Evolution of New Zealand alpine and open-habitat plant species during the late Cenozoic

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Abstract: Understanding the evolutionary history and biogeography of the New Zealand alpine flora has been impeded by the lack of an integrated model of geomorphology and climate events during the Late Miocene, Pliocene and Pleistocene. A new geobiological model is presented that integrates rock uplift age, rate of uplift and the resulting summit elevations in the Southern Alps (South Island) during the last 8.0 million years with a climate template using the natural gamma radiation pattern from the eastern South Island Ocean Drilling Program Site 1119 that covers the past 3.9 million years. This model specifically defines the average treeline in relation to mountain height, allowing predictions as to the timing of the formation of the alpine zone and other open habitats. This model predicts open habitats such as rock bluffs, tussock grasslands and riverbeds would have been available from about 4.0–3.0 Ma, coinciding with the initiation of summit uplift and a cooling climate providing an opportunity for the evolution of generalist alpine and open-habitat herbs and shrubs. Alpine habitats began to form at about 1.9 Ma and were a permanent feature of the Southern Alps from about 0.95 Ma. Specialist alpine plants confined to alpine habitats can have evolved only within this period once the alpine zone was persistent and widespread. Bog habitats are likely to date from the Late Miocene (c. 6.0 Ma), and the specialist bog species would have evolved from this time. Molecular-clock dates for DNA sequences from species of specialist alpine habitats, generalist open habitats, and bog habitats are consistent with predictions made on the basis of the model.

Keywords: biogeography; climate; ecological diversification; geology; Miocene; New Zealand flora; Pleistocene; Pliocene; Southern Alps

Introduction

The Southern Alps of New Zealand are home to about 600 plant species and the centre of numerous radiations of alpine (above the altitudinal treeline) and open-habitat species. As the closest alpine areas to New Zealand are in Tasmania and south-eastern Australia, separated by 1500–2000 km of ocean, the origin and evolution of the New Zealand alpine flora has been a subject of speculation and debate for well over 150 years (e.g. Hooker 1853; Cockayne 1928; Dawson 1963; Fleming 1963, 1980; Wardle 1968, 1978; Raven 1973; McGlone 1985; Winkworth et al. 2005). Phylogenetic, evolutionary and ecological studies are today challenging long-held assumptions and providing new insights into the origin and evolution of New Zealand's alpine flora (e.g. Joly et al. 2009; Mandáková et al. 2010; Smissen et al. 2011; Lee et al. 2012). In light of these studies it is timely to reconsider the formation of the alpine zone in the South Island of New Zealand and its associated alpine habitats.

Uplift of the Southern Alps occurred during the Plio-Pleistocene period (i.e. from 5.33 Ma, including the Holocene) (e.g. Batt et al. 2000) and was accompanied by a cooling climate. The emergent mountains provided new alpine habitats that a range of plants have exploited (McGlone et al. 2001), as prior to this, alpine habitats did not exist as the topography was of low relief, the climate subtropical to warm-temperate, and the vegetation predominantly rainforest (Mildenhall & Pocknall 1989; Hornibrook 1992). Biogeographers, phylogenetic systematists and ecologists have generally given little attention to the detail of the geomorphology and associated geological and climatic history of the Southern Alps. Instead, a broad statement in general terms is usually made as to the timing of uplift as a background to a discussion of the evolution or biogeography of the taxa involved. For example, 'alpine endemics … may have evolved at any time since the start of mountain uplift 3–5 Ma' (McGlone 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' (Winkworth et al. 2005); 'For the alpine species in particular, there is evidence that many are evolutionarily young lineages that have speciated rapidly in newly formed high-elevation habitats within the last five million years' (Meudt & Bayly 2008). For their part, geologists have only occasionally shown any interest in detailing the subaerial evolution of the New Zealand landmass. With geological information difficult of access, and climatic histories of daunting complexity, biologists have tended to fall back on the same handful of papers, sketchy diagrams, and rounded dates.

A great deal of geological and climate data are now available and these should be more widely and systematically used. The question of most relevance to the origin of the alpine flora of New Zealand is: when were the Southern Alps high enough and the climate cool enough for the diversification of specialist alpine plants? To answer this critical question we present here an integrated model of geomorphology and climate history for the Southern Alps, relating mountain uplift and climate change to treeline to establish when and where habitat suitable for alpine plants would have been available.

