for individual taxa, assuming that there has been a history of range-expansion or dispersal rather than vicariance (Bremer, 1992, 1995; Ronquist, 1994, 1995). The 'cost' of dispersal is traded off against extinction. Ronquist (1997) has refined the method to take vicariance into account, at no extra cost. Unlike the narrative dispersalist biogeography of Darlington *et al.* (above), this method offers the possibility of corroboration by recurrent single patterns where concerted dispersal has occurred, or by geological hypotheses. Hypothesised migrations of sets of floristic elements, e.g. across Torres Strait or the Tasman Sea, could be explored by these methods. This sort of analysis should be especially applicable where a history of island-hopping with speciation is suspected, such as along the Hawaiian chain (Wagner & Funk, 1995) and the Melanesian arcs (Turner, 1995; Polhemus, 1996). Swenson & Bremer (1997) applied this approach to *Abrotanella* (Asteraceae), which occurs in Australia and across the Pacific.

Are general explanations possible in biogeography?

Although cladistic biogeography is based on the expectation of congruent geographic patterns among different taxa, this assumption may be false. It appears that in some areas of endemism, such as South America, co-existent elements of the biota have different area-patterns suggesting different biogeographic histories (Parenti, 1981; Humphries & Parenti, 1986; Crisci *et al.*, 1991a, 1991b; Nelson & Ladiges, 1996: 52–53). Such areas are sometimes termed 'composite'. Composite patterns probably arise via diverse causes: sequential accretion of land fragments carrying different organisms to form present-day land masses and biota; taxa responding differentially to vicariance events; patterns of different age overlain in the same areas; and patterns reflecting different causes, e.g. migration versus vicariance. It seems reasonable to suppose that any ancient area would be affected by such complexities.

In the face of such complexity, is it possible to find general patterns with common cause, or should every taxon be considered to have its own unique history, incongruent with any other? Some would believe that the search for congruent patterns is delusive:

'Nothofagus probably had a similar centre of origin to many other southern taxa, but its history of dispersal is unique. There have almost certainly been some episodes of long distance dispersal involved, which would not have been followed exactly by other taxa, and even its land based dispersal is unique. The overall message is that biogeography is not amenable to sweeping generalisations, and when they are applied it is more an expression of ignorance than of profound understanding.' (Hill, 1996).

If this conclusion is true, then biogeography cannot progress beyond the narrative stage. However, there is good theoretical and empirical evidence that congruent area patterns exist (Edmunds, 1981; Cracraft, 1986, 1991; Crisci *et al.*, 1991a; Seberg, 1991; Page, 1993b, 1994a; Linder & Crisp, 1995; Nelson & Ladiges, 1996). Moreover, general patterns and general explanations will never be found if they are not sought. Therefore, the only option is to continue to seek general area-patterns, and also to subject the results to rigorous test. Page (1988, 1989) has proposed statistical tests of congruence among area-cladograms and has implemented them in his programs. Further studies are needed in this area, especially in developing null hypotheses for statistical tests. More work is needed also in developing methods that can discover multiple, overlain general patterns, if such exist, and statistical tests as to whether these are different. Where overlain patterns are of different age, the molecular clock may be used to distinguish them (Page, 1993b). Methods already exist that can hypothesise dispersal as an *ad hoc* event against a background of cospeciation (vicariance), but for greater explanatory power a method is needed that combines both processes in a single optimised procedure (Page, 1994a, 1994b).

Analytical studies in search of general pattern

Some studies, unfortunately relatively few, have looked for general patterns through combined analysis of multiple taxa. Phenetic studies have usually had an ecological emphasis and aimed to define 'phytochoria' (floristic regions), often within particular taxonomic groups, e.g. rainforests (Webb & Tracey, 1981; Webb *et al.*, 1986; Whiffin & Hyland, 1986), freshwater aquatics (Jacobs & Wilson, 1996), grasses (Simon & Macfarlane, 1996), Triticeae (Poaceae) throughout Australia (West *et al.*, 1988) and *Acacia* (Hnatiuk & Maslin, 1988).

Invoking processes: palaeobotany, geology, ecophysiology and climate

Once floristic patterns have been identified and described, biogeographers attempt to explain them by recourse to various earth processes. During the 1980s and 1990s studies have continued in the quest to understand the past geological and climatic complexity in the Australian region and how these have impacted upon the flora and fauna. These studies are summarised in the present volume by Frakes and Hill *et al.*, where it is shown that the history of the Australian flora and fauna is far more complex than previously suspected. As well as the gross sorting of the biota resulting from the fragmentation of Gondwana, major climatic changes have apparently driven migrations of floras backwards and forwards over the continent. These migrations have been accompanied by periods of major extinction. Expansion of floras back into areas decimated by aridity, glaciation and other factors have also undoubtedly led to major episodes of rapid speciation. For example, Schodde (1989) hypothesised that the central arid zone has acted as a sink, which was filled by speciation out of the near-coastal regions during wetter periods, then emptied by extinction in the subsequent arid periods. Present biogeographic patterns, then, represent just one iteration of biotic sorting, and past distributions were often quite different.

Some papers in this re-evaluation through climatic and palaeobotanical studies are particularly worth mentioning. Truswell *et al.* (1987) addressed the biogeographic consequences resulting from reassessment of geophysical activities that have taken place on the northern margin of the Australian plate. The accumulated fossil data indicate that the Indo-Malayan element of the Australian flora, as postulated by Burbidge particularly, might

not be entirely Laurasian, but that there has been some floristic interchange between Australia and regions to the north in the late Cretaceous and early Tertiary. However, Truswell *et al.* (1987) found little fossil pollen evidence for any 'massive influx of taxa' into Australia from the north following the Miocene contact about 15 Ma.

This view was supported by Webb *et al.* (1986), who doubted that Australian rainforests arrived by dispersal from external sources and put forward a different interpretation, based on floristic comparisons between rainforest provinces. They suggested that Australia's rainforests, rather than being depauperate samples of those of south-east Asia, are 'remnants of the ancient Gondwanan flora that once covered Australia'.

In an analysis of the origins of the flora of Australia's wet tropics, Barlow & Hyland (1988) concluded that the tropical rainforests of northern Australia are the complex products of a sequence of palaeogeographic and palaeoclimatic events. They invoked a combination of refugial surges and contractions, and intermixing of autochthonous New Guinea and Australian rainforest flora elements with those of Malesia. This scenario recapitulated that of Van Steenis (1979), who suggested that the Malesian and Australian floras are re-mixing after a long separation, as exemplified by palms now found in Australia and New Guinea.

Hooker's elements today

We have reviewed the history of thinking about the origins and relationships of the various 'elements' that comprise the present-day Australian flora. In a sense this has come full circle. Hooker's primary concern was to identify broad-scale patterns by teasing out the different 'elements' in the Australian flora. Each element denoted a different floristic affinity between Australia and other regions of the world; thus his elements are essentially similar to the 'tracks' which we discuss below. Note that Hooker's elements, like tracks, are not mutually exclusive areas on a map - they intermix and overlay in space and time. He speculated about the processes that might cause strong affinities to cross oceans, suggesting that they are relics of ancient and widespread floras that were broken up by climatic and geological upheavals. However, he was careful not to commit himself to any explanation, such as migration in a particular direction: that was in the past and therefore unobservable.

