THE VEGETATION HISTORY OF SNOWDONIA SINCE THE LATE GLACIAL PERIOD

PETER RHIND AND BARBARA JONES
Countryside Council for Wales, Plas Penrhos, Ffôrdd Penrhos, Bangor, Gwynedd LL57 2LQ

ABSTRACT
Snowdonia has one of the most intensely studied pollen records in Britain. It has, therefore, been possible to provide a detailed description of all of the major vegetation types that developed since the last ice age. The account extends from the late glacial period (some 12,000 years BP), when pioneer plants were struggling to colonise the newly exposed, barren landscapes, through to the development of various climax woodland communities, and on to the ever-increasing impact of man. A number of plants occurring in the late glacial and early post-glacial period, such as Iceland purslane (Koenigia islandica), wild azalea (Loiseleuria procumbens) and dwarf birch (Betula nana) are no longer found as far south as Snowdonia, whilst others such as alpine saxifrage (Saxifraga nivalis) and dwarf willow (Salix herbacea) have managed to survive on the higher mountains. During the early stages of glacial retreat, a number of calcicoles (lime-loving plants), such as hoary plantain (Plantago media), Jacob’s ladder (Polemonium caeruleum), meadow saxifrage (Saxifraga granulata) and rock-rose (Helianthemum sp.) appear to have been widespread, suggesting that the soils were much less acidic than they are today. The early colonists also included various weedy species, such as Artemisia sp., black bindweed (Fallopia convolvulus), plantains (Plantago sp.), and nettle (Urtica sp.), some of which have continued to be members of the lowland flora of Snowdonia through to the present day.

INTRODUCTION
Snowdonia has one of the most thoroughly investigated pollen records in Britain, revealing a fascinating vegetation history that can be traced back some 12,000 years to when the first pioneer plants were struggling to colonise the newly exposed, barren landscapes of the late glacial period. Prior to this, the area had been subject to prolonged periods of glaciation in an ice age stretching back some 120,000 years, with most of its terrain under deep ice sheets and glaciers for much of this period. Even at the height of the last glaciation, however, when conditions were very hostile to plant life, Snowdonia was probably not a plant desert. Lichens, algae, and possibly some mosses would have been present on exposed rock, and there may even have been some higher plants, such as horsetails, some hardy ferns and, possibly, flowering plants in places where the soil remained unfrozen for at least a part of each year. These would have been plants we now call arctic-alpines - essentially species of arctic or alpine regions that reach into temperate latitudes on high mountains, e.g. the Snowdon lily (Lloydia serotina), several saxifrages and mountain avens (Dryas octopetala).

Possibly one of the earliest pollen studies in the area was carried out by Woodhead & Hodgson (1935) who concentrated on such places as Cwm Idwal, Nant y Benglog, Gwern y Gof, Flynnnon Lloer, Blaen y Nant, Cwm Cywion, Ty’n y Maes and Llyn Cororion. Since then other studies have been carried out in Cwm Idwal (Godwin, 1955; Tipping, 1993), Cwm Dwytwch and Nant Ffrancon (Seddon, 1962), Cwm Melynlllyn (Walker, 1978), Cwm Cywion and Llyn Llydaw (Ince, 1983), Clogwynygarreg, Llyn Cororion, Llyn Irddyn, Erw-wen and Moel y Gerddi (Chambers & Price, 1988), Cors Geuallt, the Llewesig basin (Crabtree, 1972) and Llyn Gwernan (Lowe & Lowe, 1989). In addition, there has also been a detailed study of the plant fossil record in Nant Ffrancon (Burrows, 1974;1975).
During the late glacial period, as glaciers started to retreat, the ground became free of ice for the first time in many thousands of years; the exposed barren land of rocks and mineral sediments once again provided conditions for vegetation to develop. For many years, the area was exposed to arctic or sub-arctic conditions and, initially, there was a prevalence of open conditions with areas of bare immature soils and newly exposed rock surfaces. Initially, the main colonists would have been lichens and mosses but, as warming progressed and the ground remained unfrozen for part of the year, higher plants would have begun to play a part. In the early stages, they would mainly have been species with the ability to complete their life cycles very rapidly, but as fertility built up and temperatures rose, more and more perennial species appeared. Many of the species that colonised the area during this harsh period survived well into the post-glacial period and a number of these cold climate species still survive today in the higher parts of the Welsh mountains. Pollen studies in various parts of Britain and Europe have indicated that the climate up until about 12,000 years BP was initially very cold, and because of the abundance of mountain avens (*Dryas octopetala*) over this time, it has been described as the Lower (Older) Dryas Period. Subsequently, during the so-called Allerod interstadial period, the climate ameliorated and for the next 1,500 years or so the temperature increased sufficiently for birch woodlands to develop. This was followed by a short return to Arctic conditions, allowing a resurgence of tundra type vegetation with abundant mountain avens. Consequently, the period leading up to the end of the Ice Age has been dubbed the Upper (Younger) Dryas. However, the sequence of events may not have been as clear-cut in the uplands of Snowdonia, although there is evidence that similar climatic oscillations took place in the Nant Ffrancon.