We develop a geobiological model (Figs 1 & 2) for the evolution of the alpine habitat in the Southern Alps,
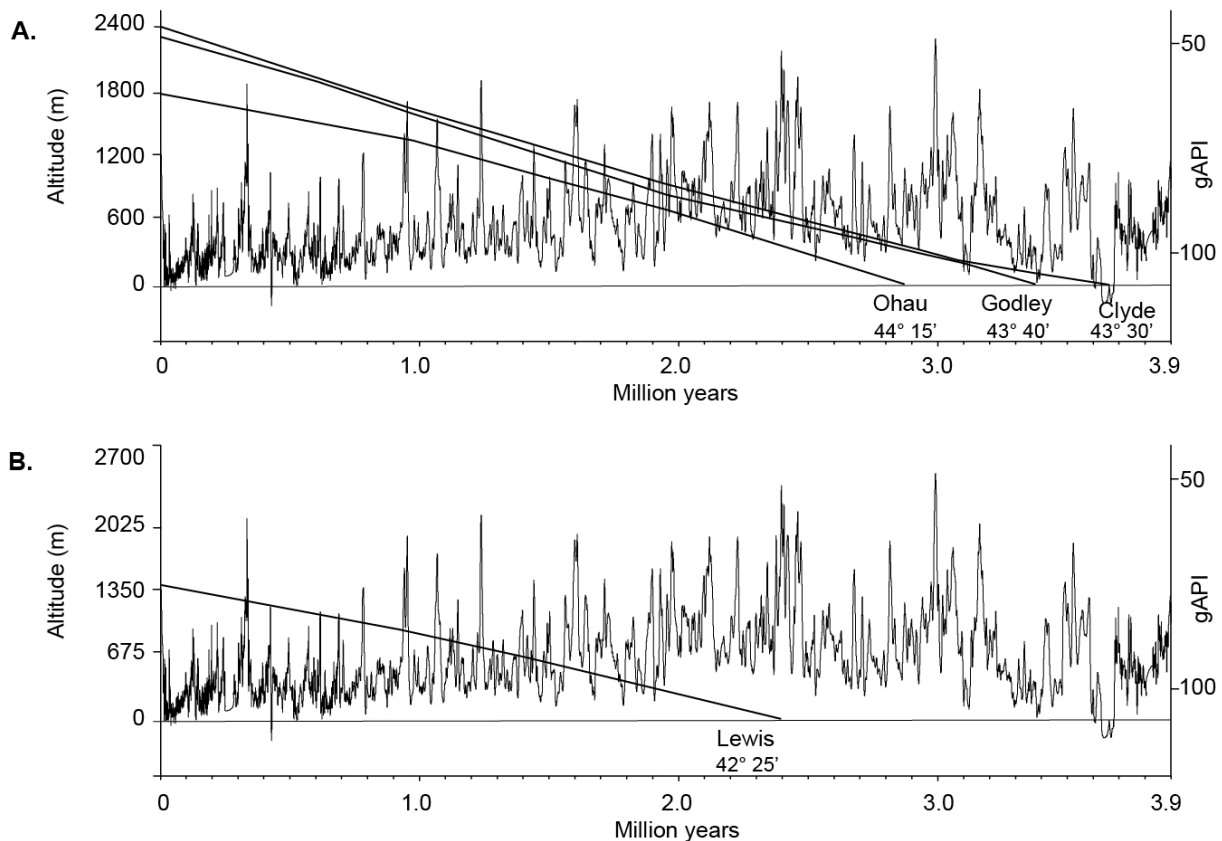
Figure 1. Geobiological model relating treeline to mountain uplift rates in four areas of the Southern Alps of New Zealand. Treeline is indicated by natural gamma ray measurements (gAPI) from ODP Site 1119 (Carter 2005). Start of mountain uplift for Lewis Pass (2.4 Ma), Ohau (3.0 Ma), Godley (3.5 Ma), and Clyde (3.8 Ma) areas, with a line representing each of their mean summit heights from 3.9 Ma to the present (Tippett & Kamp 1995a). In the early (3.9–2.9 Ma) period of uplift treeline is above mountain summit height, in the middle (2.9–1.2 Ma) stages treeline oscillates above and below mountain summit height, and in the latest (1.2 Ma–present) phase treeline is mostly below mountain summit height. (a) Mountain uplift for Ohau, Godley and Clyde areas with the treeline set at 1200 m. (b) Mountain uplift for Lewis Pass area with treeline set at 1350 m.

South Island, New Zealand; the North Island mountains are not considered as they are young, some probably less than 200 000 years old (Ghani 1978), and they have few endemic alpine taxa (McGlone 1985). We first summarise the geomorphological evolution of the Southern Alps as proposed by Tippett and Kamp (1995a, b). Particular emphasis is given to rock uplift age, rate of uplift, and the resulting summit elevations in the Southern Alps. We then review the climate data based on the natural gamma pattern from Ocean Drilling Program (ODP) Site 1119 that covers the past 3.9 million years (Carter et al. 2004; Carter & Gammon 2004; Carter 2005). We then summarise literature on treelines as this is crucial to interpreting the gamma curve as a proxy for the average treeline. Finally, we integrate the geomorphological (Tippett & Kamp 1995a, b) and climate models (Carter et al. 2004; Carter & Gammon 2004; Carter 2005) into a new geobiological model that identifies mountain height and the position of the treeline and higher elevation alpine habitat. We then use molecular clock dating and distributional information on alpine plants to test the utility of the model.