For most of the 20th century, biogeographers accepted Hooker's main elements and debated their origins, whether by the 'invasion theory' (Burbidge, 1960; Barlow, 1981; Beadle, 1981), by *in situ* differentiation (Herbert, 1935, 1950, 1960, 1964, 1967) or by plate tectonics (Barlow, 1981; Schodde, 1989). Many present-day biogeographers, like Hooker, prefer to eschew causal explanations of distributional patterns until these patterns have been elucidated, analysed and tested for generality (Rosen, 1978; Nelson & Platnick, 1981; Ladiges, 1998). This is the approach we use in the following sections.

Diversity and endemism of the Australian flora

The earliest botanists to visit Australia were struck by the unique character of its plants. As pointed out by Hooker (1860) and Barlow (1981) this curious characteristic is partly the result of the ubiquity of a few genera (*Eucalyptus* and *Acacia* in particular) and partly of high diversity and endemism in some distinctive groups (Proteaceae, Myrtaceae, Casuarinaceae, Epacridaceae and some of the conifers). However, on analysis this peculiarity is mainly limited to lower taxonomic levels, e.g. species and genus. (Data for this analysis are drawn from various sources: Morley & Toelken, 1983; Harden, 1990; Groombridge, 1992; Boden & Given, 1995; Mabberley, 1997 and the *Flora of Australia*, including figures for unpublished volumes). At higher taxonomic levels the uniqueness diminishes, with few families being confined solely or largely to the continent. The composition of the Australian flora above family level is virtually identical with that of other areas. For example, the proportions of species in major groups of vascular plants in Australia are very similar to those for the world as a whole (Table 17).

Table 17. Numbers and proportions of species in major groups of vascular plants in Australia

		Vascular plants	Pteridophytes	Gymnosperms	Monocots	Dicots
Australia	No.	18 640	470	75	3723	14 372
	%	100	2.5	0.4	20.0	77.1
World	No.	260 140	9800	840	55 800	193 700
	%	100	3.8	0.3	21.4	74.5

Comparison of the ten largest families in Australia (cf. Introduction, Table 3) with those in the world as a whole (Table 18) again shows our flora to be a fairly representative sample. Seven families are common to both lists. The three large Australian families that are not in the world top ten (Proteaceae, Epacridaceae and Goodeniaceae) are among those that give the Australian flora its distinctive aspect. It is interesting to note that 140 years ago, Hooker (1860), working with a sample of only 8000 known species, gave a nearly identical list of the largest Australian families.

Table 18. The ten largest families of Australian vascular plants, in descending order of size, compared to those in the world as a whole.

Australia		World	
Fabaceae <i>s. lat.</i> ¹	2400	Asteraceae	22 750
Myrtaceae	1858	Orchidaceae	18 500
Poaceae	1302	Fabaceae <i>s. lat.</i> ¹	18 000
Asteraceae	1221	Rubiaceae	10 200
Proteaceae	1116	Poaceae	9500
Orchidaceae	650	Euphorbiaceae	8100
Cyperaceae	650	Lamiaceae	6700
Epacridaceae	424	Scrophulariaceae	5100
Euphorbiaceae	395	Myrtaceae	4620
Goodeniaceae	377	Cyperaceae	4350

¹ The legumes are here treated as a single family, *contra* Cronquist but the consensus view of legume systematists.

Australia is recognised as a major centre of floristic endemism. The concept of an area of endemism is fundamental to historical biogeography. Authors have long observed that small geographic regions often contain many endemics – species that occur nowhere else. These endemics are often unrelated or, when they are closely related, they have differing ecological requirements. Moreover, geographically distant areas of endemism often contain species that are closely related and have similar ecological tolerances (Candolle, 1820; Wallace, 1855; Croizat, 1958, 1962; Nelson, 1978; Nelson & Platnick, 1981). An excellent example is the *Nothofagus* forests and alpine floras of the distant southern continents that so struck Hooker (1860). Surprisingly, narrow endemism is often maintained despite the apparent vagility of the organisms. For example, Wallace (1855) noted that birds did not cross the 25 km strait between Java and Sumatra. These authors inferred that if widely separated areas contain related taxa then perhaps the areas were united in the past but subsequently separated, causing the taxa within them to speciate (Croizat, 1958, 1962; Nelson & Platnick, 1981;

Page, 1993b). Thus, areas of endemism are units of evolutionary history, rather than of ecology.

Islands are the most easily defined areas of endemism; they have an obvious boundary — the sea (Wagner & Funk, 1995). However, islands often occur in groups, and there may have been a history of successive differentiation events among them, as in the Malesian region. This history may be represented as a tree, with the branch-points representing divergence of areas (vicariance events), analogously with a phylogeny of organisms (Nelson & Platnick, 1981: 398–409). Islands vary continuously in size, up to the scale of continents, and virtually all are (or contain) areas of endemism (Major, 1988; Andersson, 1994). At the scale of continents, the break-up of Gondwana into the present-day southern continents during the last 160 million years is well known as a series of events reflected in the phylogeny of their endemic biota (Rosen, 1978; Humphries & Parenti, 1986; Weston & Crisp, 1994; Linder & Crisp, 1995). Further, within each continent and larger islands there are areas of endemism such as mountain ranges, lakes and other more subtly delimited regions. These may have a history of differentiation also. Thus areas of endemism may be expected to form a hierarchy, reflecting history at different geographic scales and different time scales.

Given this hierarchy of scales, how are areas of endemism to be defined for biogeographic analysis? Some authors (Platnick, 1991) suggest that we should use the smallest recognisable units, analogous with species at the base of the hierarchy of organisms. Henderson (1991) states that we should not use areas at all, for fear of circularity when we later draw inferences about areas from the results of biogeographic analysis of taxa. This is analogous to rejecting the circumscription of taxa before phylogenetic reconstruction for fear of prejudicing conclusions about taxa (Vrana & Wheeler, 1992). However, there is no need to restrict areas of endemism to the smallest diagnosable unit. Just as one can reconstruct a phylogeny using accepted higher taxa as the terminal units, so it should be possible to reconstruct a history of areas using more inclusive units, such as the southern continents. In both cases, one would be reconstructing a deeper history than if one were using less inclusive taxa as terminal units.

Takhtajan (1986) treats the continent of Australia as a high-level area of endemism. It is one of only six floral kingdoms in the world, and the second smallest in extent, after the Cape Kingdom of southern Africa. Of the 280 vascular plant families in Australia, Takhtajan considered 18 endemic. His list has been outdated by considerable change in family delimitations, resulting from molecular phylogenetic studies. However, in the most recent family-level classifications (Bremer *et al.*, 1998; Chase *et al.*, in press), 16 angiosperm families are recognised that are endemic to Australia. In systematic sequence, these are Austrobaileyaceae, Atherospermataceae, Blandfordiaceae, Boryaceae, Doryanthaceae, Xanthorrhoeaceae, Dasyopogonaceae, Anarthriaceae, Ecdeiocoleaceae, Tetracarpaeaceae, Cephalotaceae, Tremandraceae, Akaniaceae, Emblingiaceae, Gyrostemonaceae and Eremosynaceae). To these should be added the fern family Platyzomataceae. This total of 17 families is high compared with the other small floral kingdoms: the Cape Kingdom has eight endemic or near-endemic families, and the Holantarctic Kingdom has 12 (Takhtajan, 1986). Other families, such as Eupomatiaceae, Casuarinaceae, Centrolepidaceae, Hydatellaceae, Epacridaceae, Stackhousiaceae, Myoporaceae, Goodeniaceae and Stylidiaceae are near-endemic, having few species outside the continent. Also very characteristic of the Australian flora are the Chenopodiaceae, Proteaceae, Cunoniaceae and Pittosporaceae. At species level, Australia has one of the highest levels of endemism in the world (c. 80%, Groombridge, 1992; c. 95%, Boden & Given, 1995) compared with other large countries, e.g. South Africa (70–80%), Madagascar (68–80%), New Caledonia (c. 80%), Indonesia (67%), China (40–56%).

