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The nature of the lower North Island floristic gap

G. M. ROGERS*

Forest Research Institute
Private Bag
Rotorua, New Zealand

Abstract Patterns of regional endemism and disjunction of higher plants in the lower North Island are reviewed in relation to the plants' habitats. A redefinition of the lower North Island floristic gap emerges. A northern boundary in the southern central North Island uplands replaces the previous one at 39°S latitude. Southern boundaries occur either in Cook Strait or in southern Wellington-southern Wairarapa. Most endemic and disjunct species defining the gap occur in non-forest habitats. Previous explanations for these distribution patterns centre either on the disruptive effects of glacial ice and harsh climates of the Last Glaciation or on the tectonic modification of the New Zealand land mass since the Oligocene. It is suggested that regional discontinuities in the availability of non-forest habitats account for many disjunctions. Furthermore, patterns of endemism and disjunction most closely equate with the tectonic alteration of lower North Island. In particular, fault displacement of large land masses, obliteration of habitats by marine transgression and the regionally differential effects of mountain building have acted to preserve habitats of elements of an old flora in tectonically stable regions.

Keywords New Zealand flora; plant biogeography; floristic gap; endemism; disjunction; Pliocene; Pleistocene; marine transgression

INTRODUCTION

Though many plant species in lower North Island have geographic ranges explicable in terms of environmental factors, others show patterns

unaccountable by these means. Several unusual patterns of endemism and disjunction are seemingly unrelated to climatic or geographic zones. Cockayne (1928) and Wardle (1963) recognised a prominent phytogeographical boundary at approximately 38–39°S latitude. Both recognised the comparatively low degree of endemism in lower North Island compared to central and northern North Island. In addition, Wardle (1963) and McGlone (1985) identified a small group of plants disjunct between northern North Island and South Island. Later, Druce (1984), in an analysis of plant distribution in North Island and northern South Island recognised endemic-rich zones in the northern half of North Island and the northern portion of South Island, and an endemic poor zone in southern North Island, supporting the conclusions of Wardle (1963) and Burrows (1965). Druce found the central North Island mountains support a moderate number of endemics and identified a large group disjunct between the central North Island uplands and South Island. Yet another group has a discontinuous North Island range between southern Wellington-southern Wairarapa and central North Island. Clearly the central and southern North Island are biogeographically quite different.

Currently, two prominent biogeographic hypotheses are under evaluation to explain these biogeographic patterns. Both Wardle (1963) and Burrows (1965) concluded that many plant distributions in New Zealand were determined primarily by the effects of the Oiran Glaciation, both glacial ice and harsh climates, and subsequent climatic change in the postglacial. Redistribution of species out from refugia has subsequently modified these distributions, as has the climatic optimum of the postglacial and central North Island vulcanism. Later, McGlone (1985) concluded that anomalous plant distributions can be related to the Cenozoic tectonic and palaeogeographic history of New Zealand. He found explanations based on the disruptive effects of glacial ice and severe climates, with subsequent migration from refugia in a warm climate, largely unconvincing. As an alternative, McGlone makes appeal to the "tectonic hypothesis"

*Miss E. L. Hellaby *Indigenous Grasslands Research Fellow*.

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by proposing that those areas with the most diverse and endemic-rich floras were least disrupted by tectonic processes since the Oligocene.

The present work re-evaluates the nature of the lower North Island floristic gap and attempts to reach a biogeographic synthesis for lower North Island that is compatible with our current knowledge of plant distribution, plant ecology, and earth history. The validity of the two current biogeographic hypotheses is assessed.

With some 16% of the total, scientifically recognised, indigenous vascular species unnamed (Druce 1982), our knowledge of the flora is far from stable and will undergo further refinement. Although the taxonomy and distribution of the woody flora are well known (see, for example, Druce 1980a), there is a paucity of accessible, detailed distributional records for the herbaceous flora. The present exercise draws heavily on the distributional information in Druce (1984).

PATTERNS OF ENDEMISM AND DISJUNCTION

An analysis of the floristic biogeography of Moawhango Ecological Region (MER) (Simpson 1982) is placed in the wider and related context of that of central and southern North Island. Several geographic patterns emerge involving groups of endemic and disjunct species which show similar distributions; these are used to define a lower North Island floristic gap. The predominant habitat of each species is shown, based on assumed habitats in pre-human landscapes. Explanations for these congruent patterns in distributions and habitats are reviewed, firstly in relation to habitat availability and secondly in the light of late Cenozoic and Quaternary earth history, by examining what is known of the palaeogeography, tectonic deformation, and palaeoclimate of lower North Island.

Rather than impose latitudinal limits on species distributions, more informative regional or environmental zones are defined. Central North Island, as defined here, includes those upland districts, predominantly above 650 m, as shown in Fig 1. The Ruahine Range is included as it shows close physiographic, floristic, and vegetation relations with ranges to the north. Several lowland species, with southern North Island limits in southern Hawke's Bay, Taupo, and Taihape are considered to have central North Island distributions.

Biogeographic species groups

Initially, six groups of species with unusual lower North Island distributions are identified. Three groups of largely endemic species are shown first, followed by three groups of disjunct species. The lists show taxon, habitat, and southern limit and were compiled by G. M. Rogers and A. P. Druce.

Nomenclature

Druce et al. (1987) and Druce & Williams (1989) use lower-case letters as tag names for unnamed taxa, e.g., *Melicytus* sp. (a), *Helichrysum intermedium* var. (a). This system is continued in the present paper. To avoid any confusion, the same taxon is given the same tag letter in all three papers.

If the name used is different from that used in the standard floras (Allan 1961; Moore & Edgar 1970; Cheeseman 1925 – grasses only) the previous name is added in square brackets.

Habitat classification

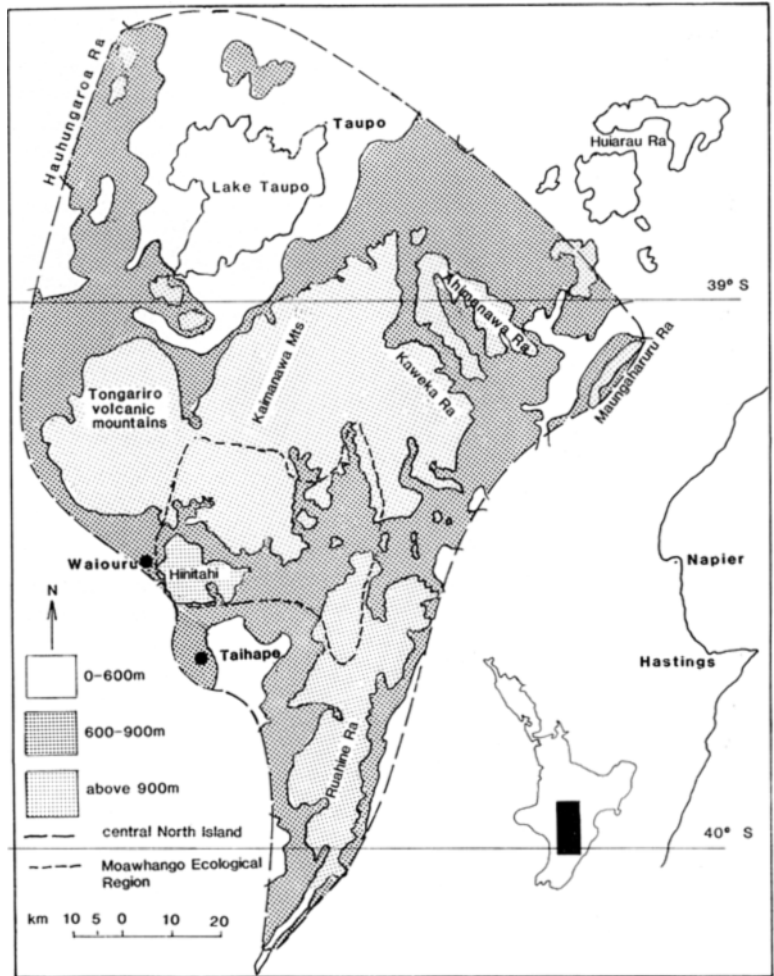
In the species lists, bioclimatic, landform, hydrological, and vegetation structural class terms are used to classify habitats. Species that reach the alpine zone are classed as alpine irrespective of lower altitude occurrences.

- alpine – (extends to alpine zone but not necessarily confined there)
- shrubland – (see Atkinson 1985)
- tussockland – (includes tussock and non-tussock grassland)
- unconsolidated substrate – (includes dunes, loose talus, levées)
- mire
- cliff
- basin – (sites of cold-air inversion)
- wet depression – (periodically flooded depressions, and lake margins subjected to fluctuating water levels)
- riparian
- forest margin
- forest – (see Atkinson 1985)
- aquatic

Classification of southern limits in central North Island

- Lowl – lowland (lowland districts of Hawkes Bay, Taupo, and inland Taranaki)
- Hauh – Hauhungaroa Ra.
- Tvm – Tongariro volcanic mountains
- Ahim – Ahimanawa Ra.
- Maung – Maungaharuru Ra.
- Kaim – Kaimanawa Mts
- Kaw – Kaweka Ra.

Fig. 1 An outline of the region defined as central North Island.



MER – Moawhango Ecological Region (including adjoining Taihape district west of Taihape)

nR – northern Ruahine Ra.

cR – central Ruahine Ra.

sR – southern Ruahine Ra.

Groups of species with southern North Island limits in the central North Island uplands

Group 1

2 species endemic to M.E.R.

Acaena sp. (b) (aff. *A. microphylla*) – riparian, MER

Logania depressa – wet depression, MER

Group 2

16 species endemic to central North Island with nearly all occurring in M.E.R.

