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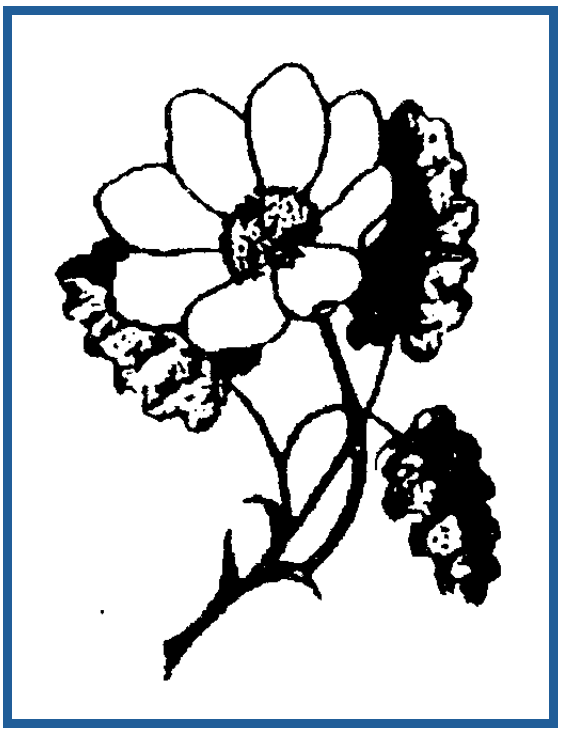

Alpine Plants and Climatic Change

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Alpine Plants and Climatic Change

Brian Huntley

To discuss the this topic, we must first define our terms. In horticulture the term *alpine plant* is often used synonymously with *rock plant*, which the SRGC defines as *any plant suitable for the rock garden, bog garden, wild garden or alpine house*. This implies that a *plant* in this context is a vascular plant: an angiosperm (flowering plant), gymnosperm (conifers and their allies) or pteridophyte (ferns, clubmosses, horsetails, and others). Such a broad definition encompasses vascular plants (hereafter *plants*) found naturally in a wide range of unforested habitats, from Arctic tundra to steppe grassland and arid regions such as the Karoo of south-west Africa, as well as above the treeline in mountainous regions. Ecologically, these habitats differ in

The Aletsch Glacier (Image: Gavin Rummery)

important ways, not least in the climatic factors that prohibit forest cover, some having an insufficiently warm growing season, whereas in others the soil moisture deficit—seasonally or year-round—is too great. In this article I use *alpine plants* to refer only to species found principally above the treeline in mountainous regions or beyond the northern or southern polar treelines. In both cases temperature is the principal factor determining the treeline. Although authors differ as to what specific temperature measure they consider most important, their consensus focuses either on an annual mean temperature threshold, particularly in the rooting zone[1], or a minimum annual temperature sum above 5°C, the limit for trees' metabolic activity[2].

Climatic Change

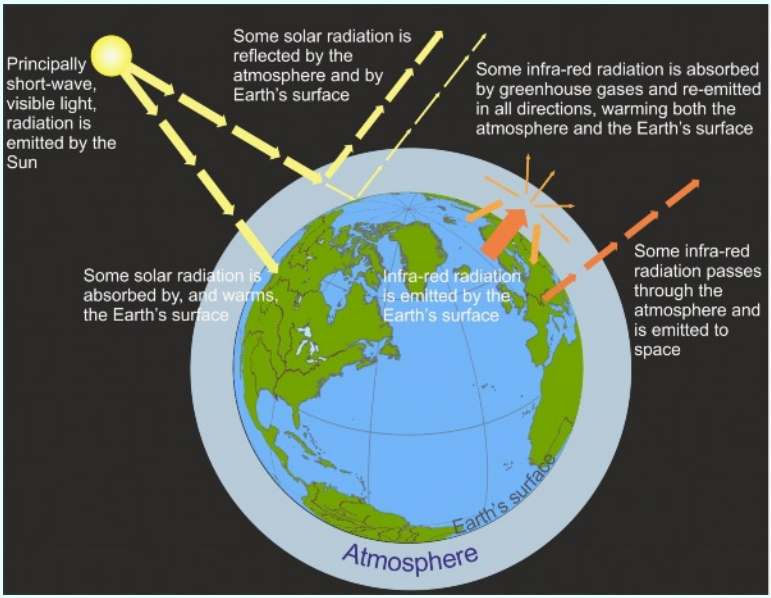
The term *global warming* is often used misleadingly, especially in the media, as if interchangeable with *climatic change*. Although recent climatic changes are consequences of increasing global mean temperature, that in turn results from humankind's emissions of so-called *greenhouse gases*, especially carbon dioxide and methane, climatic change involves much more than a simple increase in global mean temperature. Depending where you look, changes relate principally to any or all of: higher seasonal—especially winter—temperatures; more extreme, longer or more frequent periods of high temperature (heat waves), droughts or floods; stronger winds and heavier rain from storm systems, including hurricanes, typhoons and cyclones, according to geographical region.

Taking the long view, climatic changes are not new phenomena associated only with human alterations of the atmosphere; climatic conditions vary at many timescales from seconds to millions of years. Meteorologists talk about climate as a thirty-year mean of daily or monthly conditions, meaning we may exclude shorter-term variability as *weather*. In writing about the effects of varying climate and seasonality on alpine plants, I focus here principally on temperature, precipitation and snow cover, with humidity, sunshine, wind speed and wind direction also having some relevance.