While juniper was probably present very early, true woodland was not established until about 10,000 years BP. Birch was the most important tree initially, but after about 1,500 years, or so, oak, and in some places pine, began to displace it, and the woodlands generally became more diverse. Apart from a few perturbations involving shifts in species dominance and changes in altitudinal limits of certain species, it is essentially this woodland phase that has persisted right through to the present day. The fact that natural woodland now covers only a relatively small part of Snowdonia is almost entirely the result of human activity.

**Snowdon’s early colonists**

Prior to about 12,000 years BP, there was still much glacial and periglacial activity, and the climate must have been extremely harsh. The vegetation was very sparse, with few flowering plants, but the number of mosses over this period started to increase. In Nant Ffrancon, the earliest colonists included *Antitrichia curtipendula*, a moss known to occur in wet places near to Norwegian glaciers, and *Sphagnum imbricatum*, a bog moss that is common in certain types of tundra; both are now rare in Snowdonia. Slightly later colonists have been more enduring, and a number of them still have a strong presence. *Aulacomnium palustre*, *Bryum* sp, *Climacium dendroides*, *Drepanocladus cf aduncus*, *Fontinalis squamosus*, *Hylocomium splendens*, *Philonotis fontanum* and *Poblia* sp, are still frequently encountered in lowland habitats. Other mosses, including *Polytrichum alpinum* and *Racomitrium lanuginosum*, have remained exclusively montane plants.

The first flowering plants to colonise Nant Ffrancon included tufted saxifrage (*Saxifraga cespitosa*) and pearlwort (*Sagina* sp.), shortly followed by dwarf willow (*Salix herbacea*). Although not found in the pollen record at this site, it is likely that alpine meadow-grass (*Poa alpina*), alpine hair-grass (*Deschampsia alpina*), alpine chickweed
(Cerastium alpinum), mountain sorrel (Oxyria digyna), starry saxifrage (Saxifraga stellaris) and moss campion (Silene acaulis) were amongst these first colonists. These species all occur as pioneer colonisers at the foot of retreating glaciers in northern Europe. Indeed, S. acaulis has been used to estimate the age of glacial deposits in the Canadian Rockies, using growth rates and maximum diameters of this cushion plant (McCarthy, 1992).

Some of these species may not have been new to the area, but had survived at least the latter part of the Ice Age in unglaciated refuges that existed on the west coast of Britain. For example, unglaciated peaks within ice masses known as nunatacks, and coastal refugia bordered by the sea, are known to support a limited flora in Greenland. Peaks, such as Snowdon and Glyder Fawr, were probably free from ice throughout later ice advances (McCarroll & Ballantyne, 2000), and this may help explain the isolated occurrence of certain alpine plant species, such as the Snowdon lily (Lloydia serotina) and mountain avens (Dryas octopetala). Both species may have survived on these isolated 'island refuges'. There is some evidence for this in the genetics of the Snowdon lily, since the genetic distance between the Welsh populations and their nearest Alpine neighbours, from which the Welsh plants presumably descended, was found to be greater than would be expected based on geographical distance alone, (Jones et al, 2001). This implies that the Welsh populations have been separated for longer than 12,000 years suggesting that the plants in Snowdonia were extant for at least part of the Ice Age.

In the period shortly after the glaciers retreated, up until about 10,000 years BP, the initially-open habitats allowed colonisation by a variety of species producing apparent mixtures of arctic-alpine plants and plants we now often regard as lowland weeds. In the area around Llyn Llydaw, the vegetation at this time was dominated by various grasses and docks (Rumex sp.), whilst less common species included juniper (Juniperus communis), mountain avens (Dryas octopetala), purple saxifrage (Saxifraga oppositifolia), alpine saxifrage (Saxifraga nivalis), alpine saw wort (Saussurea alpina), meadow-rues (probably both alpine meadow-rue and lesser meadow-rue; Thalictrum sp.), and a variety of ferns and clubmosses, including moonwort (Botrychium lunaria), parsley fern (Cryptogramma crispa), fir clubmoss (Huperzia selago) and interrupted clubmoss (Lycopodium annotinum). Intermixed with these were various weedy species, such as Artemisia sp. (possibly Scottish wormwood, A. norvegica), black bindweed (Fallopia convolvulus), plantains (Plantago sp.), nettle (Urtica sp.), and various members of the goosefoot family (Chenopodiaceae). Most of these can still be found in Snowdonia, but the interrupted clubmoss appears to have recently disappeared. It was recorded above Llyn y Cwm in 1690 and then on several subsequent occasions on the Glyderau up until the start of the 19th century (Jones, 1996).

