

Evolution of the New Zealand mountain flora: Origins, diversification and dispersal

Richard C. Winkworth^{a,*}, Steven J. Wagstaff^b, David Glenny^b, Peter J. Lockhart^c

^a*Department of Ecology and Evolutionary Biology, Yale University, P.O. Box 208105, New Haven, CT 06520-8105, USA*

^b*Manaaki Whenua Landcare Research, P.O. Box 69, Lincoln 8152, New Zealand*

^c*The Allan Wilson Centre for Molecular Ecology and Evolution, Massey University, Private Bag 11222, Palmerston North, New Zealand*

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Abstract

The New Zealand mountains provide a unique system in which to study the evolution of alpine plants. The relationship between the recent uplift of mountain habitats (5–2 million year ago (mya)) and floristic diversity has polarized hypotheses on the evolution of the alpine flora; suggestions have ranged from an ancient history in New Zealand to recent arrival by long distance dispersal from the Northern Hemisphere. Molecular phylogenies are now available for numerous New Zealand alpine plant groups and these provide insights into the evolution of this unique flora. Taken together with the fossil record, these studies suggest that many alpine lineages first arrived in New Zealand during the late Tertiary and subsequent radiations accompanied environmental upheaval in the Pliocene and Pleistocene. Ongoing studies are investigating the processes that contribute to morphological and ecological diversity in the New Zealand alpine flora.

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Introduction

“With regard to general problems of biogeography, the biota of New Zealand has been, perhaps, the most important of any in the world. It has figured prominently in all discussions of austral biogeography, and all notable authorities have felt obliged to explain its history: explain New Zealand and the world falls into place around it” (Nelson 1975).

The New Zealand biota has developed on an ancient continental landmass that was progressively isolated during the late Cretaceous and early Tertiary. Originally linked to the Gondwanan supercontinent, New Zealand has been separated from its closest continental neighbor, Australia, by 2000 km for the last 60 million years (my). The long isolation of New Zealand is reflected in the generally oceanic character of its biota, and in this respect it is similar to Hawaii and the Galápagos. However, New Zealand has a much older heritage than these strictly oceanic archipelagos, with a long pre-history of dramatic environmental change that has helped shape its biota. More complex than most oceanic islands yet more tractable than many continental

*Corresponding author. Tel.: +1 (203) 436 4992;
fax: +1 (203) 432 3854.

E-mail address: Richard.Winkworth@yale.edu (R.C. Winkworth).

systems, New Zealand provides unique opportunities to study evolution.

The biogeographic history of New Zealand has, as Nelson (1975) points out, attracted the attention of many biogeographers. In this regard, the flora of its mountains (referred to here as the alpine flora) has been one of the most extensively studied elements. However, despite numerous detailed studies and several syntheses, hypotheses about the origins and diversification of the New Zealand mountain flora have remained polarized – largely due to contrasting views on the relative importance of dispersal, geological change, and climatic fluctuations (McGlone et al. 2001). Recent advances in our knowledge of New Zealand's geological and climatic history, and phylogenetic studies for a growing number of lineages have provided important insights into the origins and evolution of the alpine flora. In this review we have two goals: (i) to discuss insights from recent molecular phylogenetic studies, and (ii) to highlight avenues for future research. As a framework for this discussion, we first briefly summarize the alpine setting in New Zealand and biogeographic hypotheses concerning the alpine flora.

Discussion

The New Zealand mountains

Mountains dominate much of the New Zealand landscape. With the exception of the central North Island volcanoes, the alpine zone is restricted to a single, rugged mountain chain that extends from Stewart Island in the south, along the Southern Alps of the South Island, and through the North Island to East Cape (Fig. 1). Although largely contiguous, the New Zealand axial mountains vary considerably in geomorphology, with five regions recognized based on the underlying parent material. For example, the eastern mountains of the Southern Alps (e.g., the Craigieburn Range) are composed of greywacke and argillite rocks. These formations underwent complex faulting during their uplift and are highly prone to frost shattering that results in the extensive talus and scree slopes characteristic of this region. In contrast, folding and tilting of crustal sections formed the Otago mountains (e.g., the Old Man Range). These more rounded, undulating mountains are composed of harder schist rocks and were not subjected to extensive glacial erosion (Holloway 1982; Whitehouse and Pearce 1992). Such geological differences, as well as striking differences in past and present climates, have resulted in a diverse array of habitat types in the New Zealand mountains (Whitehouse and Pearce 1992).

