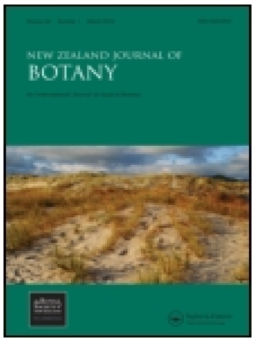

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Plant biogeography and the late Cenozoic history of New Zealand

M. S. McGLONE

Botany Division, DSIR
Private Bag, Christchurch
New Zealand

Abstract Patterns of regional endemism, vicariance, and disjunction in New Zealand higher plants are reviewed. These are discussed in relation to the post-Oligocene history of the geology, climate, and vegetation. Previous explanations for such distribution patterns have centred on the disruptive effects of ice and severe climates during the Last Glaciation, and subsequent migration of plants from glacial refugia during the postglacial. It is concluded that these explanations are largely inadequate. It is suggested that many endemic, vicariant, and disjunct plant distributions are related to the large-scale modification of the New Zealand land mass which has occurred as a result of active tectonism since the Oligocene. The more stable regions of New Zealand (in particular Northland, northwest Nelson, and Otago) have retained diverse floras partly as a result of retention of older elements of the flora which more radically altered areas (southern North Island, central South Island) have tended to lose. The rapidly rising Southern Alps may have acted as a centre of speciation because of its provision of novel alpine and subalpine environments. Glaciations have affected distribution patterns mainly through permitting the wide spread of glacial environment specialists.

Keywords New Zealand flora; plant biogeography; plant migration; evolution; endemism; vicariance; disjunction; *Nothofagus; Agathis; Phyllocladus; Dracophyllum*; Plate tectonics; Alpine Fault; Quaternary; Pleistocene; Miocene; Neogene

INTRODUCTION

Plant biogeography has always attracted considerable scientific attention in New Zealand, primarily because these islands are isolated and the flora distinct. As well as numerous studies dealing with plant distribution and plant fossils, distinguished reviews have been made, beginning with the first systematic treatment of the New Zealand flora and continuing to the present (Hooker 1855; Cockayne 1928; Fleming 1962, 1975; Dawson 1963; Raven 1973; Wardle 1978; Mildenhall 1980). These reviews have concentrated on what has been for many the central issue: the ultimate origins of the New Zealand flora.

Distribution of plants within New Zealand has not been neglected. Cockayne (1928) recognised a major discontinuity in the flora through the centre of the North Island, and was the first to divide the country into botanical districts based on plant distributions. Cockayne also made the important observation that there was a gap in the distribution of *Nothofagus* species in central Westland which he suggested was related to the Pleistocene distribution of glacial ice (Cockayne 1926). Willett (1950) discussed evidence for the effect of the Last Glaciation on New Zealand vegetation and Holloway (1954) stressed the role of both the Last Glaciation and recent climate change in controlling the broad features of forest composition in the South Island. Wardle (1963) and Burrows (1965) provided detailed analyses of the present distribution of some key plant taxa and mapped concentrations of local endemics, and disjunct, and vicarious plants. Both suggested that the Last Glaciation and subsequent climatic change were the primary determinants of many plant patterns within New Zealand.

Acceptance of the hypothesis that past glaciations and climatic change influence the present distribution of many plants entails very important consequences for ecological theory. As Wardle (1983) points out, it must follow that many plants have not reoccupied their potential range, and therefore historical factors are as important as environmental ones in understanding their ecology.

In the 20 years since the last substantial review of plant biogeography within New Zealand (Burrows 1965), much progress has been made in understanding the history of the vegetation and the landscape on which it grows. In particular, plate tectonics has revolutionized geology, and it is now appreciated just how exceedingly mobile the New Zealand region is, and that many of the events which have shaped the present landscape are relatively recent (Stevens 1980). It seems likely that the dynamic nature of the New Zealand landmass has

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affected distribution of plants, but to what extent is uncertain. This review is devoted to this question.

I first briefly discuss the present distribution of higher plants in New Zealand, and the late Cenozoic vegetation and climate record. From this basis, I examine evidence for and against the hypothesis that many anomalous plant distributions can be explained by appeal to ice distribution and severe climates during the Last Glaciation, subsequent climatic events, and migration. I show that the effects of the Last Glaciation and subsequent plant migrations have been exaggerated to the detriment of other explanations. In particular, I stress the hypothesis that late Cenozoic changes in the configuration of land and sea have affected present plant distributions.

BIOGEOGRAPHIC TERMINOLOGY

Biogeographic terms elude strict definition as they depend to a very large extent on the scale at which a phenomenon is examined.

An *endemic* is a taxon restricted to a given area; at some scale or other, all plants are endemic. *Pandemics* are taxa which occur throughout a given area; as with endemics, there is always a scale at which all plants are pandemic. Here, if no qualification to these terms is given, they may be taken as synonyms for restricted and widespread distributions on a New Zealand basis.

Discontinuity or *disjunction* is the occurrence of a taxon in separate areas. All taxa are discontinuous at some scale unless represented by a single plant. Cain (1944) therefore defines disjunction as indicating populations more widely spaced than 'the normal dispersal capacity of the type'. Kloot (1984) points out, there is not enough information on the normal dispersal capacities of most taxa for there to be any certainty as to what the norm is. More so than in most definitions, the term 'disjunction' is totally dependent on a subjective decision as to what is or is not 'widely spaced'.

Vicariant distributions are those in which two closely related taxa, derived from one initial form, occupy mutually exclusive areas (Stebbins & Major 1965).

Discontinuities in plant distributions arise either by fragmentation of a once continuous distribution, or by long-distance dispersal. Fragmentation of a once continuous range can occur by:

(1) elimination of populations from intermediate areas by temporary occurrences such as disease, browsing, fire, volcanism, or ice advance;

(2) elimination of habitat by such changes as those consequent upon permanent climatic change, mountain building, marine transgression, etc;

(3) by the splitting and movement apart of once continuous land masses.

It is important to note that these categories are not mutually exclusive, and that any combination may act to produce a discontinuous distribution.

Migration is difficult to define satisfactorily. If a plant successfully establishes in an area from which the taxon was previously absent, whether or not migration is taking place depends entirely on the magnitude and direction of the movement in relation to the general distribution of the taxon. I will not refer to migration, but to either range expansion or population growth. Movement of a taxon into an area from which it was previously absent, with movement not being towards other members of the taxon within normal dispersal distance, I will term *range expansion*. Other dispersal events resulting in the establishment of plants are best referred to as *population growth.*

THE DISTRIBUTION OF ENDEMIC, DISJUNCT, AND VICARIOUS SPECIES

Leonard Cockayne proposed a comprehensive scheme for dividing New Zealand into floristic and ecological districts (Fig. 1a). He delimited 16 botanical districts (Cockayne 1917) using a variety of criteria — which included exotic plants, agricultural and horticultural status — but relied primarily on the distribution of endemic and rare or restricted plants, as well as the general nature of the native vegetation. He continued to refine his scheme (e.g., Cockayne 1928), although it remained in essence the same.

Wardle (1963) showed that the North Island south of approximately latitude 39°S, and the South Island between latitudes 42–43°S and 44–45°S have relatively low numbers of endemics (Fig. 1b). Burrows (1965) developed a more elaborate scheme for the South Island alone, recognising 3 broad endemic-rich areas (Fig. 1c). A northern South Island and a southern South Island endemic-rich area delimited an endemic-poor central region as in Wardle (1963), while a third overlapping endemic-rich area included most of the central mountain chain. The northern area was further divided into western and eastern sub areas, as was the southern, with an additional overlapping area in the far south which included western Fiordland, Stewart Island, and coastal Southland.

There is a broad similarity in the three schemes for the subdivision of New Zealand, in that both Wardle and Cockayne recognise a major phytogeographic boundary running at approximately 38–39°S, and all split, in some manner or other, the South Island into a northern, central, and southern area. Despite the inevitably arbitrary nature of the

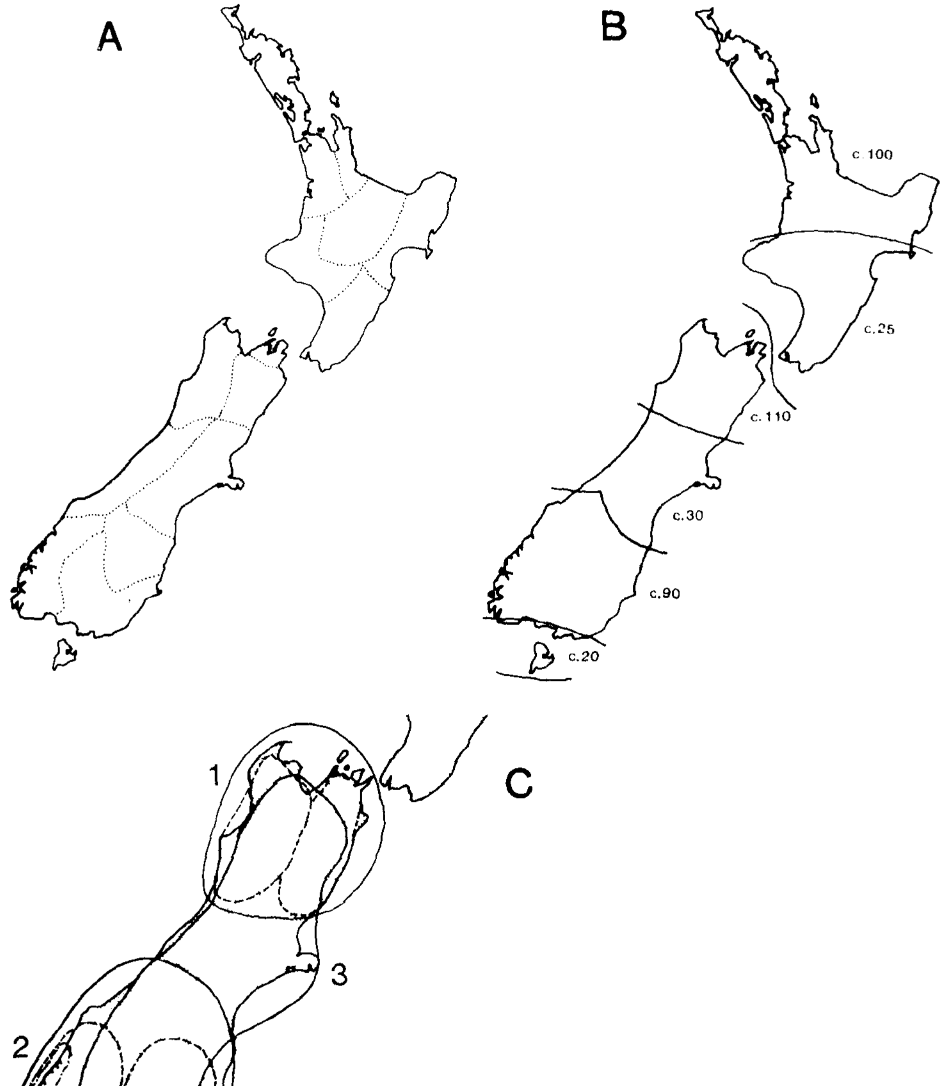

Fig. 1 Botanical regions: (A) Cockayne (1917); (B) Wardle (1963); (C) Burrows (1965).

