

## Disjunction of Tree Species in Mountain Forests, Southern North Island, New Zealand: A Review of Paleobotanical Evidence<sup>1</sup>

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**ABSTRACT:** Dominant trees of New Zealand forests, particularly *Nothofagus*, which has low seed mobility, show major distribution gaps, associated with past glacial and volcanic destruction of forest. In the southern North Island there are forest tree discontinuities distant from volcanic destruction and subject only to periglacial activity in the Pleistocene. Here there is absence of one taxon of *Nothofagus* and of some mountain coniferous trees, including podocarps, with bird-carried seeds, and *Libocedrus*, with winged seeds. The southern North Island, from 40° S to 41° 30' S, shows a progressive southward loss in montane and subalpine tree species. These species are common, often dominant, to the north of the area described, and in the northern South Island. In order of increasingly southern limits in the North Island they are *Halocarpus bidwillii*, *Nothofagus solandri* var. *cliffortioides*, *Libocedrus bidwillii*, *Halocarpus biformis*, and *Phyllocladus alpinus*. Their pollen and macrofossil history is reviewed. *Libocedrus bidwillii* was present in the southern North Island 80,000 yr ago, and *Halocarpus* and *P. alpinus* until ca. 10,000 yr ago. Various glacial episodes since 80,000 yr ago have severely limited their distribution. The postglacial reoccupation by forest of southern North Island sites was influenced by rapid climatic warming. This warming not only flooded the Cook Strait landbridge, cutting off tree migration from the south, but also allowed lowlands around the gorge bisecting the axial mountains to be occupied by temperate forest, effectively blocking access southward by *L. bidwillii* and *N. solandri* var. *cliffortioides*. The mountain podocarps, *H. biformis* and *P. alpinus*, now abundant just south of the gorge, are in a particularly cloudy climate, which lacks *Nothofagus*. Farther south, under less cloudy conditions, the rapid expansion of *N. menziesii* forest from lowland refugia could have excluded the two small podocarps, which were present in pollen records in the early postglacial.

IN COMPILING AN ACCOUNT of the present vegetation of New Zealand, many distributional anomalies of forest trees are encountered. At the present time we are approaching a better understanding of vegetation history, mostly by palynology.

This paper reviews Pleistocene and Holocene paleobotanical studies and some past and present species distribution patterns in montane and subalpine forests in the southern North Island of New Zealand. New Zealand is a relatively large land mass dating back at

least to Devonian times and was part of Gondwanaland until 80 million years ago. New Zealand has on its present land mass a mixture of trees, some with seeds of low mobility such as *Nothofagus*, which are unattractive to birds for transport; others such as the Podocarpaceae and some angiosperm trees, with seeds capable of transport by birds; and *Weinmannia* and *Metrosideros*, having very small seeds capable of distant dispersal by wind.

This then is the unique context of the distribution patterns in central New Zealand, with the rationale that anomalies in present distribution can, through recent research, be explained by Pleistocene environmental histo-

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ry. Plant names used are those of Allan (1961) and Connor and Edgar (1987).

### *New Zealand's Forest Pattern*

The forest pattern of New Zealand is complex. Even after extensive human clearance in the lowlands, four major floristic types can be recognized, and their history and dynamics studied.

The four types are (1) *Agathis* forests, north of latitude 38° S; (2) Conifer-dominated forests, mostly of Podocarpaceae, but also of *Libocedrus*, in the Cupressaceae. These forests, as they mature, include dicotyledonous trees that may ultimately supplant the conifers; (3) Pure *Nothofagus* or southern beech forests; and (4) *Nothofagus* mixed with conifer forests.

Only the last three types contain species that can tolerate mountain climates. In the southern North Island such climates are in the montane zone from 600 to 900 m and the subalpine zone from 900 m to the treeline at 1200–1300 m. These two zones are subtended by the temperate zone, from 0 to 600 m (zone designations: Wardle 1964).