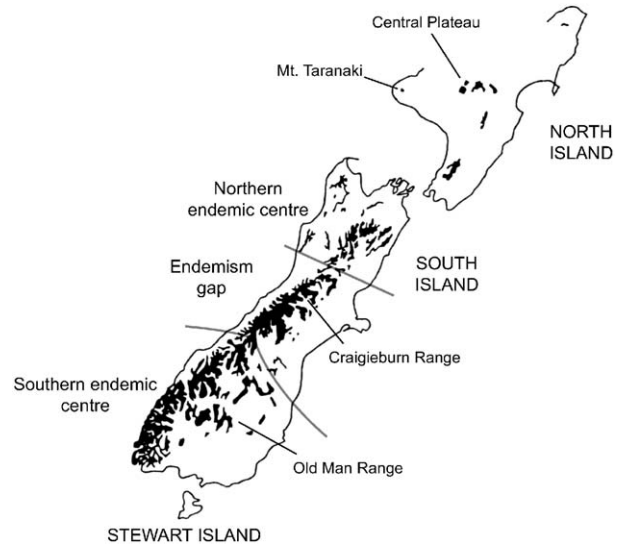


Fig. 1. Extent of alpine areas in New Zealand and alpine plant distribution patterns. Areas above alpine tree line are indicated as black silhouettes; montane habitats are more extensive, especially in the North Island. Gray lines indicate generalized boundaries for two endemic-rich centers and an intervening endemic-poor gap. Several individual mountains or mountain ranges described in the text are marked.

There is little doubt that mountains are a geologically recent feature in New Zealand. For much of the last 85 my New Zealand has been an isolated landmass of limited topographic relief. Having broken away from Gondwana in the late Mesozoic, New Zealand continued to separate from Australia until the early Paleocene. Throughout the late Cretaceous and early Tertiary the ancestral New Zealand landmass suffered steady erosion. By the latest Oligocene only a scattered archipelago of low-lying islands remained (Cooper and Cooper 1995). The general form of contemporary New Zealand is the result of tectonic uplift that began approximately 25 million year ago (mya) with the activation of the modern Pacific-Australian plate boundary (Cooper et al. 1987; Kamp 1992). Miocene tectonism led to rapid changes in distribution and topography, but the general uplift trend resulted in a narrow, elongate landmass of rugged relief. It was not until the Pliocene (5–2 mya) that the formation of the Alpine Fault system and the increasing tempo of tectonic activity led to the rapid elevation of the axial mountains in New Zealand (Ollier 1986; Cox and Findlay 1995; Batt et al. 2000). Although the overall form of these mountains reflects the original pattern of tectonism, many details of the contemporary relief are the result of extensive modification following uplift. In particular, the alpine landscape of the South Island was heavy modified by glaciation during the latest Pliocene and Pleistocene. From about 2.5 mya large areas of the Southern Alps were repeatedly glaciated, and many contemporary landforms relate directly to glacial

modeling or modification of glacial constructions. Although glaciation was more limited in the North Island, cold climate processes, such as periglacial mass movement, have strongly influenced lower North Island landscapes (Beu and Edwards 1984; McGlone 1985; Suggate 1990; Pillans et al. 1992; Markgraf et al. 1995). Post-glacial erosion has also played an important role in shaping the modern alpine landscape (Suggate 1990; Pillans et al. 1992).

The most distinctive North Island mountains are the four volcanic peaks, three on the Central Plateau (Mt. Ruapehu, Mt. Ngauruhoe, and Mt. Tongariro) and one to the west (Mt. Taranaki). These mountains are younger than those of the axial ranges, having reached their present elevations during the last Pleistocene glacial or more recently. Their contemporary relief has been shaped by both volcanic activity and erosion (Holloway 1982).

Biogeographic themes in the New Zealand mountain flora

The origins of the New Zealand mountain flora have been a longstanding biogeographic problem. Of the approximately 600 vascular plant species that occur in the New Zealand mountains more than 90% are endemic. In contrast, no plant families and less than 10% of the genera are endemic to the New Zealand mountains (Mark and Adams 1995). Consistent with this observation, numerous authors (e.g., Hooker 1853; Dawson 1963; Fleming 1963; Wardle 1963, 1968; Raven 1973; McGlone 1985; McGlone et al. 2001) have noted the diverse affinities of the lineages represented in the alpine flora. Two dramatically different hypotheses have been suggested to explain this diversity: (i) that these lineages have an ancient history in the Southern Hemisphere, or (ii) that they have arrived much more recently from the Northern Hemisphere.