The Greenhouse Effect

The principal source of energy for Earth's climate is the radiation emitted by the Sun. The peak wavelength of the radiation emitted by what is referred to as a blackbody depends upon its surface temperature; the Sun and the Earth behave as blackbodies. According to Wien's Law, the peak wavelength emitted by a blackbody $\lambda = 2897/T$ μm, where T is its surface temperature in Kelvin. Because of its high surface temperature (*ca*. 6000 K), the Sun emits radiation principally in the visible part of the spectrum. Although some solar radiation reaching Earth is reflected, especially by clouds and by snow- and ice-covered surfaces, a substantial fraction is absorbed by, and warms, the Earth's surface. The Earth also emits radiation, but because its surface is much cooler (*ca*. 288 K) this is primarily of much longer wavelengths and in the infra-red portion of the spectrum.

Four 'greenhouse gases' occur naturally as minor components of Earth's atmosphere: carbon dioxide (CO_2); methane (CH_4); nitrous oxide (N_2O); and water vapour (H_2O). These gases absorb infra-red radiation and hence absorb Earth's emitted radiation. This both warms the atmosphere and is re-emitted, some to space but also some back towards the Earth's surface, leading to further warming. This so-called 'greenhouse effect' is a natural phenomenon, without which life as we know it could not be sustained, because the average surface temperature in the absence of the greenhouse effect would be *ca*. -20°C, rather than *ca*. 15°C.

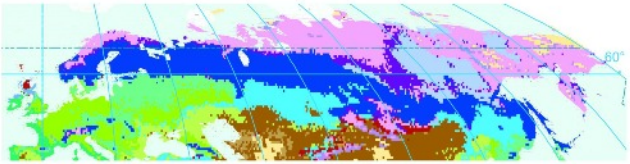


Concentrations of these natural greenhouse gases have varied throughout Earth's history, changes in the atmospheric concentration of carbon dioxide [CO_2]atm in particular being generally positively correlated with temperature. Thus, during the Quaternary, [CO_2]atm has been lower during glacials and higher during interglacials, a pattern generally followed also by the concentrations of CH_4 and N_2O. Since 800 ka and prior to the industrial period (pre-1750 CE), [CO_2]atm varied between *ca*. 174 and 299 ppmv. Human activities, however, especially large-scale burning of fossil fuels (including peat, lignite, coal, oil and gas), but including also the manufacture and use of cement, deforestation, paddy-field rice cultivation, large-scale application of artificial nitrate fertilisers, and husbandry of cattle for milk and meat production, led to rapid and still accelerating increases in concentrations of CO_2, CH_4 and N_2O, primarily since the industrial revolution and especially since the mid-twentieth century.

In May 2023, global [CO_2]atm had reached 424 ppmv (*https://climate.nasa.gov/vital-signs/carbon-dioxide/*)*, *ca*. 50% higher than pre-industrial level and >40% higher than at any time between 800 ka and 1750 CE. In August 2023, global CH_4 concentration had exceeded 1919 ppbv (*https://gml.noaa.gov/ccgg/trends_ch4/*)*, >280% of pre-industrial concentration and >240% of the highest value between 800 ka and 1750 CE. N_2O concentration has also increased since the industrial revolution, reaching 336·75 ppbv (*https://gml.noaa.gov/ccgg/trends_n2o/*)* in August 2023, an increase of >28% above its pre-industrial value and >11% greater than its highest value between 800 ka and 1750 CE. Although this relative increase is not as great as those of the other two gases, N_2O is more persistent in the atmosphere and thus has a 100-year global warming potential per molecule 265 times that of CO_2.

* *Links queried 29 December 2023*

1



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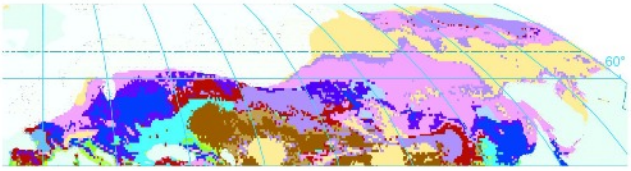

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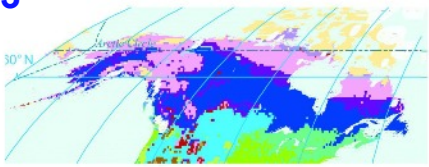

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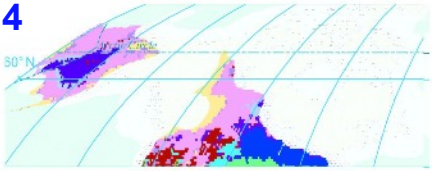

- Desert
- Semi-desert
- Tropical Grassland
- Savanna
- Tropical Raingreen Forest
- Tropical Evergreen Forest
- Temperate Shrubland
- Unclassified
- Warm Temperate Woodland
- Temperate Broad-leaved Evergreen Forest
- Temperate Summergreen Forest
- Temperate Needle-leaved Evergreen Forest
- Temperate Mixed Forest
- Temperate Parkland
- Steppe
- Ice sheet
- Boreal Parkland
- Boreal Evergreen Needle-leaved Forest
- Boreal Summergreen Needle-leaved Fore
- Boreal Summergreen Broad-leaved Fores
- Boreal Woodland
- Shrub Tundra
- Tundra
- Ocean or lake

Glacial versus Interglacial Palae-ovegetation and Ice Sheets

The upper maps 1&3 show boreal vegetation simulated for the climate of the last interglacial, 120ka (thousand years ago). The lower maps 2&4 show the simulation at the last glacial maximum, 24ka. They also show the extent of large ice sheets covering north-western Eurasia and northern North America; note the much reduced extents of temperate and boreal forests and greater extents of shrub tundra, tundra and polar desert compared to the upper maps 1&3, the exception being persistence of forest in eastern North America close to the ice sheet. Reduced sea level of the glacial maximum, by about 130 metres, is reflected by the increased land area north of Siberia and the land bridge spanning the Bering Sea.