Model development

Formation of the Southern Alps

Tippett and Kamp (1995a, b) proposed a model for the geomorphic evolution of the Southern Alps that encompassed mean surface uplift, surface elevation, rock exhumation, and topography. Rock uplift began 8 million years ago when mean land height was close to sea level, although it did not initiate or occur evenly across the Southern Alps. For the first two million years of rock uplift there was little mean surface uplift as the overlying soft rock was rapidly eroded away. As a result, mean surface uplift throughout the Southern Alps lagged the start of rock uplift. Only when erosion-resistant greywacke was exposed after removal of 1400–2600 m of the overlying soft rock did substantial surface relief form. Rock uplift propagated from south to north. It began at 8 Ma in the southern sector (Fiordland) of the Southern Alps; at 5 Ma in the northern parts of the alps (Lewis Pass area); and along the eastern margins at 3 Ma. In southern sectors greywacke was exposed at 4 Ma and relief began to form around 3.7 Ma. In northern regions, greywacke was exposed as recently as 1.7 Ma and relief formed around 1.3 Ma.

As well as latitudinal variation in initiation of mountain building, uplift rates have also varied. For example, in the Mt
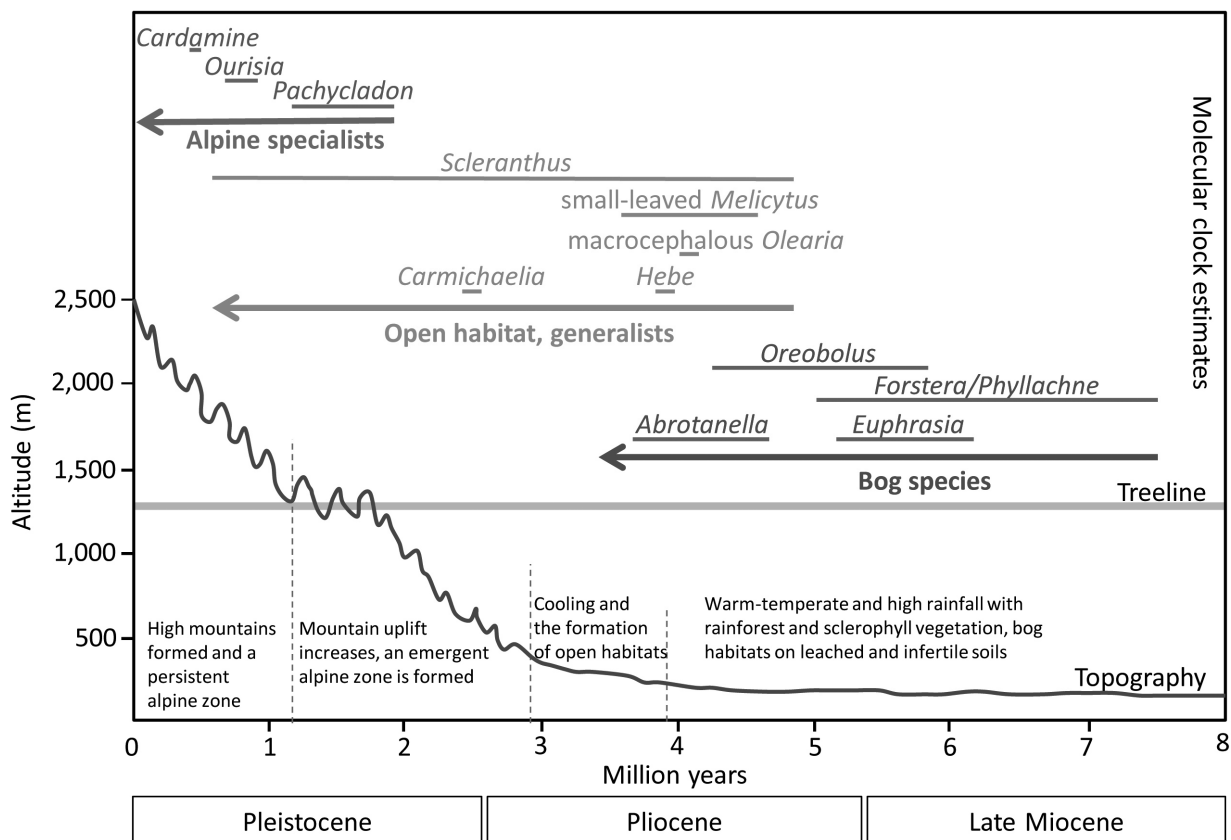
Figure 2. Geobiological model relating mountain uplift rate and topography to treeline in the Southern Alps of New Zealand. Genera with species that have evolved to occupy major habitat types are shown with their corresponding major habitat type; the bar below each genus name represents the estimated molecular clock age (see text for details).

Cook area, uplift has accelerated over time: it proceeded at 0.8 mm year^{-1} from 6.7 to 1.3 Ma; at 6 mm year^{-1} between 1.3 and 0.8 Ma; and at 9 mm year^{-1} from 0.8 Ma to the present. For four localities in the Southern Alps, Table 1 (see also Fig. 1) summarises the start of rock uplift (6.4–5.7 Ma), start of mountain uplift (3.5–2.4 Ma), and mean summit height during the past 3.0 million years (data from Tippett & Kamp 1995a). Note that the mean summit heights did not reach 1000 m until less than 2.0 Ma.