Several authors (e.g., Cockayne 1928; Fleming 1962, 1963; Wardle 1963, 1968, 1978) have favored the idea that New Zealand alpine lineages have long histories in the Southern Hemisphere. Whilst these hypotheses all involve an ancient presence they suggest quite different scenarios for the origin and survival of these plants. The earliest hypothesis is that of Cockayne (1928) who suggested the modern flora was descended from groups present in Cretaceous age mountains. Following initial uplift in the late Jurassic and early Cretaceous, the ancestral New Zealand landmass was mountainous, and Cockayne (1928) suggested that lineages occurring in these mountains might have survived the Tertiary in temperate, low-lying habitats, radiating into contemporary alpine habitats as they arose. Specifically, it has been suggested that areas of cool, wet, and infertile soils may have provided conditions suitable for the development of a cool temperate assemblage prior to renewed mountain building in the late Pliocene (Wardle 1968,

1978). In contrast, Wardle (1963) and Fleming (1963) speculated that Tertiary New Zealand would not have provided suitable environments for cool temperate plants. Instead they suggested that ancestors of modern alpine lineages may have spent this period in cool temperate areas to the south of New Zealand, re-establishing in New Zealand only after suitable habitats became available in the late Pliocene and Pleistocene. Wardle (1963) hypothesized that a southern extension to New Zealand (or perhaps islands to the south; see Dawson 1988) would have provided cool climates, whereas Fleming (1963) favored Antarctica as a potential refuge for cool-adapted lineages.

A link between the New Zealand alpine flora and floras of the northern temperate zone has long been recognized. For example, in an analysis by Dawson (1963) genera with north temperate affinities formed the largest component of the alpine flora. However, Raven (1973) was the first to explicitly suggest that much of the New Zealand alpine flora was recently derived from Northern Hemisphere ancestors. Whilst recognizing the presence of a potentially ancient element, Raven (1973) proposed that most lineages had dispersed to New Zealand during the Pliocene and Pleistocene. More specifically, he suggested that the mountains of southeast Asia and New Guinea – also uplifted during the late Tertiary and Pleistocene – served as stepping stones for the dispersal of pre-adapted alpine lineages to Australia, with dispersal of these groups to the New Zealand mediated by West Wind Drift (Raven 1973; Raven and Raven 1976). Recently, Pole (1994) and Macphail (1997) have also argued that Australia was an important source for the New Zealand flora. They suggest that New Zealand was completely or nearly completely inundated for at least part of the Oligocene, and consequently that the extant flora must have arrived from Australia since renewed uplift began in the Miocene.

A second focus for biogeographical research in New Zealand have been patterns of distribution within the alpine flora, especially with respect to regions of endemism and range disjunctions. Strikingly, approximately 6% of alpine species are restricted to the northern third of the South Island, whereas approximately 8% are confined to the southern third (Mark and Adams 1995). There are also numerous examples of taxa that are disjunct between these two endemic centers (Fig. 1). Three distinct explanations have been proposed. The first hypothesis favors vicariance (McGlone 1985; Heads 1998). Over the last 25 my the Pacific-Australian plate boundary has experienced 480 km of lateral displacement along the alpine fault, with as much as 100 km of lateral displacement northeast relative to the Pacific Plate occurring as recently as the mid-Pliocene (Sutherland 1994). This model suggests that historically continuous distributions may have begun to split apart during the Miocene (McGlone 1985; Heads

1998). In contrast, the two other hypotheses invoke more recent events. One suggests that the origin of the endemic centers relates directly to mountain building (McGlone 1985). Geological evidence indicates that the endemic centers have been relatively stable over then last 5 my, whereas the central Southern Alps have been tectonically much more active. This explanation implies that tectonically stable areas have maintained species diversity or provided opportunities for the evolution of local endemics, and that habitat instability has limited such opportunities in the intervening region (McGlone 1985). The final hypothesis suggests that contemporary distribution patterns are the result of glaciation and glacial climates over the last ~2.5 my. During the late Pliocene and Pleistocene repeated climatic changes and glaciation strongly influenced New Zealand environments. In particular, geological evidence suggests that the central portion of the Southern Alps were more heavily glaciated than areas to the north and south. Several authors (e.g., Cockayne 1928; Wardle 1963, 1988; Burrows 1965) have argued that alpine taxa may have been restricted to these relatively ice-free regions during glacial maxima, and that contemporary range disjunctions are explained by failure to recolonize the central Southern Alps (Fig. 1).

There are also distinct differences between the alpine floras of the North and South Islands. Specifically, the alpine flora of North Island is smaller in size and has lower diversity. Several factors may have limited the evolution of alpine plant diversity in the North Island. These include: (a) the younger age and more limited extent of mountain habitats; (b) a post-glacial climatic regime that probably further reduced the extent of North Island alpine habitats; (c) the relative isolation and instability of habitats on the volcanic peaks (McGlone 1985; Wardle 1988).

Insights from molecular data

Pre-molecular studies of the New Zealand alpine flora have provided important clues to the evolutionary history of these plants. However, these studies have been unable to distinguish between competing hypotheses of origin. Recently, attention has focused on the use of molecular phylogenetic approaches as a means to help test hypotheses and provide additional insights into the history of New Zealand alpine plants. Here we review recent phylogenetic studies that are contributing to our understanding of the origins and evolution of the mountain flora.