As might be expected, endemism at the generic level is intermediate between family- and species-level endemism. About 566 of the 2500 genera recognised in Australia are endemic, and the largest families (not surprisingly) contain the largest numbers of genera. Endemism at generic level is spread very unevenly across families, and the largest genera (Introduction, this volume, Table 19) have most of their species richness outside the tropics.

Within Australia endemism is spread unevenly, and several centres of endemism have been recognised. According to Takhtajan (1986), there are over 150 endemic genera in his North-

east region (being the north and east coasts and adjacent inland), 125 endemic genera in the South-west and 85 endemic genera in the Eremaean region. On an areal basis, this represents a heavy concentration of endemics in the south-west. Similarly, at species level, endemism is greatest in the south-west, with 68% of species endemic and 83% near-endemic (Boden & Given, 1995). Burbidge (1960) recognised four floristic areas of 'special interest and importance', being centres of high diversity and endemism: the South-west Province, Tasmania, North-east Queensland and the McPherson-Macleay overlap. Cracraft (1991) recognised 14 areas of endemism for the purpose of a cladistic biogeographic analysis of Australia, based on bird distributions and Burbidge (1960). Crisp *et al.* (1995) adopted Cracraft's scheme with modification (Fig. 76).

The 'centres of plant diversity and endemism' recognised by Boden & Given (1995) for mainland Australia include four that are more or less the same as Burbidge's (South-west Botanical province, Western Tasmanian Wilderness, Wet Tropics of Queensland and the Border Ranges), plus five others (Table 19). In a comparison among these areas (Table 19), again the south-west is exceptional in both species richness and endemism, although it should be noted that its area is an order of magnitude greater than most of the others. When area is taken into account, the Wet Tropics of north-east Queensland is perhaps an even more outstanding centre of diversity and endemism. The species richness and endemism are not much less than in the south-west, but in an area only one thirtieth the size (Table 19). Moreover, this region has 43 endemic genera and is noted for its concentration of the world's primitive angiosperm families (13 out of 19; Boden & Given, 1995).

Table 19. Centres of plant diversity and endemism recognised in mainland Australia by Boden & Given (1995), showing their estimated number of vascular plant species and the percentage of these that are endemic.

	Area (km ²)	No of species	% endemic
Australian Alps	30 000	780	11
Border Ranges	6000	1200	7
Central Australian Mountains	168 000	1300	9
Kakadu-Alligator Rivers	30 000	1430	3
North Kimberley	99 000	1476	7
South-west	310 000	5500	68
Sydney Sandstone	24 000	2200	2
Western Tasmania	14 000	800	?
Wet Tropics	11 000	>3400	43

In many ways, the South-west and Wet Tropics present a complete contrast as centres of endemism. The South-west has a mediterranean climate and sclerophyllous vegetation of heath, mallee and eucalypt forests and woodlands, while the Wet Tropics has a tropical wet climate and rainforest vegetation. As Hooker (1860) first noted, the large and characteristically Australian families (e.g. Goodeniaceae, Epacridaceae, Stylidiaceae, Casuarinaceae, Proteaceae, Myrtaceae, Myoporaceae etc) have most of their diversity in the south-west, or in the south-east, but never in the tropics. This same pattern is shown by the largest two genera, *Acacia* (Hnatiuk & Maslin, 1988) and *Eucalyptus s. lat.* (Wardell-Johnson *et al.*, 1997). By contrast, the Wet Tropics has more genera and families, many of which are scarcely seen outside the rainforest pockets of the east coast, and which therefore are not considered 'characteristically Australian' (Webb *et al.*, 1986).

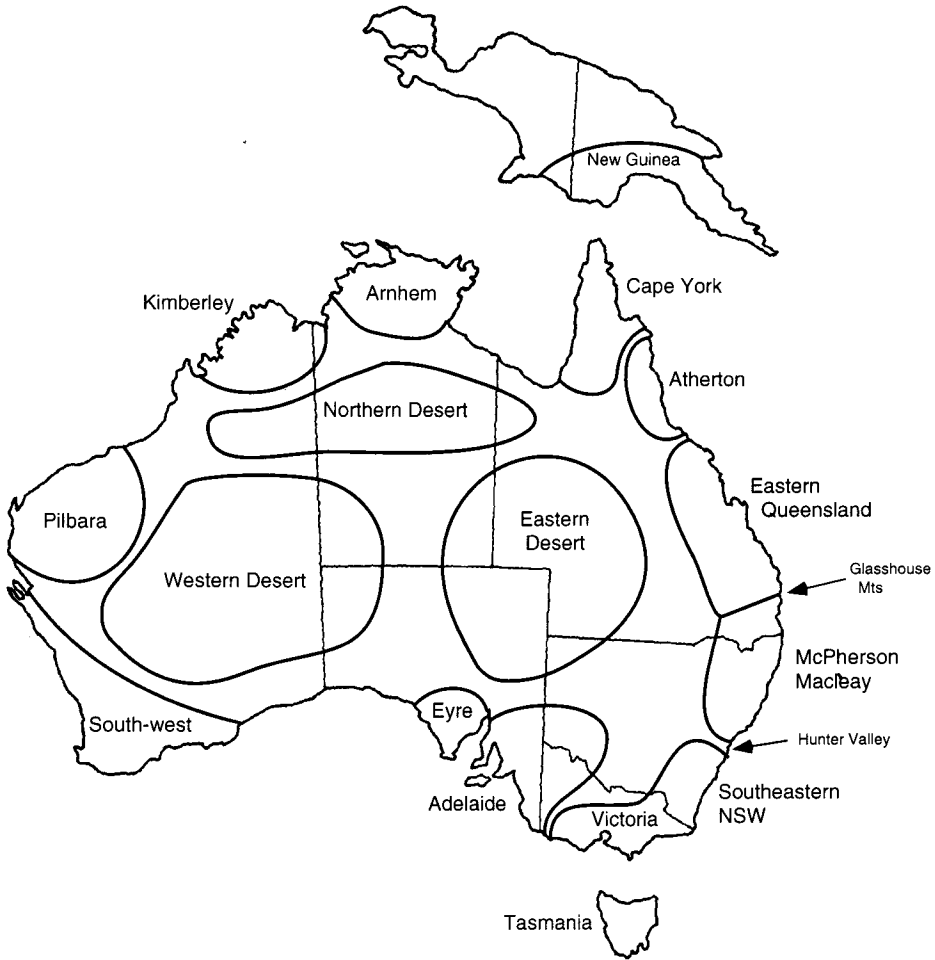


Figure 76. Map of Australia and New Guinea, showing major areas of endemism as in Crisp *et al.* (1995: fig. 3). Modified from Cracraft (1991) by adding 'New Guinea', splitting his 'Southeastern forest' into 'Southeastern New South Wales' and 'Victoria', and by splitting his 'Eastern Queensland' into 'McPherson-Macleay' and a smaller 'Eastern Queensland'. Note that there are gaps between the mapped areas, by contrast with maps of biotic regions (Figs 73 & 74). These gaps occur because areas of endemism represent coincident sets of range-restricted species, and ignore widespread species (and minor areas of endemism) that occur in the gaps.