These maps are extracts from a global simulation of vegetation cover[49]. The methods of generation have been used for a series of equivalent maps extending to 800 ka at 4000 year intervals[49].

Mountain Ranges

Throughout Earth's history, mountain ranges and volcanic mountains have been generated by tectonic movements and collisions between continental plates. Erosion, over many millions of years, can reduce high mountain ridges to river valleys, so the balance and timing of tectonic uplift and erosion together have led to the topography we see today. Since the first vascular plants colonised the land about 470 Ma (million years ago), mountain ranges have come and gone, giving opportunities for plants to evolve adaptations to the alpine zone. These opportunities have been scattered in space and time, as various ranges have come and gone. Consequently, although many of today's alpine plant families, and some genera, may have evolved in mountain ranges of the Mesozoic Era (252–66 Ma) and subsequently dispersed to evolve further in ranges uplifted during the Cenozoic Era (66 Ma to now), many genera, and probably all the species, of today's alpine plants are of geologically recent origin[3].

We can distinguish three main groups of mountain ranges. Those today having extensive alpine zones above their treeline arose mainly during the Cenozoic Era. They include: the Himalayas, uplifted about 60–50 Ma as the Indian sub-continental plate moved northwards colliding with the Asian plate; the Cantabrians, Pyrenees, Alps, Apennines, Carpathians and other European ranges, uplifted about 37–24 Ma as the African and Arabian plates moved northwards, squeezing various plate fragments against the European plate; the Southern Alps of New Zealand, uplifted since around 25 Ma along the Alpine Fault and as the Pacific and Australian plates collide; and the Alaska Range, whose rise began only 5–6 Ma in the Miocene Epoch as the Pacific plate moved northwards to subduct beneath the North American plate[4]. A second group, whose uplift began during the Mesozoic and continued during the Cenozoic, today also have extensive alpine zones. They include the Andes, whose uplift began about 90 Ma during the Upper Cretaceous Period, and the Rocky Mountains, uplifted since around 70 Ma. Finally, some present ranges have a longer and more complex history. The Scandes, for example, were originally uplifted during the Palaeozoic Caledonian Orogeny around 490–390 Ma, along with today's Scottish Highlands and the mountains of East Greenland, but were later largely eroded, fell below sea level and were covered by Mesozoic sedimentary rocks. They were uplifted again after about 23 Ma in the later Cenozoic, their principal phase of uplift being after 5 Ma in the early Pliocene. Continued erosion removed most of the Mesozoic rocks, exposing older rocks from the Caledonian Orogeny and long before, resulting in the present mountain ranges and high-level plateaux, at least in southern Norway[5].

Evolution of the Arctic Flora

The extensively treeless regions of today's Arctic are, like many mountain ranges, geologically recent. Forests dominated the Arctic during the early Cenozoic, although global cooling caused a shift from broadleaved to coniferous trees. Substantial climatic fluctuations were superimposed on this cooling trend. Hyperthermal events, like the Paleocene–Eocene thermal maximum at 55·5 Ma[6], saw warmth-demanding taxa including *Taxodium*, *Metasequoia*, Arecaceae (palms) and Bombacoideae (baobabs) forming high Arctic forests[7], whereas a late Miocene cooling event (7–5·4 Ma)[8] brought transient northern hemisphere glaciations and ecosystem restructuring. Nonetheless, high Arctic boreal forests reaching a treeline around 80°N[9] persisted through most of the Miocene and into the Pliocene. Gymnosperm forests occupied the Canadian high Arctic islands during the Miocene and Pliocene[10,11] and dark taiga of *Tsuga*, *Picea* and *Abies* the Novosibirskie Islands in the Arctic Ocean during the Miocene[12]. Only in the middle Pliocene around 3 Ma did the forest persistently retreat southwards, initially replaced by more open woodlands before modern-like tundra and forest–tundra developed. Even so, there were boreal forest trees in northern Greenland as late as the end of the Pliocene at 2 Ma[13]. The land area beyond the Arctic treeline was thus generally very limited at least until the Pliocene, perhaps as late as 2 Ma. Opportunities for the evolution of plants adapted to the conditions typical of today's Arctic tundra were therefore limited to the past few million years.

Evidence suggests most modern Arctic herbaceous plants derive from ancestors occupying the alpine zones of ranges that extended sufficiently northwards to permit migration into the Arctic once the polar treeline retreated[14,15]. Others, especially woody taxa, may have evolved from ancestors occupying the earlier Cenozoic Arctic forests. Whatever their ancestry, it seems that present-day Arctic and alpine plant species evolved only since the late Pliocene or early Pleistocene, with many evolving in even more recent times.

Quaternary Climatic Changes and Alpine Plants

The last two million or so years of the Quaternary Ice Age saw massive global climate fluctuations[14], undoubtedly contributing to evolution of today's alpine species. The last million years has brought an alternation, roughly every hundred thousand years, between interglacials, with conditions broadly similar to the present, and glacials.