The importance of dispersal

Molecular phylogenetic analyses have provided important insights into the origins of New Zealand alpine plant lineages. To date, these studies have consistently

suggested a late Tertiary, or more recent, arrival of these plant groups in Australasia (Table 1). For example, uncertainty about the phylogeny and taxonomy of *Myosotis* had made it difficult to differentiate between hypotheses suggesting either Northern Hemisphere or Australasian origins (e.g., Grau and Leins 1968; Raven 1973). However, molecular phylogenetic analyses of the nuclear ribosomal ITS (nrITS) and three chloroplast loci have clarified relationships within *Myosotis* (Winkworth et al. 1999, 2002a). These analyses strongly suggest a Northern Hemisphere origin; furthermore, the level of genetic divergence between austral taxa and Northern Hemisphere relatives implies that long distance dispersal has played an important role in establishing the current geographic range of *Myosotis*. Indeed molecular age estimates based on nrITS sequences suggest that the austral lineage was derived from an ancestor that most likely arrived from the Northern Hemisphere within the last 15 my (Winkworth et al. 2002a).

Molecular phylogenetic studies have supported Raven's (1973) assertion that many of New Zealand's alpine plant lineages are recent arrivals from the Northern Hemisphere. In addition to *Myosotis*, analyses of Asteraceae (Breitwieser et al. 1999), Brassicaceae (Heenan et al. 2002), the *Hebe* complex (Wagstaff et al. 2002), *Ranunculus* (Lockhart et al. 2001), and *Scleranthus* (Smitsen et al. 2003b) suggest Northern Hemisphere origins. However, these phylogenetic studies are not consistent with the route of dispersal suggested by Raven (1973). That is, these analyses do not provide evidence that the mountains of southeast Asia and Australia acted as stepping-stones. An expectation of stepping-stone models is that taxa from southeast Asia and Australia would be basal to the New Zealand radiation in gene trees. However, to date species from stepping-stone locations have been nested within predominantly New Zealand clades, suggesting that they are derived rather than ancestral. In *Myosotis*, for example, Winkworth et al. (2002a) suggest that lineages currently present in the mountains of Australia and New Guinea arose following dispersal from New Zealand. Although stepping-stone hypotheses are not currently supported by molecular phylogenies, we should remain cautious about these inferences since phylogenetic analyses may be limited in this respect. Specifically, if Pleistocene climatic fluctuations resulted in the extinction of stepping-stone populations, then it would be misleading to draw conclusions based on extant lineages. One possible approach to this problem would be to use molecular age estimates; if contemporary species were shown to have persisted in the stepping-stone regions throughout the Pleistocene, then it would be difficult to explain survival of these species and not the stepping-stone forms (Winkworth et al. 2002b).

Although recent analyses have suggested the importance of the Northern Hemisphere as a source for

Table 1. New Zealand alpine plant taxa for which molecular phylogenetic analyses suggest recent origins and diversification

Taxon	Approx. number of New Zealand species ^a	Inferred origins	Molecular age estimate for lineage	Reference
Apiaceae/apioid genera ^b	60	Northern Hemisphere	n/a ^c	Mitchell et al. (1998), Radford et al. (2001)
Asteraceae/Gnaphalieae	75	Equivocal ^d	n/a	Breitwieser et al. (1999), Wagstaff and Breitwieser (2002), Smissen et al. (2004)
Asteraceae/ <i>Brachyglottis</i>	30	Equivocal ^e	n/a	Wagstaff and Breitwieser (2002, 2004)
Boraginaceae/ <i>Myosotis</i>	34	Northern Hemisphere	2.0–14.7 mya	Winkworth et al. (2002a)
Brassicaceae/ <i>Pachycladon</i> and relatives	8	Northern Hemisphere	1.0–3.5 mya	Heenan et al. (2002)
Caryophyllaceae/ <i>Scleranthus</i>	3	Northern Hemisphere	1.2–7.7 mya	Smissen et al. (2003b)
Gentianaceae/ <i>Gentianella</i>	30	South America	1.4–2.7 mya	von Hagen and Kadereit (2001), Glenney (2004)
Ranunculaceae/ <i>Caltha</i>	2	South America	n/a	Schuettpelz and Hoot (2004)
Ranunculaceae/ <i>Ranunculus</i>	41	Northern Hemisphere	n/a	Lockhart et al. (2001)
Scrophulariaceae/ <i>Ourisia</i>	10	South America	n/a	Meudt and Simpson (in press)
Scrophulariaceae/ <i>Hebe</i> complex ^f	100	Northern Hemisphere	3.9 mya	Wagstaff et al. (2002)
Stylidiaceae/ <i>Forstera</i> and <i>Phyllache</i>	7	Equivocal ^g	6.0 mya	Wagstaff and Wege (2002)
Stylidiaceae/ <i>Oreostylidium</i>	1	Australia	2.0 mya	Wagstaff and Wege (2002)

^aSpecies numbers compiled from individual references and additional sources (Mark and Adams 1995; Wilton and Breitwieser 2000; McGlone et al. 2001).