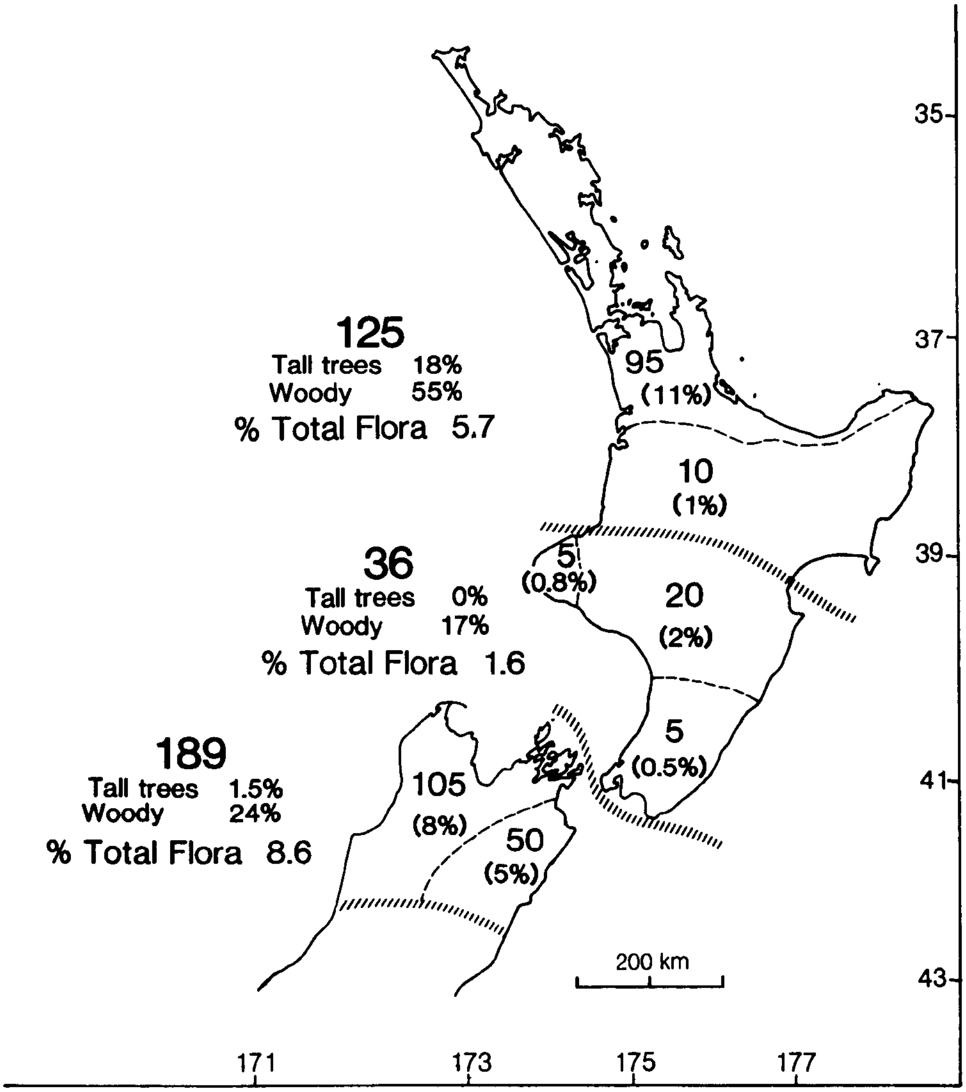

Fig. 2 Endemism in higher plants. Hatched lines divide the North Island and northern South Island into 3 zones. Total number of endemics in each zone, and endemics as percentage of total flora of that zone are given. Each zone is further divided into subzones by broken lines. Numbers of endemics and their percentage of the total flora of the subzone are given. Figure is drawn from data presented in Druce (1984).

boundaries, there can be no doubt that real discontinuities of the flora occur at these latitudes.

Figure 2 shows numbers of endemic higher plants in the North Island and the northern half of the South Island, based on intensive field work by A. P. Druce. The broad conclusion that the north of the North Island and the north of the South Island are relatively endemic-rich, and the southern North Island is endemic-poor is supported by this more detailed study.

The nature of the endemics in each region is of as great importance as their number. Northern North Island endemics are predominantly woody (Fig. 2). The percentage of endemic trees in the northern North Island is nearly 3 times greater than the percentage of trees in the flora as a whole, and endemic shrubs are nearly twice as common. In southern districts, the percentage of endemic woody plants is lower than their percentage in the New Zealand flora as a whole, and endemic trees rare.

In the entire South Island there are only about 7 endemic tall trees, whereas about 30 tall trees are endemic to the North Island, and most of those are endemic to the north of the North Island.

The contrast in type between endemics of the northern North Island and those of more southerly regions can be shown by comparing the endemics of the Three Kings Islands in the far north, and those of Stewart Island and adjacent islands. There are 13 endemic plants on the Three Kings group, including 6 trees, 4 shrubs, and 1 woody climber. On Stewart Island, only 3 shrubs occur among approximately 28 endemics (Wilson pers. comm. 1984). Nearly 30% of the Three Kings flora is woody (Oliver 1948), and approximately 20% of the Stewart Island flora (Wilson 1982). However, approximately 85% of the endemics on the Three Kings are woody, but only 10% on Stewart Island. The concentration of woody endemics in the northern North Island reflects the greater woodiness of the northern flora as a whole, and the concentration of endemic herbs in the south the greater numbers of herbs in the South Island flora. Even so, it is likely that there is a disproportionate number of endemic trees in the northern North Island.

Close to 30% of the vascular flora is classified as alpine (Mark & Adams 1973) and, as pointed out by Cockayne (1917), these plants are concentrated in the high mountains of the South Island. Only a depauperate extension of the alpine flora occurs in the North Island, reflecting the much smaller area of alpine habitats. Alpine plants share in the general pattern of having an abundance of endemics in the northern part of the South Island (6% of the total alpine flora) and in the southern part of South Island (8%), while having relatively few endemics in the central alpine regions of Canterbury and Westland (2%) (Marks & Adams 1973).

As well as these gross patterns of endemism there are others which involve groups of taxa which form patterns seemingly unrelated to major climatic zones or geography. Many of these patterns consist of major disjunctions, but not all disjunctions are equally informative. There are, for instance, a number of spectacularly large disjunctions. *Ourisia modesta* occurs only on Stewart Island and one small area of northwest Nelson. *Drosera pygmaea* is found only in the southernmost region of the South Island and also in the far north of the North Island. Long-distance disjunctions such as these which involve only one species are not very informative as to the general causation of plant distributions. It is only when several species are involved that common factors can be assessed, the possibility of chance dispersal or very recent extinction of intermediate populations ruled out, and biogeographically significant information obtained. Several such patterns are known.

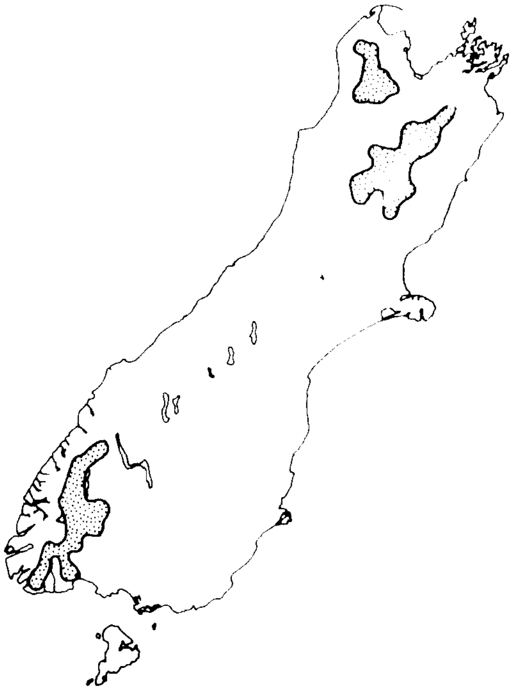

Fig. 3 Distribution of *Celmisia traversii*; after Given (1984).

Firstly, Wardle (1963) and Burrows (1965) listed disjunctions and vicariant species pairs between southern South Island and northern South Island. *Celmisia traversii* is a typical example (Fig. 3). Such disjunctions link the regions of high endemism, the endemic-poor central South Island coinciding with the gap. These disjunctions involve mainly herbaceous alpine or upland taxa. The four *Nothofagus* species are also disjunct, or partially disjunct across the central South Island (Wardle 1984). Some of the disjunct species are habitat limited in the central South Island, as they are plants of upland bogs; such bogs are rare because of the steep broken terrain (Burrows 1965). However, most of the disjunct taxa are considered to be capable of thriving in the central region (Burrows 1965, Marks & Adams 1973).

A second group of wide disjunctions is that between the South Island upland areas and the central uplands (Tongariro Volcanoes; Kaimanawa and Kaweka Ranges; northern Ruahines) of the North Island. Approximately 200 species share this pattern (Druce 1984), and nearly all are of upland to alpine habitats. Many are specialists in disturbed or unstable habitats.

Table 1 Plants present north of approximately latitude 39°S in the North Island, absent in the southern half of the North Island, but present in the South Island.

Taxon	Altitudinal zone
Dacrydium intermedium	montane
Dacrydium colensoi	montane-lowland
Libocedrus plumosa	lowland
Phyllocladus trichomanoides	lowland
Dracophyllum traversii	montane
Melicytus novae-zelandiae	lowland
Metrosideros parkinsonii	montane
Quintinia serrata	montane
Archeria racemosa/traversii	subalpine/montane
Hebe rigidula	lowland
Hebe townsonii	lowland
Alseuosmia macrophylla	lowland
Epacris pauciflora	lowland
Astelia trinervia	lowland
Tmesipteris lanceolata	lowland

A third group of wide disjunctions (Table 1) was first pointed out by Wardle (1963). A small group of species occur no further south than approximately latitude 39°S in the North Island, but reappear in the South Island. Unlike those of the other patterns mentioned above, these species are mainly trees or tall shrubs of lowland to montane habitats.

A final two groups of plant distributions do not involve disjunction but abrupt floristic breaks. Some 55 species extend from the South Island across Cook Strait into the North Island but do not penetrate any further than about latitude 40°30′S, or the area of the Manawatu Gorge. Another pattern involves some 460 species which occur in the central North Island, but do not occur in Taranaki (Druce 1984).

HISTORY OF THE VEGETATION AND CLIMATE SINCE THE OLIGOCENE

Fleming (1975), Kemp (1978), and Mildenhall (1980) provide overviews of the floristic and palaeoclimatic evolution of the New Zealand region during the Tertiary, and only the very broadest outline of pre-Pleistocene change is given here.

New Zealand was separate from Australia and Antarctica by at least 70 m.y. ago. During most of the early to mid Tertiary (65–30 m.y. ago) New Zealand was a low-lying archipelago at high latitudes (as far poleward as 78–68°S). In the early Eocene (55 m.y. ago), the opening up of a wide sea gap between Australia and Antarctica established the westerly oceanic circulation and associated winds which have been a feature of the region ever since (Kemp 1978). Marine trangressions which had been in progress since the late Cretaceous (65 m.y. ago) reached their maximum extent in the early Oligocene (c. 35 m.y. ago) at which time very little of the New Zealand region remained above sea level, except in Otago and Southland.

During the early to mid Tertiary, New Zealand, despite its high latitude, had a flora of predominantly temperate to subtropical affinities which suggests a warm and not excessively seasonal climate (Mildenhall 1980). Palaeotemperature curves for surface waters in the New Zealand region (Shackleton & Kennett 1975) support this inference. These warm temperature conditions continued into the Miocene, with subtropical climates experienced in some regions (Mildenhall 1980).

A major break, and one of crucial importance in the evolution of the New Zealand flora came in the Late Miocene and earliest Pliocene (c. 5 m.y. ago). Westerly circulation increased in intensity, and glaciation of Antarctica resulted in major polar ice sheets, as is evidenced by the presence of ice-rafted debris in deep sea cores around 5 m.y. ago (Kennett & Brunner 1973). During the Late Miocene many herbaceous taxa make their first appearance in the fossil record, and temperate taxa are prominent in most fossil assemblages (Mildenhall 1980). Rapid changes of vegetation types within sequences and the appearance at times of shrubland and grassland dominated vegetation reflect increasingly variable climates. By middle Pliocene time, grasslands periodically extended to sea level (Mildenhall 1980) in the north of the South Island. At the same time the flora was gradually depleted of taxa of tropical and subtropical affinities. With the beginning of the Pleistocene (c. 1.7 m.y. ago) the last tropical and subtropical taxa disappeared, although extinctions continued through to at least the middle Pleistocene (Mildenhall 1980).

During the last 2 million years (latest Pliocene and Pleistocene) there has been at least 20 glacio-eustatic sealevel cycles (Beu & Edwards 1984) which indicate repeated glacial-interglacial alternations. These glacial-interglacial cycles gave rise to a pattern of cool, and largely deforested periods, alternating with warm, mild episodes during which forest cover was near complete. Although many sites have been examined for both micro- and macro-plant fossils, we have no continuous record for vegetation change which extends back beyond the maximum of the Last Glaciation (25–15 000 years ago). Nevertheless, it seems clear that the New Zealand sequence correlates closely with long, complete records of palaeoclimates elsewhere (Pillans 1983, Beu & Edwards 1984). These records reveal that present climatic conditions are typical of only about 10% of Pleistocene time; for most of this period conditions have been colder (Bowen 1978). We know most about the most recent interglacial-glacial cycle which extends from the maximum of the Last Interglaciation at around 120 000 years ago through to the present. I assume here that this has been a typical cycle, and it will be used here as a model for the repetitive changes in climate and vegetation which have lasted for most of the last 2 million years.