Much of the vegetation in Nant Ffrancon, during this period, remained open with much sheep’s sorrel (Rumex acetosella). Other species included willow herb (probably chickweed willow herb (Epilobium alsinifolium), now restricted to a few upland crags, such as Craig y Dulyn, and wild azalea (Loiseleuria procumbens), now confined, in Britain, to the mountains of northern Scotland. Also amongst the early flowering plants of this period were various lowland calcicoles (lime-loving plants), such as bulbous buttercup (Ranunculus bulbosus), great burnet (Sanguisorba officinalis), hoary plantain (Plantago media), hutchinsia (Hornungia petraea), Jacob's ladder (Polemonium caeruleum), meadow saxifrage (Saxifraga granulata) and rock-rose (Helianthemum sp.). They quickly disappeared as leaching progressed and the soils became more acidic. However, if these species were able to survive the arctic or sub-arctic conditions of that time, it is unclear why they did not continue to grow in some of the more calcareous upland areas. On the other hand, these are not typical
alpine species, and may be unable to tolerate the more exposed conditions found in uplands.

Jacob’s ladder, in particular, appears to have been widespread during the late glacial period (Pigott 1958) and, although it now has a limited distribution - being largely confined to grasslands and open woodlands on limestone - in Britain, in northern Germany it can be found in fenland habitat. Its presence in Snowdonia during the late glacial period may indicate the occurrence of a similar fenland habitat at that time.

Other surprising inclusions in this early flora were thrift (Armeria maritima), sea plantain (Plantago maritima) and, possibly, sea campion (Silene uniflora). They all appear to have been fairly widespread at that time, occurring in both upland and lowland areas, such as the Nant Ffrancon but, as their names suggest, they are now mainly associated with maritime cliffs. There are still places in upland Snowdonia where these species can be found, such as Clogwyn Du’r Arddu and Cwm Idwal, but only where there is a degree of base enrichment. One explanation for these unusual distributions is that, because these plants were unable to tolerate the competition and shady conditions caused by the post-glacial spread of forests, they became restricted to upland crags and sea cliff ledges which remained open during this period, providing isolated but disconnected refuges. Such anomalous distributions also apply to several other species, including the lesser clubmoss (Selaginella selaginoides) and mosses, such as Amblyodon dealbatus, Catoscopium nigritum and Meesia uliginosa. They are all found in either upland base-rich flushes and rock crevices, or coastal calcareous sand dunes. This again probably relates to the possibility that sand dunes remained open even when forest spread was at its maximum.

Plants of recently exposed rocky surfaces and scree slopes
By about 9,900 years BP, the rocks in Cwm Cywion had been colonised by a variety of bryophytes; dominant amongst these were the arctic-alpine species Racomitrium cf aquaticum and R. cf fasiculare, whilst less specialised species included Hypnum cupressiforme, Philonotis fontana, Mnium sp., Dicranum sp. and Bryum sp. All of these species and genera are still relatively common. It is also likely that the rocks, at that time, supported various arctic-alpine lichens, including Cetraria islandica, Sphaeoporus globosus and Ochrolechia tarture, since all three of these cold-climate species can still be found, although the former is mainly restricted to the uplands. At that time, scree slopes were rapidly developing in the periglacial zones and, just as today, parsley fern (Cryptogramma crispa) seems to have been one of the main pioneer plants of this habitat. It is also characteristic of late snowpatch vegetation, and became very common towards the end of the glacial period. There was also a corresponding increase in alpine saw-wort (Saussurea alpina) which, like parsley fern, can grow on newly-developed scree, but only where the rocks are calcareous.

Tundra
For a relatively brief period during the late glacial period, a form of tundra developed; dominated by dwarf birch (Betula nana). It appears to have been fairly widespread and was relatively abundant in both Nant Ffrancon and Cwm Dwythwch. However, in the immediate post-glacial period (ca 9,700 years BP) only scattered stands occurred in the area around Llyn Cororion and, by that time, much of the vegetation seems to have been a form of dwarf-heath tundra with stands of crowberry (Empetrum nigrum). It also included a large herbaceous element with many of the above-mentioned flowering plants and a comparatively large number of dwarf pteridophytes. Spores of fir clubmoss (Huperzia selago), interrupted clubmoss (Lycopodium annotinum), lesser clubmoss (Selaginella
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Selaginoides), moonwort (Botrychium lunulata) and adder's-tongue (Ophioglossum vulgatum), have all been found, suggesting that there was at least some open vegetation. But the record also tells us that there was a scattering of juniper (Juniperus communis) and sea buckthorn (Hippophae rhamnoides) scrub. Today, juniper is rare in Snowdonia, and restricted to a few upland sites, such as Cwm Graianog, whereas both dwarf birch and sea buckthorn later disappeared from Wales altogether. In Britain, sea buckthorn was eventually relegated to a few coastal sand dune systems in southern England, but it has since been introduced to a number of dune systems in Wales. In Scandinavia, it occurs in both mountain and coastal habitats where trees are lacking. Today, the nearest we have to tundra vegetation in Snowdonia are the stands of dwarf willow (Salix herbacea) communities restricted to a few upland sites such as Elidir Fach.