During glacials, ice sheets covered most of Canada, northern USA, northern Europe and north-west Siberia. Mountain glaciers were more extensive, with ice caps over major ranges, including the European Alps. These ice sheets displaced and fragmented distributions of Arctic and alpine plants. Where temperate zone lowlands were dominated by

interglacial forests, cooler glacial climates reduced tree cover and led to conditions suitable for Arctic and alpine plants. These distributional changes are clear in the Quaternary palaeobotanical record, that includes sub-fossil remains of pollen, fruits, seeds and vegetative material. For example, seeds of *Papaver radicatum*, today found in Iceland, the Faeroes and Fennoscandian mountains, occur in lake sediments in the Scottish Borders and the Eastern Highlands[16] dating from the Younger Dryas episode at the end of the last glacial stage about twelve thousand years ago; the Younger Dryas is so named from the abundance of *Dryas octopetala* leaves found in Danish sediments of this episode. Even the distributions of species today endemic to a limited geographical area were in some cases displaced, seed of *Primula scotica* being identified in Cambridgeshire sediments of last glacial age[17], from a time when its present haunts were ice covered[18,19].

The wider spread of forest cover during interglacials also fragmented and displaced distributions. In the Fennoscandian mountains, for example, some alpine plant species have bicentric distributions, being found in the south and north Norwegian (and north Swedish) mountains, but missing from the generally lower elevation intervening ranges. Notable amongst these species are *Rhododendron lapponicum*, *Pinguicula alpina* and *Viola rupestris*, genetic analyses of

Papaver radicatum, Grødalen, Norway

Dryas octopetala, Abisko, Sweden

Primula scotica, Sutherland, Scotland

the latter revealing that it probably spread north from Europe through the British Isles to the Fennoscandian Mountains following retreat of the last glacial ice sheets[20].

These frequently repeated patterns of displacement, fragmentation, restriction and population isolation, followed by further displacement, expansion and the reunions of isolated populations, have led to the great diversity of Arctic and alpine plant species that we can find today. This constant environmental 'stirring' shaped the recent evolution of both Arctic and alpine floras, in which most species originated as hybrids, often between species themselves of hybrid origin, with such hybrids stabilised by doubling of their chromosomes (allopolyploidisation). The result is a

Rhododendron lapponicum, Abisko, Sweden

Pinguicula alpina, Ötztal, Austria

higher proportion of polyploid Arctic and alpine species than in the floras of lower latitudes and elevations. Arctic and alpine polyploidy is often associated with a fixed high level of heterozygosity that, it is argued, offers greater ecological flexibility than for diploid species, with an associated increased capacity to colonise new regions and environments. Diploid species are associated mainly with unglaciated regions, in the case of Arctic species most notably Beringia (eastern Siberia, Alaska and much of the Yukon Territory), whereas high polyploidy is principally associated with repeatedly glaciated areas, notably the mountains and Arctic regions of western Eurasia[21]. Even within a largely glaciated region such as north-western Europe, some species that range from the southern and central European mountains and north through Fennoscandia, for example *Parnassia palustris*[21], have mainly diploid populations more or less south of the last

Parnassia palustris, Ötztal, Austria

glacial ice limits, but mainly autotetraploid populations in northern regions that were ice covered at the last glacial maximum. With so much environmental stirring, autopolyploidisation has taken place more than once, tetraploid northern European populations of *P. palustris* being polyphyletic (having multiple originations).

Some *Primula* Studies

A similar, albeit more complex, pattern can be seen amongst members of *Primula* sect. Aleuritia subsect. Aleuritia—otherwise *Primula farinosa* and its allies, familiar to growers of alpine plants. Of 21 species in this subsection, 20 are distributed around higher northern latitudes, with one, *P. magellanica*, in southern South America. Eight diploid species (2*n* = 18) are found primarily in unglaciated regions of western and south-eastern Europe, the Great Plains region of North America, Beringia and Japan, and include the European *P. farinosa*, North American *P. mistassinica* and Japanese *P. modesta.* The remainder are polyploids, found today in formerly glaciated regions and ranging from tetraploids (2*n* = 36) such as *P. halleri* of the European Alps, through hexaploids, including the Scottish endemic *P. scotica*, and octoploids, like *P. scandinavica* with its disjunct range in the Norwegian mountains, to the 14-ploid *P. stricta* that ranges widely from north-east Canada and west Greenland eastwards through Iceland and Fennoscandia to Novaya Zemlya. Cytological and genomic research

Primula farinosa, Yorkshire, England

Primula stricta, Abisko, Sweden

shows that these polyploid species too are allopolyploid stabilised hybrids between species of lower ploidy levels[22].

Our endemic hexaploid, *Primula scotica*, apparently derives from a hybrid between a diploid *P. farinosa*-like and a tetraploid *P. halleri*-like species[22]; it probably originated south of the ice sheet during the last glacial stage, perhaps in south-east England where sub-fossil seeds of *P. scotica* and *P. halleri*[17,23] occur in sediments from that time. As with many allopolyploids, genetic evidence indicates it originated from more than one independent hybridisation. Furthermore, genetic evidence indicates that octoploid *P. scandinavica* is probably an allopolyploid from a hybrid between *P. scotica* and *P. farinosa*[22]. In addition to the possible advantages of a fixed high level of heterozygosity in such allopolyploids, all but one polyploid species are homostylous. Homostyly allows the possibility of self-fertilisation of a single colonising individual, thus increasing the potential for successful long-distance colonisations and hence rapid extensions of species' distributions into formerly glaciated regions. The exception is the tetraploid *P. borealis* that, with all the diploids, displays the heterostyly of most *Primula* species. In this context it is notable that *P. borealis* is also exceptional amongst the polyploids in being distributed principally in unglaciated coastal regions of northern Beringia.