The Last Glaciation (c. 100 000–10 000 years ago) was itself a complex event in which there were at least three major interstadials during which forest occupied much of both the North and South Islands. (McGlone & Topping 1983; Mildenhall 1973; McGlone, Howorth & Pullar 1984). These interstadials were separated by severe intervals during which forest was extremely restricted throughout the country, and shrubland and grassland communities dominant (McGlone, Neall & Pillans 1984). The most recent of these stadial periods, the glacial maximum (25 000–15 000 years ago), is the most intensively studied. It is also the most important, as if any period of the Last Glaciation has left its mark on the present distribution and composition of the vegetation, it is likely to be this one.

Figure 4 depicts New Zealand as it was at the height of this stadial. Sea levels had dropped by at least 120 m and thus North, South, and Stewart Islands were united by dry land, as were numerous offshore islands. Mean annual temperatures were at their lowest, and glaciers extended along the chain of the Southern Alps in the South Island. Glaciation was not heavy in the northernmost part of the South Island, and in the North Island was confined to small cirque glaciers in the Tararua Ranges (Stevens 1974) and on the Tongariro Volcanoes (Mathews 1967, McGlone & Topping 1977). Soons (1979) estimates that the depression of snowline in central South Island was of the order of 830–850 m, which corresponds to a depression of annual temperatures of about 4.5°C, and this value appears to be of approximately the right order for other areas of the country (McGlone & Topping 1983, McGlone & Bathgate 1983).

In the South Island the peak of the glaciation was associated with the construction of broad outwash plains by debris filled rivers, and deposition of loess over much of the eastern side of both islands (McCraw 1975, Bruce 1973). Erosion occurred on steep to moderate slopes throughout the South Island northwards to the Waikato Basin. Increased load of shattered material from the eroding uplands is reflected in the often spectacular flights of terraces, large alluvial plains, and outwash fans in many of the major river systems. Dunes were activated or formed in some areas, for example in Taranaki (Neall 1975). A result of heightened erosion and deposition during the glacial maximum has been that a very large proportion of soils in New Zealand — especially in southern and upland areas — date from this time or later. As far as the vegetation is concerned, fertility was vastly increased by an abundance of fresh soils.

Pollen diagrams dating to the glacial maximum reveal a landscape in which grassland and shrubland dominated in the uplands, and over broad swaths of the lowlands (Moar & Suggate 1979; McIntyre 1970; Mildenhall 1973; McGlone & Topping 1983; McGlone, Neall & Pillans 1984; McGlone, Nelson & Hume 1978). How abundant forest was during the glacial maximum is difficult to say, as most of the sites from which our information is derived are in areas of rapid accumulation of sediments which are likely also to be sparsely vegetated. In some regions, such as the eastern side of the South Island (Moar 1980), tree pollen is virtually absent, supporting the conclusion that forest was exceedingly restricted. In other regions such as western South Island and North Island, variable but often high levels of *Nothofagus* pollen are recorded, in particular *N. menziesii*, which was probably the most abundant tree for most of the period. Given that *Nothofagus* pollen is among the best distributed in the country (Macphail & McQueen 1983), it is highly likely that *Nothofagus* forest was scattered in isolated, favourable sites throughout largely grass and shrubland dominated landscapes. Present evidence suggests that hilly terrain may have provided more favourable microclimate sites, and thus had more extensive forest (McGlone, Howorth & Pullar 1984). Podocarp pollen is so rare that there can only have been extremely small, fragmented areas of podocarp-hardwood forest. The present distinction between the wetter western half of the country and the drier, more drought-prone east seems to have been maintained, as shrublands seem to have been more dense and variable in the west, and organic deposits far more frequent (Moar & Suggate 1979).

The open, shrub and grassland dominated landscapes of the glacial maximum cannot be interpreted in terms of postglacial vegetation patterns. Even given a depression of annual temperatures of close to 5°C, the limit to tree growth would have been sufficiently high that forest should have, if this had been the only change, covered lowland and montane regions of the North Island, and the lowlands of the South Island. It is therefore probable that other factors such as strong, constant winds, episodic drought, and freezing air masses moving up from the polar region acted to confine forest to the most sheltered and climatically favoured sites.

Abrupt amelioration of the climate began c. 14 000 years ago; forest spread in the North Island

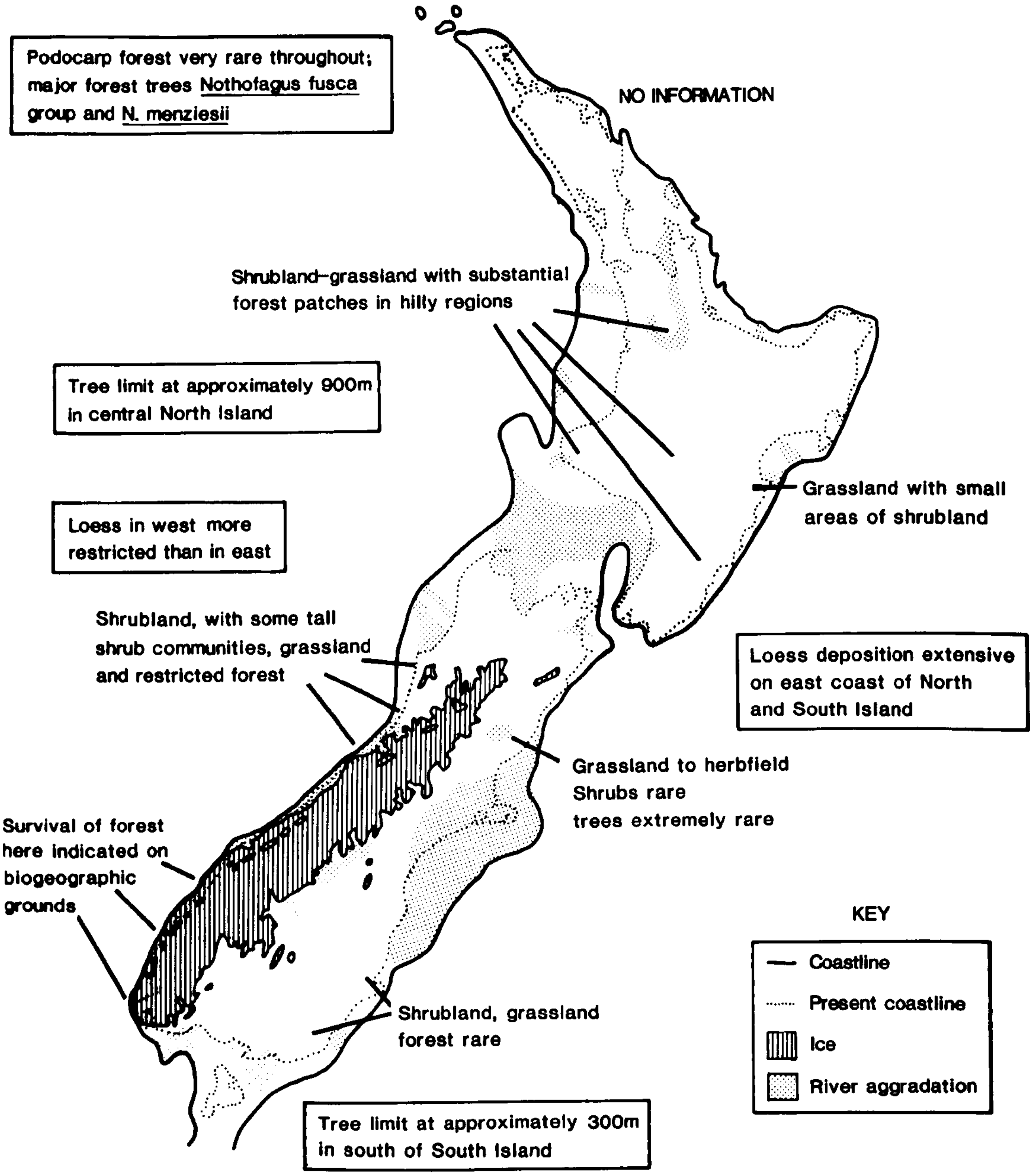

Fig. 4 New Zealand at the height of the Last Glaciation. Base map after Suggate et al. (1978).

both in lowland and upland sites (McGlone 1983a) and, by 12 000 years ago, all but the Wellington region was covered with podocarp-hardwood dominant forest. At around 12 000 years ago, shrubland began to replace the previously more abundant grasslands in the South Island (McIntyre & McKellar 1970, Moar 1971, McGlone & Bathgate 1983). At 10 000 years ago a major climatic amelioration led to the abrupt expansion of forest in the southern tip of the North Island and all but the driest eastern districts of the South Island (Mildenhall & Moore 1983, Moar 1971). In the North Island, there was a significant shift in the composition of the late glacial podocarp forest as *Dacrydium cupressinum* and warm temperate elements such as *Ascarina lucida* became abundant.

There are several points worth stressing about the late glacial afforestation of New Zealand (McGlone 1983a). First, there was apparently no steady north to south progression of forest; nor was there earlier afforestation in the lowlands. Afforestation occurred at roughly the same time throughout a district, regardless of latitude and altitude. Second, the change from grassland-shrubland to forest occurred with surprising abruptness both at an individual site and throughout a large region, such as the South Island. From available dates, it seems as though the afforestation of the South Island may have taken something in the order of only 500 years. Third, there is no hint in most areas of any progression from a shrubland phase through forests typical of high altitudes to lowland forest types. Instead, podocarp-hardwood forest seems to have directly replaced the previously dominant non-forest vegetation. In the North Island, these podocarp-hardwood forests had elements such as *Libocedrus* and *Nothofagus menziesii* during the late glacial, but these appear not to have been dominant at any stage. In fact, at 10 000 years ago, *Nothofagus* forest was less common than it was before and has been since.

The conclusion which can be drawn from the suddeness with which forest reoccupied the landscape, and the lack of migratory waves or extended successions, is that podocarp-hardwood forest was close to nearly every site yet investigated. Survival of some forest throughout New Zealand has been proposed on biogeographic grounds, particularly as regards the *Nothofagus* species which are reputedly slow movers (Nicholls 1963, P. Wardle 1963). If *Podocarpus spicatus* and *Ascarina lucida* could survive the glacial maximum in the southern regions of New Zealand, there is every reason to suppose that nearly all other southern trees and shrubs could also. It therefore seems that this model of widespread survival of forest trees can be expanded to cover nearly every plant at present resident within a region.

During the early part of the postglacial (10 000 to 7 000 years ago) mild, temperate climates permitted the growth of podocarp-hardwood forest throughout the country and at all altitudes with very few exceptions. By 7 000 years ago change had begun with the population growth of *Nothofagus* in upland regions of both the North and South Islands (Moar 1967, 1971; Russell 1982), and increasing restriction of *Ascarina*, *Dacrydium cupressinum*, and presumably other podocarp-hardwood species of mild wet climates (McGlone & Moar 1977). In the north of the North Island, *Agathis australis* populations began to expand (McGlone, Nelson & Todd 1984). These changes continued to affect forest in nearly all parts of the country until at least 1000 years ago, when the effects of human interference blur the picture (McGlone 1983b).

The changes in both lowland and upland forests which occurred during the latter half of the postglacial are almost certainly not a consequence of migration of plants back to areas from which they had been excluded during the glaciation. Rather, it was the result of increasing population size of plants better adapted to withstand the stresses of a deteriorating, windier, cooler and more continental climate which has characterised the last 7000 years (McGlone & Bathgate 1983; McGlone, Nelson & Todd 1984).

Several general conclusions can be made about the Last Glaciation and the present postglacial cycle. First, sequences observed appear to follow the general pattern noted in older Quaternary deposits: podocarp-hardwood forest dominates during the early phase of a climatic amelioration; in the latter phases, *Nothofagus* and subalpine forest types spread, eventually giving away to shrubland and grassland. Only in central Westland (Moar pers. comm. 1984) has an interglacial sequence terminated by the passing of podocarp-hardwood forest directly through to shrubland and grassland communities. Second, during the most severe glacial events, the forest flora of a region is not eliminated, but is reduced to very small patches in an otherwise shrubland and grassland dominated landscape. Third, some plants extend their range during a glaciation, examples being *Nothofagus menziesii* and *Phyllocladus alpinus*, and are eliminated during the abrupt climatic amelioration and reafforestation which concludes a glaciation. Others are confined during postglacial periods to upland areas, or exposed sites, and poor soils where competition from the dominant lowland forest communities is non-existent or weak.

If the above statements are accepted, it can be seen that there is no reason to believe that the flora of any region has recently arrived, or is in the process of rapid floristic alteration. Changing climates and edaphic conditions favour one group of plants over another, but the composition of the flora apparently remains more or less static with only minimal floristic change from one glacial-interglacial cycle to another.