Acaena sp. (c) (aff. *A. anserinifolia*) – forest, MER

Aciphylla sp. (a) (described as *A. squarrosa* var. *flaccida* by Kirk 1899) – alpine, cR

Carex astonii [*C. druceana* var. *astonii*] – wet depression, MER

Craspedia sp. (i) – mire, MER

Dichondra sp. (c) (aff. *D. brevifolia*) – tussockland, cR

Dracophyllum subulatum – basin, MER

Hebe colensoi – cliff, MER

Hypericum sp. (a) (aff. *H. japonicum*) – wet depression, MER

Myosotis eximia – cliff, cR

Myosotis sp. (g) (aff. *M. forsteri*) – shrubland, sR

Myosotis sp. (h) (aff. *M. pygmaea*) – wet depression, MER

Ourisia vulcanica – alpine, Tvm

Parahebe spathulata – alpine, cR

Pittosporum turneri – forest margin, MER
Raoulia sp. (d) (R. “australis north” of Ward 1982)
 – tussockland (especially unconsolidated
 substrate), MER

Pimelea sp. (a) (aff. *P. aridula*) – cliff, Maung

Group 3

13 species with wider distributions but still (mostly)
 endemic to North Island and with southern limits in
 central North Island

Acaena microphylla s.s. – tussockland (especially
 unconsolidated substrate), MER

Aciphylla sp. (b) (aff. *A. squarrosa*) – tussockland,
 cR

Alseuosmia turneri – forest, Tvm

Anaphalis sp. (b) (aff. *A. keriensis*) [*Gnaphalium*] –
 cliff, MER

Coprosma sp. (f) (aff. *C. cheesemanii*) – alpine, sR

Coriaria pteridoides – unconsolidated substrate, sR

Dracophyllum recurvum – alpine, sR

Dracophyllum strictum – cliff, Lowl (Hawkes Bay)

Gaultheria colensoi – alpine, cR

Gaultheria oppositifolia – cliff, Lowl (inland
 Taranaki)

Gaultheria paniculata – cliff, Lowl (inland Taranaki)

Gentiana sp. (e) (aff. *G. spenceri*) – forest, MER

Hebe macrocarpa – forest, cR (var. a, incl. *H.*
corriganii, at southern limit)

Hebe sp. (f) (described as *H. stricta* var. *egmontiana*,
 and as *H. stricta* var. *lata*, by Moore 1961) –
 alpine, cR

Isolepis crassiuscula [*Scirpus crassiusculus*]* – mire,
 cR

Ixerba brexioides – forest, Ahim

Pimelea buxifolia – alpine, sR

Pittosporum kirkii – forest, Tvm

*Prasophyllum suttonii** [*P. patens*] – mire, MER

Ranunculus nivicola – alpine, cR

*Schoenus carsei** – mire, Lowl

*Schoenus fluitans** – mire, MER

*Thismia rodwayi** – forest, Tvm

Group 4

17 species confined to M.E.R. in North Island and
 disjunct to South Island

Acaena inermis – unconsolidated substrate, MER

Agrostis imbecilla [*A. tenella*] – wet depression,
 MER

Cardamine sp. (j) (*C. debilis* agg.; “slender var.” of
 Allan 1961) – riparian, MER

Carex berggrenii – wet depression, MER

Carex petriei – riparian, MER

Elymus laevis [*Asperella laevis*] – riparian, MER

Euphrasia disperma – mire, MER (var. a endemic to
 MER)

Gnaphalium ensifer – wet depression, MER

Koeleria sp. (a)¹ (*K. novozelandica* agg.) [*K. kurtzii*]
 – tussockland, MER

Luzula sp. (c) [*L. rufa* var. *albicomans*] –
 unconsolidated substrate, MER

Myosotis tenericaulis – riparian, MER

Myosotis sp. (i) [*M. pygmaea* var. *glauca*] –
 unconsolidated substrate, MER

Nertera sp. (b) (aff. *N. balfouriana*) – riparian, MER

Ourisia modesta – riparian, MER

Ranunculus recens – wet depression, MER (var. a
 endemic to MER)

Tetrachondra hamiltonii – wet depression, MER

Uncinia strictissima – tussockland, MER

Group 5

55 species confined to the central North Island
 uplands in North Island and disjunct to South Island

Agrostis pallescens – alpine, cR

Agrostis sp. (aff. *A. subulata*) – alpine, cR

Carmichaelia enysii [*C. orbiculata*] – unconsolidated
 substrate, MER (var. *orbiculata* [*C. orbiculata*]
 endemic to central North Island)

Carex carsei – mire, Tvm

Carex druceana s.s. [*C. druceana* var. *druceana*] –
 alpine, cR

Carex enysii – unconsolidated substrate, Maung

Carex rubicunda – wet depression, MER

Carex uncifolia – mire, MER

*Chiloglottis gunnii** – forest, Lowl (east of Taupo)

Centrolepis pallida – alpine, cR

Colobanthus acicularis – alpine, cR

Coprosma cheesemanii s.s. – tussockland, cR

Coprosma petriei – tussockland (especially
 unconsolidated substrate), MER

Deschampsia novae-zelandiae – alpine, cR

Elymus tenuis – tussockland, MER

Epilobium hectorii s.s. – unconsolidated substrate,
 MER

Epilobium pycnostachyum – alpine, cR

Festuca sp. (a)¹ (aff. *F. rubra*) – alpine, cR

Galium sp. (b) (aff. *G. perpusillum*)[†] – wet
 depression, MER

Gnaphalium traversii – tussockland, cR

Halocarpus bidwillii – alpine, cR

Hebe subalpina – forest margin, sR (var. a, incl. *H.*
truncatula, endemic to Ruahine Ra.)

Iphigenia novae-zelandiae – wet depression, Maung

Korthalsella clavata [*K. lindsayi* var. *clavata*] –
 forest margin, MER

Lachnagrostis sp. (c)¹ (aff. *L. filiformis*) [*Deyeuxia*]
 – mire, nR

Lagenifera cuneata – tussockland, cR

- Lagenifera montana** – mire, MER
Lagenifera petiolata s.s. [*L. purpurea*] – forest margin, MER
Lagenifera pinnatifida – forest, MER
Leptinella sp. (c) (aff. *L. squalida*) [*Cotula*] – mire, cR.
*Leucopogon suaveolens** [*Cyathodes colensoi*] – alpine, cR
Luzula leptophylla – alpine, cR
Luzula rufa s.s. – alpine, Kaw
Luzula sp. (b) [*L. crinita* var. *petrieana*] – alpine, cR
Melicytus sp. (d) (*M. angustifolius* auct. NZ) [*Hymenanthera*]³ forest margin, MER
Myosotis sp. (e)² (*M. australis* agg.) – alpine, MER
Oreomyrrhis sp. (a) (described as *O. colensoi* var. *delicatula* by Allan 1961) – tussockland, MER
Oreostylidium subulatum – tussockland, cR
Pernettya alpina – alpine, cR
Pernettya macrostigma – tussockland, MER
Pimelea microphylla [*P. prostrata* in part] – unconsolidated substrate, MER
Pittosporum anomalum – forest margin, MER
Poa lindsayi – alpine, cR
Pseudognaphalium sp. (b)¹ (*P. luteoalbum* agg.) [*Gnaphalium*] – unconsolidated substrate, MER
Ranunculus cheesemanii – alpine, cR (var. (a), incl. *R. carsei*, endemic to central North Island)
Ranunculus ternatifolius – riparian, MER
Ranunculus sp. (c)¹ (described as *R. lappaceus* var. *macrophyllus* by Kirk 1899) – tussockland, MER
Raoulia sp. (e) (*R.* “sp. K” of Ward 1982) – unconsolidated substrate (and wet depression), MER
Rytidosperma pumilum [*Triodia pumila*]* – tussockland, MER
Rytidosperma tenue – tussockland, MER
Scleranthus brockiei – unconsolidated substrate, Maung
Selliera microphylla [*S. radicans* in part] – wet depression, MER
Senecio glaucophyllus (ssp. *toa* [ssp. *raoulii*] – endemic to central North Island) cliff, MER
Senecio sp. (a) (described as *S. glaucophyllus* ssp. *discoideus* by Ornduff 1960) – unconsolidated substrate, cR (ssp. a endemic to central North Island)
Uncinia rubra – tussockland, cR
- Group 6
67 species with broader northern North Island distributions with southern limits in central North Island, and then disjunct to South Island
- Asplenium richardii* – cliff, Tvm
Bulbinella hookeri – tussockland, MER
*Carex echinata** – mire, cR
Carex fasciculata – wet depression, Lowl (Taupo)
Celmisia glandulosa – alpine, cR
Celmisia incana – alpine, sR
Celmisia sp. (b)¹ (aff. *C. gracilentata*) – alpine, cR
Chenopodium pusillum – wet depression, Lowl (Taupo)
Clematis quadribacteolata – basin, Lowl (Hawke’s Bay)
*Coprosma obconica*³ – forest, MER (ssp. *obconica* in central North Island)
Deyeuxia sp. (b) (*D. quadriseta* agg.) – mire, MER
Drosera arcturi – alpine, sR
Drosera pygmaea – wet depression (and mire), MER
Drosera spathulata – mire, cR
*Empodisma minus** [*Calorophus minor*] – mire, sR
Epacris alpina – alpine, cR
Epilobium gracilipes – cliff, MER
Euphrasia zelandica – alpine, cR
Festuca novae-zelandiae – tussockland, cR
Gentiana bellidifolia s.s. – alpine, cR
Gentiana grisebachii s.s. – tussockland, sR
Geum leiospermum – alpine, cR
Gnaphalium laterale – mire, Tvm
Gnaphalium sp. (d) (aff. *G. paludosum*) – riparian, MER
Gratiola nana – riparian, Lowl (Hawke’s Bay)
Helichrysum depressum – unconsolidated substrate, Lowl (Hawke’s Bay)
Herpolirion novae-zelandiae – tussockland, cR
Hydrocotyle sulcata – mire, MER
Hymenophyllum malingii – forest, sR
Hymenophyllum rufescens – forest, sR
*Isolepis fluitans** – mire, MER
Kelleria sp.(a)¹ [*Drapetes laxus*] – tussockland, sR
Koeleria cheesemanii – alpine, cR
Lagarostrobos colensoi – forest, MER
Lepidothamnus laxifolius – alpine, cR
Libocedrus bidwillii – forest, sR
Luzula decipiens – tussockland (especially unconsolidated substrate), MER
Lycopodium deuterodensum – shrubland, Tvm
Microtis oligantha – mire, MER
Montia sp. (a) (*M. australasica* agg.) – alpine, cR
Myosotis petiolata s.s. – cliff, Lowl (Hawke’s Bay)
Myosotis sp. (c)¹ (*M. pygmaea* var. *drucei*) – alpine, cR
Nertera balfouriana s.s. – mire, sR
Olearia capillaris – forest margin, Tvm

- Olearia nummulariifolia* – alpine, cR (var. *nummulariifolia* endemic to North Island)
Phyllocladus trichomanoides s.s. – forest, Ahim
Pimelea suteri var. (a) (incl. *P. oreophila*)¹ – alpine, cR
Plantago triandra s.s. – wet depression, MER
Podocarpus nivalis – alpine, cR
Pseudopanax ferox – forest, MER
Pterostylis humilis – shrubland, MER
Pterostylis tristis [*P. mutica*] – tussockland, Lowl (Hawke's Bay)
Quintinia serrata (incl. *Q. acutifolia* and *Q. elliptica*) – forest, Tvm
Ranunculus simulans [*R. depressus* var. *stewartiae*] – riparian (and mire), MER
Ranunculus royi – alpine, cR
Rytidosperma viride – unconsolidated substrate, cR
Schizeilema allanii – shrubland, sR
Schizeilema colensoi – forest, cR
Senecio sterquilinus – cliff, Lowl (Hawkes Bay)
Stackhousia minima – tussockland, MER
Stellaria elatinoides – riparian, Lowl (Hawkes Bay)
Stellaria gracilentia – alpine, cR
*Tetraria capillaris** – mire, Tvm
Trisetum sp. (d)² (aff. *T. antarcticum*) – alpine, sR
Uncinia drucei – alpine, cR
Uncinia egmontiana – alpine, cR
*Utricularia australis** (incl. *U. protrusa* and *U. mairii*) – aquatic, Lowl (Taupo)

*species not endemic to New Zealand.

†possibly also occurs at Lake Wairarapa.

¹Species tag name appears first in Druce et al. (1987).

²Species tag name appears first in Druce & Williams (1989).

³Two species that occur near Taihape, *Coprosma obconica* and *Meliclytus angustifolia*, are included in Group 5 because the western Taihape district has close physiographic and biological affinities with lowland MER.

A summary of the distributional parameters and numbers of species in each group appears in Table 1.