Primula sect. Auricula, endemic to the European mountains, also diversified almost entirely during the Quaternary. Unlike *Primula* sect. Aleuritia subsect. Aleuritia, however, the 25 extant species are all polyploids, all but two being hexaploid ($2n$ = 66) or hypohexaploid ($2n$ = 64 or 62), the exceptions being *P. marginata*, that is (approximately) dodecaploid ($2n$ = 126), and *P. clusiana*, that is 18-ploid ($2n$ = 198). In marked contrast to the section Aleuritia subsection Aleuritia polyploids, the section Auricula species are all heterostylous and self-incompatible. Section Auricula apparently originated in eastern Asia *ca*. 3·6 Ma, sharing a common ancestor with *Primula* sects. Cuneifolia, Parryi and Dodecatheon (formerly the genus *Dodecatheon*). Following dispersal of their Asian ancestor to Europe

Primula marginata ‘Drake’s Form’, in cultivation in Wigtownshire, Scotland

the section diverged into two distinct clades *ca*. 2·4 Ma, close to the onset of the Quaternary Ice Age marked by the first extensive northern hemisphere glaciations[24,25]. Species diversification in both clades apparently then occurred relatively early in the Quaternary, probably driven by recurrent alternations between glacial and interglacial conditions, the more severe climatic fluctuations of the last million years apparently not leading to further speciation.

Ten species of the ‘eastern’ clade, found mainly in the eastern Alps and eastern European mountains, include *P. clusiana*, *P. glutinosa* and *P. minima*; just one, *P. integrifolia*, extends to the western Alps, Pyrenees and Cantabrians. The ‘western’ clade species, including *P. allionii*, *P. auricula* and *P. marginata*, occur principally in the western Alps, extending also to the Apennines (*P. apennina*), Calabrian Mountains of southern Italy (*P. palinuri*), Pyrenees (*P. latifolia*) and Cantabrians (*P. pedemontana*). The two clades’ distributions have limited overlap in the Alps, *P. villosa* and *P. carniolica* of the ‘western’ clade occurring in the eastern Alps[26]. Divergence of the two clades is hypothesised to have resulted from glaciation of the Alpine region, ancestral taxa becoming restricted to distributions east and west of the highest central Alps that were most extensively glaciated. Present occurrences of ‘eastern’ species west to the Cantabrians and of ‘western’ species in the eastern Alps are proposed to have arisen

Primula clusiana ‘Murray Lyon’, in cultivation in Wigtownshire, Scotland

secondarily by dispersal through the central Alps during interglacial periods with minimal ice sheets.

The greater number of ‘western’ clade species principally reflects seven of the 15 species being local endemics, five restricted to small areas in the (south)-western Alps[26]. This region is noted for its high topographical diversity and far richer flora than the central or northern Alps. Three of the four regional endemics in the ‘eastern’ clade are also found in the southern Alps, suggesting glacial conditions north of the main Alpine ranges were unsuitable for persistence of *Primula* sect. Auricula species.

Primula glutinosa, Ötztal, Austria

Some New Zealand Examples

The importance of Quaternary climatic fluctuations in the evolution of the present flora has been globally ubiquitous[27], especially in mountainous and arid regions. Nonetheless, as in biology generally, no single factor accounts for all of the present patterns. In New Zealand, uplift of the Southern Alps is geologically very recent, the mountain tops first consistently exceeding the treeline only about 0·95 Ma[28]. Evolution of specialised alpine plants has principally occurred since that time, the resulting alpine flora comprising several elements with different origins. Many species of alpine mires evolved from ancestors occupying waterlogged treeless sites at lower elevations, some as long ago as around 5·5 – 8 Ma (late Miocene). Species of alpine stream- and riverbeds include species with wide elevation ranges or with close relatives found at lower elevations. The species or its relatives occupy similar disturbed habitats below treeline that were available long before the mountain tops consistently exceeded the treeline. In contrast, species restricted to alpine zone habitats (including fell-field, scree, and communities dominated by cushion herbs or snowgrass (*Chionochloa* spp.)) evolved only since such habitats became permanently available after around 0·95 Ma[28]. Nonetheless, the New Zealand alpine flora contains a high proportion of polyploids, many of which are allopolyploids of hybrid origin. *Plantago*[29,30], for example, has diploid, tetraploid, octoploid, decaploid, dodecaploid and 16-ploid species, some of the polyploids having genomes derived from three or more parent species[30]. In other genera the polyploids are autopolyploids, their two or more chromosome sets originating from one parent species through the same process of chromosome doubling that leads to allopolyploidy. For example, two of the four *Leucogenes* species, *L. neglecta* (tetraploid, $2n = 56$) and *L. tarahaoa* (octoploid, $2n = 112$), are autopolyploids derived from diploid *L. leontopodium* ($2n = 28$)[31].

Thus, although at the family and even generic level alpine plant lineages mainly evolved earlier, most present species evolved during the Quaternary, some probably since the last glacial maximum around 24 ka. Hybridisation followed by allopolyploidisation played a key role in this evolution, the repeated isolation and merging of species' distributions as a result of Quaternary climatic changes undoubtedly stimulating such hybridisation. Thus the alpine plants we know and grow evolved in the recent geological past as a product of past climatic changes.

Alpine Plants and Climate

Despite climatic differences between polar, mid- and high-latitude alpine, and tropical alpine zones, a shared characteristic is that their plants must tolerate low, often freezing, temperatures. Outside some

Oxyria digyna, Ötztal, Austria

tropical and warm temperate regions, alpine plants must also be able to utilise a short growing season. For several months there will be no daylight in polar zones, seasonal snow cover in polar and sub-polar regions and in mountains, freezing—potentially including around the roots—in polar, sub-polar and mid- and high-latitude alpine zones, or seasonal drought in alpine zones of warm temperate and tropical mountains. Even on tropical and equatorial mountains with no such growing season restrictions, plants must instead tolerate marked diurnal temperature fluctuations, from sub-zero (°C) overnight to daytime peaks of more than 30°C.