^bIncludes *Aciphylla*, *Anisotome*, *Gingidium*, and *Lignocarpa*. A fifth member of this clade, *Scandia*, has no alpine representatives.

^cn/a = a divergence time estimate is not available, although relative branch lengths are consistent with recent events.

^dMolecular analyses suggest close affinities to Australian taxa, with multiple independent dispersals between New Zealand, Australia, and New Guinea. However, the root position remains equivocal, and therefore it is difficult to make strong inferences.

^eOrigins of the group in New Zealand are equivocal. This morphologically extremely diverse genus is closely related to several Australian species, but exact relationships remain uncertain.

^fIncludes *Chionohebe*, *Hebe*, *Heliohebe*, and *Parahebe*.

^gThe two genera are not monophyletic, *Phyllache* being nested within *Forstera*. The New Zealand radiation is most closely related to a South American species, and in turn this clade is sister to the Tasmanian *Forstera*. Therefore, South American and Tasmanian origins are equally parsimonious.

lineages in the New Zealand alpine flora, several studies have highlighted lineages with origins in southern South America. Molecular phylogenetic analyses of *Caltha* (Schuettpelz and Hoot 2004), *Gentianella* (von Hagen and Kadereit 2001), and *Ourisia* (Meudt and Simpson in press) all indicate South American origins for the New Zealand representatives. Phylogenetic analyses of morphological characters suggest similar origins for *Abrotanella* (Swenson and Bremer 1997a, b). As for lineages with Northern Hemisphere origins, the route of dispersal between South America and New Zealand remains uncertain. Phylogenies based on contemporary species could be interpreted as favoring direct long-

distance dispersal. However, fossil evidence suggests that Antarctica may have acted as a corridor for movements between these two regions until relatively recently (e.g., Webb and Harwood 1991; Ashworth and Cantrill 2004), a possibility recognized by many authors (e.g., Darwin 1859; Skottsberg 1960; Swenson and Bremer 1997a; Wardle et al. 2001). In this case distinguishing between alternative dispersal routes will require a much more detailed knowledge of the fossil record.

Taken together, molecular phylogenetic and palynological studies (e.g., Fleming 1979; Mildenhall 1980) provide convincing evidence that many alpine plant

lineages are recent additions to the New Zealand flora. Indeed dispersal appears to have played a very important role in the assembly of this element, lineages having arrived at different times and from different sources. The apparent influx of alpine lineages into the New Zealand mountains since the late Tertiary may be directly linked to the uplift of montane environments. However, this correlation might also reflect an increase in the availability of open niches, both in montane and lowland environments. That is, compared to the environmental stability of the early Tertiary, the rapidly changing environments of the late Pliocene and Pleistocene may have created a range of new, open habitats that offered opportunities for the establishment of dispersing lineages. Although long-distance dispersal clearly has been an important influence on the composition of the New Zealand alpine flora, the overall contribution of dispersed lineages to this assemblage remains uncertain. Our current knowledge is biased towards larger, morphologically and ecologically diverse groups, and understanding the assembly of the alpine element requires the inclusion of lineages that potentially represent alternative evolutionary histories. For example, several predominantly lowland forest groups also have representatives in the mountain flora (e.g., *Coprosma*, *Myrsine*, *Pittosporum*, and *Podocarpus*). It has been suggested that such lineages might have long histories in New Zealand, with the alpine forms arising only after the onset of mountain building and climate change (Smith 1986; Dawson 1988). Indeed molecular phylogenetic analyses appear to support such an explanation for the origin of *Phyllocladus alpinus* (Podocarpaceae). In this case, despite a long fossil record, molecular evidence indicates that the modern species diversity arose very recently; indeed the mountain ecotype of *P. alpinus* appears to have arisen from a lowland form within the last 6.3 my (Wagstaff 2004).