Central North Island endemism and disjunction

All except 5 of the 18 central North Island endemic species (groups 1 and 2) are of comparatively wide distribution. Of the restricted species, two are confined to Ruahine Ra., two to MER and one to Maungaharuru Ra. Only one of the endemic species is a tree and only four are shrubs, all of which occur below the regional treeline in open vegetation habitats, i.e., forest margins, cliffs, and pumice-

infilled basins. Of the remainder all but one are non-forest herbaceous species of wet or arid habitats.

Outside Northland and its offshore islands, by far the most significant centre of endemism in North Island is the central North Island mountains (Druce 1984). This region accounts for 43% of the non-Northland endemism in North Island. However, the number of species originally believed to be central North Island endemics, has been reduced with recent discoveries of some "North Island" species in western Canterbury and Otago.

South of Ruahine Ra., only three endemic species are recorded (Druce 1984): *Hebe evenosa* and *Euphrasia* sp.(a) restricted to Tararua Ra., and *Chionochloa beddiei* restricted to eastern Wairarapa and Rimutaka Ra.

For such a small geographic area, MER contains a large number of species disjunct to South Island. Ten species are restricted to non-forest habitats of the Moawhango River headwaters east of the Desert Rd in the southern Kaimanawa Mts. Another six non-forest species are confined to Reporoa Bog, Makirikiri Tarns, and other open vegetation on Mangaohane Plateau in the southern sector of MER in NW Ruahine Ra. Most of these southern species occur on medium to high fertility (commonly calcareous) sites such as periodically flooded damp depressions, seepages, and stream banks. These special habitats in upper montane, undulating topography are restricted to MER in the North Island.

Although the distribution of New Zealand mosses is poorly known, J. K. Bartlett (pers. comm.) recognised the elevated limestone capped plateaux of MER as a significant area for mosses restricted there in North Island and disjunct to South Island (e.g. *Bryum harriottii*, *Bryum tenuidens*, *Fissidens adianthoides*, *Gigosperrum repens*, and *Sphagnum squarrosum*). Two others, *Bryum muehlenbeckii* and *Bryum inclinatum* are disjunct from Mangaohane Plateau, MER to Mt Arthur, NW Nelson (Bartlett 1984).

One lichen, *Diploschistes hypsaceus*, is endemic to Mangaohane Plateau, MER, and possibly one undescribed species of *Sphagnum* (J. K. Bartlett pers. comm.). The *Libocedrus bidwillii* forest at Hihitahi, MER has a rich diversity of corticolous lichens including three endemic species, *Cetraria chlorophylla*, *Xanthoria candelaria* and *Parmeliella granulata*, while *Pseudocypbellaria crassa* is disjunct from there to western South Island (J. K. Bartlett pers. comm.).

The central North Island mountains, excluding MER, contain 55 species disjunct to South Island (group 5). All except two are non-forest species (Table 1); open vegetation sites at montane-subalpine elevations are most common where waterlogged or droughty soils exclude forest communities. Although the majority can be classed as upland species, most descend to lower-montane altitudes with the availability of suitable microhabitats. The exceptions, obligate alpiners, in the North Island are a limited group, e.g., *Pernettya alpina*, *Luzula leptophylla* (Makirikiri Tarns below treeline is a rare exception — CHR 249128), *Uncinia drucei*, *Agrostis* sp. (c) (aff. *A. subulata*), and *Colobanthus acicularis*.

Most of these 55 disjunct species are widely distributed in the central North Island ranges. No one mountain range, therefore, appears biogeographically or ecologically unique except possibly the Maungaharuru Ra., to which three species are restricted in North Island, that is *Scleranthus brockieii*, *Iphigenia novae-zelandiae*, and *Carex enysii*, (*Pimelea* sp. (a) is endemic there).

With possibly one or two exceptions, the endemic and disjunct species of central North Island are not restricted to volcanic substrates. This suggests that little speciation has resulted from the novel environments generated by the onset of volcanism in central North Island some 1.35 Myr ago (Brothers 1984).

For the species confined to or disjunct in the central North Island mountains (groups 1, 2, 4, 5), some 95% are non-forest plants, the majority in open sites below the treeline (Table 1). Approximately 55% occur in reliably moist sites and sites with a high water table. For groups 3 and 6, species of wider northern North Island occurrence, 83% are non-forest species (Table 1) and, again, the majority occur below treeline.

Northern boundary of the gap

The nature of the lower North Island gap and, in particular, the northern boundary can now be evaluated. Dealing with endemism only, two northern boundaries are recognised by McGlone (1985:726,

Table 1 Summary of the predominant habitats of species appearing in the endemic and disjunct species groups.

The distributional parameters and numbers of species in each group are as follows:

Group 1 : 2 species endemic to MER.

Group 2 : 16 species endemic to central North Island with nearly all occurring in MER.

Group 3 : 23 species with wider distributions but still endemic to North Island and with southern limits in central North Island.

Group 4 : 17 species confined to MER in North Island and disjunct to South Island.

Group 5 : 56 species confined to the central North Island uplands in North Island and disjunct to South Island.

Group 6 : 65 species with broader northern North Island distributions and with southern limits in central North Island, and then disjunct to South Island.

	Alpine	Shrubland	Tussockland	Unconsolidated substrate	Mire	Cliff	Basin	Wet depression	Riparian	Forest margin	Forest	Aquatic
Group 1								1	1			
Group 2	3	1	2		1	3	1	3		1	1	
Group 3	6		2	1	4	4					6	
Group 4			2	3	1			5	6			
Group 5	17		12	8	5	1		4	1	5	2	
Group 6	20	3	8	2	10	4	1	4	4	1	9	1
Total	46	4	26	14	21	13	2	17	12	7	18	1
Appendix 1	17	3	1	13	4	9		3		1	1	
Appendix 2	2	13	3	12	9	15		7	3	1	17	
Total	19	16	4	25	13	24		10	3	2	18	

fig. 2 based on Druce 1984). A boundary drawn at 38°S, from Kawhia to East Cape, is more compelling than that drawn at 39°S based on numbers of endemics in the two northern regions.

Table 2 summarises the southern North Island limits of species in groups 1–6. Based on patterns of endemism and disjunctions this exercise redefines the boundary to the gap in the southern part of the central North Island uplands. The boundary is best defined as a series of geographically associated, but dispersed, mostly montane regions dominated by MER and central Ruahine Ra (Fig. 2). If latitudinal limits are considered, this range spans 39°20'S to 39°50'S. Lowland Taranaki, Taihape, and Hawke's Bay also feature prominently as does southern Ruahine Ra.

Southern boundary of the gap

Although Wardle (1963) and McGlone (1985) show a southern boundary to the gap in Cook Strait the patterns of two large groups of disjunct species would suggest otherwise. Fifty-two species, with predominantly South Island distributions, have northern range limits about the southern Wellington–southern Wairarapa district (Appendix 1). Species ranges terminate either in the southern Taranaki and Rimutaka uplands, or in the southern Wellington and southern Wairarapa coastal lowlands. Several of the upland group stop at the Mitre–Mt. Holdsworth Ridge of Taranaki Ra., despite outwardly suitable habitats further north, (e.g. *Hebe canterburiensis*, and *Brachyglottis adamsii*). Only *Pimelea gnidia*, *Hoheria* sp. (a), and *Coriaria* sp. (a) do not fit this altitudinally demarcated pattern; they are found in both the lowlands and uplands (Appendix 1).

Another large and significant group of over 80 species (Appendix 2) shows North Island disjunctions between the southern Wellington–southern Wairarapa lowlands and northern–central North Island districts. Most are recorded from South Island. A number of species of this group have links between the northern Cook Strait lowlands and the central North Island uplands, for instance, *Coprosma wallii*, *Rytidosperma merum*, *Carex flaviformis*, *C. buchananii*, *Leptinella pusilla*, *Scleranthus uniflorus*, and *Mazus radicans*.

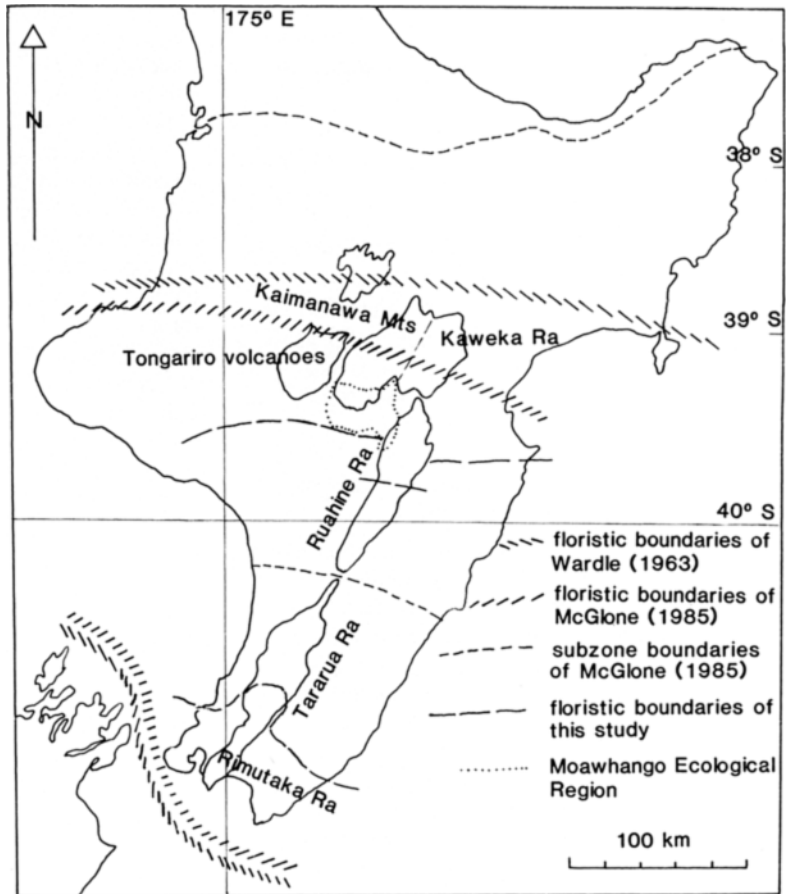
The great majority of species listed in Appendices 1 and 2 occur in non-forest habitats (Table 1). The coastal greywacke cliffs and screes, typified by seasonal drought, support species such as *Aciphylla squarrosa*, *Luzula banksiana*, *Muehlenbeckia astonii*, *Pellaea* sp. (b), *Pimelea aridula*, and *Pleurosorus ruitifolius*. More commonly, unconsolidated substrates on coastal platforms are the characteristic habitat for such species as *Carex buchananii*, *Leptinella pusilla*, *Myosotis* sp. (j) [*M. pygmaea* var. *minutiflora*], *Muehlenbeckia ephedroides*, *Acaena pallida*, and *Myosurus minimus* ssp. *novae-zelandiae*. Others grow in moist sites associated with stream levées and banks, or lagoons, salt marshes, and lake margins subject to fluctuating waterlevels (e.g., *Carex cirrhosa*, *Carex flaviformis*, *Crassula sinclairii*, *Glossostigma submersum* and *Leptinella maniototo*). Several other species are confined to stable and low fertility soils with high clay content, e.g., *Lindsaea linearis*, *Morelotia affinis*, *Pterostylis nana*, *Pterostylis trullifolia*, and *Schizaea bifida*.