The coniferous forests and the beech forests alternate throughout New Zealand in a way not fully explicable by present climate. A major example of this is on the west coast of the South Island. Here there is a long gap in the beech forests, otherwise continuous to the north and south. Beech is more common, although not continuous, on the east face of the mountains, a discontinuity corresponding to the western beech gap. Heavy Pleistocene glaciation of the highest parts of the mountains and the resulting outwash material denuded the piedmont, destroying the forest. Beech forest survived on what is now the seabed (Moar and Suggate 1973), but its very low seed mobility prevented reinvasion by it of the piedmont before the bird-carried conifer seeds and the wind-carried angiosperm seeds enabled forest development, from 10,000 yr ago.

Beech is invading the conifer–angiosperm forests at each end of the gap, but very slowly, as the beech is quite light-demanding. How-

ever, beech dispersal can be relatively widespread down waterways.

There are other areas of beech absence. On the North Island these may be related to the Holocene vulcanism of Mt. Taranaki, in the west, active until the seventeenth century. The central North Island was devegetated by the violent Taupo Pumice eruption of A.D. 130, and beech is likewise absent from the forests reoccupying the new surface.

### *Forests of Central New Zealand*

The area of concern here, the southern part of the North Island axial mountains, had only slight Pleistocene valley glaciation, but extensive solifluxion to low altitudes (Stevens 1974). Volcanoes are too distant to have destroyed vegetation. Thin tephra beds from volcanoes are sometimes present, right down to Cook Strait, and are valuable dating tools. Dominant soil parent material is Jurassic greywacke, with varying depths of Pleistocene greywacke-derived loess on gentler slopes. The Tararua and Ruahine Mountains (Figure 1) are part of the axial Mesozoic sedimentary chain aligned NE to SW over much of the length of New Zealand. They were uplifted from a peneplain starting only 340,000 yr ago (Te Punga 1954, Rogers 1989), at least in their southern part. A large remnant portion of the central peneplain extends for about 30 km on either side of the antecedent Manawatu Gorge, which bisects it (Figure 1).

The mountains are otherwise very dissected and rise to a maximum of 1750 m. The climate is cool and oceanic, with up to 5000 mm of annual precipitation. Below the alpine tree-line, at about 1200–1300 m, most of this precipitation is as rain and fog. At a climate station above the Manawatu Gorge, at ca. 900 m, gales with windspeed >96 km/hr are reported on 74 days annually and fog on 220 days (New Zealand Meteorological Service 1980). Both the Manawatu Gorge and Cook Strait act as weather funnels concentrating the cloud and rain of the predominant westerlies.

The mountain forests, except on and near the peneplain remnants on either side of the gorge, are dominated by *Nothofagus*. In the

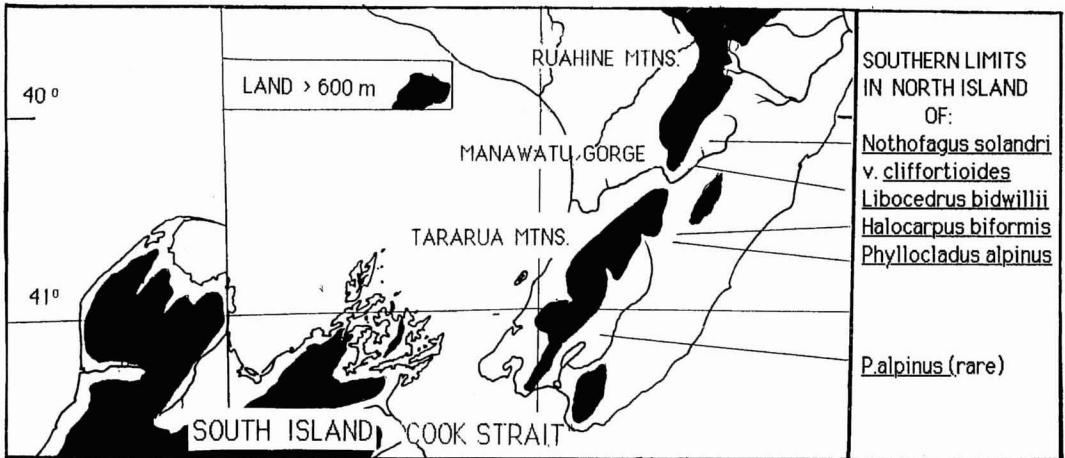


FIGURE 1. Map of the central portion of New Zealand, showing the extent of land > 600 m altitude (i.e., in the montane and subalpine [Wardle 1964] zones). The southern limits of trees of these zones are shown for the North Island. All these species are present, and frequently dominant, in the northern South Island.