Rapid morphological differentiation

The New Zealand mountain flora is characterized by numerous large, morphologically and ecologically diverse genera. For example, *Aciphylla*, *Celmisia*, *Epilobium*, *Hebe*, and *Ranunculus* each contain more than 35 species and have many montane species (Mark and Adams 1995; Wilton and Breitwieser 2000). Despite uncertainty about the origins of this flora, it has generally been assumed that speciation during the Pliocene and Pleistocene explains the presence of these large, morphologically and ecologically diverse lineages (Wardle 1968; Raven 1973). Recent molecular phylogenetic analyses are also consistent with this suggestion. Specifically, species with striking morphological and ecological differences exhibit little or no genetic differentiation at commonly assayed marker loci (e.g., nrITS and chloroplast loci), suggesting that differentiation has occurred over a relatively short period of time. Examples

of recent diversification in the New Zealand mountains include the Australasian Apioideae (Mitchell et al. 1998; Radford et al. 2001), *Brachyglottis* (Wagstaff and Breitwieser 2004), the Gnaphalieae (Breitwieser et al. 1999; Smissen et al. 2003a, 2004), the *Hebe* complex (Wagstaff and Garnock-Jones 1998, 2000; Wagstaff et al. 2002), *Myosotis* (Winkworth et al. 1999, 2002a), *Ourisia* (Meudt and Simpson in press), the *Pachycladon* complex (Heenan et al. 2002; Heenan and Mitchell 2003), and *Ranunculus* (Lockhart et al. 2001).

Rapid diversification of plant lineages in the New Zealand mountains appears to be correlated with a period of environmental instability during the late Pliocene and Pleistocene. Molecular clock analyses of nrITS sequence data from *Myosotis* (Winkworth et al. 2002a), *Pachycladon* (Heenan et al. 2002), and *Ranunculus* (Lockhart et al. 2001) suggest that the contemporary diversity arose within the last 5 my, a period of rapid geological uplift and frequent climatic fluctuations in New Zealand. Certainly the expansion of montane habitats during this period may have provided opportunities for the diversification of contemporary mountain plant lineages (Raven 1972). That is, we might expect that the topography of the newly formed mountains would have introduced barriers to gene flow, thereby promoting the evolution of novel, local variants (Wardle 1963). However, it also seems likely that the repeated climatic fluctuations during the late Pliocene and Pleistocene have played an important role in alpine plant diversification. Several authors have previously implicated cyclical environmental change in models of plant speciation (e.g., Ehrendorfer 1958; Rattenbury 1962; Morton 1972; Stebbins 1984; Hewitt 1996; Ferris et al. 1999), and it seems possible that the intense selective regimes imposed by Pliocene and Pleistocene glacial cycles may have influenced the radiation of New Zealand mountain plant lineages. A potential cyclical model might involve a two phases: (i) climate change produces new habitats that allow range expansion and provide opportunities for the differentiation of local morphological or ecological variants; (ii) ongoing climate change leads to range contraction, which may result in the formation of additional local variants either by local differentiation or perhaps hybridization (Fig. 2). Through multiple climatic cycles such a model might be expected to produce many variants, especially if additional habitats become available or changing migration paths result in interactions (e.g., hybridization or introgression) between previously isolated forms.

Given the large environmental changes associated with glacial cycles, as well as smaller fluctuations within each cycle, we might expect that such a model of species diversification would result in considerable admixture, and therefore complex patterns of phylogenetic relationship. Indeed this expectation is consistent with several recent molecular analyses. For example, Lockhart et al.