Sedimentation rates on the continental shelf off the Canterbury coast reflect the increased rate of rock uplift in the Southern Alps. For the period 11.5–6.0 Ma sedimentation rates were <15 mm year^{-1}, with high sedimentation rates of 21 mm year^{-1} (6.0–2.64 Ma) and 25 mm year^{-1} (2.64 Ma to present) supporting increased plate convergence and uplift of

the Southern Alps from 6.0 Ma (Lu et al. 2005). Furthermore, the high rate of sediment supply from 2.64 Ma may reflect the increasing importance of mountain glaciation during that period.

Plio-Pleistocene climate

The climate model used here is primarily based on the composite total gamma-ray record from ODP Site 1119 for the past 3.9 million years (Carter et al. 2004; Carter & Gammon 2004; Carter 2005; Fig. 1). Site 1119 is 93 km off the eastern South Island at 44°45.3' S, 172°23.6' E, south of Banks Peninsula and east of Timaru, and is on the upper continental slope about 5 km downslope from the shelf edge. Glacial and interglacial periods in the Site 1119 core are identified by their stratigraphy: rapidly sedimenting terrigenous micaceous muds and silts

Table 1. Start of rock uplift, start of mountain uplift, and mean summit height for selected areas of the Southern Alps. Data taken from Tippett & Kamp (1995a, figs 6 & 7).

Area	Start of rock uplift (Ma)	Start of mountain uplift (Ma)	Mean summit height (m)			
			3 Ma	2 Ma	1 Ma	Present
Lewis	5.7	2.4	-	250	800	1400
Ohau	5.8	3.0	150	750	1350	1800
Clyde	6.0	3.8	300	900	1650	2300
Godley	6.4	3.5	350	850	1600	2400

(glacial periods) alternate with more slowly accumulating muddy and calcareous sands (interglacial periods). The natural gamma-ray curve is derived from formation radiation and five-window spectroscopy and resolves the spectrum into the three commonest naturally occurring radioactive elements, potassium (^{40}K), thorium (^{232}Th), and uranium (^{238}U) (Carter & Gammon 2004). K and Th are the principal radioactive elements present in clays, and a high overall gamma-ray signature is associated with mud-rich sediments (glacial period), and a low gamma-ray signal with the presence of sand or carbonate sediments (interglacial). The terrigenous sediment that reaches Site 1119 is from low grade metamorphic greywackes and schists of the central and eastern South Island.

The summed natural gamma-ray curve has been shown to be a sensitive indicator of mean annual temperature. The natural gamma-ray record from Site 1119 features a significant long-term cooling trend since c. 3.0 Ma and exhibits marked cyclicity at 100- and 41-ka Milankovitch periodicities, which are associated with Earth's orbital changes (Carter & Gammon 2004). These gamma-ray data also indicate conditions different from the Holocene with eight unusually warm interglacial periods and eight severely cold glacial periods (Carter & Gammon 2004). The natural gamma-ray record corresponds with an overall decline of 6°C in atmospheric temperature over the South Island since 2.45 Ma, and a temperature amplitude of 12°C between glacial and interglacial periods.

Treeline

Alpine treelines are now widely agreed to be controlled by the warmth of the growing season. A global analysis of soil temperatures at treeline (Körner & Paulsen 2004) established a mean growing season temperature of 6.7° ± 0.8°C. It has been argued, for instance by Wardle et al. (2001), that New Zealand treelines are unusually low and warm, presumably because of lack of alpine lineages or sufficient time to evolve true, cold-hardy alpine trees. Körner and Paulsen (2004) appeared to confirm this by recording unusually warm soil temperatures at their two New Zealand sites. However, a recent study of New Zealand treelines (Ellen Cieraad unpubl. data) has shown they are close to the international norm as regards both soil and air temperatures. A 3-month summer average of 10.5°C approximates the treeline isotherm. For southern New Zealand, treeline lies between 1530 m and 1040 m, the highest treelines being in the north-east and the lowest in the south-west – the average elevation of the treeline being close to 1200 m.

Present-day treelines are as high as they have been during the Holocene period, and can be taken as representative of a typical interglacial (McGlone & Basher 2012). The issue as to full glacial treelines is more complex (McGlone et al. 2010). The typical depression of mean annual temperatures by 5°C during full glacial conditions should, all things being equal, lead to a lowering of treelines by 800 m, which would place them 300–400 m above current sea level. However, pollen, macrofossils and geomorphic indicators demonstrate that forest during full glacial conditions was confined to small patches in southern New Zealand, and shrubland, grassland and herbaceous and prostrate shrub communities of open ground formed the dominant vegetation cover (McGlone et al. 2010). An explanation for this is that outbreaks of ultra-cold polar air were more frequent and, given the well-documented low level of frost resistance in New Zealand trees (Bannister 2007), were sufficient to keep forest confined to frost-sheltered localities. We can assume that full glacial conditions provided widespread

and abundant open habitat, with cold-tolerant species down to and below current sea level, but specialist alpine species largely confined to regions 300 m or more in elevation.