Relationship of Australian flora to other floras

Track analyses

In this analysis, first we compile general tracks, then we relate these to phylogenies where available, and finally we make process interpretations. We do not attempt to overlay the vast number of distribution maps available, but rather synthesise from the literature the generalised tracks that have been used. Where there is a dearth of these, we develop the general maps without rigorous analysis, using coincident widely distributed taxa. Widespread taxa are difficult to interpret. Often they are regarded as the results of dispersal, and thus uninformative (Morat, 1986; Nelson & Ladiges 1991, 1996). However, it could be argued that a recurrent widespread pattern is a track, and possibly informative on plant history.

We summarise the distributional data into four general tracks: the South Pacific track; the Equatorial track; the Trans-Indian Ocean track and the Pan-temperate track.

South Pacific track

The South Pacific track consists of two sections. The first is the disjunction across the southern Pacific, illustrated by the very numerous taxa shared between Australia, New Zealand and southern South America. This is possibly one of the best documented and studied disjunctions. It was first noted by Hooker (1853), and subsequently there have been many enumerations of the taxa that span it (Croizat, 1958; Thorne, 1972, 1978, 1986; Good, 1974; Takhtajan, 1986; Crisci *et al.*, 1991b). Some 50 genera and seven families are restricted to southern South America and Australasia. In addition, there are several closely related generic groups, e.g. *Drimys/Tasmania/Pseudowintera* and *Austrotaxus/Pilgerodendron/Libocedrus/Papuacedrus*. The conifer flora is almost entirely restricted to this track (Page & Clifford, 1981).

The South Pacific track has long been recognised, and was called the Antarctic element by Hooker (1860) and Burbidge (1960), a term widely used in the 'pre-drift' literature. Subsequent to the acceptance of continental drift the track has generally been called 'Gondwanan' (e.g. Turner, 1995 and many other references). Since Gondwana contained many more components than this track, this is a misleading usage. It would be tempting to call it the *Nothofagus* track, as this well-studied genus spans the whole track, but it may also be misleading to call a general track after a particular taxon.

The fossil evidence for a common flora from southern South America (Axelrod *et al.*, 1991), Antarctica (Dettmann, 1989; Askin, 1990; Truswell, 1990), Tasmania (Hill & Read, 1987; Hill, 1992), New Zealand (Pole, 1993) and southern Australia (Truswell, 1993; Hill *et al.*, this volume) from the Late Cretaceous to the early Tertiary is extensive. The flora, often described as the Gondwanan flora (or the *Nothofagidites* floristic province), contains many of the floristic elements still associated with the *Nothofagus*-dominated forests of the same areas, as well as several taxa now found in the montane uplands of New Guinea. Prominent taxa included *Nothofagus*, *Araucaria*, Proteaceae (*Beauprea*, *Banksia*), Winteraceae, *Ilex*, Podocarpaceae, and many others. The vegetation has been described as cool temperate, with no temperature extremes – a climate currently associated with the cool uplands of tropical areas (Specht *et al.*, 1992). The fauna associated with these forests has been shown to be sharply discontinuous with that of the surrounding vegetation types (McQuillan, 1993), thus corroborating the uniqueness of this biota.

The second, northern part of the track has been less studied, and shows complex patterns around the northern and eastern borders of Australia, encompassing New Guinea, West Malesia, New Caledonia and eastwards to Fiji. There is very little fossil evidence from these northern areas (Veblen *et al.*, 1996), so reconstruction of this track can only be based on extant distributions (Turner, 1995; Weston & Crisp, 1996).

Table 20. Selected distribution patterns of members of the South Pacific track.

Taxon	New Guinea	New Caledonia	Monsoon Australia	Temperate Australia	Tasmania	New Zealand	Temperate South America
<i>Nothofagus</i>	+	+	+ ¹	+	+	+	+
<i>Drimys/ Tasmannia/ Pseudowintera</i>	+	+	+	+	+	+	+
<i>Cupaniopsis</i> ¹	+	+	+				
<i>Jagera</i>	+		+				
<i>Carpina</i>	+			+	+	+	+

Source: ¹ fossil evidence only (Veblen *et al.*, 1996)

The presence of a wide range of taxa associated with the *Nothofagidites* flora, including *Nothofagus*, in New Guinea firmly establishes the island as part of the South Pacific track. Similarly, many of these taxa also occur on New Caledonia, which also shares the largest two components of its flora with Australia and New Guinea (Morat *et al.*, 1986). This establishes the north-eastern part of Australia, New Guinea and New Caledonia as part of this general track, and enables us to include in this track taxa more or less restricted to these areas (Table 20). We therefore argue that patterns which apply to part of the track, can be taken to apply to all taxa of that particular track. This acceptance of at least a portion of the monsoonal forests as part of the 'Gondwana' biota is well established in the Australian literature (Barlow, 1981; Webb *et al.*, 1986; Turner, 1995).

Equatorial track

This track encompasses the equatorial regions of the world: Amazonia in South America, equatorial Africa (as scattered forests), Madagascar, India and south-east Asia (Croizat, 1968). This track has been called the tropical element in Australia (Burbidge, 1960), although her concept may have included taxa present only in the monsoonal parts of New Guinea and north-eastern Australia, taxa which we would ascribe to the South Pacific track. Schodde's (1989) Irian element clearly belongs to this track.

Specht (1981) showed that some 177 genera (10% of the Australian genera) show Afro-Indo-Malesian distribution patterns. These genera are most common in the tropical and subtropical closed forests. This assessment is corroborated by Hartley (1986), who documented the distribution ranges of 716 genera of New Guinean rainforest species. Based on these data it is evident that there is substantial evidence of the equatorial track reaching Australia (Table 21). The most common pattern includes Africa and Indo-Malesia (57.7%, 413 of the 716 genera), while a further 20% (140 of 716 genera) are amphi-equatorial. Only 20% of the genera are more or less restricted to New Guinea, New Caledonia and Australasia.

The equatorial track is largely coincident with the Late Cretaceous *Palmae* palaeo-floristic province, which included most or all of Africa and Madagascar, eastern South America, India and probably south-east Asia (Herngreen & Chlonova, 1981; Crane, 1987). Interestingly, all of Australia is usually mapped to the *Nothofagidites* province, but it is not clear how good the fossil evidence is for the northern margins of the continent. Thus the possibility that the northern parts of Australia may have been part of the *Palmae* palaeofloristic province cannot be discounted on the plant evidence.

Table 21. Selected genera showing the equatorial track. All genera are present in Australia.

Taxon	New Guinea	SE Asia	India	Madagascar	Africa	South America
<i>Celtis</i>	+	+	+	+	+	+
<i>Beilschmiedia</i>	+	+	+	+	+	+
<i>Ilex</i>	+	+	+	+	+	+
<i>Eugenia s. str.</i>	+	+	+	?	+	+
<i>Flagellaria</i>	+	+	+	+	+	
<i>Antiaris</i>	+	+		+	+	
<i>Garcinia</i>					+	
<i>Myristica</i>	+	+				
<i>Freycinetia</i>	+	+				
<i>Cansjera</i>	+	+				
<i>Macadamiinae</i>	+				+	+

Trans-Indian Ocean track

This track is not well documented (but see Croizat, 1968), and consists mainly of temperate elements (e.g. Proteaceae subfam. Proteoideae, Restionaceae, Haemodoraceae, *Wurmbea*, *Ehrharta/Microlaena*, *Schismus/Plinthanthesis*, *Anacampseros*). These are taxa which cross the Indian Ocean, but which do not occur in Malesia, India or Sri Lanka. This absence distinguishes this track from the Equatorial track (above). Those taxa which occur in South America are more or less restricted to eastern South America (e.g. Haemodoraceae; Simpson, 1990). Earlier phytogeographical studies over-emphasised this track (see comments in Burbidge, 1960), possibly because of the ecological prominence of the Restionaceae and Proteaceae in the south-western tip of South Africa and south-western Australia.