North of Aorangi Mts, in south-east Wairarapa, outcropping sandstone pinnacles at low altitudes ("taipos") support various woody or semi-woody

Table 2 Summary of southern North Island distribution limits of species endemic to central North Island or disjunct from there to South Island.

	Lowland	Hauhungaroa Ra.	Tongariro Volcanic Mountains	Ahimanawa Ra.	Maungaharuru Ra.	Kaimanawa Mts	Kaweka Ra.	Moawhango Ecological Region	Northern Ruahine Ra.	Central Ruahine Ra.	Southern Ruahine Ra.
Group 1								2			
2			1		1			9		4	1
3	4		3	1				6		5	4
4								17			
5	1		1		3		1	26	1	21	1
6	10		6	1				16		23	11
Total	15		11	2	4		1	78	1	53	17

Fig. 2 The northern and southern boundaries of the lower North Island floristic gap as defined by endemic and disjunct distributions of higher plants. Previous boundaries of Wardle (1963) and McGlone (1985; after data in Druce 1984) are shown based on patterns of endemic higher plants.



disjunct species e.g., *Clematis afoliata*, *Coriaria kingiana*, *Hebe venustula*, and *Pimelea gnidia*.

Within these Cook Strait groups, some species have been recorded only once or from one locality in the Wellington–Wairarapa lowlands, e.g., *Hierochloa fusca*, *Isolepis praetextata*, *Mazus radicans*, *Mentha cunninghamii*, *Muehlenbeckia astonii*, *Myosotis* sp. (k), *Simplicia laxa*, *Utricularia novae-zelandiae* and *Utricularia lateriflora*. Others are probably extinct, e.g., *Pleurosorus rutifolius*, *Hebe speciosa*, *Lepidium tenuicaule*, and *Lepidium obtusatum*.

The southern boundary of the gap can now be reviewed in relation to these Cook Strait patterns. An analysis of endemism in northern South Island and southern North Island places a boundary in Cook Strait (Wardle 1963; McGlone 1985). This analysis highlights a southern boundary in lower North Island in the region of southern Wellington–southern Wairarapa (Fig. 2). No absolute boundary can be identified. What is evident is the

strong biogeographic affinities between central North Island and southern Wellington–Wairarapa, and conversely, the biogeographic incongruity between these regions and northern–central Tararua Ra. and the flanking lowlands. Clearly, a more restricted lower North Island gap than previously recognised (Wardle 1963, McGlone 1985) has emerged, confined to southern Ruahine and northern–central Tararua Ranges and the bordering lowlands.

DISCUSSION

To what can we ascribe these coincident patterns and minor centres of endemism in lower North Island? The groups of plants identified have diverse ecological requirements and probably display widely differing dispersal mechanisms, yet they exhibit numerous, coincident disjunct patterns. Chance dispersal events appear to be an improbable explanation. Long-distance disjunctions of just one

species, e.g., *Ourisia modesta*, disjunct from MER to NW Nelson and E Nelson and then to Southland and Stewart Island, are rather uninformative in obtaining an explanation for plant distributions (McGlone 1985). It is coincident patterns that enable common factors to be assessed and explanations of chance dispersal or recent extinction of intermediate populations to be ruled out.

With this redefinition of the lower North Island gap, I will attempt to rationalise these patterns firstly in relation to habitat availability, then for those species unaccountable by these means, with historical explanations. The latter will be used to assess the applicability of the "Otiran Glaciation" and the "tectonic" hypotheses.

Discrepancies between available habitats and species ecological requirements

It seems clear that several of the disjunct and endemic species ranges accord with discontinuities in available habitats. The absence in the gap of lakes with fluctuating margins may account for the absence of *Leptinella maniototo* and *Carex cirrhosa*, for instance. Furthermore, coastal greywacke cliffs and gravel beaches, prominent around northern Cook Strait shores, are absent from the gap. A group of forest and forest margin species, e.g., *Coprosma virescens*, *C. wallii*, and *Olearia hectorii* have lower North Island distributions broadly correlated with markedly summer-dry climates in southern Wairarapa and parts of central North Island but these species are absent from central Hawke's Bay in the gap, also noted for summer aridity. However, other specialist habitats of group 1-6 species at lower altitudes within the gap, such as mires, riparian sites, unconsolidated substrates, and non-greywacke cliffs, are common around coasts and lowlands rendering an environmental explanation for the absence of these species untenable.

Whereas central Ruahine Ra. is an important southern limit for disjunct species, southern Ruahine Ra. is far less so (Table 2). Significant habitat discontinuities correlate with this pattern. The southern range is narrow and at lower elevations than the northern and central Ruahine Ra. (Elder 1965). Frequent cloud and mist and increased windiness, associated with the Manawatu Gorge depression affect both the southern Ruahine Ra. and northern Tararua Ra. Montane beech forest is absent from both areas either side of the gorge depression. In southern Ruahine Ra., continuous *Olearia colensoi* scrub above *Libocedrus bidwillii*-*Halocarpus*

biformis forest dominates summit surfaces, and habitat diversity compared to the northern and central range is lower. Tussockland, wet depression and certain mire habitats for non-forest species are very local.

Treeline morphology and montane-subalpine vegetation indicate profound environmental differences between the Ruahine and Tararua Ranges. Elder (1965) in Ruahine Ra., and Zotov et al. (1938), Wardle (1962), and Franklin (1967) in Tararua Ra., detail the dominant vegetation patterns. In general terms, extensive *Nothofagus menziesii* forest allied to a complete absence of *Nothofagus solandri* var *cliffortioides* indicates low insolation and high humidity climates in Tararua Ra. Treelines are lower than those of Ruahine Ra. and extensive subalpine scrub and, higher still, tussockland replace the alpine habitat diversity to the north. Extensive peat bogs are rare. On the other hand, montane northern and central Ruahine forests are physiognomically dominated by *Nothofagus fusca* and *Nothofagus solandri* var *cliffortioides* which indicate climates are sunnier and less consistently wet (Wardle 1984: 308).

Unstable detrital substrates favoured by many disjunct species abound in Ruahine Ra. but are uncommon in Tararua Ra. Moreover, in general, Ruahine Ra. has a diverse, unstable-habitat flora, in contrast to the Tararua Ra. which is noteworthy for the general absence of herbaceous species of unstable habitats (A. P. Druce pers. comm.). An equably cool, superhumid Tararua climate results in cliff faces stabilised with a complete cover of vegetation. Solifluction debris that accumulated as fans and screes in cold Pleistocene climates (Kamp & Vucetich 1982) are now almost entirely stabilised by *Chionochloa pallens* tussockland, effectively excluding lower stature species.

While the presence of competing species and habitat discontinuities may account for the absence of many high-altitude disjunct species in the gap, there are several "generalist" bog species absent from southern Ruahine and Tararua bogs although habitats appear to be suitable, e.g., *Halocarpus bidwillii*, *Centrolepis pallida*, *Luzula leptophylla*, *Drosera arcturi*, and *D. pygmaea*. Similarly, conditions appear suitable for the widespread species, *Libocedrus bidwillii*, *Lepidothamnus laxifolius*, and *Podocarpus nivalis*.

The concentration of endemic and localised disjunct species in MER is explained by specialist habitats restricted there in North Island. Unusual wet depression habitats, periodically flooded hollows

and seepages, and high-fertility riparian zones, all associated with Tertiary sediment plateaux uplifted to upper montane elevations, are restricted to MER in North Island. Maungaharuru Ra. similarly supports local specialist microhabitats of Tertiary sediment for its three disjunct and one endemic species.

In conclusion, although it is difficult to be precise with the ecological attributes of habitats, it appears that discontinuities in both lowland and upland non-forest habitats can account for some of the conspicuous lower North Island disjunctions. But many taxa, both ecologically “specialist” and “generalist” species of alpine bogs and lowland mires, riparian sites and unconsolidated substrates, are absent from ostensibly suitable habitats within the gap.

Care must be taken in attempting to assess the age of current habitats as an index of the age of patterns of endemism and disjunction. The current realised niche of a species may only be a fraction of the potential when assessed in relation to stochastic disturbance factors, changing palaeoenvironments, and presence of competing species. The fossil record may be equally unreliable in assessing habitat age, as only select environments are favourable for fossilisation, presenting a very restricted range of the ecological diversity represented at any one time.

The influence of Pleistocene climates on endemism and disjunction

Attempts to use Pleistocene climates to explain biogeographic patterns must be equally convincing when applied to zones either side of a phyto-geographic boundary. In applying the “glacial refugia” hypothesis to lower North Island, Wardle (1963) contends that there were fewer opportunities for plant survival there than northward. Observations on Otira Glaciation snowlines have been used to infer a lowering of mean annual temperature of first 6°C (Willett 1950) and later 4.5°C (Soons 1979). This, in turn, is used to infer an 850 m lowering of altitudinal vegetation sequences (Wardle 1963) with an attendant elimination of the lowermost 750 m of the sequence adjusted for lowered sea-levels. Wardle notes the regionally lower treeline in Tararua Ra. and Wellington compared with further north and suggests that if the relative suppression of treelines was sustained, this is sufficient to explain the (near) absence of endemics (and disjunct species) from this region.

Admittedly, there is good evidence from the depressed altitude of the *Nothofagus menziesii*

treeline and the upper altitudinal limit of other species such as *Dacrydium cupressinum* and *Nothofagus fusca*, that climate is significantly different between in turn Tararua Ra., Ruahine Ra., and the mountains further north. But the limit of continuous woody growth in Tararua Ra., particularly subalpine shrubs, is quite a different matter. *Olearia colensoi* in Tararua Ra. attains 1450 m (4750 ft.) in steep well-drained sites, comparable to its limit in Ruahine Ra, while *Brachyglottis bidwillii* and *Dracophyllum uniflorum* occur to the highest peaks in Tararua Ra. (Wardle 1962). Therefore, it cannot be argued (see Wardle 1963) that there may have been less potential in the Tararua region than northward to accommodate the Otiran depression of lower montane-subalpine vegetation zones. Further, today’s regionally distinct mountain climates, particularly frequent cloud in Tararua Ra., may not model the regionalism of harsh weather of glacial climates. Additionally, Shepherd (1987) has cast doubt on the concept of Pleistocene glaciation of Tararua Ra. (see e.g., Stevens 1974) that originally implied more regionally severe cold climates only in Tararua Ra. in the North Island axial ranges.

There are also striking local climatic differences between Tararua and Rimutaka Ranges with the effect of much greater exposure evident in the latter (Franklin 1967). This zone of harsher climates overlaps the zone where 52 “South Island” species extend into southern Wairarapa–southern Wellington (with 23 occurring in the Tararua–Rimutaka uplands) (Appendix 1). In addition, the majority of the 80 species with disjunct distributions between central North Island and southern Wellington–southern Wairarapa (Appendix 2) have ranges overlapping this zone. If, as Wardle (1963) suggests, Wellington experienced differentially harsher climates than areas to the north and south, why then were the mainly temperate, disjunct species of Appendix 2, preserved in south Wellington–south Wairarapa lowlands, but eliminated in the greater, lower North Island?