In this study the current mean treeline in the central Southern Alps (e.g. Clyde, Godley, and Ohau areas; Fig. 1A) is set at 1200 m elevation and in the northern Southern Alps (e.g. Lewis Pass; Fig. 1B) is estimated to be 1350 m (estimates from Google Earth, accessed July 2011).

Alpine plant distributions

There are approximately 571 species of vascular plants that regularly occur above treeline, and these species have been documented as to habitat and distribution (Mark & Adams 1995). This compilation was the basis for an analysis of alpine plant distribution (McGlone et al. 2001), and these data are reanalysed here. The alpine regions of New Zealand are divided into 19 geographical regions, based on the distribution descriptions given in Mark and Adams (1995). Using the data provided by Mark and Adams (1995) each species is scored according to the number of alpine regions in which they occur, the predominant habitat type (cushion vegetation, fell field, scree, rock outcrop, snow bank, open vegetation, tussock grassland, wet hollow, stream and riverbed, or peat bog), elevation range, and if they were specialist or non-specialist (generalist) alpines based on whether or not they regularly occurred below treeline.

The data on alpine plant distributions are collected from alpine areas throughout New Zealand, but predominantly from the largest alpine area, the Southern Alps, and are therefore of relevance to the discussion presented here. These data are used to elucidate the geobiological model for the evolution of alpine and open-habitat plants in the Southern Alps, with particular emphasis on the formation of alpine and open habitats and in identifying general patterns of species' distribution in different geographic regions and habitat types.

Integrated model

Below we summarise the three episodes of climate change and uplift included in our model, and discuss the consequences of these changes for alpine plant evolution.

By combining the geomorphological model for the evolution of the Southern Alps in the past 8.0 million years with the climate history of the South Island for the past 3.9 million years a geobiological model is developed for the evolution of the alpine and open-habitat flora (Figs 1 & 2). Since the geomorphological and climate models are time bound, these temporal scales can be used to calibrate the new model.

The gamma-ray curve of Carter (2005) can be used as a proxy for treeline through the last 3.9 million years. During the full-glacial, tree cover fell to less than 10% (McGlone et al. 2010) at current sea level (0 m elevation). These open environments (i.e. bare-ground, herbfield, grassland and shrubland) can be regarded as providing 'effective' alpine habitat for all but specialist high alpine species. Along with present-day treeline, this full-glacial datum is used to calibrate the *y*-axis of the gamma-ray curve in terms of treeline and mountain summit elevation. Therefore, the simplest interpretation of the integrated model is to compare treeline against mountain summit height and this relationship can be used to estimate when land above treeline would be available for alpine and open-habitat plants.

Early cooling and the emergence of open habitats (3.9–2.9 Ma period)

The most significant event during this period is the cooling between 3.7 and 3.6 Ma, with the temperature lowering by c. 4.5°C to a level equivalent to the last glacial maximum (LGM) (Fig. 1). Nevertheless, glaciers cannot have formed in the absence of tall mountains. Rock uplift is well established, but hill and valley topography has just begun to form with the beginning of summit uplift. For example, the Godley summit uplift starts at 3.5 Ma and the Clyde uplift at 3.8 Ma; by 3.0 Ma the summits at these locations are only about 300–350 m (Tippett & Kamp 1995a; Table 1, Fig. 1). The 10°C warmest-month isotherm that equates with the modern treeline would have fallen by c. 750 m. Treeline in the Godley area now sits at close to 1200 m. Therefore, in the Godley area at 3.0 Ma the summits would have failed to reach treeline by some 100–200 m but would have been well within the subalpine forest zone. Even low summits such as these would have begun to cast a rain shadow to the east, and cool, dry eastern biomes formed. It is likely that some open areas may have formed in the eastern rain-shadow areas. This is the first period when climate space would have been present for the evolution of plants tolerant of cool and dry climates with increasing open habitat.

Mountain uplift increases and an emergent alpine zone (2.9–1.2 Ma period)

The period between 2.9 and 1.9 Ma is warm, and the treeline is well above the mountain summits for much of the time (Figs 1 & 2). Few, if any, alpine habitats can have been available, but open habitats such as rock outcrops, slips, and gravelly riverbeds would have increased in number and extent as mountain uplift continued. On these sites there would be suitable habitats for low-growing plants of unstable ground, and for shrub and herbaceous species to evolve and diversify.