EXPLANATIONS FOR THE DISTRIBUTION OF NEW ZEALAND PLANTS

In general terms, we may speak of two floras: there is the largely lowland - montane forest flora; and there is the largely montane - alpine non-forest flora. To which of these a species belongs has profound influence on when and where it is capable of spreading or surviving.

At present, and by extension during any interglaciation, the forest flora is more or less continuous. Cook Strait and Foveaux Strait are barriers to north-south spread, and the Southern Alps are a narrow east-west barrier for about half the length of the South Island. Otherwise there are few significant geographic barriers. By and large, each area of lowland forest is connected to another, or separated by minor barriers such as rivers. In contrast, upland habitats are extremely fragmented in the North Island and, with the exception of the central system of the Southern Alps, cut into separate upland blocks in the South Island.

It is likely that this pattern of extensive lowland forest communities and fragmented upland non-forest communities was reversed during the glaciations. Many of the generalist upland species must have had greatly extended ranges, while forest was confined to very small patches, separated by ice, unstable slopes, large braided rivers, and wide extents of exposed, treeless plains. During at least the last 2 million years, and almost certainly for several million years before that, there has therefore been regular alternation in both dominance, and degree of connectedness of these forest and non-forest components of the flora. The fact that many New Zealand plants have wide distributions, in which most areas providing suitable habitats are occupied, is a consequence of the opportunity which they have had to spread by connected land routes at some point in the course of a glacial-interglacial cycle.

It must be stressed that environmental factors appear to account in a reasonably straightforward manner for the distribution of most species in New Zealand. The southern limit of many northern species at close to 38°S where the warmer northern climate gives way to a cooler southern climate being a good example (Garnier 1958). However, as shown in the last section, there are features of the distribution of some New Zealand plants which are not

the ecological requirements of the plants, broad climatic zone, nor geography can predict where the plants can be found. These features are:

(1) concentrations of endemics in certain regions, and their paucity in others;
(2) long-distance disjunctions of species, or groups of closely related species;
(3) the abrupt halt of many species at approximately the same boundary, despite the absence of substantial geographic or climatic barriers, and the apparent ineffectiveness of seemingly major barriers.

In the South Island and the southern North Island both endemics and long-distance disjunctions tend to be of montane to alpine non-forest species, whereas in the northern North Island, most are forest trees and shrubs of lowland to montane habitats. Both endemics and long-distance disjunctions are centred on the same regions.

These features of the distribution of New Zealand plants must be explained by any hypothesis dealing with biogeographical patterns. It is, of course, easy to provide *ad hoc* and mostly untestable explanations by appeal to special circumstances related to an individual taxon's ecology, means of dispersal, or postulated history. Thus, the distribution of *Metrosideros parkinsonii*, which occurs on Little Barrier Island in the far north and in a limited area of north-west South Island, is suggested by Carlquist (1965) to be a result of seed dispersal by petrels which have nesting sites in these two areas. Such special appeals — however valid they may appear to be for a given taxon — cannot hope to explain patterns which are shared by many species of differing ecology and means of dispersal. In these cases long-distance dispersal can be discounted as a satisfactory interpretation of the data.

If long-distance dispersal is considered improbable as an explanation of shared disjunction pattens, there appear to be only two other possibilities:

(1) Plants may have achieved their distribution by population spread during times when there existed a more continuous favourable habitat;
(2) or the plants may have once occupied a continuous block of land which has since split and separated.

Explanations for concentrations of endemics in a particular region include four options:

(1) The endemics may be of very recent origin, that is, have arisen during the postglacial and have lacked time to spread;
(2) they may have been restricted by extinction events in surrounding regions, and are in the course of reoccupying their range;
(3) they may have their originally restricted range, and be incapable of further spread;

part of a once more extensive range, and be incapable of spread.

Options 1 and 2 do not require that the plants involved be ecologically or environmentally restricted; options 3 and 4 do require restriction to spread. Option 1, that the endemics are of very recent origin, seems improbable in most cases, and will not be discussed further.

There are two current hypotheses which seek to explain the distribution of the New Zealand biota. First, there is the *glacial refugia* hypothesis elaborated by Wardle (1963) and Burrows (1965) particularly in relation to plants, but also adopted to explain animal distributions (e.g., cicadas *in* Fleming 1975). Second, there is a hypothesis which is based on late Cenozoic tectonic change in the landscape. Climo (1975) was the first in New Zealand to make extensive use of tectonism to explain biogeographic distributions in his review of landsnail biology, although Lee (1959) suggested marine transgression had been an important factor in earthworm biogeography and Fleming (1975) made similar suggestions with regard to the bird genus *Nestor* (kaka and kea). Here I extend this hypothesis — which I call the *tectonic* hypothesis — to higher plants.

Glacial refugia hypothesis

The glacial refugia hypothesis assumes that at some point before the peak cold of the Last Glaciation, endemic and disjunct plant taxa had a wider or more continuous distribution. Expansion of ice with the onset of the glacial maximum at around 25 000 years ago physically excluded plants from many of the mountainous regions of the Southern Alps, particularly in central and southern regions. In lowland ice-free regions which are now characterised by low numbers of endemics — such as the Canterbury Plains, and the Wellington region — it is claimed that harsh climatic conditions and unstable land surfaces effectively eliminated a wide range of plants. As a result, it is suggested plants tended to become concentrated in refugia. In the South Island these putative refugia were scattered along the lowered coastline and coastal ranges of north-west Nelson, Marlborough, southern Fiordland, Southland, and south Otago. In the North Island, major refugia are thought to have occurred north of latitude 38–39°S, and in particular on peninsulas and islands now submerged or created by the postglacial rise in sea level.

With the warming which occurred at the end of the Last Glaciation between 14 000 and 10 000 years ago, plants spread out from refugia at rates controlled by their dispersal ability and competition from already established vegetation. An important corollary of this hypothesis is that many species forced from certain regions during the glaciation have not yet recovered their original distributions, and are presumably in the course of doing so. Both disjunctions, and endemism are therefore related to relatively recent extinctions in endemic-poor regions.

Some adjustment to plant ranges during the postglacial are claimed to be a result of changing postglacial climates. For instance, disjunctions such as those of *Phyllocladus trichomanoides* and *Astelia trinervia* (northern North Island and north-west Nelson), and *Beilschmiedia tawa*, *Nestegis cunninghamii*, and *Rhopalostylis sapida* (widely scattered populations on the northeastern coast of the South Island) involve warmth-demanding lowland species. These are considered to have been too tender to survive the rigours of the Last Glaciation in the South Island. It has been suggested that there was a range expansion of these species at the height of the postglacial warm period (9000–7000 years ago), and that subsequent deterioration of the climate during the late postglacial resulted in contraction of range (Wardle 1963, Burrows 1965). Burrows (1965) suggests that 'tender kauri associate species' — presumably *Phyllocladus trichomanoides* and *Astelia trinervia* — and probably *Agathis australis* itself, had migrated as far south as north-west Nelson during the postglacial, only to become extinct over most of their range as climates cooled during the late postglacial.

Burrows (1965) notes also a group of disjunct species in the South Island which he regards as having suffered fragmentation of range during a shift towards aridity in the late postglacial. Fire may have also played a role in the fragmentation of once continuous ranges, although Burrows regards it as secondary to climatic change.

A final modification to the glacial refugia hypothesis is that volcanism in the central North Island may have limited the range of some northern plants (Burrows 1965).

Objections to the glacial refugia hypothesis

The most fundamental objection to the glacial refugia hypothesis is that it takes as its basic proposition that there are no environmental barriers limiting the present distributions of many endemic plants. Or, to put it another way, as far as the plants are concerned, endemic-rich and endemic-poor regions are environmentally equivalent. If this proposition is accepted, naturally the problem of endemics is reduced to a search for historic factors which have restricted them. However, as will be discussed below, there is reason to believe that endemic-poor and endemic-rich regions do differ in the totality of their environmental characteristics. A further basic objection is that many endemic

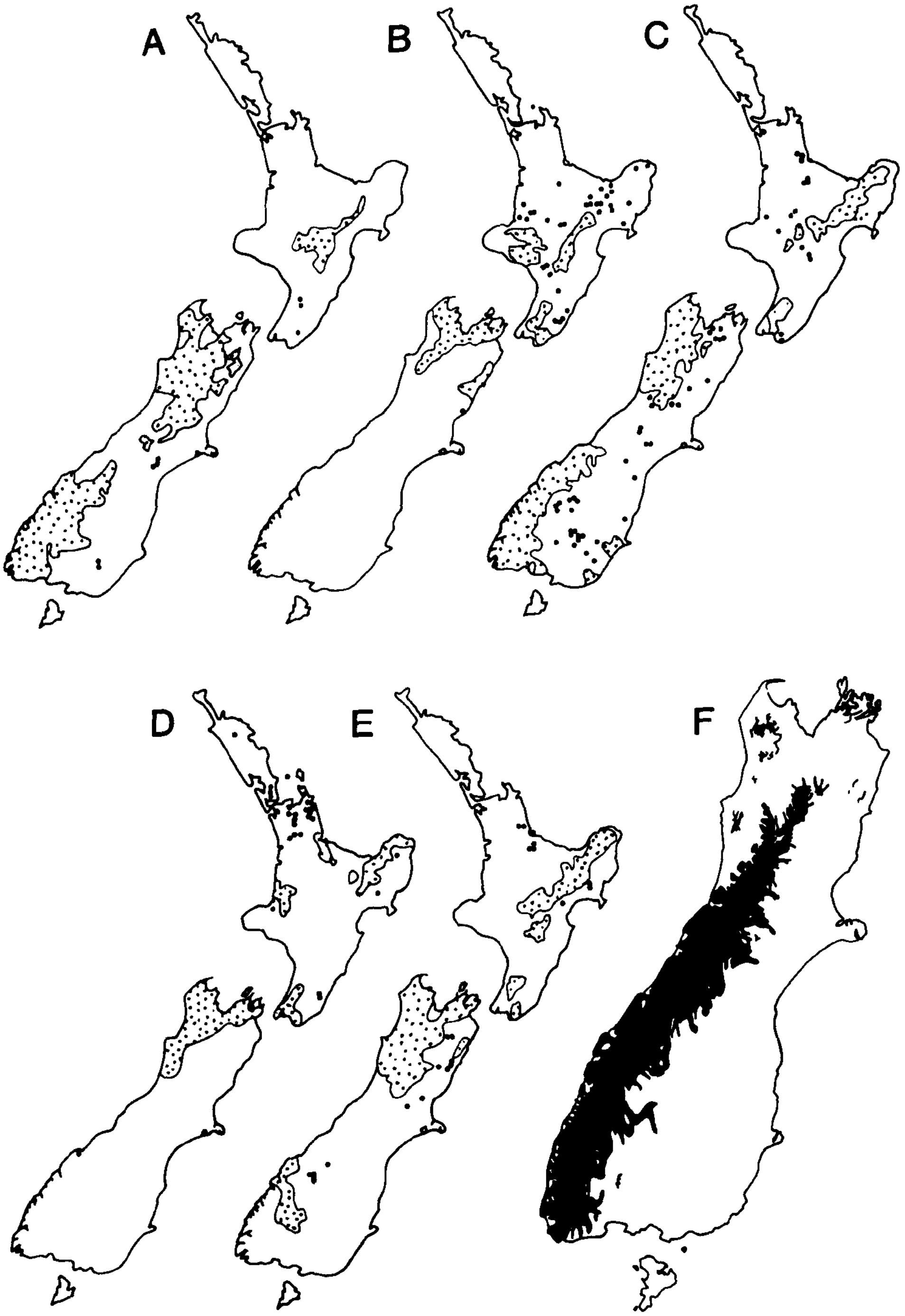

Fig. 5 Distribution of *Nothofagus* species; after J. Wardle (1984).
(A) *N. solandri* var. *cliffortioides*; (B) *N. solandri* var. *solandri*; (C) *N. menziesii*; (D) *N. truncata*; (E) *N. fusca*;
(F) Maximum extent of ice at the height of the Last Glaciation.

plants show no relationship to ice distribution, or any potential refugium. For instance, *Aciphylla leighii* occurs only on the Darran mountain range in Fiordland, which was heavily glaciated. Therefore, *Aciphylla leighii* must have already spread from some ice-free area, in which it now no longer occurs, to its present site. Others, for example, *Clematis marmoraria*, are found in a single locality or in a very few closely separated locations. Such limited distributions which are, according to the glacial refugia hypothesis, within regions broadly favourable to the taxa involved, are difficult to ascribe to historic events dating back many thousands of years. It would seem more sensible to assume as a working hypothesis that such plants have specialised requirements and are thus confined to scattered patches of suitable habitats within a broader region which contains few such suitable sites.