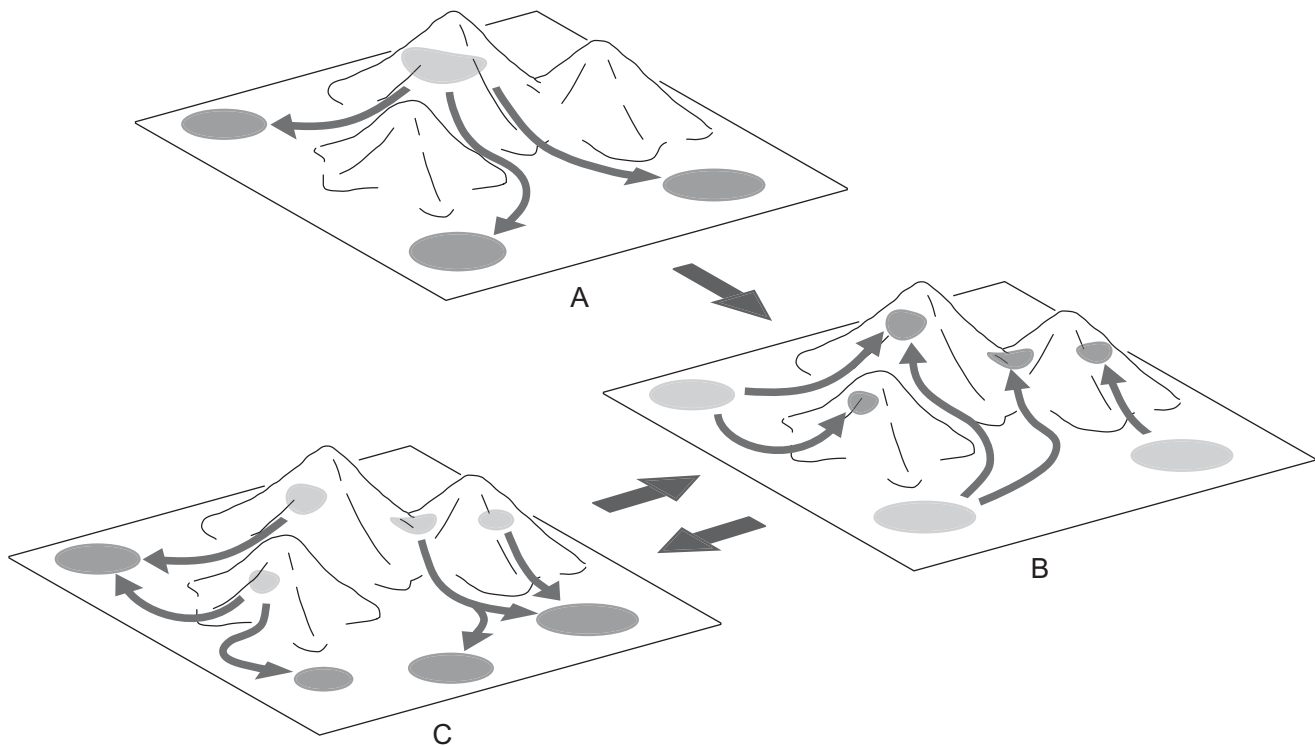


Fig. 2. Potential model for the rapid diversification of New Zealand alpine plant lineages during the Pliocene and Pleistocene: (A) Climate change leads to range expansion. An initial population (light gray) forms several isolated daughter populations (dark gray) that differentiate from one another. (B) Further climate changes result in range contraction. Due to altered migration pathways or novel ecological tolerances these new populations (dark gray) may occupy different habitats relative to the initial population. Furthermore, such range contraction may result in different local forms occurring in one area, providing opportunities for the origin of further novel variation through hybridization. (C) Repeated cycles of range expansion and contraction associated with later climate fluctuations may promote further diversification, especially if new habitats become available or interactions (e.g., hybridization or introgression) between previously isolated forms are possible.

(2001) identified a clade (their Group II) containing three morphologically distinct *Ranunculus* species endemic to the South Island. Analyses of nrITS sequences indicate complex patterns of relationship between these taxa perhaps linked to reticulate evolution (Lockhart et al. 2001; Winkworth et al. 2005). Similarly, incongruence between gene trees for chloroplast and nuclear loci suggest reticulate patterns of evolution in *Raoulia* (Smitsen et al. 2004) and the Australasian Apioideae (Winkworth and Lockhart, unpublished). These observations are certainly consistent with earlier suggestions that hybridization may have been of considerable evolutionary importance in the New Zealand mountain flora (Raven 1972, 1973) and with the reported frequency of hybridization – natural hybrids are known for *Ranunculus* (Fisher 1965), *Leptinella* (Lloyd 1972), *Epilobium* (Raven 1972; Raven and Raven 1976), and the Australasian Apioideae (Webb and Druce 1984). However, it remains unclear whether the apparent frequency of hybrids in the contemporary alpine flora is correlated with the evolutionary significance of this phenomenon. Phylogenetic studies that specifically

address the role of hybridization within alpine plant lineages are clearly needed.

Recent molecular systematic studies on New Zealand alpine plant lineages show striking similarities to those from both oceanic island and continental floras. In particular, the patterns of relationship exhibited by many New Zealand alpine plant groups parallel plant species radiations on other island archipelagos. Specifically, radiations on the Hawaiian Islands (e.g., Carr 1987; Robichaux et al. 1990; Baldwin 1992), the Juan Fernandez Islands (e.g., Sang et al. 1994, 1995), and the Macaronesian Islands (e.g., Böhle et al. 1996; Kim et al. 1996) all exhibit extensive morphological and ecological differentiation but limited genetic variation. For such groups analyses of morphology, biochemistry, cytology and genetics tend to favor hypotheses of recent arrival by transoceanic dispersal, followed by rapid and potentially adaptive radiation (Givnish 1997). In addition, studies on New Zealand alpine plants are also consistent with analyses of continental lineages that suggest the importance of environmental change during the late Tertiary and Quaternary. Such investigations

suggest that rapid and repeated climatic fluctuations associated with Pleistocene glaciation have had profound effects on the floras of Europe and North America (Comes and Kadereit 1998). Clearly, environmental change during the last 5 my has been an important stimulus for the evolution of modern floristic diversity at both local and global scales.

