

BIOGEOGRAPHY OF THE TERRESTRIAL FLORA

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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

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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.

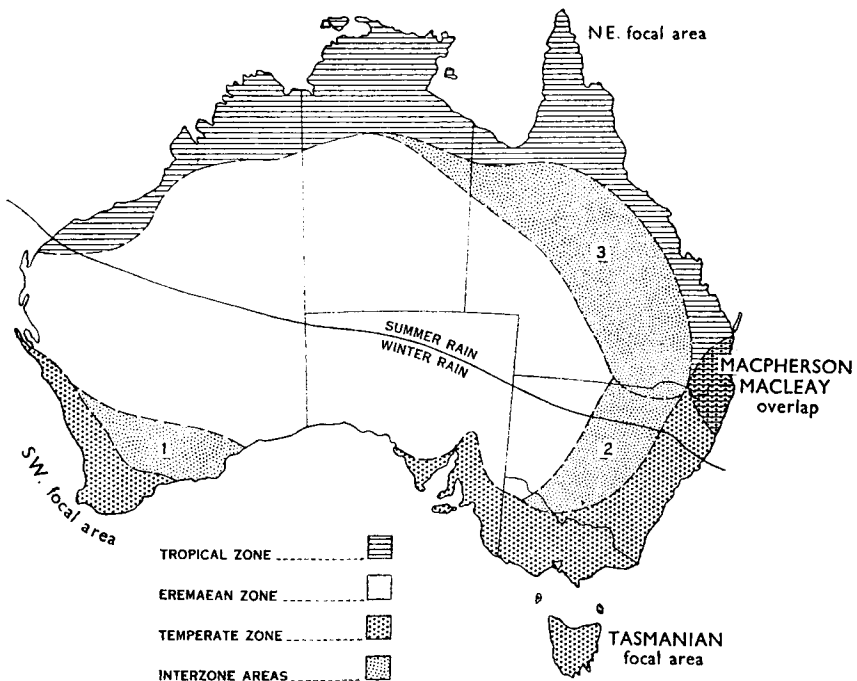


Figure 73. Map of floristic zones (equivalent to biotic regions or elements) in Australia. Reproduced from N.Burbidge, *Austral. J. Bot.* 8: 79 (1960) with permission.

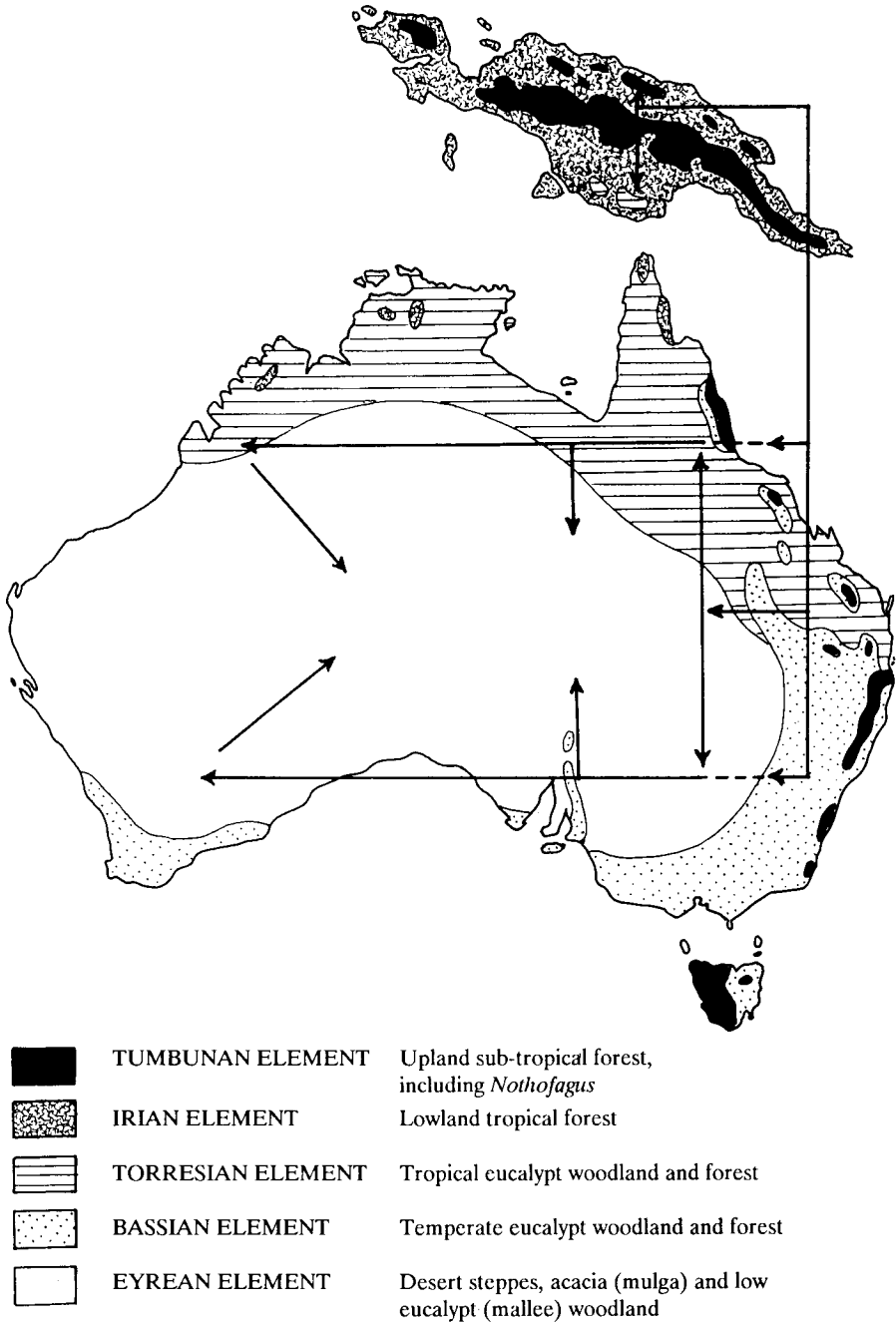


Figure 74. Map of biotic elements in Australia and New Guinea. This map is based on that of Burbidge (Fig. 73), but recognises additionally the Tumbunan and Irian elements. Arrows indicate putative pathways of migration and radiation. Reproduced from R.Schodde, Origins radiations and sifting in the Australasian 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).