Plants of lake margins, bogs and fens
In area around Nant Ffrancon, early bog and acidic flush species included the mosses Aulacomnium palustre, Dicranum scoparium, Polytrichum urnigerum, Sphagnum imbricatum, S. papillosum and the now rare Philonotis seriata which, today, is restricted to upland flushes on the Carneddau. These early bogs also provided habitat for the moss Scorpidium turgescens, which is now restricted to high altitude mires in northern Scotland. It was allegedly recorded on Cadair Idris in 1922, but the plant has not been seen in Wales since then.

From about 11,300 BP, the area around Glanllynnae Marsh provided habitat for Iceland purslane (Koenigia islandica). This, now rare, plant in Britain is restricted to the mountains of northern Scotland (Ratcliffe, 1958) but is commonly found in the Scandinavian mountains. It tends to occur on damp mud and bare ground, and can be found, for example, around the edges of small lakes in Iceland (Grontveg 1942). The late glacial marshlands of Glanllynnae possibly therefore had much in common with the habitats surrounding these Icelandic lakes.

Other marshland plants, however, were mostly those that we expect to find today, including slender spike-rush (Eleocharis uniglumis), marsh willow herb (Epilobium palustre), lesser spearwort (Ranunculus flammula), bog stitchwort (Stellaria aline), together with a variety of mosses, such as Calliergon cordifolium, Calliergon cuspidatum, Campylium stellatum, Climacium dendroides and Cratoneuron commutatum.

In the final stages of the glacial retreat (ca 10,000 BP) a tall fen community dominated by common valerian (Valeriana officinalis), meadowsweet (Filipendula ulmaria) and marsh cinquefoil (Potentilla palustris) became moderately common in Cwm Dwythwch, whilst meadowsweet and Jacob's ladder (Polemonium caeruleum) dominated the lake margins of Cwm Cywion and Llyn Llydaw. The margins and streams also supported a rich bryophyte flora including Climacium dendroides, Philonotis fontana and Racomitrium aquaticum.

It is interesting to note that, during this period, a large lake (‘Llyn Ffrancon’) formed in Nant Ffrancon and persisted for some 5,000 years. The margins supported many of the fenland species found in Cwm Dwythwch, together with the, now very rare, Scottish dock (Rumex aquaticus), which, as the name suggests, is now restricted to Scotland. The mosses included Cratoneuron commutatum and Dichodontium pellucidum. Alder and willow carr together with various sedges were also becoming common lake margin features at this time.

Aquatic plants
During the late glacial period, the aquatic vegetation that colonised some of Snowdonia's early lakes included a number of species that you would expect to find today, including
alternate water-milfoil (*Myriophyllum alterniflorum*), bulrush (*Typha latifolia*), bur-reed (*Sparganium* sp.), various pondweeds (including small pondweed *Potamogetum berchtoldii*), quillwort (*Isoetes lacustris*), and shoreweed (*Littorella uniflora*). Surprisingly, the aquatic flora of 'Llyn Ffrancon' also included two stoneworts (charophytes), *Chara* sp and *Nitella* sp. Neither of these can tolerate acid conditions, but recent studies of microscopic algae from various lake sediments have shown that the lakes of Snowdonia were generally less acidic than they are today (Walker 1978).

The aquatic vegetation in Llyn Dwythwch included water lilies (*Nuphar* sp. and *Nymphaea* sp.) and, although neither of these species is present in this lake today, white lily (*Nymphaea alba*) can still be found in Llyn Goddionduon. Later, and shortly before its disappearance, ‘Llyn Ffrancon’ provided a habitat for the pteridophyte pillwort (*Pilularia globulifera*), showing that the waters had become much more acidic. The aquatic moss *Fontinalis squamosa* appears to have been common in many of the mountain streams during this early period and, although it later went into decline, it is still comparatively common.

**THE POST GLACIAL-PERIOD**

This period is taken as beginning when the remaining ice-sheets and valley glaciers began to undergo rapid decay and the climate became sufficiently warm to allow scrub and woodland to develop. It represents the geological period known as the Holocene and started some 10,000 years ago; for much of this period the climate has continued to ameliorate. As a result, Snowdonia has seen the development of a zonation of plant communities ranging from scrub and woodland communities in the valleys to mountain grassland and moorland at higher altitudes. Arctic-alpine species became increasingly restricted to mountain tops and high altitude crags. Although oak is now the dominant tree in most natural woodlands, juniper, birch, pine, hazel, alder, and elm have also been prominent at various times.