There are also some rather bizarre disjunctions across this interval. *Bulbinella* is shared between Africa and New Zealand; *Cunonia capensis*, which is widespread in temperate African forests, is the only non-New Caledonian member of its genus; and *Dietes robinsoniana*, found on Lord Howe Island, is the only non-African member of its genus (Goldblatt, 1981). However, these examples should be regarded as anecdotal within the larger biogeographical sweep. Unique events cannot be explained.

Table 22. Examples of Indian Ocean tracks.

Taxon	Africa	Madagascar	Indian Ocean islands	Australia	New Zealand
<i>Adansonia</i>	+	+		+	
Proteaceae	+	+		+	+
Ehrharteae	+	+	+	+	+
<i>Wurmbea</i>	+			+	
<i>Anacampseros</i>	+			+	

Pan-Temperate track

This track includes all temperate areas, in both the southern and Northern Hemispheres. At higher latitudes it reaches sea-level, while at lower latitudes its members are found at higher altitudes. In Australia members of this track generally co-occur, often in the same habitat, with members of the South Pacific track. However, members of the South Pacific track are absent from the Northern Hemisphere, and from Africa. It might be argued that the South Pacific track is a subset of the Pan-temperate track, as it occurs over a subset of the areas occupied by the Pan-temperate track. However, in the South Pacific track the closest relatives of the track members in Australia are in New Zealand or South America, while it appears likely that the closest relatives of the Pan-temperate track members in Australia are in the Northern Hemisphere. If the two tracks were combined, this information might be lost, so we deem it better to keep them separate in this analysis.

Members of this track, typically, are *Festuca*, *Poa*, *Euphrasia* (Table 23) while taxa such as *Gaultheria*, *Rhododendron* and *Vaccinium* show a more limited distribution area.

This track is generally continuous along the temperate zones of Asia, Europe and North America, but its southern extensions are largely interrupted, forming small outliers on mountain tops. Burbidge (1960: 179) refers briefly to this group of taxa, including in addition to those tabulated below, *Mentha*, *Ajuga*, *Stellaria*, *Viola*, *Centaurium*, *Drosera*, *Ranunculus* and *Hydrocotyle*. Many taxa in this track are extensive in the Northern Hemisphere but reach their southern limit in New Guinea, e.g. *Castanopsis*, *Potentilla* and *Gentiana s. str.*

Table 23. Examples of Pan-temperate patterns. Sources: ¹West & Garnock-Jones (1986); ²Barker (1986).

Taxon	West Malasia	Himalayas	Europe	North America	South America	Africa
<i>Poa</i>	+	+	+	+	+	+
<i>Festuca</i>	+	+	+	+	+	+
<i>Rhododendron</i>	+	+	+			
<i>Scleranthus</i> ¹			+			
<i>Euphrasia</i> ²	+	+	+	+	+	

Differentiation within the tracks

General tracks link the individual distribution patterns of taxa (species, genera, families) into a general statement, which can be interpreted in terms of the areas occupied by those tracks (Fig. 75). If the general track is at supra-specific level, then it includes areas with different species. This differentiation in the biota along the track can be investigated using cladistic biogeography, and the patterns retrieved are indicative of the relationships among the floras from different parts of the track, and of the factors that may have led to that differentiation. Relatively few cladistic biogeographical studies have been published, thus hampering this interpretation.

South Pacific track

The Antarctic track comprises two parts. The first is the southern portion, which differentiated over Australia, New Zealand and South America. The second is the northern portion, which differentiated over the northern and eastern parts of the Australian craton, involving New Guinea, Queensland, Northern Territories, New Caledonia and further east to Fiji.

The southern portion of the Antarctic track has stimulated much research. This is largely because it poses a relatively simple question: is the biota of New Zealand more closely related to that of South America, than to the biota of Australia. In the last decade, a second question has been added: is the biota of New Zealand derived (by long-distance dispersal) from that of Australia, or are they both derived from a common ancestral biota?

The most popular tool used to address these questions has been one of the versions of cladistic biogeography. The earliest studies were by Humphries (1981, 1983), and like the later studies, these were centered on *Nothofagus*, the genus of southern beeches. These studies seek congruence in the area relationships of as big a suite of taxa as are available. Seberg (1991) used five taxa, but failed to find congruence among them, and Crisci *et al.* (1991b) similarly failed to find congruence. This lack of congruence was largely due to a faulty phylogeny of *Nothofagus*.

The most recent study on this problem (Linder & Crisp, 1995) was based on a total evidence phylogeny of *Nothofagus*, which was based on both morphological data (from Hill & Jordan, 1993) and sequence data from the chloroplast encoded *rbcL* gene (Martin & Dowd, 1993). In addition, all other taxa which are informative on these areas, and for which phylogenetic hypotheses are available, were used. Included were *Aristotelia*, *Cyttaria*, Restionaceae, Iridaceae, Haemodoraceae, Danthoniaceae, Cunoniaceae, Embotrichaceae, *Oreobolus* and Winteraceae. Component analysis was used to find the tree which best fitted the area relationships, while minimizing the number of duplications required (Page, 1993a, 1993b).

Linder & Crisp interpreted their results as suggesting that the flora of Australia and New Zealand differentiated from a common flora, shared more recently than with temperate South America. This is contrary to the results obtained for three insect groups – chironomid midges (Brundin, 1966), mayflies (Edmunds, 1981; Cranston & Naumann, 1991) and the dipterans *Symmerus* plus *Austrosymmerus* (Munroe, 1974) – which suggest that the Australian biota has a more recent connection to South America than to New Zealand. Also, Ladiges *et al.* (1997) extracted a non-paralogous subtree from *Aristotelia* in Linder & Crisp's data, showing support for the third possible relationship between these three areas: (Australia, ((New Zealand, South America))). It appears unlikely that more than one of these three interpretations can be correct, unless New Zealand is a composite area. There is substantial evidence that in fact New Zealand is a composite area, possibly with one portion linking to Antarctica and South America, and the other to Australia (Craw, 1989a; Walley & Ross, 1991; Kroenke, 1996).

Recently, Pole (1994) suggested that the New Zealand flora is entirely derived by long-distance dispersal from Australia, that is, it is a derivative biota, a specialised form of the Australian flora. The implications are that the New Zealand flora and vegetation formations would be uninformative about the Gondwanan Tertiary *Nothofagus* forests, as they are derived from the Australian, and not the Gondwanan, *Nothofagus* forests.