A corollary of the hypothesis that endemic plants were restricted by glacial ice cover and climates, is that plants so restrained are now spreading, or have spread. Only fossil evidence can give unequivocal answers to such questions. There is sufficient evidence for two taxa to attempt a preliminary test of the hypothesis.

Nothofagus is a pivotal taxon in the glacial refugia hypothesis. The celebrated Westland 'beech gap' is of major biogeographic importance because of the physiognomic dominance of *Nothofagus* in northern and southern South Island forests. Figure 5 shows the distributions of the four *Nothofagus* species in relation to the maximum extent of ice. Several features are immediately apparent. Although all the *Nothofagus* species are absent from central Westland, and this is undoubtedly the area of maximum and most complete ice cover, there are other regions where *Nothofagus* is absent, which had neither extensive ice cover at any time during the Pleistocene, nor can be expected to have had more severe than normal glacial climates. Mount Egmont and the Pouakai Range lack *Nothofagus*, and there is a large gap centred on the Manawatu Gorge in southern North Island in which all the *Nothofagus* species are either rare or absent. Besides the Westland gap, there is also a wide area without *Nothofagus* in northern Otago and South Canterbury.

Although the Westland *Nothofagus* gap is complete for at least 150 km, *Nothofagus solandri* and *Nothofagus menziesii* have isolated stations on the eastern side of the main ranges, and the gap is therefore only partial. At no point does the maximum extent of Last Glaciation ice (see Fig. 4 & 5) and modern *Nothofagus* distribution show a close relationship. *Nothofagus solandri* and *N. menziesii* are, for instance, as abundant in the once heavily ice covered ranges of Fiordland as they are in the much less extensively ice covered Nelson and Marlborough mountains. The argument that ice affected the distribution of *Nothofagus* cannot be sustained solely on this type of evidence.

There have been two studies which have claimed to show that *Nothofagus* is slowly migrating back into areas from which it had been excluded. This type of evidence is important as, if it is sustained, it would show that there is no present environmental barrier to the spread of *Nothofagus*, and the present distribution of *Nothofagus* could reflect postglacial migration from a relatively small number of refugia.

Wardle (1980) studied the distribution of *Nothofagus* in southern Westland, at the southern boundary to the *Nothofagus* gap. Palynological evidence was consistent with a model in which *Nothofagus* populations had been growing since around 7500 years ago. However, this population growth had occurred earlier (or at the same time) in inland, previously totally ice-covered locations, than it had at coastal sites where ice cover had been less extensive. *Nothofagus menziesii* populations at their range limit in south Westland consisted of younger trees than those populations inside the margin, a result interpreted as evidence for a spreading margin.

It is difficult to fit these results to a strict interpretation of the glacial refugia hypothesis as considerable mobility must be attributed to *Nothofagus*. Wardle (1980) suggests that there was an initial expansion of *Nothofagus menziesii* inland from coastal refugia at the end of the Last Glaciation, and slow population growth and range extension have taken place ever since. He also states that this is unlikely to have occurred further north in central Westland, as the smooth nature of the glacial shoreline cannot have provided sufficient suitable locations for *Nothofagus* survival.

The south Westland evidence of Wardle (1980) is just as compatible with an hypothesis that a combination of edaphic and climatic factors are restricting *Nothofagus menziesii*. Certainly the fossil evidence suggests the *Nothofagus* population is growing, but gives no evidence as to whether or not significant range expansion is taking place. Population studies at boundary margins are largely irrelevant as evidence for long-term spread which may have taken 12 000 years or more. Present distribution may have been achieved rapidly at the end of the Last Glaciation, stabilised in the mild early postglacial, and subsequent changes towards a cooler climate in the later postglacial permitted population growth.

June (1982) studied the northern margin of the *Nothofagus* gap in northern Westland. From his analysis of the

Nothofagus forests and isolated stands beyond the main distribution, he came to the conclusion that *Nothofagus* had spread at slow rates from refugia just outside the main glacier covered region. The extremely slow rates of spread he calculated (c. 0.1 m/yr), necessitated distributional jumps, at some time since the Last Glaciation, to achieve isolated distributions inside the margin of the glacial maximum ice cover.

Fossil evidence, as in south Westland, does not support all of June's conclusions. Pocknall (1980) shows in a pollen diagram close to the *Nothofagus* limit in North Westland, that *Nothofagus* pollen was at steady, low levels from at least 5000 years ago, and then abruptly increased to present day levels at around 2500 years ago. Such evidence is more compatible with a local presence of *Nothofagus* for many years, followed by population growth, than it is to a pattern of slow migration from refugia.

A better model is that *Nothofagus* survived in many locations on the western side of the South Island, both coastal and inland. At the end of the glaciation, as the ice retreated, saltationary spread of *Nothofagus* occurred. These nuclei acted as centres for spread during the late postglacial when favourable climates for *Nothofagus* became widespread. In central Westland the mild postglacial climate together with unsuitable soil conditions did not permit even limited survival of *Nothofagus* stands. Recent pollen evidence from lowland Taranaki (McGlone unpublished) has established that *Nothofagus menziesii* was eliminated from that region during the climatic amelioration which terminated the Last Glaciation and it is highly probable that a similar elimination occurred in central Westland.

On the eastern side of the Southern Alps a similar pattern has emerged. Scattered stands of *Nothofagus* in the central eastern foothills show that *Nothofagus* has maintained a presence for many thousands of years without appreciable spread. Pollen evidence from within the *Nothofagus*-clad northeastern ranges shows that *Nothofagus* was rare until it began a period of sustained population growth from 7000 to 4000 years ago (Moar 1971, Russell 1982, Burrows 1983). However, there is no discernable pattern of spread from north to south, as would be expected on the basis of the glacial refugia model; rather spread and growth have occurred at various times within the region. In both the central Westland and central eastern *Nothofagus*-free regions it would seem that the primary reason for the absence of *Nothofagus* is the presence of better adapted plant communities. These only give way when climatic change shifts the bal-

Agathis australis is another plant which has been suspected of being limited by glacial conditions in the southern half of the North Island, and is thus also in the process of slow migration south. This hypothesis has already been questioned on the basis of distributional and ecological evidence (Barton 1983). *Agathis* pollen has been identified in middle Last Glaciation sediments from the Bay of Plenty (McGlone, Howorth & Pullar 1984). Recent pollen evidence from the Waikato Basin (McGlone, Nelson & Todd 1984) and Auckland City (McGlone unpublished) reveal that *Agathis* rose to prominence about the same time (6000 years ago) in both regions, and therefore most likely from local populations. There is absolutely no evidence for an early postglacial spread south and subsequent retreat. In fact, the late timing of its population growth phase suggests that it is favoured by the cooler, more variable climates which have characterised the late postglacial (McGlone 1983a).

There is insufficient fossil evidence for it ever to be feasible to test more than a handful of the plant species involved in disjunct distributions. But the evidence for *Nothofagus* and *Agathis*, as well as the general nature of the reoccupation of the New Zealand landscape by forest at the end of the Last Glaciation, strongly supports the more conservative hypothesis that there have been no great changes in the range of most plant species since the peak of the Last Glaciation. Plants were eliminated by the postglacial rise of sea level, and also there was what appears to have been rapid expansion into regions which were largely covered by ice during the glaciation but these movements need never have been greater than 30–50 km. However, large scale migratory movements lack any confirmatory evidence.

The problem of lack of endemics in the southern half of the North Island cannot be solved by appeal to ice cover during the glacial maximum, as ice was limited to a very few corrie glaciers in the higher points of the Tararua Ranges (Stevens 1974). Wardle (1963) cites the lower altitude of the tree line in the Wellington region when compared with regions north and south, and suggests that if this relative depression was sustained during the Last Glaciation, that this alone could explain the absence of many plants, and in particular endemic plants, from the southern North Island. McQueen & Mildenhall (1983) give a list of tree and shrub species absent close to Wellington, but which are present to both the north and south (*Nothofagus solandri* var. *cliffortioides*, *Dacrydium bidwillii*, *D. biforme*, *Phyllocladus alpinus*), and which were present 19 000 years ago, just before the period of most intense cold. They suggest that these hardy woody by exceptionally harsh and windy climates created by enhanced orographic funnelling of wind at the glacial maximum.

Although there was in all probability a greater relative lowering of temperatures in the Wellington region than to the north and south, and much greater wind speeds, there is no reason to assume that these conditions would have been extreme enough to eliminate hardy plants from sheltered and sunny locations. And if they did, it is then surprising that a tree such as *Nothofagus truncata* which is definitely less hardy, apparently survived unscathed. The crucial information which is missing is the date that these hardy, cold-tolerant species became extinct in the Wellington region. It seems more probable that it was the rapid amelioration of climate which affected the Wellington region at around 10 000 years ago (Mildenhall & Moore 1983) which eliminated these cold-tolerant plants by increasing the competitive pressure exerted by podocarp-hardwood communities.

Even though glacial climates were likely to have been more severe in the general area of Cook Strait, the endemic-poor area extends much further north to latitude 39°S. These more northerly regions have higher tree lines, and are unlikely to have shared the extreme orographic effects postulated for the Wellington region. The hypothesis of exceptional climatic stress in the Wellington region during the Last Glaciation thus cannot contribute to a solution of the wider problem of the distribution of endemic plants.

Finally, the glacial refugia hypothesis cannot explain why most of the restricted endemic plants and disjunct taxa in the South Island are primarily herbs and shrubs of non-forested upland habitats. Many, moreover, are alpine or subalpine. In contrast, very few lowland or montane trees and shrubs are involved in these patterns, the paradoxical exceptions being the *Nothofagus* group which contains the hardiest trees in the flora. It seems intuitively wrong that a cold, glacial period should have such a disproportionately strong effect in restricting alpine and subalpine plant distributions.

The glacial refugia model, as put forward by Wardle (1963) and Burrows (1965) appears to have, as I have shown above, serious flaws. Unless future work (1) demonstrates close correlations between plant distributions and ice-free refugia, (2) can substantiate range expansion of supposedly restricted taxa, or (3) shows that dispersal abilities of restricted plants are markedly less than widely dispersed relatives, the glacial refugia hypothesis must be rejected as a general explanation for endemism and disjunction.

The tectonic hypothesis

The Pleistocene history of the vegetation gives little support for any concept of great mobility in the flora. For the purposes of this hypothesis it will be assumed that, unless there is strong evidence to the contrary, plants growing in a given region have been there for a long time, and in most cases for at least several glacial-interglacial cycles. I propose that floras of given regions are not recent collections of species, but rather have developed slowly as a result of migration and extinction over a very long time.

If the static nature of regional floras is assumed, it must be further asserted that there are environmental reasons for plants failing to extend their present ranges. In most cases these environmental factors will act through competitive pressure from better adapted plants. Proving or disproving this assertion will be difficult. Presence of apparently suitable, but scattered habitats for a given species within a region from which it is absent, is not sufficient reason for rejecting the assertion. There are limits to the dispersal range of most plants, and minimal areas are necessary to ensure survival. Each region has a different set of environmental factors and floristic composition; the most parsimonious explanation for a restricted distribution is that it is related to these factors.

Even if these assertions are taken as correct, they do not of themselves explain present plant distributions; they merely indicate how they are maintained. However, there are broad features of the geology of New Zealand which give clues as to how these regional floras came into existence. If the regions of lowest endemic concentration are taken, that is, the southern half of the North Island, and the central portion of the South Island, it can be seen that, although they have little in common either geologically or topographically, they share a relatively recent origin. The hypothesis which I will develop here is that, despite transformations of the land surface since the Oligocene, there are relatively stable areas which have either developed or retained endemic-rich floras. There are also recent, actively uplifting, unstable areas, which have not. Disjunctions and vicariant distributions are related mainly to these factors, although there is also an important set of distributions which may also be a consequence of a wider range for glacially adapted plants during glaciations.