**Juniper scrub**

Juniper was growing in the watershed of Nant Ffrancon well before the start of the post-glacial period, and probably became established in the area sometime prior to 12,000 years BP. Its career as a dominant plant seems to have been short, however, and by about 10,000 years BP birch had started to replace it. This period leading up to the start of the post-glacial period also saw a peak in the amount of sea buckthorn (*Hippophae rhamnoides*) scrub, which, prior to the spread of birch, is thought to have been an early colonist of morainic debris. In the upland areas, such as Cwm Dwythwch, the prostrate variety of juniper (*Juniperus communis* subspecies *nana*) is thought to have been present, whereas in the lowland areas around Llyn Cororion the juniper was found to have an associated understory of ferns including *Dryopteris* sp. suggesting, perhaps, that the taller growing *Juniperus communis* ssp. *communis* had become established. Thickets of juniper with sea buckthorn also formed in Nant Ffrancon, producing what appears to have been a relatively closed community, but in upland areas the community was probably much more open. This is supported by evidence that, during the maximum period of juniper abundance in Cwm Cywion, bedstraw (*Galium* sp.), meadow-rue (*Thalictrum* sp.), bladder fern (*Cystopteris fragilis*) and royal fern (*Osmunda regalis*) were also relatively common. Also around Cwm Cywion during this period, joint pine (*Ephedra cf. distacbya*) makes a fleeting appearance in the pollen record. Although no longer present in Britain, this small gymnosperm shrub can still be found in western France, where it inhabits sandy shores and rocks.
Mountain grassland and moorland
Grassland and moorland were already established in the early stages of the post-glacial period, some 10,000 years BP, particularly on upland slopes and sheltered plateaux. They were probably similar to the upland meadows that we have today in places like Cwm Dyli and, as today, their species composition would have varied according to soil type and the properties of the underlying rocks. On lime-rich volcanic soils, there would have been a grassy sward with sheep’s-fescue (*Festuca ovina*) and common bent (*Agrostis capillaris*), as well as alpine plants, such as lady’s mantle (*Alchemilla vulgaris*), possibly globe flower (*Trollius europaeus*) and wood bitter vetch (*Vicia orobus*). This assemblage of plants can still be seen in some of the meadows adjacent to upper reaches of the Afon Conwy and Afon Eidda. On more acidic soils, moorlands with acid grasslands dominated by mat grass (*Nardus stricta*) and heath grass (*Danthonia decumbens*) appear to have been interspersed with heaths in which heather (*Calluna vulgaris*), bilberry (*Vaccinium myrtillus*) and crowberry (*Empetrum nigrum*) were important species. These, as today, would have typically formed on acidic rhyolite lavas and tuffs.

Birch forest
By about 9,500 years BP, Snowdonia entered a relatively warm and dry era known as the Boreal Period, in which birch woodland rapidly became established over much of the lowland and semi-upland areas. Juniper, on the other hand, because of its inability to tolerate shade, went into rapid decline. Only on high ground, in conditions too harsh for birch to grow properly, were juniper and other low-growing species able to compete.

In the lowlands around Llyn Cororion for example, birch and willow dominated the vegetation for the next 500 years or so, but persistence of certain members of the rose family (*Rosaceae*), the cabbage family (*Brassicaceae*), plantain and mugwort (*Artemisia* sp.), shows that the density of the canopy varied, and mountain ash (*Sorbus aucuparia*) was able to occupy some of the more open areas. Nevertheless, over this period, there was an increase in the frequency of understorey ferns, such as hard fern (*Blechnum spicant*), lady fern (*Athyrium filix-femina*), polypody (*Polypodium* sp.) and various *Dryopteris* sp.

Hazel forest
By about 9,300 years BP, the climate had become sufficiently warm for hazel to start invading the birch woodland around Llyn Cororion and Nant Ffrancon and, over the next 1,000 years or so, to assume a dominant or co-dominant role over much of Snowdonia. In the upland forests around Cwm Cywion and Llyn Llydaw, hazel colonisation was somewhat later, about 8,350 years BP, and was accompanied by the spread of bog myrtle (*Myrica gale*), a species of *Prunus* (possibly blackthorn or bird cherry), a species of *Sorbus* (possibly wild service tree, *S. torminalis*) and a variety of ferns.

Oak forest
Oak woodland, composed largely of sessile oak (*Quercus petraea*), became the dominant woodland throughout lowland areas of Snowdonia from about 8,660 years BP onwards; within 500 years or so it had spread into upland areas, forming dense forests as high as Llyn Llydaw at 440m above sea level. It also eventually reached Cwm Cywion, at a height of 600m, but seems to have been close to its altitudinal limit and never produced closed forest at this height. At lower altitudes, sessile oak, probably mixed with some peduculate oak (*Q. robur*), formed the basis of the first truly-mixed deciduous forest to develop in the post-
glacial period, and eventually included elm (*Ulmus* sp.), small-leaved lime (*Tilia cordata*), ash (*Fraxinus excelsior*) and alder (*Alnus* sp.). Birch and hazel, on the other hand, declined over this period as oak and other tree species came to dominate the more fertile soils. Ground layer species in these primordial oak forests included common cow-wheat (*Melampyrum pratense*) and bracken (*Pteridium aquilinum*), both of which are typical of today’s ground floras, and sessile oak continues to be the main tree in much of today’s woodlands.

**Pine forest**
The only pine native to Britain today is Scots pine (*Pinus sylvestris*) but, as its name suggests, it probably only occurs naturally in northern Britain; especially in the ancient Caledonian forests of Scotland. There was a brief period after the Ice Age, however, when conditions were suitable for it to become locally dominant in more southerly parts of Britain. The spread of pine forest (assumed to be Scots pine) in Snowdonia seems to have occurred during a prolonged dry period. However, most of these forests appear to have been restricted to marginal areas, such as dried out peat bogs and lake margins, especially in lowland situations. For example, sometime after about 8,400 years BP in the area around Llyn Cororion, pine started to rapidly expand at the expense of both oak and elm, and there was a contemporary decline in the amount of willow and fen herbs. For a period of about 700 years pine continued to be the dominant tree in the area surrounding the lake.