In the absence of evidence, it is hazardous to postulate obliteration of regional floras in a cold phase by an “escalator-like” effect of lowered vegetation zones against a seashore. If this effect contributed to “floristic poverty” in the gap, there seems no reason why the impact was so regionally selective in lower North Island, i.e., only southern Ruahine and northern and central Tararua Ra.? Furthermore, McGlone (1985) argues that there were altered climatic constraints on plant growth (survival) in the glaciations from those prevailing today, e.g., persistent strong winds, episodic drought,

freezing air masses, and severe temperature inversions. He believes topography would have been a prominent determinant of vegetation patterns. Forest survival was enhanced in regions of broken relief where there was an amelioration of the harsh, more variable weather factors (McGlone & Webb 1981, McGlone et al. 1984, McGlone 1985). Conversely, areas of subdued relief, e.g., lowland plains, would have been those regions most severely affected, supporting extensive grassland with small areas of shrubland.

The topographic complexity of the central and southern North Island mountains, despite late Pleistocene intensification of relief, would have deflected the rigours of climatic deterioration by offering opportunities for survival, not only for forest, but for non-forest species in habitats such as cliff, riparian, and flush-zone sites. Whether the region was at current elevations throughout the Pleistocene is immaterial; as has been demonstrated, most of the biogeographically unusual plants are not obligate alpinists but exhibit wide altitudinal tolerances with the provision of suitable habitats. If altitude was subordinate to topography as the major control on vegetation patterns in glacial periods, an intermixing of what are now altitudinally segregated vegetation types would have been characteristic of broken terrain. Degree of exposure would have produced a complex intermixing of structurally diverse vegetation.

The dissected topography of the central North Island uplands probably also served to ameliorate and deflect the impact of paroxysmal vulcanism and thereby functioned as an enhanced refuge for habitats of restricted plants. However, some species have probably become regionally or locally extinct; *Libocedrus bidwillii* disappeared from the northern-central Kaimanawa Mts following inundation of its restricted riparian habitat by the Taupo Pumice Ignimbrite (Rogers 1987).

The palynological record pictures extensive grassland and shrubland with forest patches in hilly regions in the Last Glaciation, a reversal of the present day pattern (McGlone 1985). Although it is likely some generalist upland species had greatly extended cold-climate ranges, as demonstrated in their response to Polynesian deforestation, others of lower dispersal capacity or more confined ecological amplitude, would have exhibited far less mobility. There is some contemporary evidence for this. For instance, most of the group of disjunct species confined to MER in North Island have not spread out from their very restricted, non-forest habitats with

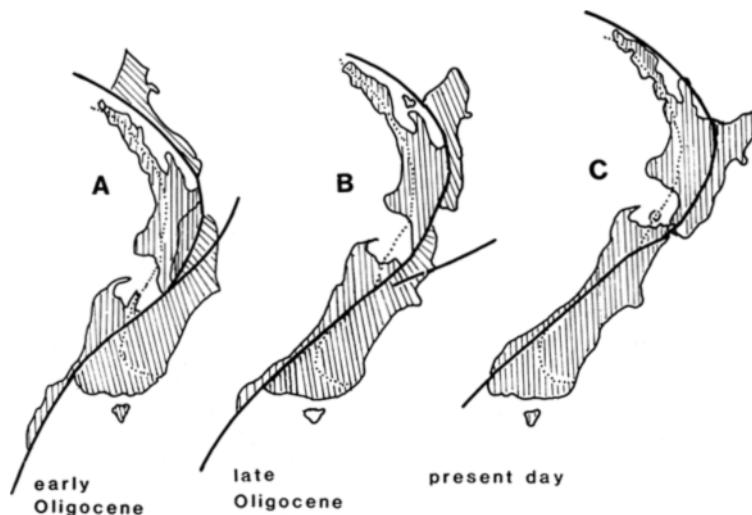
the advent of extensive Polynesian deforestation and associated spread of shrubland and tussockland.

Any suggestion of a cold climate survival centre for central North Island endemic and disjunct species in the lowlands, now partly submerged, between Taranaki and Nelson is contingent upon long-distance mobility, but is in direct conflict with the extant evidence for comparative distributional stasis of most disjunct species in response to deforestation. In addition, in this lowland region today, ostensibly suitable habitats would be expected for low altitude forest and forest margin species of the disjunct groups such as *Melicytus alpinus*, *Olearia capillaris*, *Clematis quadribacteolata*, *Coprosma wallii*, *C. virescens*, and *C. obconica*, yet they are conspicuously absent in that region. It would seem unlikely that they found a cold-climate survival centre there and subsequently disappeared. The creation of other specialist habitats within the gap in glacial climates would not necessarily result from a climate driven change from extensive forest to open shrubland and grassland. Unfortunately, as a means of testing for the cold climate presence of disjunct species within the gap, the palynological record is poor. The pollen of many restricted non-forest species is poorly differentiated and habitat and accurate community composition appears difficult to reconstruct (Pocknall 1982). However, the palyno-logical record does show that many physiognomically conspicuous and "generalist" habitat species of forest, shrubland, and tussock grassland are regionally rather mobile in response to fluctuating climates.

It is possible that the oceanic influence acted to ameliorate the variability of glacial climates. But while the maritime influence may have engendered the survival of some south Wellington-south Wairarapa disjuncts, particularly near the coasts, the groups of central North Island endemics and disjuncts could not have been similarly influenced. For some species, limited altitudinal mobility probably occurred, particularly on coastal cliffs and in mountains as a strategy for survival in response to changing climates.

In summary then, there are no grounds for believing that upland topography in either southern North Island or in the redefined gap experienced harsher glacial climates with greater species extinction when compared to central North Island. While there are regionally distinct mountain climates throughout Ruahine, Tararua, and Rimutaka Ranges, they only partly correlate with the biogeographic patterns and they may not be a reliable extant analogue for regionally distinct glacial climates.

Fig. 3 Evolution of North Island during the last 32 million years (modified after Wellman 1985).



Tectonic hypothesis

The “tectonic” hypothesis (McGlone 1985), while recognising that anomalous endemic and disjunct distributions reflect present environmental constraints, also offers a means of explaining how these distributions were achieved. McGlone (1985:737) contends that although the land surface has undergone transformation since the Oligocene, “there are relatively stable areas which have developed or retained endemic rich floras”, in contrast to those “actively uplifting, unstable areas”.

When applying the “tectonic” hypothesis to lower North Island we must assess the likely palaeo-environmental impact of three significant post-Oligocene geological events:

1. dislocation of large landmasses by fault displacement;
2. changing palaeogeographies by marine transgression and regression;
3. disruption of old environments and creation of new ones by mountain building episodes.

Numerous tectonic and palaeogeographic reconstructions covering the late Cenozoic development of New Zealand have been proposed and some can be considered as historical biogeography working models. Considered first here are models of late Cenozoic tectonic dislocation (by fault displacement) of North Island, followed by palaeogeographic reconstructions involving marine transgression. Finally, the Kaikoura Orogeny in lower North Island is considered.

Tectonic displacement

The central and southern North Island mountains are part of the axial tectonic belt of New Zealand (Walcott 1978a), which absorbs the tectonic strain between the Indian and Pacific Plates. This regime became established about 20 M yr ago when the alpine fault became active (Walcott 1978b; Kamp 1986). Kamp (1986) argues for 480 km of Cenozoic dextral transcurrent displacement in South Island on the Alpine Fault. In North Island and Marlborough, however, Kamp believes this lateral displacement of land masses did not occur, and changes in the position of the crustal plate boundary resulted in little change in overall geographic outline of southern North Island.

On the other hand, Korsch & Wellman (in press, fig 23) and Wellman (1985) (see Fig. 3) suggest dextral transcurrent movement on an extension northward of the Wellington Fault through North Island of 170 km in the last 10 M yr. (Fig. 3), and 500 km since the Oligocene resulting in a rafting southward of south-eastern North Island relative to the western portion.

Thus, the emerging picture is that the lower North Island is tectonically unstable. Whereas one model indicates dextral transcurrent movement may have substantially separated the western and eastern regions of lower North Island, the other model shows a zone of complex deformational strain but little translocation of landmasses by fault displacement.

In South Island, McGlone (1985) argues for fault displacement on the Alpine Fault to account for a separation of southern South Island and

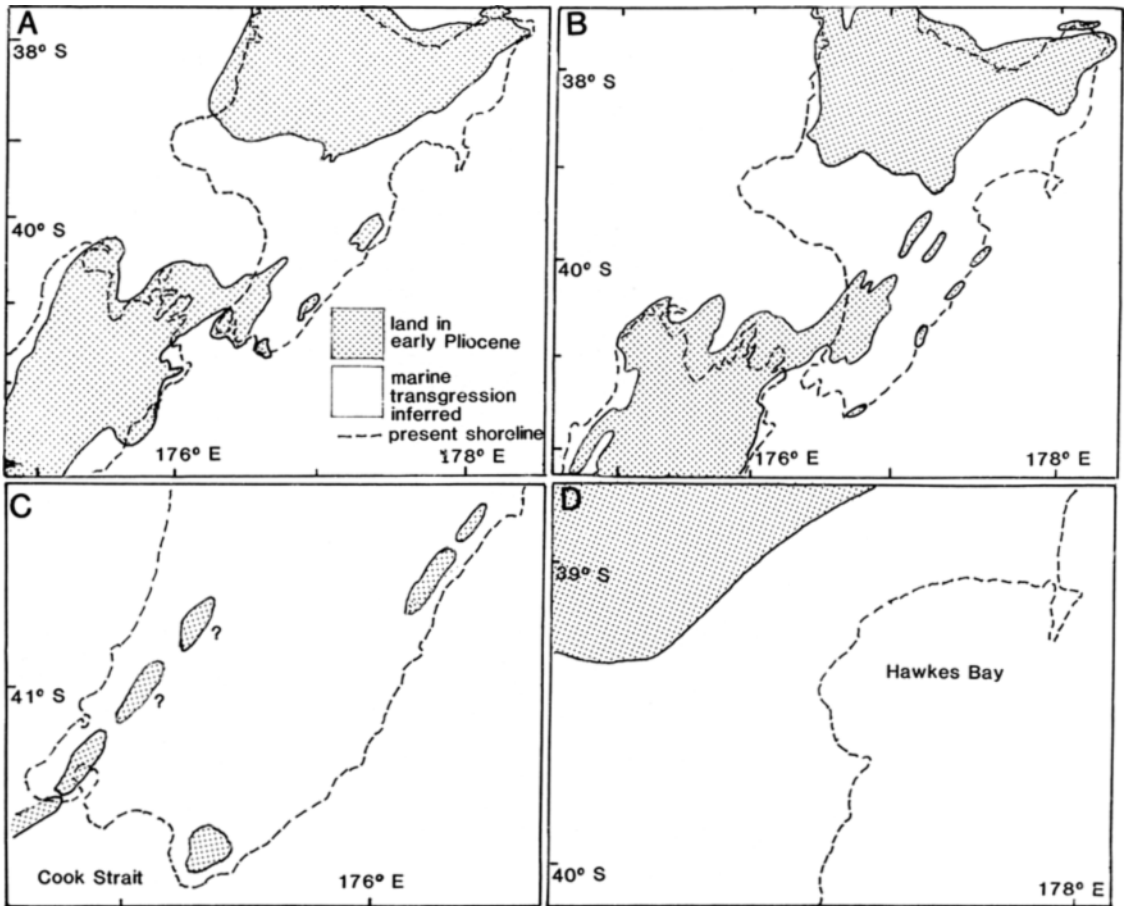


Fig. 4 Palaeographic maps for the early Pliocene at the approximate maximum extent of marine transgression of lower North Island. A After Stevens (1974); B After Suggate et al. (1978); C After Kamp (1982); D After Kamp & Vucetich (1982).