A primary and crucial adaptation of many alpines is an ability to carry on metabolic and life-cycle processes at low temperatures. Fifty years ago William Dwight Billings[3] emphasised the evolution of distinct ecotypes of many Arctic-alpine species that are adapted to the local conditions in different parts of their overall distributions. He studied especially the contrasting Arctic and alpine ecotypes of *Oxyria digyna*. Even within smaller areas, wide ranges of microclimate, generally associated with landscape influences on the depth and duration of snow lie, can lead to the evolution of ecotypes within a species exhibiting markedly different adaptations. For example, *Saxifraga oppositifolia*, shows marked ecotypic differentiation over only 5 to 10 metres between plants growing on exposed ridges and others

Saxifraga oppositifolia, Isle of Skye, Scotland

growing in hollows. Ridges have shorter and potentially discontinuous snow cover, warmer soil and possible soil water deficit; in contrast, hollows may have deep and long-lasting snow, leading to a short growing season, with waterlogged soils that are generally colder–at least during the growing season. Plants occupying ridge sites are more upright and tufted, flower earlier and have overlapping petals, whereas in hollow sites they are prostrate and mat forming, flower later and have non-overlapping petals[32]. An even more extreme adaptation is seen in populations of this and other species that experience many months of ice encasement and hence of anaerobic conditions. All plants of *S. oppositifolia* from the mountains of southern Norway and Scotland, where ice encasement is rare, died after a week in anaerobic conditions, whereas all plants from a site in Spitsbergen, where they endured months of ice encasement each winter, survived the week[33].

Notwithstanding alpines' need for metabolic activity at low mean temperatures, many of them–especially cushion-forming species and

those in exposed microsites–can experience very high leaf temperatures in summer, dropping very low during winter if not snow-covered. On a sunny summer day the temperature in a cushion plant in the European Alps frequently reaches 30–35°C, occasionally over 40°C, often exceeding air temperature by 16–25°C. The same plant may experience -20°C to -22°C in winter, whereas only a few metres away, where snow depth exceeds half a metre, temperature will fall only to about -5°C[34]. Thus, although unsurprising that alpines are able to make a net photosynthetic gain at temperatures as low as -6°C to -3°C, it is perhaps surprising that their typical optimum for photosynthesis is 12–18°C and that they can maintain a net gain up to 38–42°C[35]. However, were it not for their wide temperature tolerance they could not successfully be cultivated in our predominantly lowland gardens, nor would some of them be able naturally to occupy some lowland habitats. The Arctic–alpine *Sedum (Rhodiola) rosea*, for example, is found on sea cliffs around the western coasts of the British Isles, and on mountain cliffs and rock ledges, its absence from inland lowland sites being a consequence of its relatively slow growth rate–and hence inability to compete with vigorous lowland species[36].

Sedum rosea, Breadalbanes, Scotland

Rubus chamaemorus, Abisko, Sweden

Not all Arctic-alpine plants can survive at lower latitudes and lower elevations. In particular, species found principally in habitats with perpetually moist–and hence cool–soils, and with reliable winter snow of about half a metre or more, may be sensitive to winter soil temperatures. The rate of respiration in the rhizome of *Rubus chamaemorus*, for example, depends strongly on temperature, especially during winter[37]. Although winter temperature alone may not ultimately determine its natural distribution, as winter temperatures increase it respires more of the carbohydrate reserves stored in its rhizome during summer, resulting in less rapid or vigorous spring shoot growth that, in turn, can lead to reduced photosynthesis. Warmer summer conditions may lead to supra-optimal leaf temperatures for photosynthesis[38], and hence a reduced carbohydrate reserve for the following winter. The warmer winter and summer temperatures of lower latitudes and elevations thus lead to a downward spiral and eventually to death of the plant.

Projected Future Climatic Changes and Alpine Plants

Global climate is altering in complex ways, but the underlying change is an increase in the mean surface temperature. This 'global warming' stems primarily from release of a series of 'greenhouse gases', the best known and quantitatively most important being carbon dioxide and methane. These gases lead to warming of the lower atmosphere because they absorb radiation emitted by the Earth's surface. The warming is not uniform across the Earth, however. Warming is greater over land than over the oceans, and is generally greater towards the poles, especially in the Arctic. Warming is also greater at higher elevations in mountain regions worldwide[39]. A major contributor to amplified warming in both mountains and the Arctic is the snow–albedo feedback effect. As temperatures rise, the extent and persistence of snow cover decreases. Whereas snow-covered areas have a high albedo (i.e. are highly reflective), reflecting much of the incoming solar radiation into space, most soils, vegetation and open ocean areas have

a lower albedo, absorbing much of the solar radiation and being warmed. This snow–albedo feedback is further amplified by the offset between the season of snow cover and the seasonal intensity of solar radiation. Snow cover tends to peak in the spring, much of this snow not melting until approaching midsummer, thus reflecting a large fraction of the annual solar radiation budget. Climatic warming leads to earlier melting of the snow cover and hence a disproportionate increase in absorption of solar radiation, largely accounting for amplified warming both in the Arctic and at higher elevations in mountains.