Ruahine Mountains, to the north, *N. solandri* var. *cliffortioides* reaches the treeline, subtended by the montane *N. fusca*. To the south, in the Tararua Mountains, *N. menziesii* is the only tall tree going up to the treeline. As in the northern Ruahine Mountains, *N. fusca* is at lower altitudes.

However, the central peneplain remnants and their upper flanks on both sides of the gorge have no *Nothofagus* forest. Replacing them in the montane and subalpine zones are, successively upward: *Prumnopitys ferruginea* (Podocarpaceae) and *Libocedrus bidwillii* (Cupressaceae) and above is *Halocarpus biformis*, which merges at 900 m into a scrub of a rhododendroid composite, *Olearia colensoi*, which goes up to the treeline. It has been suggested (Zotov et al. 1939) that the presence of steady-state scrub rather than subalpine forest may be correlated with low light and temperature levels in the very foggy mountains described. To the south of the gorge, there is a similar sequence of trees, but *Libocedrus* is absent and does not occur again until the northern South Island. To summarize these floristic gaps, the area has in its mountain forests: a complete lack of *Nothofagus* in the central part, a lack of *N. solandri* var. *cliffortioides* in its southern part, and a

progressive further loss southward of a group of important mountain trees (Figure 1), which are *Libocedrus bidwillii*, *Halocarpus biformis*, and *Phyllocladus alpinus* (local only in southern area). But these missing beech and conifer species are present and often dominant in mountains north of the area and on South Island mountains just over Cook Strait.

#### Paleobotanical Evidence

Recent pollen analysis has enabled the history of these forests to be elucidated. Most of the tree taxa have lowland Pleistocene, and upland Holocene, fossil records from near Cook Strait and from both flanks of the southern part of the mountains.

A pollen sequence to the southeast of the Manawatu Gorge, at 200 m altitude, shows that the absence of *Nothofagus* from mountains to the north and south of the gorge dates from 19,000 yr ago (McLea 1990). At that time, 19,000 yr ago, it became even colder, so that *Nothofagus* disappeared from the deposition area. In lower parts of the southern North Island, there were still local refugia for *Nothofagus* (Fleming 1970, Harris and Mildenhall 1984). After the Holocene warming of 13,000 yr ago, lowland podocarp forest dominated,

instead of the pre-last glaciation *Nothofagus* forests.

The modern failure of *Nothofagus solandri* var. *cliffortioides* to invade the peneplain remnant mountains to the north and south of the Manawatu Gorge may be related to the low light intensity and reduced temperatures of this foggy upland because *N. solandri* var. *cliffortioides* has a high light requirement (Wardle 1984). However, pollen sections on the peneplain show that *Nothofagus* of the pollen group of *Nothofagus solandri* var. *cliffortioides* did not become important north of the peneplain until 2000 yr ago (Lees 1986). Other pollen evidence along the northern part of these mountains indicates a slow migration southward of *Nothofagus* (Rogers and McGlone 1989). Southward on the more dissected Tararua Mountains in less cloudy, rain-shadow areas, *N. solandri* var. *cliffortioides* is absent; it seems not to have been able to occupy an apparently suitable mountain area during the rapid Holocene warming, when lowland podocarp forest occupied the plains below the mountains and blocked the invasion of *N. solandri* var. *cliffortioides*. *Nothofagus menziesii* now forms the higher altitude forests of the Tararua Mountains south of the peneplain remnant.