The period between 1.9 and 1.2 Ma is notable for the coldest periods, having temperatures lower than those in the preceding 1.0 million years (Fig. 1). Temperature falls, but the warmest periods are warmer than or equivalent to those of the Holocene. Summit height in the southern and central Southern Alps increases rapidly from 750 m to about 1650 m (Table 1, Fig. 1). At these elevations, small shifts in temperatures would have moved the crests of the ranges and leading ridges of mountains in and out of the alpine zone. On steeper ground, rock outcrops and bluffs would become more common both above and below treeline and these would have provided suitable habitat for alpines and open-habitat species. During the latter part (1.6–1.2 Ma) of this period, in the areas with higher summits, the alpine zone must have been more persistent and therefore evolution and diversification of specialist alpine species is possible. However, caution is needed as a warming event at c. 1.25 Ma may have had an impact on the treeline and availability of alpine plant habitat.

In the northern part (e.g. Lewis Pass) of the Southern Alps rock uplift begins at about 2.4 Ma and small summits form from 2.0 Ma (Table 1, Fig. 1). In these northern areas the summits are mostly below the treeline and therefore there was limited, if any, alpine habitat.

High mountains formed and a persistent alpine zone (1.2 Ma – present period)

The general trend during this period is for cooler temperatures, with the cool intervals becoming colder (Fig. 1). The 1.2–0.95 Ma interval has only limited overlap of summit heights with treeline on the highest summits in the southern and central Southern Alps (Figs 1 & 2). This can be interpreted as providing some alpine and open habitat, but this was still likely to have been fluctuating with the changing treeline. In the northern Southern Alps, summit heights are low and treelines would not have formed. From 0.95 Ma to the present, permanent and extensive alpine habitat would have been available for the evolution of alpine plants in southern and central Southern Alps. Indeed, treeline is well below summit height and this is the first time since uplift began at 8.0 Ma that there would have been a persistent and expanding alpine zone. In the Lewis Pass area from about 0.9 Ma the treeline is intermittently above summit height providing limited alpine habitat. From about 0.3 Ma the summit height in Lewis Pass is consistently above treeline and alpine habitat would have been persistent.

Application of model

The new geobiological model proposed here allows more specific predictions to be made about the evolution of alpine and open-habitat species, and this builds on the contributions of earlier writers. For example, Wardle (1968) suggested that the alpine flora comprised two main groups of species. Firstly, those that evolved rapidly (e.g. *Celmisia*) in response to the newly available alpine habitat and, secondly, those that were derived from the pre-existing Tertiary flora that were inhabitants of the cold, wet, infertile soils on peneplained uplands. The latter – ancient cool-climate element, giving rise to plants that today occur in bog habitats – includes, for example, *Oreobolus* and *Phyllachne* (Wardle 1968).

McGlone (1985) elaborated on Wardle's (1968) suggestions and distinguished three general groupings of alpine plants. Firstly, the oldest component are plants of poorly drained and infertile sites such as bogs. The next oldest group are plants that are generalists and occur in a variety of open habitats such as rock-fall, cliff-face, ridge-top, and stream-side habitats, which became available as the first ranges appeared. Thirdly, the most recent group are specialist alpine plants of unstable-scree-slope and alpine habitats that became available only with the final phase of the uplift of the Southern Alps. In reference to these three groupings, McGlone (1985) surmised: 'If evolution of new species is strongly influenced by availability of novel habitats, the evolutionary history of taxa should broadly reflect this sequence.' The array of molecular phylogenetic data now available means that we are now in a position to test this prediction.

Bog plants

The Early to Mid-Miocene (23.0–5.33 Ma) flora of New Zealand was subtropical to warm-temperate (with high temperatures and rainfall throughout the year) with dense rainforest vegetation (Mildenhall & Pocknall 1989; Hornibrook 1992). Sclerophyll vegetation was also present and would have been induced by either aridity or nutrient-poor soils (Mildenhall 1980; Pole 1993), and has been shown to be a major contributor to diversification into a range of different biomes in the Southern Hemisphere (Crisp et al. 2009). Miocene soils, having formed on long-lived stable surfaces under a largely warm-temperate oceanic climate, were deeply weathered. These leached and infertile soils on landscapes with low elevation gave rise to wide expanses of peatland providing mosaics of stunted forest, shrubland and bog (Pocknall 1989; Pole 1993). As Wardle

(1968) suggested, 'If, during the period of the Tertiary warmth, there were infertile soils on peneplained uplands drenched by persistent mist and rain, some cool-climate plants would undoubtedly exist.'

As the Late-Miocene and Plio-Pleistocene climate cooled and the Southern Alps developed, bog habitats would have remained in cool-temperate lowland sites under persistent rainfall, as well as occupying newly created upland montane and alpine regions. Bogs, being largely rain-fed, have naturally low fertility and thus habitat-switching to bog soils by lineages evolved to tolerate low-fertility dryland soils can be expected to have been relatively common. Furthermore, the species of Miocene peat bogs and infertile soils would also have the opportunity to establish and diversify into the new higher elevation alpine bog habitats. Indeed, early-colonising taxa in the New Zealand alpine zone have been shown to co-occur more frequently and with greater cover per unit area than those from later-colonising genera (Lee et al. 2012), thereby highlighting the probable importance of priority effects and niche pre-emption in community assembly of bog habitats from the Late Miocene.