This amplification is further enhanced by the greater warming in winter, especially at higher latitudes, that results from the underlying warming mechanism. Whereas incoming solar radiation is strongest at midday and in midsummer, and zero at midnight and throughout midwinter north of the Arctic Circle, outgoing terrestrial radiation is essentially constant both diurnally and seasonally. The short days and long nights of winter are cooler largely because the daily amount of outgoing terrestrial radiation exceeds the incoming solar radiation, with the reverse being true in summer when temperatures as a result are warmer. Greenhouse gases absorb a proportion of the outgoing terrestrial radiation; as their concentrations increase that proportion increases, warming the atmosphere. This warming is greatest in winter because of the stronger influence of the amount of outgoing terrestrial radiation on temperature during this season. In turn, the extent and persistence of snow cover is further decreased, leading to increased amplification of warming by the snow–albedo feedback – a vicious circle indeed!

An increasingly frequent result of general warming in polar and mountainous regions is mid-winter episodes of temperatures well above freezing. These lead to snow and ice melting and to any precipitation falling as rain, adding to the melting. Their onset can be extremely rapid, temperature rising from -20°C to +5°C, or even +10°C, in a day or less, the higher temperatures typically lasting about a week. These episodes often severely damage plants, especially dwarf shrubs that form extensive heath-like communities that are an important component of the tundra vegetation mosaic. Extensive damage and shoot death follow in various species, notably *Empetrum hermaphroditum* in northern Fennoscandia. Experiments mimicking such events have shown shoot mortality of up to 52% in *E. hermaphroditum* and as high as 80% in *Vaccinium myrtillus*[40]. Much of this mortality results from the initiation, when snow cover is lost during warming events, of normal spring physiological processes, including loss of freezing tolerance. High shoot mortality then results from subsequent exposure to returning extreme sub-zero temperatures that are not mitigated by any insulating snow cover. The return of sub-zero conditions also freezes meltwater from the preceding warm event causing shoots to die if they become encased in ice and experience anaerobic conditions.

Warming and longer periods without snow cover are not the only climatic changes affecting alpine plants. More frequent extreme rainfall events, droughts and gales are all influencing polar and mountain regions. Given the inherent instability of mountainous landscapes, extreme rainfall and rapid snow-melt increase the frequency of landslides and avalanches. Such events can strip away vegetation and soil over large areas, leaving scars where vegetation cover will take many years fully to return.

Rain and extreme rain in mountainous areas result from moisture-bearing air masses being forced to rise, hence cooling and causing water vapour to condense. This general pattern is broken on the highest equatorial and tropical mountains above cloud level, where the summit areas may be arid. Elsewhere, drought conditions are infrequent in most mountainous alpine zones. However, with climatic warming, drought is happening more frequently in many of these zones. In tropical mountains the elevation at which condensation occurs is characterised by cloud forest. Climatic warming is causing cloud elevations to increase, however, leading some lower tropical mountains to lose their cloud forest zone, with often far-reaching impacts on many species[41,42], whilst the alpine zone above the clouds of higher tropical and equatorial mountains will reduce in extent as the cloud zone moves higher. A similar reduction in the extent of areas beyond polar and mountain treelines is expected as rising temperatures allow treelines to advance.

Plant Community Changes

Alpine forbs (broad-leaved plants) are generally more sensitive to drought than are the graminoids (grasses, sedges and rushes) amongst which they often grow. As a result, increasing drought frequency is expected to shift plant communities towards a greater dominance of graminoids, with alpine forbs decreasing. In turn, this will impact other alpine ecosystem components, notably pollinators that will encounter fewer plants with showy, animal-pollinated flowers, as opposed to the wind-pollinated flowers of graminoids.

A review of 142 published studies examining recent treeline dynamics found 66% of studies showed treelines advancing upslope or polewards, whereas only 1% found evidence of treeline retreat[43]. The mean rate of advance of elevational treelines (1·42 ± 2·44 metres per year) was very much less than that of latitudinal treelines (47 ± 82·4 metres per year), although both varied considerably. This contrast is expected, however, because temperature decreases with elevation at a mean rate (about 6·5°C per kilometre) that is three orders of magnitude faster than it decreases with latitude in extra-tropical latitudes (about 0·0067°C per kilometre in the northern and about 0·0051°C per kilometre in the southern hemisphere). A 1°C temperature increase thus equates

to a latitudinal displacement of about 149 km, around 903 times greater than the equivalent elevational displacement of 165 m. Given that the reported mean rate of advance of latitudinal treelines is only about 33 times faster than that of elevational treelines, this strongly suggests latitudinal treeline advance is lagging substantially behind the rate of warming. Although this lag might result from propagule dispersal limitations, these being much less relevant in the case of elevational treelines, palaeoecological evidence indicates that,·following retreat of the last glacial ice sheets, trees extended their ranges across the northern hemisphere continents at rates of 0·25 to 1·5 kilometres per year[44,45]. Much of the current lag in latitudinal treeline advance is thus likely to result from various human activities reducing and/or fragmenting the habitat available for trees to colonise, combined with higher than natural grazing levels leading to reduced establishment rates. Furthermore, similar lagging responses to climatic change are evident in other types of organism, including volant taxa such as birds and butterflies[46] that are expected to be less likely than trees to suffer from dispersal limitations. Whereas, between 1990 and 2008, European bird communities shifted polewards at 2·06 ± 0·17 kilometres per year and butterfly communities at 6·33 ± 0·5 kilometres per year, mean annual temperature increased at a rate equivalent to a poleward shift of 13·83 ± 1·5 kilometres per year during the same interval[46]. Bird communities thus shifted at only 14·9% and butterflies at 45·8% of the rate required to track the warming, loss and fragmentation of suitable habitat resulting from human land use likely largely accounting for these lags.