New Zealand lies on the boundary of the Pacific and Indian Plates (Fig. 6), and this feature has controlled the geological structure of the region for at least the last 40 m.y. (Lewis 1980). Horizontal movement of the plates, with the Indian Plate moving northwards relative to the Pacific Plate, has totalled close to 1000 km during this time. Not all movement has resulted in shearing of one plate past

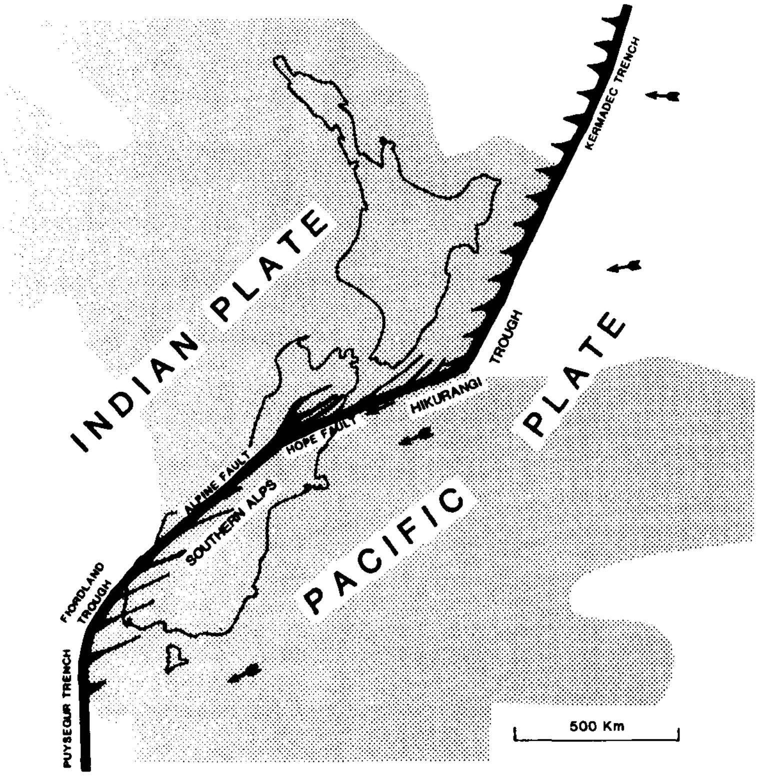

Fig. 6 Tectonic structure of New Zealand; after Lewis (1980).

the other; oblique relative movement has led to convergence and thus compression, uplift, and subduction, especially during the last 10 m.y. (Lewis 1980). In the North Island, dense oceanic crust of the Pacific Plate is sinking under the lighter continental crust of the Indian Plate. In the South Island, the boundary cuts through light continental crust on both sides, and the leading edge of the Pacific Plate is rising up on the Indian Plate to form the Southern Alps. South of Fiordland, dense oceanic crust of the Indian Plate is being subducted beneath the Pacific Plate.

The Alpine Fault which trends NE–SW along the western side of the South Island is the clearest expression of the plate boundary in New Zealand. Offsets of once contiguous rocks in Fiordland and north-west South Island reveal that there has been at least 480 km of dextral horizontal displacement along the fault. Exactly where the plate boundary runs in the North Island is disputed, but most consider it to lie offshore in the east, along the Hikurangi Trench (Walcott 1984).

Horizontal movement parallel to the plate boundary has accelerated since the end of the Oligocene towards the present, and as much as 330 km of displacement may have occurred over the last 10 m.y. (Walcott 1979). As a consequence, the east coast of the North and South Islands has gradually shifted into its present position, either from an initial position further north, alongside Northland and Coromandel (Ballance & Sporli 1979) or out to the east as shown here (Walcott 1984). Movement along the Alpine Fault has moved the northwest Nelson and Fiordland blocks apart, and stretched out the rocks of the intermediate region as a narrow zone of greywackes and schists (Walcott 1979).

These massive and geologically recent movements have not been confined solely to the immediate region of the plate boundary, but faulting, rifting, uplift, and subsidence has occurred in a broad band on both sides. A consequence has been uplift of mountain ranges or transgression of shallow seas as movement proceeded. These changes are intimately connected with the development of the present day distribution of plants.

After the height of the marine transgression had passed in the late Oligocene, a broad strip of land emerged down the axis of New Zealand (Fig. 7a). Coarse debris from the late Oligocene–early Miocene in South Island basins to the west of the Alpine Fault and to the east in the region of the Kaikoura Ranges, indicates that a broad zone of uplift and erosion had commenced (Katz 1979). Uplift of the

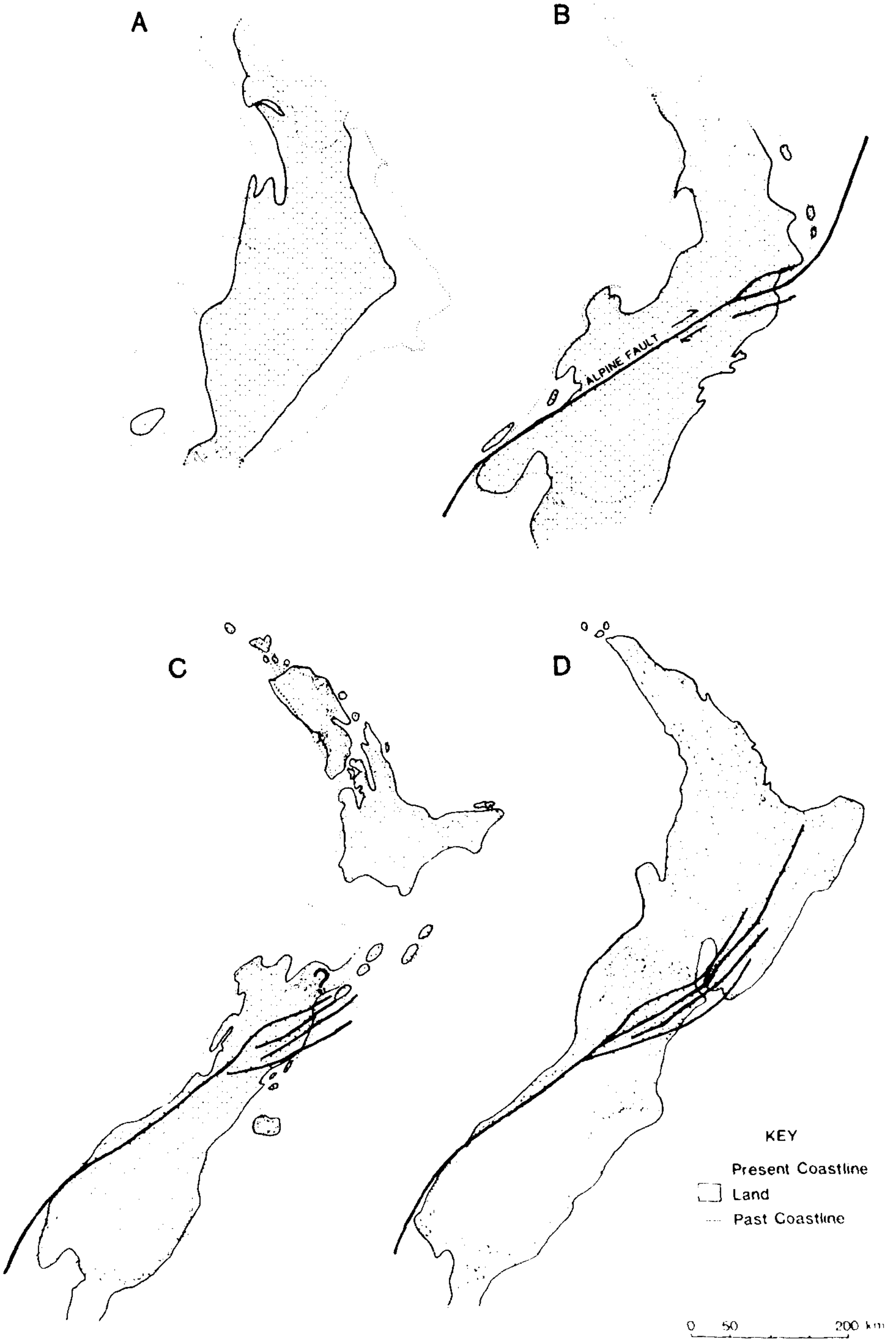

Fig. 7 Palaeographic maps of New Zealand: (A) Late Oligocene; (B) Late Miocene; (C) Pliocene; (D) 20 000 years ago. Maps (A) and (B) after Kamp (unpublished); (C) and (D) after Suggate et al. (1978).

Southern Alps proper may have begun as early as 10 m.y. ago (Fig. 7b), as compression increased across New Zealand with a shift in the relative movements of the plates (Walcott 1984). Uplift intensified at around 5 m.y. ago (Fig. 7c) and was concentrated within the present axial Southern Alp system (Katz 1979). As the mountains rose, they intercepted more rain and were more quickly eroded, a steady state being achieved for a given uplift rate (Wellman 1979). At the Pliocene-Pleistocene boundary (1.7 m.y.) a yet further intensification of the uplift rate occurred and the modern form of the Southern Alps came into being.

Events in the North Island have followed a substantially different course. Northland has been more stable than most other regions of New Zealand since its emergence during the Oligocene (Fig. 7a), although only the western extremities have been continuously above sea level. In the Pliocene (c. 5 m.y.) Northland formed an archipelago, with a narrow strait through the Auckland area, and a rather broader strait, linked by several islands, which isolated North Cape (Fig. 7c). Uplift in the Northland region has been slow and the climate warmer than more southerly regions, and it is thus characterised by deeply weathered soils (Ballance & Williams 1982).

The North Island north of latitude 39°S has had extensive land above sea level since the mid-Oligocene (Fig. 7). Major alteration of land surface has been connected with the opening of the Taupo Graben, a rift area running through the Bay of Plenty down to the Tongariro Volcanoes. Volcanism — beginning at around 0.75 m.y. ago (Healy 1982) — has covered large areas of the central North Island with ignimbrite sheets, and activity has continued to the present.

South of latitude 39°S, the emergence of land during the late Oligocene (Fig. 7a) was followed by subsidence in the late Miocene and early Pliocene (Katz 1979) in basins centred on the Wanganui region and Hawkes Bay–central Wairarapa (Fig. 7c). Land remained above sea level in the general area of Wellington–Tararua Ranges, and dry land possibly extended across to the Marlborough Sounds in the South Island. Eastern Wairarapa was initially a topographic high marked by an archipelago of small islands (Fig. 7c). At first, during the late Pliocene, there was a broad strait connecting Wanganui and Hawke Bay basins. As the rate of uplift increased, this strait was split into two by the emergence of land in the region of the Ruahine Ranges, forming northern (Kuripapango) and southern (Manawatu) seaways. Continuous land with a belt of coastal hills extended down the eastern margin of the Wairarapa–southern Hawkes Bay district. By the middle Pleistocene (c. 1 m.y. ago), sea had withdrawn from the eastern side of the southern North Island (Kamp 1982, Kamp & Vucetich 1982). The Wanganui Basin finally emerged above sea level somewhat later at around 400 000 y. ago, although lower sea levels during the glaciations (Fig. 7d) had resulted in repeated marine transgressions and regressions from at least 1 m.y. ago (Beu & Edwards 1984).

Although land was permanently emergent over most of the southern half of the North Island by 1 m.y. ago, the axial ranges in this region are much younger. Gravel conglomerates — indicating the rise of substantial hills — flooded into the southern North Island basins about 1 m.y. ago. However, measured uplift rates in the region suggest that rapid uplift giving rise to the present mountainous terrain may have occurred as late as 500 000 to 200 000 years ago (Ghani 1978).

The age of Cook Strait is uncertain; it may have formed sometime in the early Pleistocene (1.5 m.y. ago) (Kamp & Vucetich 1982), although some interpretations would place its formation at around 3 m.y. ago (Stevens 1974).

Taking this brief geological history as a basis, it is possible to develop a general narrative account of the development of the present day patterns of plant distributions. It is easier to do this if we deal with the lowland and upland floras separately, as they appear to have had very different histories.

As we have seen above, endemism in the northern half of the North Island is largely concentrated among trees and tall shrubs. With few exceptions, these plants belong to genera with few species (Millener 1960) and tend to be taxonomically isolated. It is reasonable to assume that, for the most part, the lowland tree and shrub flora is of considerable antiquity and represents the remnants of a very much richer and diverse middle Miocene assemblage, such as is hinted at in the fossil record (Pocknall & Mildenhall 1984). The current distribution limit of many trees and shrubs at approximately 39°S corresponds quite closely to the distribution of land at the height of the Pliocene marine transgression across the lower half of the North Island (Fig. 7c). Many shrubs and trees also halt at about 38°S, and this corresponds very approximately to the northern limit of intense Pleistocene volcanism although, as mentioned above, climatic factors are likely to be the controlling environmental influences here.