There are several generalisations that can be made about the species inhabiting alpine bogs. Firstly, they would occur over a wide geographic area; secondly, they would occur over a wide altitudinal range in both lowland and upland habitats; and thirdly, as noted by Wardle (1968) and McGlone (1985), they would be the oldest component of the new cool-temperate alpine flora. We show here that species of bog habitats are geographically widely distributed, as compared with species of all other alpine habitat types they occur in the most alpine regions and in comparison to species of strictly alpine habitats they occur in twice as many regions (Table 2). They also have a wide altitudinal range, and their mean minimum altitude is second only to species of riverbed habitats and less than half that of species of strictly alpine habitats (e.g. scree, snow grass, fell field, and cushion vegetation; Table 2).

Based on data from molecular phylogenetic studies the lineages of species from bog habitats are older than those of specialist alpine species (Fig. 2). The molecular-clock divergence estimates for taxa predominantly of bog habitats are, for example: *Abrotanella* stem age of 4.2 Ma for the main New Zealand lineage (Wagstaff et al. 2006); *Euphrasia* stem age of the New Zealand clade 5.7 Ma (Gussarova et al. 2008,

estimate from fig. 5c); *Oreobolus pectinatus* and *O. strictus* stem age of 5.1 Ma (Chacón et al. 2006); and *Forstera/Phyllachne* stem age 6.3 Ma (Wagstaff & Wege 2002). The stem ages for these taxa are Late Miocene to Early Pliocene, rather than dating from the subtropical and warm-temperate Early to Mid-Miocene, and from this we infer that the already cooling climate and the start of rock uplift of the Southern Alps (Table 1) may have been triggers to the evolution and diversification of these lineages. It should be noted that the bog species might have evolved any time after the bog habitat became available and so are not necessarily restricted to the Late Miocene or Early Pliocene. Additional molecular phylogenetic and dating studies are required of other genera with bog species, such as *Carpha*, *Rostkovia*, and *Donatia*.

Generalist species

A feature of the New Zealand alpine and open-habitat flora is the prevalence of generalist herbs and subshrubs. For a dataset of 571 alpine species, McGlone et al. (2001) showed that 343 (60%) were non-specialist, generalist alpines and 228 were specialist alpines. For 19 alpine areas of New Zealand the non-specialist alpine species are found in significantly more regions (8.9 ± 0.30) than specialist alpine species (3.9 ± 0.22) (McGlone et al. 2001). Furthermore, of the specialist alpine species, 65% ($n = 156$) were associated with predominantly alpine habitats (cushion vegetation, fell field, scree, rock outcrops, and snow banks) compared with only 22% ($n = 72$) of the non-specialist alpines. The non-specialist alpine species favoured open vegetation, tussock grassland, wet hollows, stream and riverbeds and peat bogs, and when compared with specialist alpine habitats have a lower mean minimum elevation and wider altitudinal ranges (Table 2). Therefore, the non-specialist alpine species occupy more alpine regions, are found over a wider altitudinal range, and occur in more habitat types.

We argue that these non-specialist alpine and open-habitat species are likely to have evolved from the time when the open habitats were forming as a result of cooling temperatures and uplift of the mountains. This began with initiation of mountain uplift between 4.0 and 3.0 Ma (Table 1, Figs 1 & 2) when rock bluffs and outcrops, open riverbeds and terraces, and tussock grassland were becoming increasingly prevalent. Another important driver is likely to be the generally cooler

Table 2. Alpine habitat types and the altitudinal range (m a.s.l.) and distribution of 571 alpine species. Sorted by mean minimum altitude. *Specialist alpine habitat.

Habitat type	No. of species	Minimum altitude (mean ± SD) (range)	Maximum altitude (mean ± SD) (range)	Mean altitudinal range (mean ± SD) (range)	Mean number of taxon occurrences in 19 alpine regions (mean ± SD)
Riverbeds	19	428 ± 56 (0–900)	1629 ± 48 (1200–2000)	1200 ± 45 (800–1500)	8.42 ± 0.99
Peat bog	77	470 ± 43 (0–1200)	1527 ± 21 (1200–2000)	1043 ± 38 (400–1900)	9.93 ± 0.69
Fen/wetland	44	538 ± 56 (0–1200)	1496 ± 30 (970–1850)	957 ± 60 (120–1700)	7.56 ± 0.83
Tussock grassland	114	548 ± 36 (0–1400)	1596 ± 23 (760–2480)	1039 ± 41 (210–2100)	7.95 ± 0.51
Open vegetation	70	574 ± 53 (0–1400)	1617 ± 29 (930–2200)	1029 ± 54 (200–2000)	7.03 ± 0.61
Rock outcrops	89	776 ± 44 (0–2300)	1701 ± 36 (900–2800)	924 ± 46 (100–2270)	6.09 ± 0.59
Scree*	38	918 ± 66 (0–1540)	1854 ± 30 (1400–2400)	904 ± 62 (300–1900)	4.65 ± 0.66
Cushion vegetation*	16	985 ± 106 (0–1600)	1728 ± 70 (1100–2000)	742 ± 84 (200–1460)	4.13 ± 0.94
Fell field*	60	1124 ± 37 (500–1800)	1936 ± 36 (1500–3000)	810 ± 45 (50–1900)	4.14 ± 0.38
Snow grass*	44	1021 ± 46 (50–1600)	1830 ± 31 (1300–2460)	772 ± 51 (100–1650)	6.34 ± 0.71