N.B. Fleming (1979: fig 11) shows a Pliocene palaeogeography similar to Stevens (1974).

Nelson–Marlborough centres of endemism. Separation of once adjacent terrain across the North Island shear belt representing what is now central North Island and Wellington–Wairarapa, with subsequent interpolation of rapidly rising axial ranges, may also go some way to explaining lower North Island disjunctions.

Marine transgression

Palaeogeographic reconstructions for the early Miocene show New Zealand as an attenuated central strip of land (Suggate et al. 1978: 737). Late-Miocene re-creations of North Island show an expanded landmass (e.g., Suggate et al. 1978: 738–739) and several re-creations span the following period of

Plio–Pleistocene marine transgression of lower North Island (Fig. 4), referred to by McGlone (1985) as important in lower North Island plant biogeography. At the maximum extent of inundation, exceptions to a complete submergence of lower North Island are land in the vicinity of Ruahine Ra. (Stevens 1974; Suggate et al. 1978: 740), some land in the Manawatu and western Tararua Ra. region and an archipelago of eastern Wairarapa islands (Suggate et al. 1978: 740; Fleming 1979: 46; Stevens 1974; Kamp & Vucetich 1982). Interestingly, Suggate et al. (1978), and Fleming (1979) show a Pliocene marine transgression covering the regions of the Tongariro volcanoes, much of the Kaimanawa Mts, Kaweka Ra. and all MER, a large portion of that central North

Island region highlighted by endemic and disjunct species distributions. Kamp (1982), however, shows land emergent in the vicinity of Kaweka Ra. (Fig. 4). Grindley (1960), shows no Cenozoic sediments within the Kaimanawa–Kaweka massif which would constitute unequivocal evidence of marine transgression of the greywacke basement.

While palaeogeographic maps function only as “snap shots” in geologic time, the consensus for late Cenozoic Wellington–Wairarapa is for some land above sea level at any one time, particularly in the vicinity of Aorangi Mts. and southern Wellington, including parts of southern Tararua Ra. (Fig. 4).

The age of lower North Island mountain landforms is also important in relation to the establishment of biogeographic patterns. According to Walcott (1978b), there is no evidence in the form of a record of large scale erosion of greywacke terrain, of the lower North Island axial ranges having been rapidly uplifted before 0.5 million years ago. Tectonic uplift of northern Ruahine Ra. commenced in mid-Pleistocene times, later than 1 M yr ago (Beu et al. 1981), and Ghani (1978) believes rapid uplift of Tararua Ra. was a comparatively recent event at 500,000 to 200,000 years ago. Nevertheless, other workers report evidence of earlier uplift in the form of greywacke gravel conglomerates, interbedded in basal, marine sediments, abutting parts of Ruahine Ra. of 3–1 M yr age (Lillie & Fleming 1941: 3, reported in Wellman 1949). In addition, Browne (1978) reports similar interbedded greywacke conglomerates in basal marine sediments of Opoitian age (6–5 M yr) from the Mangaohane Plateau, MER, bordering the NW Ruahine Ra. Browne believes this signifies a greywacke landmass in close proximity in this period well before the late Pleistocene period of rapid uplift.

Peneplain remnants and plateaux

There is evidence that many endemic and disjunct species occupy habitats associated with zones of tectonic stability. Traces of old peneplain surfaces pre-dating the Kaikoura orogeny are widespread in lower North Island. Sporli & Barter (1973) and Sporli (1987) map extensive remnants of an ancient erosion surface in the greywacke, Kaimanawa massif possibly dating to Cretaceous–early Tertiary times. In the vicinity of the upper Moawhango River headwaters and Ngamatea Plateau (M.E.R.) abutting Kaimanawa Mts, this greywacke surface of broad convexity and concavity is overlain in places by thin late Miocene–early Pliocene, marine sediments (Gregg 1960; Sporli 1987; R. Black pers. comm.).

According to R. Black (pers. comm.) this region marks the local northern limit of the marine transgression of lower North Island, i.e., in the southern Kaimanawa Mts. Ngamatea Plateau landforms represent a remarkably well preserved Miocene landscape where existing greywacke ridges of the bordering Kaimanawa Mts, and the interfingering marine sediment plateaux—resembling contemporary Marlborough Sounds topography—represent part of a MER palaeo-shoreline dating to 12–8 M yr. The conclusion is that Kaimanawa Mts were never submerged in the Pliocene marine transgression as shown on Pliocene palaeogeographic maps of Suggate et al. (1978: 740) and Fleming (1979: 46).

On top of the Ruahine Ra. is a surface defined by summit height accordance and interpreted as an uplifted fossil erosion surface by many New Zealand geologists including Cotton (1926), Lillie (1953), and Kingma (1959). Near the Manawatu Gorge the erosion surface is overlain by late Cenozoic marine strata (Lillie 1953). In addition, the Pleistocene Kaukau peneplain of Wellington is believed by Wellman (1949) and Te Punga (1954) to have once extended north to the Tararua and Ruahine regions prior to deformation by uplift some 340,000 years ago.

The plateaux of MER and the broad summits of western-central Ruahine Ra. (e.g., Mokai Patea, Hikurangi, Whanahuia) that collectively account for so many of the endemic and disjunct species southern limits are also strikingly regular uplifted surfaces. Preservation of non-forest habitat diversity during uplift is less likely for Tararua Ra. Intense folding, faulting, and rifting produce a geomorphically unstable alpine zone (Stevens 1974) with steep, dissected terrain. Not only are there current habitat absences in the gap, but severance of once more continuous species ranges by tectonic instability, particularly in eastern-central Ruahine Ra. and central Tararua Ra., could account for many species disjunctions.

Long-term local survival of species, through the process of tectonic uplift of habitats was postulated by Smith (1974), in evaluating the origin of the Mt Wilhelm alpine flora in Papua New Guinea. Fleming (1962: 95) offers the possibility of the “facultative” development of alpine plants under warm lowland Miocene conditions by suggesting certain species were pre-adapted to the new alpine environments of the Kaikoura orogeny, surviving there by a kind of “ecological opportunism”. In the alpine Ranunculi, Fisher (1965) suggests section *Epirotes* may have arisen facultatively from lowland species.

In summary, parts of lower North Island have fossil surfaces that have apparently remained largely intact despite uplift in the Kaikoura Orogeny. Regionally, these surfaces correlate broadly with the distribution of endemic and disjunct plants in lower North Island particularly in the Kaimanawa Mts, Kaweka and central Ruahine Ranges, MER, and parts of south Wellington. Furthermore, rather than a Pliocene marine transgression covering most of the Kaimanawa Mts, the northern palaeo-shoreline probably coincided with northern MER. To the south, although lower North Island was exposed to extensive Cenozoic marine transgression, palaeogeographic maps and sedimentary strata abutting Ruahine Ra. suggest that total inundation of Ruahine and Tararua Ranges and southern Wellington and southern Wairarapa was unlikely at any one time. There is also broad agreement between the patterns of species endemism and disjunction and those areas depicted in palaeogeographic maps as being above sea in the Plio-Pleistocene. The coincidence is particularly striking in southern Wellington–southern Wairarapa, southern Tararua Ra. and in central Ruahine Ra. It is also claimed that the Kaimanawa–Kaweka region escaped marine inundation despite the impression from palaeogeographic maps.

CONCLUDING REMARKS

To summarise, there are strong biogeographic relationships between central North Island and both southern Wellington–southern Wairarapa and South Island. In particular, 10 species confined to the Moawhango River headwaters, MER, in North Island, a region with a rainshadow climate have links mostly with eastern South Island; these species occur in dry and often unstable habitats. Five species confined to Mangaohane Plateau, MER, have links with South Island, particularly NW Nelson, inland central Canterbury and Central Otago basins. Another substantial group of species in the central North Island uplands has widely disjunct relationships with both the coastal and lowland Wellington–Wairarapa region and the South Island. The majority (87%) are non-forest species, particularly of alpine sites, tussockland, uncon-solidated substrates, wet depressions, and mires.

The idea of a lower North Island floristic gap is reviewed in the light of both endemic and disjunct species distribution patterns. A diffuse boundary is suggested in southern central North Island that is

particularly prominent in MER and central Ruahine Ra. The imposition of a southern boundary to the gap is more difficult; lower North Island disjunct patterns suggest a boundary in southern Wellington–southern Wairarapa. However there is evidence based on endemic patterns, for another boundary in Cook Strait as shown by Wardle (1963) and McGlone (1985).

Biogeographic analyses render explanations of long distance dispersal to account for these distributions, unconvincing, on the grounds of very low probability for all the replicated patterns. Discontinuities in range of many species are explicable in terms of unavailability of suitable habitats within the gap. For many other species, unavailability of habitat appears unconvincing. An evaluation of the “glacial refugia” hypothesis in the light of a redefined lower North Island gap has found no substantive evidence to suggest these plants were eliminated in inhospitably harsh environments.

Alternatively, several tectonic processes which have affected lower North Island, south of northern MER, may be directly implicated in the dislocation of previously more continuous species ranges in lower North Island. These are:

1. extensive, though incomplete inundation of lower North Island by the Pliocene marine transgression.
2. relative degrees of orogenic dislocation of old landforms by processes of folding, faulting, rifting, and erosion of the greywacke axial ranges.
3. rafting of landmasses along the North Island shear belt.

A striking concordance between the more geomorphically stable regions and the presence of endemic and disjunct species suggests preservation of special non-forest habitats in tectonically stable regions and their destruction in the gap.

The conclusions from this study offer support to McGlone (1985: 746) who believes that many plant distribution patterns owe their origins to changes in land and sea patterns since the Miocene and that endemic-rich centres are regions of comparative geomorphic stasis. Yet, when applying his tectonic thesis to southern North Island he suggests “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”. If these plants are of “southern origin”, individual long distance dispersal or migration events would be required to account for the current distributions on North Island ranges. Given this possibility, it is difficult to see how

extinction through phases of mobility would produce the striking, biogeographically distinct sections of the central and southern North Island mountains. We could, however, expect some local contraction in range to have accompanied phases of population mobility induced by fluctuating Pleistocene climates, especially for the less resilient species occupying small, ecologically specialised, non-forest habitats. Whether these large groups of plants are of “southern origin” is also questionable. Only detailed phylogenetic study might clarify this point.

Wardle (1978) contends that middle Tertiary habitat diversity far exceeded that conveyed by a picture of a low-lying, subtropical archipelago. Wardle (1968) also postulates the presence of cold, wet, infertile soils on Tertiary peneplained uplands to explain a pre-Quaternary element of the mountain flora showing considerable antiquity in New Zealand. Eight of the 15 genera listed by Wardle are common floristic components of MER in habitats edaphically inimical to forest. Furthermore, the range of habitats of endemic and disjunct species considered here suggests wide habitat diversity in pre-Pliocene landscapes. Detrital substrates are one example. Talus habitats are traditionally conceived as products of mountain building episodes. But these habitats could have been associated with low undulating hills and coasts in the middle Tertiary just as they are today in warm-temperate Northland and elsewhere in lowland New Zealand.