Notwithstanding that latitudinal treeline advance is lagging behind climatic warming, at current rates of advance areas beyond the elevational and latitudinal treelines, and hence available for alpine plants, are expected to decrease markedly this century. How much they will decrease depends principally upon by how much and how soon greenhouse gas emissions are reduced; how rapidly they will decrease depends mainly upon by how much treeline advances continue to lag the changes in climate. If emissions continue at similar to present levels, the combined potential area of tundra and shrub tundra simulated for 2085 by a global vegetation model was just 4·8% of their area simulated for the pre-industrial climate. Even with substantial emissions reductions their combined simulated area was only 29% of that for the pre-industrial climate. Even if vegetation responses lag behind climatic changes, an eventual 71% reduction in tundra and shrub tundra area would seriously threaten survival of many Arctic plants and Arctic populations of Arctic–Alpines.

In the case of elevational treelines, even if treeline advance lags climatic changes more vigorous herbaceous species of lower elevations may expand upslope more quickly than the treeline. If this happens, alpine plants will be outcompeted and their occurrence limited to ever

higher elevations. Evidence of such upslope shifts by lower elevation species was shown already 30 years ago by a study of Alpine and nival zone plant communities in the Alps[47]. Subsequent work showed declines of cold-adapted plant species and increases and range expansions by warm-adapted species in the alpine zone[48]. These observations led the Austrian workers involved to establish an international network to monitor alpine zone plant community responses to climatic changes (see https://www.gloria.ac.at/home). Monitoring results have generally confirmed climatic change impacts on alpine zone plant communities that remain above the treeline. Nival zone and snow-bed communities often show substantial changes because of reduced snow cover. Flushes and other communities dependent upon meltwater to sustain soil moisture during the summer months are also suffering because, as the quantity of snow decreases, the supply of meltwater is no longer maintained through the summer.

Alpines in Gardens

When it comes to the garden cultivation of alpines, although the impacts of climatic changes depend upon geographical region, they will almost always be negative. Increases in summer temperatures and in the incidence and intensity of summer droughts will negatively affect cultivation of alpines in many regions. Furthermore, supplementary watering to alleviate drought will become increasingly anti-social, if not illegal, in many places as supplies of water for human consumption become increasingly restricted. Warm winters, with a general lack of snow cover, are already becoming familiar where at least some weeks of snow cover was normal only forty or fifty years ago. Despite these generally warmer winters, periods with substantially sub-zero temperatures are nonetheless still experienced, but by plants that either have never become fully frost hardened during the mild autumn, or else have responded to a warmer interval during the winter by physiological changes that lead to the loss of frost hardiness that typically must occur prior to spring growth. In either case the result is likely to be significant shoot damage or even death. The increasing intensity of rainfall events, and in some regions a shift towards greater winter precipitation, also have negative impacts. Many species grown in rock gardens are poorly adapted to the resulting cold, wet conditions, both above ground and in the soil. They are adapted instead to freezing conditions, often with snow cover that insulates them from temperature extremes. This maladaptation, coupled to increasing over-winter survival and winter activity of many garden pests, not least slugs and snails, causes increased amounts of plant damage, and can lead to substantial winter mortality of alpines. As rock gardeners we will need to adapt the choice of plants that we attempt to cultivate taking into account the changing local climatic conditions.

Conclusions

As I have described, vascular plants that would qualify as alpine plants have almost certainly been part of the global flora since the earliest evolution of land plants, given that mountains have been a feature of global geography since very early in geological history. The angiosperm plants with showy flowers that we particularly admire, and that form the majority of those that we attempt to cultivate, were present already during the Mesozoic. By the end of that geological era many of the families, and some of the genera, that are found today in Arctic and alpine zones had evolved and were probably occupying these zones. These taxa diversified during the Cenozoic, but their major diversification, and the evolution of many of the species found today, has happened geologically only very recently. Marked global cooling, with retreat of polar and mountain treelines, occurred during the late Pliocene, around 2 Ma, opening up extensive new opportunities for alpine plants. The Quaternary Ice Age that followed was characterised by repeated cycles of climatic cooling, with extensive ice-sheet development, and climatic warming, leading to intervals with climatic conditions similar to those that have generally prevailed since about eight thousand years ago. These climatic fluctuations led to the evolution of large numbers of new species in many genera, although it is likely that they also caused the extinction of many other species.

Alpines have a range of adaptations that enable them to survive and thrive in the short growing seasons and generally low temperatures of the zones beyond polar and mountain treelines. Some adaptations enable them to take advantage of the often markedly elevated temperatures near the ground. However, alpines are generally poor competitors, compared to species from lower latitudes and elevations. Global climatic change hence has both direct and indirect impacts upon cold-adapted alpine plants as less cold-adapted herbaceous species are able to expand into polar and alpine zones. Ultimately, warming allows the expansion of shrubs and trees polewards and upwards, reducing the extent of the polar and alpine zones and shading out the low-growing and generally shade-intolerant alpines.

Climatic change also poses new challenges to those attempting to cultivate alpine plants. Although many of these challenges relate to the same adaptations of these species to their polar and alpine habitats that are leading them to decline in their natural ranges, some represent simply an amplification, as a result of climatic changes, of challenges that have always been faced, notably the lack of snow cover and the depredations of garden pests. Whilst some adaptation by those cultivating rock plants will be necessary, both in terms of the plants they attempt to grow and the cultivation methods that they employ, the aesthetic pleasure that such plants give will, I am sure, mean that rock gardeners will continue to seek ways to cultivate these splendid plants despite the additional challenges resulting from climatic changes.

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