In other lowland areas, such as Nant Ffrancon, pine became a more important component of the mixed forests, and by about 8,000 years BP, it had become established in some upland sites. During this dry period, it would have been much more able to tolerate the effects of altitude and exposure than any deciduous tree, and in Cwm Cywion it became the main tree species for a while. But even around lake margins its dominance appears to have been fairly sporadic. For example, it never appears to have become the main forest forming species around Llyn Llydaw, whereas in Cwm Idwal it became temporarily dominant over alder and birch during this period.

**Alder and upland mixed deciduous forest**
About 7,750 years BP, the climate moved into the warmer and wetter Atlantic period causing further changes to the vegetation. Evidence from Llyn Cororion shows that pine declined and, for the first time in the post-glacial period, alder and willow became prominent species. In Nant Ffrancon, it seems that alder was particularly abundant, becoming dominant along the shores of the former ‘Llyn Ffrancon’. It also became the main tree species in Cwm Idwal. Even now, the almost unaltered remains of these ancient alder trees are sometimes revealed when sub-surface layers of peat are exposed by erosion.

Away from the lake margins, oak continued to maintain its dominance but, as the climate continued to improve, alder was able to extend its range into the uplands and, by about 6,000 years BP, it had managed to colonise the lake margins of Cywion and Llyn Llydaw. Pine forests, on the other hand, started to disappear from the uplands and, as these mild conditions continued, a mixed deciduous forest of oak, hazel, birch with some ash and small-leaved lime became established in the area around Llyn Llydaw. These forests eventually reached higher altitudes where they thinned out to form scrub and, around Cwm Cywion, for example, included small amounts of elm; but in general they were less diverse than the forests around Llyn Llydaw.

While climate must have been an important influence on the spread of alder, it was also probably facilitated by the activities of beaver and Mesolithic man (see below). Beaver was
once a common feature of Snowdonia’s waterways, and according to a well-known folk tale, its damming operations used to cause serious flooding on the River Conwy. However, it was early hunted to extinction because of its valuable fur and, even by the 10th century, it was regarded as rare.

The start of human influence in Snowdonia
Man probably first started to re-colonise Snowdonia from about 8,000 years BP, during the Mesolithic period, when much of the vegetation, especially in the uplands, was dominated by mixed birch-pine woodlands. Initially, human colonists had little impact on the ecosystem. The forests and forest edges provided a rich supply of potential prey species, including aurochs, reindeer, elk, horse, wild boar, roe and red deer, with the latter two becoming more important as the broadleaved woodland developed. It is likely that browsing and debarking exerted some local control on forest development and management of herbivores would have caused some alteration to the composition and structure of the forest. Man also encouraged the development of open areas by burning the forest edges so as to increase the area of land suitable for browsing animals. This also promoted the spread of hazel, whose nuts appear to have been an important food source at that time. Evidence from the Moel y Gerddi valley near Harlech suggests that Mesolithic woodland clearance during this wet period may also have facilitated the spread of alder. Nevertheless, during the late Mesolithic period, the woodlands of Snowdonia became more extensive than at any other time during the Holocene Period, especially at lower elevations. Settlements were, therefore, often confined to upland locations such as Erw-wen and Moel y Gerddi in upland Ardudwy.

The decline of elm and the impact of Neolithic people
It has now been established that elm went into widespread decline from about 5,000 years BP onwards, and was certainly starting to disappear from areas around Llyn Cororion, Nant Ffrancon and Llyn Llydaw at about this time. At Llyn Cororion, its demise was associated with a sharp reduction in the numbers of small-leaved lime trees, and a temporary decline in oak, whereas Llyn Llydaw saw an influx of open habitat plants, such as heather (\textit{Calluna vulgaris}), grasses and sedges, indicating the development of extensive heathland and grassland communities.

Interpretation of these changes are confounded by the apparent coincidence of climatic and anthropogenic effects, since 5,000 years BP roughly marks the start of the so-called Sub-boreal Period, when the climate went through a time of increased dryness and became more continental in character. This coincided with the brief appearance of hornbeam (\textit{Carpinus betulus}) in Cwm Idwal, a species more characteristic of continental Europe and mainly confined to the south-east of Britain today. This point in time also marks the start of the Neolithic Period, when farming became much more widespread. Initially, this mainly involved a form of shifting cultivation in which forests were cleared locally and, for several years, crops were grown in the clearings.

One of the theories as to why elm went into decline over this period speculates that, as soil fertility in the man-made clearings declined and family units moved on, the clearings were occupied by rapidly colonising species such as ash, hazel, lime and oak rather than elm. However, these early farmers also kept primitive livestock and it has been suggested that elm leaves may have been preferentially gathered as animal feed. Others have argued that, because the loss of elm occurred simultaneously over large parts of Europe - even in...
areas not known to have been colonised by Neolithic peoples e.g. northern Scotland - its decline must have been induced by climatic factors with colder winters possibly affecting flower production. Yet another theory suggests the decline may have been caused by an outbreak of Dutch elm disease (Rackham 1980).