*Libocedrus bidwillii* pollen is represented as a fossil only where source trees were very close to the deposit (MacPhail and McQueen 1983). Its pollen does not appear in pollen sections on the northern part of the peneplain (Lees 1986) despite the presence of forests of *L. bidwillii* 300 m below and ca. 2 km away. Its absence from mountain forests south of the gorge can be ascribed, as for *Nothofagus solandri* var. *cliffortioides*, to the rapid growth of competing lowland podocarp dicotyledon forest in and around this barrier (Franklin 1967). Both trees have dry seeds that are not carried far by wind, and both are light-demanding colonizers and could not enter a dense lowland podocarp forest. *Libocedrus bidwillii* was recorded as pollen at a low altitude at the end of the last interglacial, ca. 100 km south of the Manawatu Gorge (Palmer and Vucetich 1989), but disappeared from the pollen section as the colder conditions of the last Stadial started, about 80,000

yr ago. There is thus no record of a southern North Island source of seed to reestablish this tree there after the last glaciation. *Libocedrus bidwillii* generally depends on episodic catastrophes such as landslides, storm damage, and fire to provide open areas for recolonization (Clayton-Green 1977, Norton 1983, Rogers and McGlone 1989).

Two important components of the forests lacking *Nothofagus* on the peneplain remnants are *Halocarpus biformis* and *Phyllocladus alpinus*. Forests of both are at their southern limit in the northern Tararua Mountains, although the *Phyllocladus* has a local occurrence on the mountains near Cook Strait. Neither have pollen specific to one taxon. *Halocarpus* pollen represents two mountain species, both absent from the southern North Island; one is *H. biformis*, a tree, also capable of dwarf growth. The other, *H. bidwillii*, is always a shrub of mires and impermeable soils. *Phyllocladus* pollen represents three species, two of temperate-zone lowland distribution and one of montane to subalpine distribution. In all the palynofloras considered here, the species accompanying *Phyllocladus* indicate montane to subalpine conditions, so the *Phyllocladus* may safely be assumed to be *P. alpinus*. Its phylloclades have been identified by the author from two localities near sea level near Cook Strait at 20,800 yr ago (Brodie 1954) and 21,000 yr ago, respectively (B. J. Pillans, pers. comm.).

Both *Phyllocladus* and *Halocarpus* have a Pleistocene pollen record near sea level in the southern North Island, indicating their presence, often in important quantities, from 30,000 to 10,000 yr ago (Lewis and Mildenhall 1985). Farther north, near the Manawatu Gorge, there is a Pleistocene pollen record of *Halocarpus* and *Phyllocladus* from 41,000 to 13,000 yr ago (McLea 1990).

There is a difference between the southern and northern localities (above) in timing of the change from nonforest, cold-climate vegetation to forest of warmer conditions. This change occurs at 10,000 yr ago in the south and at 13,000 yr ago in the north, despite there being less than 1° difference in latitude between the two sites.

The warming occurs in both sections within

a short stratigraphic distance, suggesting rapid climate change. It seems possible that the present Cook Strait climate, cooler than both the north and south, had a counterpart in more severe Pleistocene conditions then. A rapid warming would also have flooded the landbridge (Stevens 1974) in the northern part of Cook Strait and prohibited access from the South Island for plants of low seed mobility, such as *N. solandri* var. *cliffortioides* and *L. bidwillii*. In the north, at the Manawatu Gorge the rapid growth of temperate-zone forests would likewise prohibit any migration from the north and west on to the lowlands by montane and subalpine species, as was postulated by Franklin (1967) before there was much palynological evidence from this area. The postglacial lowland forests there indicated by pollen in both cases are podocarp forests.