We could expect genetic drift or evolutionary specialisation from differential selection pressures to apply in segregated populations long isolated by tectonic events. Evidence for rapid and continuing speciation within herbaceous and woody genera of the alpine regions was presented by Wardle (1978) in the form of cryptic species pairs and many species clusters that readily hybridise. Despite this evidence, very few of the disjunct species identified here, both within North Island and to South Island, show vicariance relationships or species pairings. Very few show infraspecific differentiation in widely separated regions (A. P. Druce pers. comm.). The overriding theme is of evolutionary stasis despite a probable period of geological separation extending back to at least the beginning of rapid uplift of the Tararua Ra., 200,000–500,000 years ago.* It appears

that while phylogenetic and taxonomic affinities in some alpine groups indicate recent evolutionary derivation (Wardle 1978), the general impression is of evolutionary stasis in the group of North Island–South Island disjunct species.

Several late Cretaceous palaeogeographic reconstructions of New Zealand (Kamp 1986: fig. 2) imply some widely separated provinces were once adjacent to one another, e.g., NW Nelson–Fiordland–Stewart Island; central Otago–NW Nelson–central North Island. Such ancient land configurations, with subsequent rifting apart, may be an additional influence in some widely disjunct plant distributions.

So numerous have been the major geological and climatic changes in New Zealand that biogeographers run the risk of a pre-occupation or bias for study of one possible explanatory factor or another. Major changes include Paleogene peneplanation and marine transgression, Neogene movement on the Alpine Fault, Pliocene marine transgression followed by Pleistocene tectonic upheaval, and fluctuating Pleistocene climates. Most biogeographic patterns could be linked to one or another of these influences thus providing an explanation for any one pattern. Little can be gained from such approaches; no one hypothesis can be a categorical solution for all distributions. This exercise highlights habitat discontinuities and geological history as significant in lower North Island plant distributions. Clearly a multifactorial synthesis will emerge from further detailed regional studies in the future providing a clearer understanding of biotic distribution patterns in New Zealand.

APPENDICES

Notes on the appendices

These lists were compiled by G. M. Rogers and A. P. Druce.

If the name used is different from that used in the standard floras (Allan 1961; Moore & Edgar 1970; Cheeseman 1925–grasses only) the previous name is added in square brackets.

For an explanation of alphabetic letter tag names, abbreviations, signs, habitat classification and superscript numbers see the notes accompanying the species lists within the text of the present paper.

Appendix 1: 52 species present in South Island and southern North Island but absent further north

Species confined to the uplands of Tararua–Rimutaka Ranges in North Island

Aciphylla polita – alpine (var. b, incl. *A. dissecta*, endemic)

* One notable exception is *Euphrasia disperma* where the length of the corolla tube in the only North Island population, in MER, is noticeably shorter than that in western South Island populations, e.g., Denniston Plateau (pers. obs.).

Anemone tenuicaulis – alpine
Brachyglottis adamsii [*Senecio adamsii*] – alpine
Celmisia allanii – alpine
Celmisia hieraciifolia – alpine
Celmisia sp. (a)¹ (aff. *C. gracilentia*) – alpine
Chionochoa flavescens s.s. [*Danthonia raoulii* var. *flavescens*] – alpine
Coprosma ciliata – forest (and alpine)
Dracophyllum uniflorum – alpine
Euphrasia laingii (incl. *E. drucei*) – alpine
Hebe canterburiensis – alpine
Leptinella pyrethrifolia [*Cotula pyrethrifolia*] – alpine
Lyperanthus antarcticus – alpine
Myosotis tyallii (incl. *M. elderi*) – alpine
Olearia lacunosa – forest (and shrubland) (var. a, described as *O. alpina* by Buchanan 1887, endemic)
*Oreobolus strictus*** – mire
Pterostylis australis – shrubland
Ranunculus foliosus – alpine
Raoulia eximia – alpine (var. a, incl. *R. rubra*, in North Island)
Rytidosperma nigricans [*Danthonia semiannularis* var. *nigricans*] – alpine
 Species confined to the lowlands of south Wellington and south Wairarapa in North Island
*Acaena pallida** – unconsolidated substrate
Aciphylla squarrosa s.s. – unconsolidated substrate
Asplenium obtusatum – cliff
Atriplex buehneri – unconsolidated substrate
*Atriplex cinerea** (doubtfully indigenous) – unconsolidated substrate
Brachyglottis greyi (incl. *B. laxifolius*) [*Senecio greyii*] – cliff
Brachyglottis monroi [*Senecio monroi*] unconsolidated substrate (var. a, incl. *B. compacta*, – endemic)
*Carex appressa** – mire
Coriaria sarmentosa – unconsolidated substrate
Craspedia uniflora s.s. – unconsolidated substrate (and cliff) (var. *grandis* endemic, var. *maritima* not endemic)
Crassula kirkii [*Tillaea kirkii*] – wet depression
Crassularuamahanga [*Tillaea acutifolia*] – wet depression
Dichondra sp. (a)² – unconsolidated substrate
Hierochloa fusca – mire
Isolepis praetextata [*Scirpus praetextatus*] – mire
Lepidium tenuicaule – unconsolidated substrate
Leptinella maniototo [*Cotula maniototo*] – wet depression
Leptinella nana [*Cotula nana*] – cliff (bare ground on cliff top)
Meliclytus crassifolius [*Hymenantha crassifolia*] – cliff (var. *crassifolius* in North Island)
Meliclytus obovatus [*Hymenantha obovata*] – cliff (var. a) in North Island)
Muehlenbeckia astonii – shrubland
Myosotis sp. (k) (described as *M. australis* var. *lytteltonensis* by Laing & Wall 1924) – cliff
*Myosurus minimus** [*Myosurus novae-zelandiae*] – unconsolidated substrate (ssp. *novae-zelandiae* endemic to New Zealand)
Pellaea sp. (b) (aff. *P. rotundifolia*) – cliff
Raoulia subsericea (in pasture; probably adventive) – tussockland

Raoulia sp. (a)² (*R. hookeri* “coastal form” of Ward 1982) – unconsolidated substrate
Rumex neglectus – unconsolidated substrate
Rytidosperma petrosum – cliff
Simplicia laxa – cliff
 Species confined to uplands and lowlands of south Wellington and south Wairarapa in North Island
Coriaria sp. (a) (aff. *C. plumosa* and *C. pteridoides*) – unconsolidated substrate
Hoheria sp. (a) (aff. *H. populnea*) – forest margin (and riparian)
Pimelea gnidia – shrubland

Appendix 2: 82 species with wide North Island discontinuities between northern-central North Island and the south Wellington and south Wairarapa lowland district. Most occur in South Island; 22 species are not endemic to New Zealand

*Adiantum hispidulum** – forest
Ascarina lucida – forest
Asplenium trichomanes agg.* – cliff
*Calochilus herbaceus** [*Calochilus paludosus*] – shrubland
Carex buehneri – unconsolidated substrate
Carex cirrhosa – wet depression
*Carex flaviformis** – mire
*Carex gaudichaudiana** – mire
Carex ochrosaccus – forest
Clematis afoliata – cliff
Colobanthus muelleri – unconsolidated substrate (also cliff)
Convolvulus sp. (a)² (described as *C. verecundus* ssp. *waitaha* by Sykes 1987) – unconsolidated substrate
Coprosma wallii – forest
Coprosma sp. (g) (aff. *C. parviflora*) – forest
Coriaria kingiana – unconsolidated substrate
Crassula hunua [*Tillaea pusilla*] – riparian
Crassula mataikona [*Tillaea debilis*] – unconsolidated substrate
*Crassula moschata** [*Tillaea moschata*] – mire (also wet rocks)
*Crassula peduncularis** [*Tillaea purpurata*] – unconsolidated substrate
Crassula sinclairii [*Tillaea sinclairii*] – wet depression
Dactylanthus taylorii – forest
*Deschampsia caespitosa** – mire
Dicksonia lanata s.s. – forest
Dysoxylum spectabile – forest
Einadia allanii [*Chenopodium allanii*] – cliff
Einadia triandra [*Rhagodia triandra*] – cliff
Entelea arborescens – forest
Euphorbia glauca – unconsolidated substrate
Gahnia rigida – mire
Gingidia montana [*Angelica montana*] – cliff
*Gleichenia microphylla** – shrubland
Glossostigma submersum – wet depression
Gnaphalium polylepis – riparian
Hebe elliptica – cliff (var. *crassifolia* endemic to south Wellington)
Hebe speciosa – cliff
Hebe venustula (incl. *H. brachysiphon*) – shrubland (also alpine)

Hebe sp. (g) (described as *Veronica salicifolia* var. *angustissima* by Cockayne 1918) – cliff (endemic to North Island)
Hydrocotyle sp.(a)¹ (described as *H. novae-zeelandiae* var. *montana* by Kirk 1889) – tussockland (also riparian)
*Hypolepis dicksonioides** – forest margin
Hypsela rivalis – wet depression
Isoetes sp. (cf. *I. kirkii* and *I. alpinus*) – aquatic
Lachnagrostis richardii [*Deyeuxia forsteri* var. *pilosa*] – cliff
Lepidium obtusatum – cliff (endemic to North Island)
Leptinella pusilla [*Cotula perpusilla*] – unconsolidated substrate
Leptinella tenella [*Cotula minor* in part] – wet depression
*Lindsaea linearis** – shrubland
*Lycopodium cernuum** – shrubland
*Lycopodium laterale** (incl. *L. ramulosum*?) – mire
Luzula banksiana s.s. – cliff
Mazus radicans – riparian (also mire and tussockland)
Mentha cunninghamii – shrubland (also tussockland)
Metrosideros umbellata – forest
Morelotia affinis – shrubland (endemic to North Island)
Muehlenbeckia ephedroides – unconsolidated substrate
Myosotis sp. (j) [*M. pygmaea* var. *minutiflora*] – unconsolidated substrate
Nothofagus truncata – forest
Olearia cheesemanii – cliff
Olearia hectorii – forest (var. a endemic to North Island)
*Ophioglossum petiolatum** [*Ophioglossum pedunculatum*] – mire
Phymatosorus novae-zeelandiae – forest (endemic to North Island)
Pimelea aridula – cliff
Pimelea longifolia – alpine
Pittosporum divaricatum – forest
Pittosporum obcordatum s.s. – forest
Plantago masoniae – unconsolidated substrate (in coastal herbfield)
*Pleurosorus rutifolius** – cliff
Poa matthewsii [*Poa imbecilla* var. *matthewsii*] – forest
*Pomaderris ericifolia** [*P. phyllicifolia* var. *ericifolia*] – shrubland
*Pterostylis nana** – shrubland
*Pterostylis plumosa** [*P. barbata*] – shrubland
Pterostylis trullifolia – shrubland
Ranunculus multiscapus s.s. – tussockland
Rumex flexuosus – wet depression
Rytidosperma biannulare – cliff
Rytidosperma merum – tussockland
*Schizaea bifida** – shrubland
Scleranthus uniflorus – unconsolidated substrate (also tussockland)
*Sebaea ovata** – wet depression
Streblus banksii [*Paratrophis banksii*] – forest
Thelymitra sp. (b) (aff. *T. ixioides*) – shrubland
*Utricularia lateriflora** (incl. *U. delicatula*) – mire
Utricularia novae-zeelandiae (incl. *U. colensoi*, *U. subsimilis*, and *U. vulcanica*) – mire

** Although there is a specimen in CHR collected by one of us (APD) and labelled as coming from northern MER, an intensive search to relocate the species there has been unsuccessful. We have assumed in this paper that the specimen was wrongly labelled.