Also at about this time, many of the upland blanket peat bogs in Britain started to form, partly due to climate change and a gradual impoverishment of soils as nutrients were leached out. This was especially prevalent on the igneous rocks of the uplands where podsolization was accompanied by descending tree lines, the expansion of acid grasslands and the development of blanket bog communities. However, studies of peat deposits close to the Neolithic remains of Carneddau Hengwn, north of Barmouth (Moore 1973), suggest that these peat accumulations were hastened by early woodland clearance, especially of alder. The peat deposits frequently contain wood remains in their basal layers, but the overlying layers usually include the remains of typical acid bog plants, such as cotton-grass (*Eriophorum*) and *Sphagnum* moss. Repeated canopy clearance, firing and stock grazing would have accelerated the demise of the original damp woodland and, by removing the trees, the rate at which moisture could be lost through evaporation and transpiration would have been reduced. Any prolonged waterlogging of the soils would then have encouraged the development of acid bogs. The situation deteriorated even further some 2,500 years BP when the climate became wetter and cooler, causing further waterlogging and leaching of exposed soils.

THE CONTINUING INFLUENCE OF HUMANS

Over the centuries, people and their animals continued to make inroads into the forests of Snowdonia. Trees were felled to provide fuel and constructional timber as well as to create open areas for grazing and arable lands. But, because browsing by domestic livestock, particularly goats and sheep, can seriously retard or prevent woodland regeneration, their access alone would have been sufficient to cause further loss of woodland. Both the Roman and Anglo-Norman invaders drove roads through the forests and maintained wide clearings on either side to reduce the dangers of ambush, but it was probably not until the 12th century that clearance became more systematic. For example, at about this time there was a major decline in all tree and shrub taxa around Llyn Cororion, and this coincided with the sudden appearance of hemp (*Cannabis sativa*). It was probably being cultivated to produce coarse textiles, and the amount of pollen found, suggests that this was one of the most important sites in Wales for hemp production at that time. The plant is also sown as a source of marijuana, but very little narcotic substance is produced in cold climates.

The forests continued to be cleared and, by the reign of Elizabeth I, we know that many great oaks from the forests of Snowdonia were being floated downstream on the River Conwy from Trefriw. Despite this, the oak forests of Snowdonia were still abundant when John Leland explored the area between 1536 and 1539 (Toulmin Smith, 1906). He described the heights of the main range (Craig Eryri) as being forested, but the ‘best’ woods were to be found in the Lledr and Llugwy valleys (especially by Capel Curig) and at Llanberis. ‘Meatly good woods’ were also to be seen in the Machno Valley and around Coetmor and Coed y parc near Bethesda. He also states that, apart from small quantities of oats and barley and ‘scantly rye’ there was little cultivation of crops on hill farms, because of foraging deer. Deer were not eradicated from Snowdonia until about 1626.

Between 1754-60 large numbers of oaks continued to be extracted to the extent that much of the Gwydyr Estate near Betws-y-Coed appears to have been denuded of oak by
that time (Davies, 1813). By the 18th and early 19th centuries a growth in demand for timber by the local boat-building industry of North Wales further exacerbated the situation, and by the end of the 18th century there appears to have been very little natural woodland remaining in Snowdonia.

During the 16th century, as the trade in Welsh cattle and cloth for English markets increased, large areas of alder and reedbed were cleared and subsequently drained to create additional hay meadows for winter feeding. Such developments occurred in the valleys of the Conwy and Gyffin, and around Penmachno and Dolwyddelan. The common occurrence of the word Gwern - the Welsh word for alder swamp - in field names in Snowdonia, gives an indication of the former extent of these alder swamps. During this period, and up until the early part of the 19th century, cattle were moved to grazing grounds in the uplands during summer, and then returned to the shelter of lowland pastures during winter. However, towards the latter part of the 17th century the growing importance of the woollen industry led to an increase in sheep farming at the expense of cattle (Hughes et al., 1973).