temperatures and the significant drop in temperature between 3.7 and 3.6 Ma, as this would provide a myriad of open habitats as a consequence of cold-intolerant species becoming less common. The extinction of cold-intolerant species is well documented during the Pliocene, with at least 15 families and 36 genera from the warm-temperate and humid climates of the Miocene being documented in the fossil record for the last time (e.g. Mildenhall & Pocknall 1989; Lee et al. 2001).

Most of the non-specialist alpine and open-habitat species are herbaceous or smaller woody shrubs, and molecular-clock estimates for these are consistent with the suggested timing of available habitat and cooling of the climate: e.g. *Scleranthus* stem age 4.9–2.1 or 2.3–0.6 Ma (Smissen et al. 2003); shrubby *Hebe* stem age 3.9 Ma (Wagstaff et al. 2002); macrocephalous *Olearia* stem age 4.1 Ma (Wagstaff et al. 2011); *Carmichaelia* stem age c. 2.5 Ma (Lavin et al. 2005; estimate from figs 3 & 6); and the small-leaved *Melicytus alpinus* complex stem age 4.7–3.62 Ma (Mitchell et al. 2009).

Specialist alpine species

The specialist alpine species of cushion-vegetation, snowgrass, fell-field, and scree habitats can only have evolved when a persistent and extensive alpine zone formed above treeline. Indeed, the mean minimum elevations for specialist alpine species of these habitat types are all approximately around the level of the current treeline, and their maximum elevation is well into the highest parts of the alpine zone (Table 2). The specialist alpine species of these exclusively alpine habitats also occur in the lowest number of the 19 New Zealand alpine regions (Table 2). These alpine habitats may have begun to form at about 1.9 Ma when mountain height began to exceed treeline, but they would have been consistently available only during the last 0.95 million years, once mountain summit height permanently exceeded the fluctuating treeline. The specialist alpine species are more likely to have evolved once the alpine zone was permanent and widespread, thereby providing contiguous land and opportunities for the formation of cushion-vegetation, snowgrass, fell-field, and scree habitats.

Radiations of alpine species in the Southern Alps are well known and generally show very little sequence divergence for a variety of genetic markers (e.g. *Brachyglottis* complex; Wagstaff & Breitwieser 2004). DNA sequence data with little sequence divergence are usually interpreted as indicating recent and rapid radiation and/or speciation. An objective measure of the timing of divergence of alpine species is provided by molecular-clock dating and these analyses support a recent origin for alpine specialists. These include, for example, species of *Pachycladon* whose stem age is 1.6 Ma (Joly et al. 2009), New Zealand species of *Ourisia* with a stem age of 0.8 Ma (Meudt et al. 2009), and New Zealand and Australian *Cardamine* with a stem age of 0.42 Ma (Bleeker et al. 2002). These three genera also include lowland or forest species, but the important point is that they are predominantly alpine and these alpine species can only have evolved after the formation of the specialist alpine habitats in which they occur.

Conclusions

We have provided an explicit temporal and spatial framework to consider the evolution of New Zealand alpine and open-habitat plants by integrating a model for the uplift of the Southern Alps (Tippett & Kamp 1995 a, b) with a 3.9-million-year climate template (Carter et al. 2004; Carter & Gammon 2004; Carter

2005). By using molecular-clock divergence estimates from published studies we have shown that the specialist alpine species have evolved much more recently than the bog and generalist species, thus providing an evolutionary time frame and ecological context that is consistent with the geological and climate events of the late Cenozoic. To provide specific tests of the model, future molecular phylogenetic studies of alpine and open-habitat species should endeavour to use molecular-clock estimates and incorporate these with analyses of habitat types and altitudinal ranges (e.g. *Chionochloa*; Pirie et al. 2010).

Although the geobiological model is developed from the perspective of the evolution of plants of alpine and open habitats, it has general application to the whole New Zealand alpine biota. For example, in an evolutionary study of alpine cicadas (*Maoricicada* spp.), Buckley and Simon (2007) found that estimates of molecular-clock divergence times were correlated with shifts in habitat type and altitudinal range during the Miocene, Pliocene and Pleistocene. The deepest lineages of alpine cicada are lowland and associated with open habitats (e.g. riverbeds and clay banks), the next lineages to diverge are of subalpine scrub and open surfaces, and the most recently derived lineages are above the treeline among alpine herbs and boulder fields. This temporal and spatial pattern of diversification for *Maoricicada* during the late Cenozoic is consistent with our geobiological model.

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