Species distributions

Previous hypotheses have invoked ancient tectonism (e.g., Heads 1998), mountain building (e.g., McGlone 1985), or glaciation (e.g., Wardle 1988) to explain distribution patterns in the New Zealand alpine flora. Although molecular phylogenetic analyses provide insights into the origin and divergence of these lineages, they have made little impact on our understanding of distribution patterns. In general this reflects the limited resolution provided by commonly used molecular markers such as the nrITS and chloroplast loci in what appear to be recently differentiated groups. In most studies relationships between the austral species are poorly resolved, either represented as polytomies or, if clades are resolved, relationships are weakly supported (e.g., Wagstaff et al. 2002; Winkworth et al. 2002a). Whilst our understanding of distribution patterns remains limited, several recent studies have provided some preliminary insights (e.g., Lockhart et al. 2001; Heenan and Mitchell 2003; Smissen et al. 2003a).

Combined analyses of morphological and nrITS data produced a largely well-resolved phylogeny for *Pachycladon*, a group of about 10 species distributed primarily in the mountains of the South Island, but with a single representative in Australia (Heenan and Mitchell 2003). In this tree the New Zealand species fall into three clades, two of which are restricted to mountain habitats. The two alpine lineages are differentiated both morphologically and ecologically – one is restricted to schist substrates in the southern South Island, whereas the other occurs on greywacke substrates to the north. Heenan and Mitchell (2003) hypothesize that adaptation to geological substrates may have stimulated the initial diversification of *Pachycladon*. However, they suggest that the disjunct distribution of *P. fastigiata* and restricted distributions of several species (e.g., *P. wallii* and *P. stellata*) reflects range contraction into isolated glacial refugia during the Pleistocene.

Studies on *Raoulia* and *Ranunculus* also suggest that glaciation has been important for shaping contemporary patterns of alpine plant biodiversity. Lockhart et al. (2001) described molecular phylogenetic analyses of nuclear and chloroplast loci for a broad sample of New Zealand alpine *Ranunculus*. These analyses identified four major lineages and provided some resolution of relationships within these groupings. In two of these major lineages, accessions from southwestern populations are genetically distinct from those in the central

Alps (Lockhart et al. 2001; Lockhart, unpublished). This pattern was interpreted as consistent with restricted gene flow due to range contraction into separate refugia during Pleistocene glaciations (Lockhart et al. 2001; McGlone et al. 2001). Lockhart et al. (2001) also suggest that lower sea levels during the glacial may have facilitated the movement of *Ranunculus* into the mountains of the North Island and Stewart Island. In other work, analyses of ISSR markers and nrITS sequences have been used to investigate phylogenetic relationships within *Raoulia* (Asteraceae). Phylogenetic analyses recover two well-supported clades: one containing exclusively North Island populations, and the other only representatives of South Island populations (Smissen et al. 2003a). These results suggest that, although Pleistocene climate change may have been an important influence on contemporary species diversity and distribution, it is insufficient to fully explain patterns of endemism in *Raoulia*. Specifically, the level of genetic differentiation between North Island and South Island populations suggests that this divergence occurred prior to glaciation, although glacial cycling might have influenced patterns of distribution in the South Island (Smissen et al. 2003a).

To date, molecular phylogenetic studies provide only preliminary insights into the origin of distribution patterns in the New Zealand mountains. However, these studies do suggest that the alpine flora is a more recent assemblage than previously thought (e.g., Heads 1998). In particular, molecular-clock analyses suggest that environmental change during the latest Tertiary and Quaternary has been most important for determining contemporary patterns of diversity and distribution. Furthermore, these studies indicate that no single factor can fully explain patterns of alpine plant diversity; for a given plant group, patterns of diversification and distribution appear to have been determined by a complex, and potentially unique, set of influences related to climate, geology and ecological tolerances (McGlone et al. 2001).

Conclusions and outlook

Molecular systematic studies are contributing greatly to our understanding of the New Zealand alpine flora. Phylogenetic analyses, in conjunction with palynological and distributional data, suggest that contemporary patterns of diversity and distribution in this assemblage have arisen only recently. More specifically, these studies indicate two general patterns: (i) that ancestors of many New Zealand alpine plant lineages arrived by long-distance dispersal during the late Tertiary or Quaternary, and (ii) that alpine lineages have diversified recently, perhaps in response to environmental

instability during the Pliocene and Pleistocene. Furthermore, molecular data suggest that alpine plant distribution patterns are unlikely to have been determined by a single factor, but instead appear to be influenced by both climate and geology. These findings mirror results from molecular systematic studies on island plant radiations and continental floras.

Despite these advances we are still far from a detailed understanding of the evolutionary patterns and processes in the New Zealand mountains. Many of the questions that remain also have implications for understanding wider problems in plant evolution. Addressing these issues will require synergistic approaches drawing on numerous disciplines. We expect future studies in New Zealand will provide important insights into (a) the evolutionary significance of hybridization in plant diversification, (b) the role of plant breeding systems in adaptive radiation, (c) the concept and evolutionary significance of glacial refugia, (d) the development of analytical methods and ecological models for studying species radiation, and (e) the genetics underlying morphological and physiological adaptation.

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