On the mountains above the two pollen sections, one near Cook Strait and the other near the Manawatu Gorge, one would expect to find the successors to cold-climate Pleistocene forests formerly growing at low altitudes. It is only on and near the peneplain remnants on either side of the Manawatu Gorge that *Halocarpus* and *Phyllocladus* survive in forests today. They do not occur near Cook Strait. There, *N. menziesii* survived the last glaciation (Fleming 1970, Harris and Mildenhall 1984), but was then displaced upward by expanding temperate-zone forests on to steeply dissected and superhumid mountains. The vigor of *N. menziesii* under such conditions would eliminate *Halocarpus*, a genus often of waterlogged soils, and *Phyllocladus*, which does not tolerate shade. To the north near the Manawatu Gorge, *N. menziesii*, a potential successor to *Halocarpus* and *Phyllocladus*, has been absent from this area since 19,000 yr ago (McLea 1990) and has still not migrated to within ca. 50 km of the gorge.

Present-day distribution of mountain plants, mostly herbs and shrubs, can help in interpretation of effects in the southern North Island of the last glacial episode, from 18,000 to 10,000 yr ago. Some 121 taxa are disjunct from central North Island to the South Island (Rogers 1989). The disjunctions, and the very low degree of endemism in the southern part

of the North Island (Druce, 1984, unpublished report on distribution of indigenous higher plants in North Island and northern South Island), also suggest that cold conditions were more severe near Cook Strait than to the north or to the west. Certainly, the postglacial warming was 3,000 yr later than within 1° latitude farther north.

### Conclusions

The absence of several montane and subalpine trees in the mountains on the north of Cook Strait can be explained by a series of mechanisms, based on paleobotanical evidence. The chronology is summarized in Figure 2: (1) In the southern part of the Tararua Mountains *Phyllocladus alpinus* and *Halocarpus* disappeared beneath forests of *Nothofagus menziesii* advancing upward from refugia near sea level, following a probably rapid climate warming 10,000 yr ago. (2) Farther north, near the Manawatu Gorge, *N. menziesii* had disappeared 19,000 yr ago, so the two mountain podocarps, *Phyllocladus* and *Halocarpus*, near sea level at the postglacial warming 13,000 yr ago advanced up on to the peneplain remnants, on both sides of the gorge. (3) *Nothofagus solandri* var. *cliffortioides* has not migrated on to the southern Ruahine Mountains nor onto the whole of the Tararua Mountains farther south. *Nothofagus menziesii*, refuged in the south, has possibly been retarded by foggy conditions in its occupation of the northern Tararua Mountains, conditions better tolerated by *Halocarpus biformis* and subalpine scrub of *Olearia*. (4) *Libocedrus bidwillii* has been unable to cross from forests to the north of the barrier of the Manawatu Gorge and its surrounding dense postglacial lowland forests because *L. bidwillii* seeds do not carry far and because it is a light-demanding tree.

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SOUTHERN MOUNTAINS, NEAR COOK STRAIT

YEARS	30,000	20,000	10,000	TODAY
<i>Nothofagus menziesii</i>	=====	-----	=====	=====
<i>N. solandri</i> var. <i>cliffortioides</i>				
<i>Libocedrus bidwillii</i> (>80,000 yr B.P.)				
<i>Halocarpus</i> : 2 spp.	=====	=====		
<i>Phyllocladus</i> cf. <i>alpinus</i>	=====	=====	-----	(Rare)

NORTHERN MOUNTAINS, ABOUT MANAWATU GORGE

YEARS	30,000	20,000	10,000	TODAY
<i>Nothofagus menziesii</i>	=====			
<i>N. solandri</i> var. <i>cliffortioides</i>				-----
<i>Libocedrus bidwillii</i>				=====
<i>Halocarpus</i> : 2 spp	=====	=====	=====	=====
<i>Phyllocladus</i> cf. <i>alpinus</i>	=====	=====	=====	=====

FIGURE 2. Summary of the paleohistory of mountain tree taxa, now mostly disjunct in the south of the North Island. The fossil records in the Pleistocene come from localities of cool-climate floras, all near sea level, in areas now occupied by temperate-zone vegetation. The present records ("TODAY") are from montane and subalpine areas, all >600 m altitude. For the fossil records, above: ===== = pollen present in sufficient quantity to indicate that the species formed a substantial part of the vegetation close to the deposition site. ----- = slight quantities of pollen, suggesting distant provenance, or limited quantities of the species close to the deposition site.

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