A group of plants halt close to latitude 39°S, but are then disjunct to the South Island (Table 1). Distributions such as these are very likely to reflect the disruption of a widespread Miocene flora by marine transgression. The taxa involved have several features in common. In the first place, most of them belong to groups with a long, rather than short history within New Zealand; nearly all of them have a fossil record at the generic level dating back to the Eocene or earlier (Mildenhall 1980). Conifers are, for instance, much more common in the group than would be expected on the basis of a random sample of the woody flora, as they make up about one quarter of the total. Most are plants which favour infertile, leached, or poorly drained soils. These disjunct taxa may reflect ecological conditions prevalent in New Zealand before the post-Miocene widespread uplift: that is, a landscape with an abundance of low-lying, poorly-drained, and highly infertile soils, but possibly with enough relief that development of a montane flora had begun to take place. We can speculate that this group represents a remnant of a once widespread Miocene flora which has been preferentially concentrated in the north of the North Island where conditions best resemble those under which it developed. Three possible factors may have played a role in this post-Miocene development.

(1) Progressively cooler and windier climates in the post-Miocene period may have eliminated cold intolerant plants from the South Island, a loss which would have accelerated during the early Pleistocene.

(2) Sensitivity to cold, windy conditions cannot explain the restriction of all northern endemics, as a number of them will grow also in the montane zone, for example, *Dracophyllum latifolium* and *Phyllocladus glaucus*, which indicates that cold and windiness are, not of themselves primarily restrictive. It is likely that the disruption and destruction of old, infertile, and leached lowland soils in the South Island during the creation of the Southern Alps played a crucial role in reducing and eliminating such taxa.

(3) Rapidly changing configurations of land and sea, and climatic fluctuations, may have put at a disadvantage trees and shrubs of forest habitats which were not adapted to a pioneering role. They may have lost their foothold within a region and have been unable to regain the scattered areas which remained potentially suitable for them.

I will now look at a set of distributions which may be read as a series, indicating the stages by which a taxon could be eliminated from southern regions (see Fig. 8). *Agathis australis* is now confined to areas north of about latitude 38°S (Ecroyd 1982). *Agathis* cf. *australis* was present in the south of the South Island during the Miocene (Fleming 1975) and fossil pollen of *Agathis* is found in (?glacial) lacustrine sediments near Wellington that are older than 340 000 years and younger than 520 000 years (Mildenhall 1984, pers. comm; in prep.). It seems probable that *Agathis* was widely spread in New Zealand during the Miocene, and at the time of the Pliocene sea strait formation was in the southern half of the North Island if not further south. Later, it became progressively confined to shrinking patches of stable, infertile soils and milder climates until, in an event possibly hastened by repeated glaciations, it became extinct in the south. Volcanism in the central North Island may have pushed it further north by destroying old soils and replacing them with fresh volcanic soils.

Phyllocladus trichomanoides (Fig. 8b) and *Astelia trinervia* are both common associates of *Agathis australis* in the north. They share a common distribution pattern, being both present north of approximately latitude 39°S, and then occurring in scattered stations in northwest Nelson. As with *Agathis*, they have been eliminated from the southern half of the North Island by the Pliocene strait. They may represent an intermediate stage, in that sufficient suitable soils and microclimates remain in the extremity of the South Island for their precarious survival. *Quintinia* (Fig. 8c) has a similar North Island distribution to that of *Agathis australis* and *Phyllocladus trichomanoides* and is presumably affected by the same factors. In the South Island it occurs only in a narrow coastal strip extending down the western side of the South Island from Wanganui Inlet in the north to Bruce Bay in South Westland. It favours infertile, poorly drained soils and wet climates, and is apparently limited further south by cool climates. *Quintinia* indicates a taxon which is certainly not close to extinction in the South Island, but relies for its continued existence on a rather narrow geographic and habitat range.

Not all of this putative Miocene group have faced extinction in the south. Some species have made their headquarters in the South Island, although they are restricted or absent from southern North Island. *Nothofagus truncata* — often associated with *Agathis* in the north of the North Island — has a scattered northern distribution with a distinct gap between the position of the ancient Kuripapango and Manawatu Straits in the southern North Island (Fig. 8d). It is found on old leached soils with warm microclimates in the Wellington region, and is abundant in northwestern South Island on similar sites (J. Wardle 1984). *N. truncata* has almost certainly been reduced from a once wider distribution in the south of the South Island. It occurs as a handful of small closely spaced stands on granitic outcrops in South Westland (June 1977).

In the tree dracophyllums (subgenus *Dracophyllum*), post-Miocene isolation may have led to the evolution of several species. *D. fiordense* has a distribution centred on Fiordland and south Westland, *D. townsonii* in northwestern South Island and *D. latifolium* in the North Island, north of latitude 39°S. Such a distribution suggests an ancestral species split into three lineages by the movement of the Fiordland block away from northwestern South Island, and the subsequent submergence of

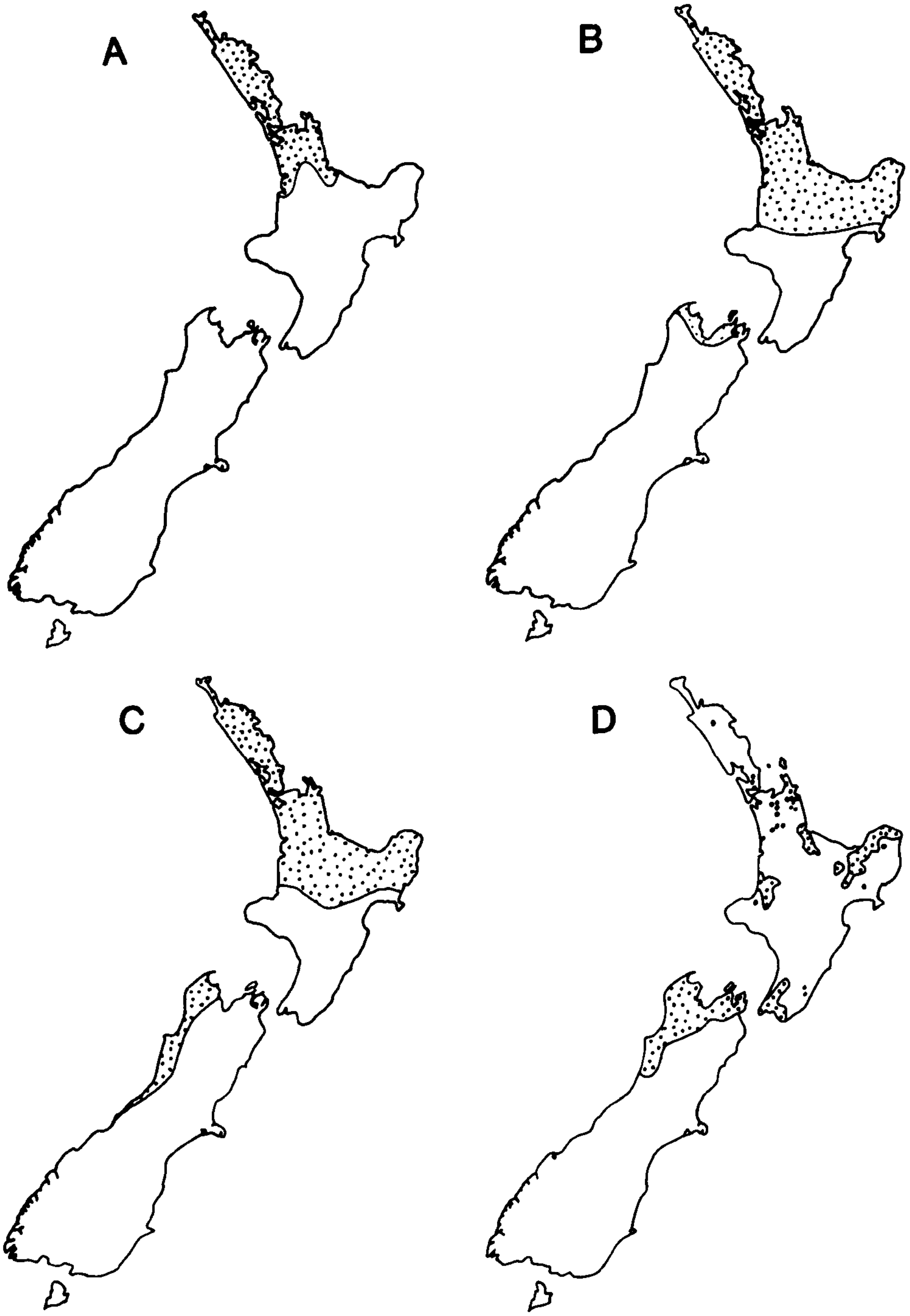

Fig. 8 Distributions of: (A) *Agathis australis*; (B) *Phyllocladus trichomanoides*; (C) *Quintinia serrata*; (D) *Nothofagus truncata*.

the southern North Island.

It is clear, therefore, that there were a variety of fates of the original constituents of the Miocene flora, although the main tendency was towards extinction in both the south and north, but with greater survivorship in the more northerly regions. There was thus a general depauperisation of the lowland and montane forest and tall shrub flora, a process which was only to a limited extend counteracted by the evolution of new tree and shrub species. It is this conservatism of the lowland and montane forest flora which ensures that it shows so clearly the imprint of post-Miocene events.

It must be stressed that a relatively small group of trees and shrubs have adapted well to the changed conditions, and therefore have virtually pandemic distributions. Trees such as *Dacrydium cupressinum, Weinmannia racemosa, Beilschmiedia tawa* have very broad ranges, and show no trace of having been influenced in a major way by ancient land and sea dispositions. Likewise, many small trees and shrubs such as *Fuchsia excorticata* and *Pseudopanax arboreus*, are found throughout.

A further aspect of the development of the forest flora is the presence of species pairs, one of predominantly southern and/or upland habitats, the other of northern or warm lowland sites. Examples are *Podocarpus hallii-P. totara; Weinmannia racemosa-W. sylvicola; Cyathea colensoi-C. smithii; Libocedrus bidwillii-L. plumosa;* and *Dacrydium bidwillii-D. kirkii.* Most of these species pairs are either parapatric or sympatric, but it is possible that their origin as distinct species was made possible by isolation within a cool, windy South Island, separated from the northern North Island landmass by the Pliocene sea strait. The present distribution of these species pairs may be possibly a result of two way exchange since the closure of the straits. A similar explanation has been proposed for the origin of the upland kea and lowland kaka species pair (Fleming 1975). A more complex explanation would call for isolation within the developing Pliocene-Pleistocene mountain chains giving rise to montane species, rather than the invoking the need for the large scale isolation within the marine-bisected Pliocene landmass.

Subalpine and alpine herb and low shrub species are concentrated in southern regions simply because that is where nearly all the suitable habitat is. The North Island upland flora is but a depauperate extension of the South Island flora, and has few endemic species. Nevertheless, there are aspects of the distribution of these plants which suggest that they reflect geological events.

Upland floras probably developed during the late Miocene-early Pliocene. It is likely that they include groups of plants which have had a long history of adaptation to leached, poorly drained and infertile sites where forest competition was slight (Wardle 1968). A certain proportion of upland species has arrived from extra-New Zealand sources (Dawson 1963, Raven 1973), although it is difficult to be certain if they were strictly alpine or subalpine plants at the time of arrival.

The first tectonic movements during the Miocene, which began to create steep hills and low mountain ranges, would not have at first created permanently treeless uplands. However, there would have been a greatly increased number of sites with little or no forest, such as exposed ridges, rockfalls, cliff-faces, and boulder-edged and coarse-bedded streams and rivers. Concurrent climatic changes leading to cooler temperatures and increased windiness, would have begun to favour shrub and herbaceous dominated floras. The rate at which old, leached soils were destroyed and replaced by younger soils, formed as a result of increased erosion and associated deposition of alluvium and colluvium, must have accelerated greatly.

During the Miocene and Pliocene, the original compact grouping of the older gneisses, granitic rocks, and marbles of the present Fiordland and north-west Nelson regions became extended in a NE–SW direction, as this once continuous block was wrenched apart by movement on the Alpine Fault. Uplift occurred at the same time, as well as periodic episodes of near full glacial conditions. We can speculate that the developing upland vegetation formed a near continuous, NE–SW elongated shape also. This late Miocene-Pliocene age upland flora, adapted to slowly rising mountain ranges of moderate elevation, was disrupted by the eruption of fast-growing, schist and greywacke mountains of the Southern Alps between 5 and 2 million years ago. These tall mountains, some with permanent ice cover on their highest peaks, radically transformed the soils and climates of the central South Island. An apron of broad outwash gravel plains formed to the east, and in the west, fast-flowing rivers created steep gravel-bottomed valleys in the narrow coastal shelf. Old, stable, leached uplands were destroyed. As a result, the once continuous upland flora was split into northern and southern regions, where the rate of uplift was low and average age of surfaces older, and a rapidly uplifting central zone.