It is evident that the relationships between the floras of Australia and New Zealand are complex. For some taxa, commonality appears to be based on trans-Tasman dispersal. Garnock-Jones (1993) showed that a dispersalist explanation for the occurrence of *Hebe* in Australia and New Zealand is more parsimonious than a vicariance explanation. This was also postulated for *Scleranthus* species shared between New Zealand and Australia (West & Garnock-Jones, 1986). Similarly, Swenson & Bremer (1997) explained the occurrence of two related species of *Abrotanella* in Australia-New Guinea and New Zealand by dispersal from the latter. However, for many other taxa (Linder & Crisp, 1995, and in prep.) this is not the case. It is possible that concerted dispersal down the westerlies might produce a similar pattern to vicariance; this can be tested by establishing the ages of the disjunction using molecular clocks. Vicariance would predict a similar age for all taxa, while concerted dispersal might predict different ages.

Martin & Dowd (1993) suggested that it might be possible to date the divergence among the subgenera of *Nothofagus*, using the *rbcL* DNA sequence. They used the first fossil occurrence of *Nothofagus* pollen at 83 Ma as a reference point, and this suggested a divergence date of 66 Ma for subgen. *Lophozonia* and 48 Ma for subgen. *Fuscuspora*, the two subgenera disjunct between South America, New Zealand and Australia. These dates are

substantially less than the estimated date of geological isolation between New Zealand and Australia, and indicate either long-distance dispersal, or errors either in their calculations or in the geological reconstructions.

Another differentiation in the South Pacific track is around the northern margins of the Australian craton, and the fragments separated from the craton during the Late Cretaceous and Tertiary. Much of this flora is found in the monsoonal forests of this region (Webb *et al.*, 1986). A number of pertinent questions arise from this area:

- (1) What was the sequence of isolating events in this area? Was the Kimberley region isolated before central New Guinea?
- (2) Could the extension of the track to New Caledonia (and by implication to the other islands of the Inner Melanesian Arc) and Fiji be ascribed to dispersal or vicariance?
- (3) Is the frequent extension of Gondwanan species to Western Malesia (Java, Sumatra, Borneo, Sulawesi) reflecting ancient distribution patterns, or dispersal?

The most informative work on the biogeography of this area has been by Van Welzen *et al.* (1992) and Turner (1995), working mostly on the Sapindaceae. Turner's analyses of eight genera (*Mischarytera*, *Arytera*, *Rhysotoechia*, *Cnesnocarpon*, *Guioa*, *Cupaniopsis*, *Lepidopetalum* and *Jagera*) presents the most detailed review of the current understanding of the biogeography of the area. Turner delimited 25 areas of endemism, ranging from the western end of New Guinea to Samoa in the east and Lord Howe Island to the south (Fig. 77).

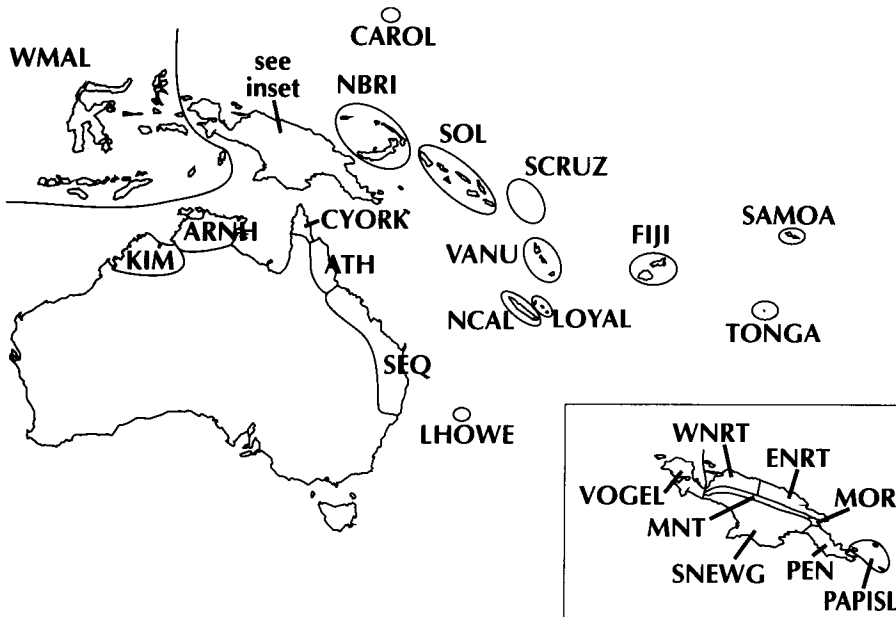


Figure 77. The 25 areas of endemism employed by Turner (1995) in his biogeographical analysis of eight genera of Sapindaceae. Abbreviations: SEQ, south-east Queensland and northern New South Wales; ATH, Atherton Tableland; CYORK, Cape York; ARNH, Arnhem Land; KIM, Kimberley Plateau; SNEWG, south New Guinea; PEN, peninsula; MOR, Morobe; ENRT, east north New Guinea; WNRT, west north New Guinea; MNT, central mountain range; VOGEL, Vogelkop; WMAL, west Malesia; NBRI, New Britain; PAPISL, Papuan Islands; SOL, Solomon Islands; SCRUZ, Santa Cruz archipelago; VANU, Vanuatu archipelago; LOYAL, Loyalty Islands; NCAL, New Caledonia; LHOWE, Lord Howe Island; FIJI, Fiji Islands; SAMOA, Samoa; TONGA, Tonga; CAROL, Carolina Islands. Reproduced with permission.

Turner obtained the following results:

- (1) The eastern Australian areas consistently form a monophyletic group with south-eastern New Guinea.
- (2) Eastern Australia + south-eastern New Guinea are sister to the rest of New Guinea.
- (3) These areas are sister to the Outer (Fiji, Samoa) and Inner (New Caledonia, Loyalty Islands, Lord Howe Island) Melanesian Arcs. These arcs are either monophyletic or paraphyletic at the base of the area cladogram.

In order to return to explanations of individual taxa, Turner optimised the cladograms for each of the taxa onto the selected area cladogram, and assessed the number of dispersal and extinction events required for each node on the area cladogram. This allows subjective assessment of the likelihood of vicariance or dispersal explaining the patterns.

Turner interpreted these results as suggesting two vicariance events; the first separating the Inner Melanesian Arc (IMA) from the Australian craton, the second separating New Guinea (not including south-eastern New Guinea) and Australia (Fig. 78). The presence of the sapindaceous genera to the west of New Guinea, and on the Outer Melanesian Arc (OMA), he ascribed to dispersal. Similarly, he suggested that the West Malesian extensions are the result of dispersal. Non-congruence among area-cladograms for different taxa is taken as evidence for dispersal: for example the sister-position of West Malesia differs among the different area cladograms, indicating different sources for the migration.

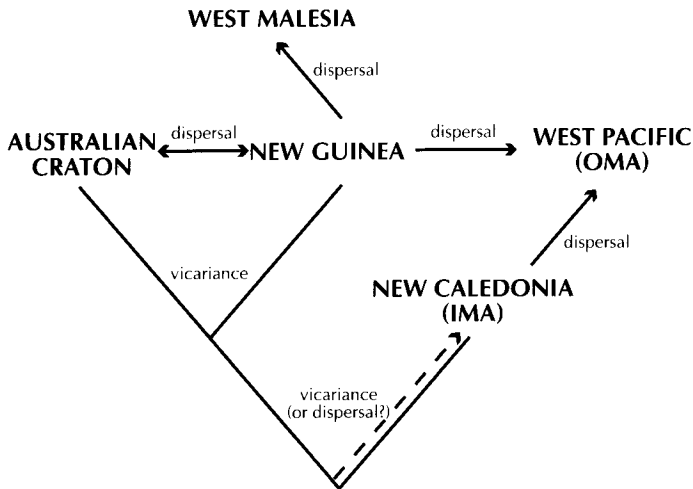


Figure 78. Summary of the major events affecting the Sapindaceae in the Gondwanan biota, from Turner (1995). Areas in this diagram are groupings of those in Fig. 77 as follows: Australian Craton (KIM, ARNH, CYORK, ATH, SEQ); West Malesia (WMAL); New Guinea (VOGEL, WNRT, MNT, ENRT, MOR, SNEWG, PEN, PAPISL); New Caledonia/IMA (NCAL, LOYAL, HOWE); West Pacific/OMA (CAROL, NBRI, SOL, SCRUZ, VANU, FIJI, SAMOA, TONGA). Reproduced with permission.