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REFERENCES

- Allan, H. H. 1961: Flora of New Zealand, Vol. I. Wellington, Government Printer.
- Atkinson, I. A. E. 1985: Derivation of vegetation mapping units for an ecological survey of Tongariro National Park, North Island, New Zealand. *New Zealand journal of botany* 23: 361–378.
- Bartlett, J. K. 1984: New and interesting records of mosses from New Zealand. *National Museum of New Zealand records* 2(17): 181–189.
- Beu, A. G.; Browne, G. H.; Grant-Taylor, T. L. 1981: New *Chamys delicata* localities in the central North Island and uplift of the Ruahine Range. *New Zealand journal of geology and geophysics* 24: 127–132.
- Brothers, R. N. 1984: Subduction regression and oceanward migration of volcanism, North Island, New Zealand. *Nature* 309: 698–700.
- Browne, G. H. 1978: Wanganui strata of the Mangaohane Plateau, northern Ruahine Range, Taihape. *Tane* 24: 199–210.
- Buchanan, J. 1887: On some new native plants. *Transactions of the New Zealand Institute* 19: 213–216.
- Burrows, C. J. 1965: Some discontinuous distributions of plants in New Zealand and their ecological significance II: Disjunctions between Otago–Southland and Nelson–Marlborough and related distribution patterns. *Tuatara* 13: 9–29.
- Cheeseman, T. F. 1925: Manual of the New Zealand flora. Ed. 2. Wellington, Government Printer.
- Cockayne, L. 1918: Notes on New Zealand floristic botany including descriptions of new species, etc., 3. *Transactions of the New Zealand Institute* 50: 161–191.
- 1928: The vegetation of New Zealand. Leipzig, Englemann.
- Cotton, C. A. 1926: Geomorphology, Ed. 7 (revised) 1958. Wellington, Whitcombe and Tombs.
- Druce, A. P. 1979 (revised 1987): Indigenous vascular plants of Ruahine Range. Unpublished report, Botany Division, D.S.I.R.

- 1980a: Trees, shrubs and lianes of New Zealand (including wild hybrids). Unpublished report, Botany Division, D.S.I.R.
- 1980b (revised 1987): Indigenous vascular plants of Tararua Range. Unpublished report, Botany Division, D.S.I.R.
- 1982 (revised 1987): Indigenous higher plants of North West Nelson and indigenous higher plants of New Zealand not in North West Nelson. Unpublished report, Botany Division, D.S.I.R.
- 1984: Distribution of indigenous higher plants in North Island and northern South Island, New Zealand. Unpublished report, Botany Division, D.S.I.R.
- Druce, A. P.; Williams, P. A.; Heine, J. C. 1987: Vegetation and flora of Tertiary calcareous rocks in the mountains of western Nelson, New Zealand. *New Zealand journal of botany* 25: 41–78.
- Druce, A. P.; Williams, P. A. 1989: Vegetation and flora of the Ben More–Chalk Range area of southern Marlborough, South Island, New Zealand. *New Zealand journal of botany* 27: 167–199.
- Elder, N. L. 1962: Vegetation of the Kaimanawa Range. *Transactions of the Royal Society of New Zealand, Botany* 2: 1–37.
- 1965: Vegetation of the Ruahine Range: an introduction. *Transactions of the Royal Society of New Zealand, Botany* 3: 13–66.
- Fisher, F. J. F. 1965: The alpine *Ranunculi* of New Zealand. *New Zealand Department of Scientific and Industrial Research Bulletin* 165.
- Fleming, C. A. 1962: New Zealand biogeography – a palaeontologist's approach. *Tuatara* 10: 53–108.
- 1979: The geological history of New Zealand and its life. Auckland, Auckland University Press/Oxford University Press.
- Franklin, D. A. 1967: The synecology of the Tararua indigenous forests. *New Zealand Forest Research Institute, Technical paper no. 53*.
- Ghani, M. A. 1978: Late Cenozoic vertical crustal movements in the southern North Island, New Zealand. *New Zealand journal of geology and geophysics* 21: 117–125.
- Gregg, D. R. 1960: The geology of Tongariro Subdivision. *New Zealand Geological Survey bulletin no. 40*.
- Grindley, G. W. 1960: Sheet 8, Taupo, Geological Map of New Zealand 1:250 000. Wellington, New Zealand Department of Scientific and Industrial Research.
- Kamp, P. J. J. 1982: Landforms of Hawke's Bay and their origin: a plate tectonic interpretation. In: Soons, J. N.; Selby, M. J. ed. *Landforms of New Zealand*. Auckland, Longman Paul. Pp. 233–254.
- 1986: Late Cretaceous–Cenozoic tectonic development of the southwest Pacific region. *Tectonophysics* 121: 225–251.
- Kamp, P. J. J.; Vucetich, C. G. 1982: Landforms of Wairarapa in a geological context. In: Soons, J. M.; Selby, M. J. ed. *Landforms of New Zealand*. Auckland, Longman Paul. Pp. 255–268.
- Kingma, J. T. 1959: The tectonic history of New Zealand. *New Zealand journal of geology and geophysics* 2: 1–55.
- Kirk, T. 1899: The student's flora of New Zealand. Wellington, Government Printer.
- Korsch, R. J.; Wellman, H. W. 1985: The geological evolution of New Zealand and the New Zealand region. In: Nairn, A. E. M.; Stehli, F. G.; Uyeda, S. ed. *The ocean basins and margins. Volume 7B. The Pacific Ocean*. New York, Plenum Press.
- Laing, R. M.; Wall, A. 1924: The vegetation of Banks Peninsula: Supplement 1. *Transactions of the New Zealand Institute* 55: 438–444.
- Lillie, A. R. 1953: The geology of Dannevirke subdivision. *New Zealand Geological Survey bulletin n.s. 46*. Wellington, Government Printer.
- McGlone, M. S. 1985: Plant biogeography and the late Cenozoic history of New Zealand. *New Zealand journal of botany* 23: 723–749.
- McGlone, M. S.; Webb, C. J. 1981: Selective forces influencing the evolution of divaricating plants. *New Zealand journal of ecology* 4: 20–28.
- McGlone, M. S.; Howorth, R.; Pullar, W. A. 1984: Late Pleistocene stratigraphy, vegetation and climate of the Bay of Plenty and Gisborne regions, New Zealand. *New Zealand journal of geology and geophysics* 27: 327–350.
- Moore, L. B. 1961: *Hebe* (except whipcord species). In: *Flora of New Zealand, Vol. I*. Wellington, Government Printer.
- Moore, L. B.; Edgar, E. 1970: *Flora of New Zealand Vol. II*. Wellington, Government Printer.
- Ornduff, R. 1960: An interpretation of the *Senecio lautus* complex in New Zealand. *Transactions of the Royal Society of New Zealand* 88: 63–77.
- Pocknall, D. T. 1982: Modern pollen spectra from mountain localities, South Island, New Zealand. *New Zealand journal of botany* 20: 361–371.
- Rogers, G. M. 1987: Landscape history of Moawhango Ecological District. Unpublished Ph.D. thesis. Victoria University of Wellington.
- Shepherd, M. J. 1987: Glaciation of the Tararua – fact or fiction? In: Le Heron, R.; Roche, M.; Shepherd, M. ed. *Geography and Society in a Global Context. New Zealand Geographical Society conference series no. 14*.
- Simpson, P. (Compiler) 1982: Ecological regions and districts of New Zealand. A natural subdivision. *NZ Biological Resources Centre publication no. 1*. DSIR, Wellington.

- Smith, J. M. B. 1974: Origins and ecology of the non-forest flora of Mt. Wilhelm, New Guinea. Unpublished Ph.D. thesis, Australian National University, Canberra, Australia.
- Soons, J. M. 1979: Late Quaternary environments in the central South Island of New Zealand. *New Zealand geographer* 35: 16–23.
- Sporli, K. B. 1987: Airphoto lineaments and fracturing in the axial ranges of the central North Island, New Zealand. *Journal of the Royal Society of New Zealand* 17: 139–156.
- Sporli, K. B.; Barter, T. P. 1973: Geological reconnaissance in the Torlesse Supergroup of the Kaimanawa Ranges along the lower reaches of the Waipakihi River, North Island. *Journal of the Royal Society of New Zealand* 3: 363–84.
- Stevens, G. R. 1974: A tramper's geology of the Tararua. Wellington, Government Printer.
- Suggate, R. P.; Stevens, G. R.; Te Punga, M. T. ed. 1978: The Geology of New Zealand. Vols I and II. Wellington, Government Printer.
- Sykes, W. R. 1987: In: Connor, H. E.; Edgar, E. Name changes in the indigenous New Zealand flora, 1960–1986 and nomina nova IV, 1983–1986. *New Zealand journal of botany* 25: 115–170.
- Te Punga, M. T. 1954: The geology of western Wellington. Unpublished Ph.D. thesis. Victoria University of Wellington.
- Walcott, R. I. 1978a: Present tectonics and late Cenozoic evolution of New Zealand. *Geophysics journal of the Royal Astronomical Society* 52: 137–164.
- 1978b: Geodetic strains and large earthquakes in the Axial Tectonic Belt of North Island, New Zealand. *Journal of geophysical research* 83: 4419–4429.
- Ward, J. M. 1982: A key, synopsis and concordance for *Raoulia. Mauri ora* 10: 11–19.
- Wardle, J. A. 1984: The New Zealand beeches: ecology, utilization and management. Wellington, New Zealand Forest Service.
- Wardle, P. 1962: Subalpine forest and scrub in the Tararua Range. *Transactions of the Royal Society of New Zealand, botany* 1: 77–89.
- 1963: Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. *New Zealand journal of botany* 1: 3–17.
- 1968: Evidence for an indigenous pre-Quaternary element in the mountain flora of New Zealand. *New Zealand journal of botany* 6: 120–125.
- 1974: Facets of the distribution of forest vegetation in New Zealand. *New Zealand journal of botany* 2: 352–366.
- 1978: Origin of the New Zealand mountain flora, with special reference to trans-Tasman relationships. *New Zealand journal of botany* 16: 535–550.
- Wellman, H. W. 1949: Tararua Range summit height accordance. *New Zealand journal of science and technology* B30: 123–127.
- 1985: Evolution of the North Island during the last 32 million years. *Newsletter of the Geological Society of New Zealand* 68: 38–40.
- Willett, R. W. 1950: The New Zealand Pleistocene snowline, climatic conditions and suggested biological effects. *New Zealand journal of science and technology* B32: 18–48.
- Zotov, V. D.; Elder, N. L.; Beddie, A. D.; Sainsbury, G. O. K.; Hodgson, E. A. 1938: An outline of the vegetation and flora of the Tararua Mountains. *Transactions of the New Zealand Institute* 68: 259–324.