Formation of high alpine habitats and associated unstable slopes and soils, and the extension of these environments during peak cold periods of the glaciations, may have led to a final burst of speciation. High alpine endemics of the central mountains and also much of the widespread flora of the central mountain axis (zone 3 of Burrows 1965) must date to this period.

We can expect, therefore, that the oldest component of the upland flora will be adapted to stable, infertile sites and poorly drained sites, such as those that occur at present on poorly drained infertile lowland terraces such as the pakihi of Westland, and uplifted exposed plateaus. The next oldest group should consist of plants which specialise in rock-fall, cliff-face, ridge-top, and stream-side habitats, which became available as the first ranges appeared. Unstable scree slope and true alpine habitats became available only with the final phase of the uplift of the Southern Alps, and high alpine habitats appeared last of all. If evolution of new species is strongly influenced by availability of novel habitats, the evolutionary history of taxa should broadly reflect this sequence.

Each glaciation, with its provision of unstable, eroding, exposed habitats throughout the South Island and the southern half of the North Island must have permitted the spread of alpine and unstable environment specialist species. It seems probable that in this fashion the volcanic uplands area of the central North Island and the newly emergent ranges of the southern North Island received the subalpine-alpine component of their flora.

The long glacial periods, with their largely deforested landscapes, were regularly interrupted by the brief (10 000–15 000 years), almost entirely forested periods of the interglaciations. Upland plants were confined in the North Island to reduced patches of bog and tussock grassland clearings on poorly drained soils or to small, often eroding areas above tree-line on the taller ranges. Once widespread species, such as *Phyllocladus alpinus, Dracophyllum* species, *Dacrydium biforme/bidwillii*, which formed such a prominent component of glacial floras in lowland situations, thus became reduced to scattered outposts. Northern sites such as Moehau (Coromandel Peninsula) and Te Aroha which have reduced upland floras including such species as *Phyllocladus alpinus, Podocarpus nivalis, Libocedrus bidwillii*, and *Celmisia incana* (Moore 1973), may thus retain remnants of a once dominant glacial flora.

During the mild, moist, equable warm peaks of the interglaciations, the very survival of some upland plants in the southern half of the North Island must have been threatened. The low number of endemic species and the generally low diversity of the non-forest flora on southern North Island ranges may be not only a result of the short time available for speciation since the uplift of the ranges to their present height, but also a consequence of loss of habitat during periods of mild interglacial climate.

TESTING THE HYPOTHESIS

As a science, biogeography is very good at producing hypotheses and poor at testing them. New Zealand plant biogeography has produced over the last 50 years a diversity of explanations for the origin and distribution of plants within this country. With Wardle (1963) and Burrows (1965) it appeared that a consensus had been achieved. Most anomalous plant distributions were seen as either a direct result of the rigours of the Last Glaciation, or a consequence of subsequent migratory movements. I have suggested that there is a connection between plant distributions and the late Cenozoic tectonic events which have affected the distribution of land and sea within the New Zealand region. We therefore have a complex mix of competing explanations for plant distributions within New Zealand: how can they be tested?

We should therefore look at the specific predictions made by the various hypotheses, and ways in which those predictions can be tested.

Predictions of the Glacial refugia hypotheses

Firstly, the glacial hypothesis predicts that many disjunct and endemic distributions of plants are young, and date to, or since, the peak of the last interglaciation, 125 000 years ago. Some distributions may have been created by earlier glacial disruptions but, even so, they are unlikely to be much older than 2 million years. Populations which are assumed to be disjunct as a result of range extensions during the postglacial climatic optimum and subsequent contractions will be of the order of 9000 years old or less.

Secondly, as many disjunct and endemic species are not restrained by environmental factors, they will be spreading, at various rates, back into regions from which they were excluded by glacial ice or climates.

Thirdly, restricted species should have, by and large, less well-developed dispersal abilities than widespread relatives.

Predictions of the tectonic hypothesis

Firstly, disjunct and endemic plant distributions should be old; in most cases dating back to 500 000 years, and in many cases back to 5 million years, and in some, back to the late Miocene.

Secondly, disjunct and endemic species should be restrained by environmental factors, or by competition from other plants. Such range extension that has occurred has been tightly tied to environmental change.

Thirdly, there should be no difference in dispersal ability between restricted species and widespread relatives.

Tests

The glacial refugia hypothesis predicts that some endemic and disjunct plant species had greater ranges before the peak of the Last Glaciation, or during the warmest period of the Holocene. It follows that the finding of these species as fossils outside their present geographical range in deposits of either Last Interglacial or early Holocene age would help verify the model. Thus the find of *Phyllocladus trichomanoides* leaves in any deposit in southern North Island younger than the age of the Plio-Pleistocene marine transgression would be vital evidence supporting the glacial refugia model, and cast much doubt on the validity of the tectonic hypothesis.

Fossil evidence of the sort in the above example is sparse and thus is unlikely to provide any clear-cut answers, although continued palaeoecological research should tend to suggest that one hypothesis is more likely than another. Nevertheless, finds of key fossil taxa in crucial areas have the potential to greatly weaken the tectonic hypothesis.

Besides fossil evidence, recently developed techniques permit relative dating of the timing of the split of phylogenetic lineages by analysis of the gradual, and apparently steady change of amino acid sequences in proteins (Wilson et al. 1977). This technique has recently been used to solve a long-standing biogeographic problem involving frog speciation in Australia (Maxson & Roberts 1984). The tectonic model predicts that the ages of most lineage splits caused by disjunction will be older than 2 million years, with a number extending back to 20 million years or even before. The glacial refugia model — where it does predict lineage splits caused by disjunction — will have most of them younger than 2 million years, and the majority very much younger.

Biogeographical classifications are best derived from sound phylogenetic classifications. Tested phylogenies of large, diverse genera such as *Hebe*, *Aciphylla*, *Coprosma*, *Celmisia*, and *Pittosporum* are therefore a further way of distinguishing the two hypotheses. If plant distributions do reflect geological history there should be strong relationships between biogeographic and phylogenetic patterns. The glacial refugia hypothesis takes as one of its basic tenets that endemic plant distributions are a result of contraction during glacial times. It follows that continued expansion and contraction of range with repeated glacial-interglacial cycles will have obscured any close link between distribution on the pre-Pliocene landmass and present distribution pattern. However, if plants have evolved more or less *in situ*, or often retain pre-Pliocene distributions, there should be a good relationship between phylogeny and area. In other words, geologically young areas should have young endemics, while older, more stable areas should have retained disproportionate numbers of old endemics.

To give an example, a vicariance between north Auckland and Nelson should involve taxa which stem from the base of a given phylogenetic tree, while vicariance between northern and southern South Island should involve taxa of moderate advancement. Vicariance between the mountains of the North Island and those of the South Island will involve only the most advanced taxa. Exactly the same analysis can be applied to disjunctions, except that recent disjunctions can affect groups of any phylogenetic age, whereas old disjunctions can only affect older taxa. As an example of this sort of analysis we can take the oldest and least advanced group of dracophyllums in the country, the subgenus *Dracophyllum*. This subgenus is involved in the vicariant and disjunct distributions between North Auckland and the South Island. However, the disjunctions between the mountain ranges of the North Island and the South Island, exclusively involve the more advanced shrub subgenus *Oreothamnus*.

Analysis of the methods of dispersal may assist in distinguishing between the two hypothesis: widespread plants with pandemic distributions should, according to the glacial disjunction hypothesis, be better adapted to dispersal than restricted relatives. The tectonic hypothesis makes no such claim, as stress is placed on environmental factors in restricting distributions; widespread, pandemic, and endemic species of the same group should show no, or random, differences in dispersal effectiveness.

An inappropriate method of testing the hypothesis is to examine the population structure of species at the limit of their ranges to try and determine whether or not they are spreading. This cannot give reliable evidence, as it is to be expected that all plant populations will show dynamic movements at the edge of their distributions, just as they do within it (Carter & Prince 1981). It is to be expected that a range margin will be characterised by young populations for as an environmental limit is approached mortality rates should be higher, and turnover of individuals correspondingly greater. Range extension is on a timescale of hundreds and thousands of years, not the decades and centuries available to a population study.

SUMMARY AND CONCLUSIONS

The southern half of the North Island and the waist of the South Island are characterised by low numbers of endemic plants. In contrast, the northern half of the North Island, and northwestern and southern South Island, are relatively endemic-rich. Plants with disjunct distributions tend to occur in these regions.

Previous workers have tended to explain these apparently anomalous distributions as being primarily the consequence of past environmental events. Most favoured explanations have been glacial ice extension and accompanying severe climatic conditions (especially during the peak of the Last Glaciation), the postglacial thermal maximum and subsequent climatic deterioration, and volcanism. A necessary, but unacknowledged assumption of this historic approach is that present environmental conditions do not provide a satisfactory explanation for these plant distributions. It follows that such plants are constrained primarily by their intrinsic dispersal and colonising ability.

According to this historic approach (here called the glacial refugia hypothesis), glacial conditions eliminated many plants from the middle of the South Island and from the southern half of the North Island, while numerous plants survived in refugia in what are now endemic-rich regions. These distribution patterns have been modified by migration out from the refugia since the climatic amelioration at the end of the Last Glaciation. Accordingly, many plants are supposed to be in the process of spreading at present, solely as an adjustment to postglacial conditions. The thermal maximum of the postglacial is suggested to have led to a temporary extension of range of some cold sensitive plants, which have since retreated, leaving isolated pockets remote from the main distribution of the species. Volcanism has supposedly truncated the range of some plants in the central North Island. The evidence supporting the glacial refugia hypothesis is weak. The vegetation history of the last 100 000 years is more conducive to the hypothesis that most plant species typical of given region have survived there during the Last Glaciation, and have since expanded or contracted in population size in response to environmental conditions, but have not substantially altered their distributional boundaries. There is no strong evidence for plant migration over substantial distances (greater than 40 km) during the postglacial period.

The hypothesis proposed here (called the tectonic hypothesis) is based on the following assertions:

(1) plants are restricted primarily by present environmental conditions;
(2) restricted plants are not usually extending their range; and
(3) the flora of a given region is likely to have been essentially stable in composition over a long time (i.e. several glacial-interglacial cycles).

Anomalous and disjunct distributions therefore reflect present environmental constraints, but require explanation as to how those distributions were achieved.

Long-distance dispersal of propagules is ruled out as a satisfying explanation for repeated patterns of vicariance and disjunction on the basis of improbability. It is suggested that many distribution patterns owe their genesis to land and sea changes since the Miocene. In particular as a result of:
(1) movement of land as a consequence of large-scale fault displacement;
(2) changing dispositions of land and sea, particularly the Plio-Pleistocene submergence of the southern half of the North Island;
(3) creation of new environments as a result of mountain building, especially the rapid uplift of the Southern Alps during the last 2 million years, and the very recent (less than 500 000 years) uplift of the southern North Island ranges.

It follows that the more stable regions of New Zealand have tended to retain a greater proportion of older taxa, which have been lost by inundation or destruction of habitat in more mobile regions. Younger regions (especially southern North Island) have not had the time to develop new floras, hence have low levels of endemism.

A non-tectonic explanation must be invoked to explain the distributions of upland plants of southern origin which occur in scattered locations in central and southern North Island. Here, migration during the repeated glaciations of the Plio-Pleistocene period is likely to have been the cause.

Testing and developing these hypotheses is likely to be a long and complex matter. The recent upsurge of interest in vicariance biogeography and application of cladistic methods to biogeography (*see* for instance, Sims et al. 1983 and Nelson & Rosen 1981) have provided a rich variety of conceptual frameworks and methodological techniques but little agreement. It is clear, however, that the foundations for biogeography must rest on sound taxonomy and thorough distributional data. It is apparent that there is a long way to go before the New Zealand biota is known well enough to give great confidence in the deciphering of our internal biogeography by this means (Brownsey & Baker 1983). Biochemical methods will eventually become an integral part of this endeavour, especially with regard to the timing of events in the biological history of New Zealand.

It should not be thought that these ideas are restricted to the plant kingdom alone; in fact they have been elaborated from suggestions originally put forward to explain the biogeography of landsnails within New Zealand (Climo 1975). Other groups, for instance, earthworms (Lee 1959), alpine grasshoppers (Bigelow 1967), and moths (Gibbs 1983), show patterns which match those of the higher plants. Eventually, a coherent biogeography will emerge which will encompass the entire biota.

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