Both New Zealand and New Caledonia form part of the Inner Melanesian Arc. Yet their floras are rather different (Morat *et al.*, 1986). If both floras shared a terrane separated from Australia, they should have rather similar floras. This lack of similarity has not yet been adequately investigated.

The northern border of the track is assumed to coincide with the complex boundary between Asian- and Australian-derived terranes and microcontinents (Michaux, 1994).

Equatorial track

This track is poorly understood, and there appear to be no cladistic biogeographic analyses of any members of the track. However, there are several hypotheses on the relationships between the Australian members of the track and those from other areas. Hooker (1860) recognised the track but was non-committal about any direction of migration. Several authors have suggested that the Australian members of the track invaded from Malesia (the 'invasion theory' discussed above, see Barlow, 1981). Herbert (1967 and earlier cited references) argued that they differentiated *in situ* from an ancient, pan-tropical flora. Specht (1981) suggested that these taxa are a remnant of a Gondwanan flora. Truswell *et al.* (1987) indicated that there is no fossil evidence of the monsoonal rainforest taxa being relative newcomers in Australia: the fossil record precedes the collision between the Australian and Sunda Shelf plates. They support various suggestions that the tropical flora is ancient, part of a pan-equatorial flora that may have flanked the Tethys in the Late Cretaceous.

The continental reconstructions of Audley-Charles (1987) do not provide for a continuous landmass linking south-east Asia and Australia, but Audley-Charles suggests that there has been a continuous traffic of continental fragments from Australia across the Tethys to south-east Asia. These may have been sufficiently close together to have acquired the developing equatorial flora. However, Veevers (1984, 1991) presents a different view, of the Sunda and Melanesian arcs having been more or less continuously in contact in the mid-Tertiary. Australia pushed through this line after about 20 Ma, broke it and distorted Sundaland. This scenario does not include a regular traffic of north-moving terranes and may provide a better model for integrating the northern portions of Australia into the Equatorial track.

Cladistic biogeographical studies of this biota are required to establish whether the elements of the equatorial track in northern Australia are part of a differentiating ancient *Palmae* flora, or whether they are derivative elements that established recently due to long-distance dispersal from West Malesia.

Trans Indian Ocean track

There have been few studies of this track. Linder & Crisp (1995) included several taxa from this track in their global analysis, and these do not indicate any close relationships. However, a number of rather striking, and common, taxa are shared between Africa and Australia.

The recognition of this track in cladistic biogeography is dependent on a pattern of (Australia, (Africa, South America)) rather than the typical *Nothofagidites* pattern of (Africa, (Australia, South America)). There are several plant taxa that show this areal relationship, including Haemodoraceae (Linder & Crisp, 1995) and *Anacampseros* (Gerbault, 1992). In addition, recognition of the track is based on a composite South America, where the eastern, tropical portion is assumed to have a different history from the southern, temperate portion. This division was suggested by Humphries (1981), Parenti (1981) and Crisci *et al.* (1991b).

The track can be accounted for by vicariance, but the dates for the opening of the Indian Ocean (c. 120 Ma; Veevers, 1984; Scotese *et al.*, 1988) are rather early for angiosperm differentiation. The pattern is consistent with an earlier disjunction across the Indian, rather than across the central Atlantic Ocean. But such a scenario would predict that the absence of these taxa from India is secondary. Another possibility is dispersal eastward across the Indian Ocean. Support for this hypothesis is found in the scattered occurrence of African taxa on the Indian Ocean islands: *Ehrharta* sp. (Gibbs Russell & Ellis, 1987) and *Disa borbonica* (Linder, 1981) on Reunion and *Pentaschistis insularis* (Linder & Ellis, 1990) on Amsterdam

Island. In these cases, the species on the islands is not a basal member of the clade, but has close relatives on the African mainland. It is possible that some of the patterns may be due to vicariance (Restionaceae, Proteaceae), but others may be due to dispersal (*Wurmbea*, *Ehrharta*). Baum *et al.* (1998) postulated on the basis of a molecular clock that the disjunction in *Adansonia* between Africa, Madagascar and Australia is due to long-distance dispersal across the Indian Ocean. They argue that the relatively short branches separating the species within *Adansonia*, compared to the branchlengths separating *Adansonia* from related genera, also indicate a recent diversification within the genus. There is a need for further studies on unrelated groups to establish the generality of this pattern.

The occurrence of Restionaceae and Casuarinaceae on Ninetyeast Ridge (Kemp & Harris, 1975) dated to the Paleocene or Late Oligocene could indicate either relictual fragments of a wider Indian flora, or secondary dispersal from Australia.

This still leaves the nature of the relationship between the floras of Africa and Australia open. Clearly there is a direct link, but how it was established is not yet clear.

Pan-Temperate track

The occurrence of Eurasian temperate taxa in Australia has generally been interpreted as the result of long-distance dispersal from Eurasia down the Malesian mountains to Australia (Burbidge, 1960; Raven, 1973). There are relatively few cladistic analyses of these widespread taxa: most of the taxa are large (e.g. *Festuca*, *Poa*, *Euphrasia*), and hence present great difficulties to the phylogenetic systematist. However, the analyses of West & Garnock-Jones (1986) of *Scleranthus* and Barker (1986) of *Euphrasia* present some evidence that if migration occurred along the track, it may have been from Australia north to Eurasia.

There is as yet no continental drift model postulating continuous land between Australia and Eurasia, along which vicariance could have developed. Hence a long-distance dispersal model appears the most feasible, but the dispersal could have been in either, or both, directions.

Relationships among the four tracks

Tracks can be arranged in a hierarchical fashion, from the narrowest track to a single global explanation (cf. Amorim & Tozoni, 1994). It could, for example, be argued that the track linking temperate Australian rainforests with those of New Zealand and South America is a distinct track from that linking the monsoonal forests of New Guinea, Queensland and New Caledonia. However, the analysis of taxa spanning these two tracks indicates that there are two nodes of differentiation along the same track, and that they are united at a higher level of generality. Similarly, there should be a similar relationship among the four general tracks discussed above. Only a global analysis can resolve this relationship. Current indications are that the equatorial and the South Pacific tracks are the major vicariant patterns, and that these probably differentiated shortly after the origin of the angiosperms. The relative timing and position of the Trans-Indian Ocean track is not known. The Pan-temperate track may also have developed rather later, and if the indications that its presence in the southern Hemisphere is due to dispersal, then it cannot be related to the other two tracks.

Of interest here could be the biogeographical patterns of some of the widespread Proteaceae subtribes, like Macadamiinae and Hicksbeachiinae (Weston & Crisp, 1996). It is possible that the Proteaceae contain elements in the equatorial, trans-Indian and South Pacific tracks: consequently an understanding of their relationships could be informative.

Synthesis

The flora of Australia is most closely related to that of its Gondwanan neighbours: in the south, New Zealand and southern South America; to the north New Caledonia and New Guinea. These relationships appear to be most parsimoniously explained as sister-group relationships, rather than derivative, ancestor-descendent relationships. This implies that all

these areas have autochthonous floras relative to each other, all are informative on the ancestral biota that once covered the whole area.

This implies that there are derivative floras within Australia. The most striking must be the savanna floras associated with the eucalypt woodlands on richer soils, and the sclerophyllous heaths, mallees and eucalypt forests of the oligotrophic soils.

However, this picture is partially upset by elements that do not fit: the trans-Indian Ocean links to Africa, and south-east Asian links. It is not clear whether there were any other island or continental links across which their biota could have vicariated, or whether these links are the result of long-distance dispersal across the Indian or Tethys Oceans. The relationship to the equatorial track is also enigmatic, and requires the analysis of members of this track, to determine the extent of its presence on mainland Australia, and whether these taxa are here as a result of dispersal, or whether they were originally part of a pan-equatorial flora.

Phytogeography within Australia-New Guinea

Here we present a descriptive classification of the biotic regions of Australia and New Guinea and a narrative account of their origins. Then we review recent analyses of distributional patterns using cladistic methods. This section covers only the most recent studies on the Australian flora.

Biotic regions

The most recent attempt to synthesise Australia's flora in a few broad biotic regions is that of Schodde (1989). Giving credit to a long line of predecessors, from Hooker (1860) to Burbidge (1960), Schodde states that his scheme contains only 'minor but significant modifications to the traditional concepts of Australian biotic elements'. This claim is too modest, for he is the first author to use both animal and plant distributions as evidence, and he adds two rainforest elements that have not been recognised explicitly before - at least, not since Hooker.

Note the subtle distinction between two kinds of biotic units: 'elements' (defined by hypothesised origin) and 'regions' or 'zones' (defined geographically). Hooker (1860) and Herbert (1967) described elements, whereas Spencer (1896) and Burbidge (1960) mapped regions or zones. Schodde integrated both kinds in a single system of mapped 'elements' (Fig. 74), each of which is defined by content (floristics and faunistics) as well as hypothesised history.

Schodde mapped most of mainland Australia and Tasmania with three elements: Torresian, Bassian and Eyrean (Fig. 74). These correspond closely with Spencer's faunistic regions of the same names and Burbidge's Tropical, Temperate and Eremaean floristic zones. The Torresian element comprises tropical eucalypt savannah woodland and semi-deciduous forest with a monsoonal climate. This element also occurs in southern New Guinea and has strong links with south-east Asia and beyond, for instance the Eurasian sylvid warblers have radiated here. The Bassian element is temperate eucalypt woodland and forest with a sclerophyll shrub understorey, dominated by autochthonous genera of the Myrtaceae, Fabaceae (especially *Acacia*), Proteaceae and Epacridaceae. The climate is mostly cool to warm temperate with winter rainfall, grading to a summer maximum in the north-east. There is strong differentiation between and endemism within the disjunct south-eastern and south-western regions. The Eyrean element is the arid-adapted biota of central Australia, vegetated by desert steppes (Chenopodiaceae), hummock grassland (*Triodia*), and tall shrubland to low woodland of mulga (*Acacia*) and mallee (*Eucalyptus*). Reptiles are diverse here but otherwise this element is the poorest in vertebrates. However, there is a very rich fossil vertebrate fauna from central Australia (Vickers-Rich *et al.*, 1991). Taken together, these three elements largely correspond with Hooker's Australian element ('autochthonous' element of later authors). However, the monsoonal component of Hooker's Indian element falls into Schodde's Torresian element.

Schodde recognised two additional elements, Tumbuna and Irian, both being rainforest types (Fig. 74). These reach their maximum extent in New Guinea, which was not included in previous biotic classifications of Australia. It has now become clear that at least southern New Guinea has always been part of the Australian craton. The Tumbunan element is cool temperate to subtropical rainforest dominated by trees of *Nothofagus*, Podocarpaceae, Lauraceae, Myrtaceae, Proteaceae, Cunoniaceae, Elaeocarpaceae and Winteraceae. The vertebrate fauna includes the primitive myobatrachid and leiopelmatid frogs, side-necked land turtles, ratite birds, parrots, other non-passerines, the ancestral specialised songbirds, monotremes and the major lineages of marsupials. The Irian element is tropical rainforest with strong Malesian affinity, which dominates the lowlands of New Guinea but in Australia occurs only in small pockets on Cape York Peninsula, Arnhem Land and the Kimberley. To a considerable extent, these two elements revive Hooker's scheme. Tumbuna corresponds closely with his Antarctic element, and Irian is his Indian element minus the monsoonal component.

In hypothesizing origins, Schodde took full advantage of the plate tectonics paradigm, which was not available to his predecessors. This led directly to his recognition of the Tumbunan element, which is now widely considered to be a scarcely modified, *in situ* relic of the Eocene forests of Gondwana (cf. Hill *et al.*, this volume), hence the derivation of the name Tumbuna, from a Melanesian pidgin word meaning ancestor. Not surprisingly, this element is also found in those fragments of Gondwana that still have cool to warm, humid temperate climates: New Zealand, southern and tropic-montane Africa ('Afromontane forest') and southern South America. Schodde considered the Tumbunan element ancestral to the autochthonous biota of the Torresian, Bassian and Eryean elements. As the climate dried out and became more seasonal from the late Miocene onwards, and fire became a major influence, the characteristically Australian sclerophyll flora radiated. With onset of aridity in the Pliocene, the Eryean element appeared in the centre of the continent. This is the most depauperate of the elements: Schodde viewed the arid zone as a sink, 'fed by the plumbing and taps' of the surrounding scleromorphic flora, only to be emptied by extinction during the arid cycles of the Plio-Pleistocene. Thus Schodde largely abandoned the old invasion theory of mass immigration. The only exception is the Irian element and the monsoonal forest component of the Torresian element, which were seen as a southerly extension of Malesian (and even pantropical) biotas.

Tracks within Australia

Here we turn our attention to evidence of floristic tracks within Australia. Tracks are not the same as a biotic region, which is a coherent mapped area circumscribed by a characteristic floristic content, climate and geography.

Identifying tracks within continents is problematic. Clearly there has been geographical differentiation within the Australian flora, as recognised by previous authors from Hooker to Schodde. For the purpose of analysis, it is necessary to partition this variation into geographic units - areas of endemism (as distinct from biotic regions). Continents and islands define themselves as areas by their coastline. By contrast, the continuous land mass of a continent seldom has sharp internal boundaries, except lakes and high mountain ranges, which are often likened to islands. Where there are no sharp boundaries, one cannot expect sharply differentiated areas of endemism (or tracks).

A further problem is that through geological history a succession of taxa is likely to have differentiated within the same (or parts of the same) areas at different periods. This is more likely to have happened within continuous land masses, where there are fewer barriers to the dispersion of flora. This too leads to an expectation that different subsets of the present flora are likely to show different tracks for the same areas.

Continent-wide tracks

The only published cladistic analyses of areas across the whole of Australia using multiple taxa have concerned vertebrates, mainly birds (Cracraft, 1982, 1986, 1991) and several