Today, most of the uplands of Snowdonia are grazed by sheep, whilst the less numerous cattle tend to be confined to the lower slopes. In fact, grazing by sheep is probably the single most important factor affecting upland vegetation, and there are now up to 25 times more sheep in some areas than there were during the mediaeval period (Hughes et al., 1976), resulting in a reduction in the diversity and range of plant communities and the restriction of most herbs and arctic-alpines to crags inaccessible to grazing animals. In the absence of sheep, the vegetation would be very different. This was clearly demonstrated when a series of sheep exclosures were established in Cwm Idwal, Pen y pass, Moel Eilio, Llyn Llydaw and Crib Coch between 1957 and 1968 (Hill et al., 1992). When these were examined some 25 years later, much of the acid grassland, dominated by mat grass (Nardus stricta), had developed into heathland with both heather (Calluna vulgaris) and bell heather (Erica cinerea), whilst grasses, such as purple moor-grass (Molinia caerulea) and wavy hair-grass (Deschampsia flexuosa) had become much more abundant, often at the expense of mat grass and sheep’s fescue (Festuca ovina). In less acidic grasslands, characterised by common bent (Agrostis capillaris), there was less of a tendency for any one or two species to become dominant - a feature attributed to the disturbance caused by the large numbers of voles that inhabit these grasslands. On wetter soils, species such as cotton grasses (Eriophorum sp.) and bog asphodel (Narthecium ossifragum) were able to grow and flower far more than in the heavily grazed grasslands. Apart from a few mountain ash and birch, trees have not yet managed to colonise these experimental plots, but on other larger areas of mountain pasture that have been free from grazing for many years, the heathland communities that initially developed have now been colonised by various trees including birch, hawthorn and mountain ash. On the open hills, the natural succession to scrub and open woodland is likely to be slow due to the relative scarcity of seed sources.

In addition to sheep, there is also a small feral goat population in Snowdonia, which is thought to be the remnant of a herd that was introduced during the Neolithic period and, therefore, considered to be worth preserving. However, they are responsible for a certain amount of ecological damage within the Park and have been blamed for preventing regeneration of the Wildlife Trust woodland reserve at Coed Dolbebin (Brown, 1981). In the Rhinogs, they principally feed on heather during the summer and gorse during the winter, but their diet also includes a large variety of other species including bracken, bog myrtle, oak, holly and ivy. Therefore, if their population size increases (which appears to be
happening now possibly due to the series of mild winters, which reduces kid mortality),
they could have a major impact on both the remaining woodlands and the heathlands
of Snowdonia. There is also concern at their potential effects on important tall-herb and
arctic-alpine ledge and crevice vegetation as they are more agile than sheep and can access
a number of these otherwise ungrazed situations.

General degradation of heaths and blanket bog occurred throughout the twentieth
century due to overgrazing, burning, drainage and afforestation, often resulting in their
replacement by acid grassland and purple moorgrass-dominated communities. Montane
Racomitrium heaths, which reach their southern British limit in Snowdonia, have been
severely damaged in the past 50 years (Turner, 1993) by overgrazing, trampling damage by
walkers and, possibly, the effects of acid rain (Edwards et al., 1990). Open waters have
suffered from acidification, and also from nutrient enrichment, affecting their ability to
support their characteristic plant communities.

Tree planting and introduced species
Contrary to popular belief, tree planting in Snowdonia was not restricted to the 20th
century. Large numbers of trees were planted in the parishes of Ysbyty and Penmachno
between 1795-97 (Davies, 1813), and the ash trees of Nant Gwynant are thought to be the
remnants of an 1804 plantation. However, following the founding of the Forestry
Commission in 1920, large areas of Snowdonia were converted to conifer plantations,
including stands of Douglas fir (Pseudotsuga menziesii), Japanese larch (Larix leptolepis),
lodgepole pine (Pinus contorta), Sitka spruce (Picea sitchensis), western hemlock (Tsuga
heterophylla), and western red cedar (Thuja plicata). The usual practice is to plant pine on the
higher and drier ground, spruce in the hollows and bogs, with larch and Douglas fir on the
better-drained slopes. Today there are over 22,670 ha of mature conifer plantation as
compared with just 6490 ha of broadleaved woodland. The plantations are spread
throughout the National Park, with over 300 stands, and have a huge impact on its
landscape. In addition, rhododendron (Rhododendron ponticum), which was brought in for
amenity planting during the 19th century, has spread to become a serious pest, threatening
native woodlands in many parts of Snowdonia.

Quarrying and mining
Exploitation of Snowdonia’s mineral riches can be traced back over 4,000 years to the
Neolithic axe factories, such as Craig Llwyd (Penmaenmawr), and certain early settlers,
including the Romans, may have been enticed to North Wales because of its mineral wealth
(Jenkins, 1989). Exploitation of Snowdonia’s natural resources, including arsenic, copper,
gold, iron, lead, manganese, sulphur, zinc, igneous rocks and slate, continued intermittently
over the centuries, eventually to reach a peak during the industrial revolution of the late
18th, 19th and early 20th centuries. These industries have since declined, but their legacy
in the form of many spoil-heaps, quarries, mines and old workings remain. Some of these
are major landscape features and could be regarded as unsightly. However, despite being
classed as derelict land they often provide habitat for rare plants, and some are now deemed
to be of major conservation interest.

The, normally toxic, waste tips left over from heavy metal extraction, such as copper,
lead and zinc provide a habitat for various so-called metaliferous species that are able to
tolerate such conditions. The lead and zinc waste tips in the Gwydyr Forest around
Coedmawr, for example, are some of the few sites in Snowdonia where the rare alpine pennycress (*Thlaspi caerulescens*) and 'lead-loving' moss *Ditrichum plumbicola* can be seen. Other species, such as forked spleenwort (*Asplenium septentrionale*) and the lichen *Stereocaulon vesuvianum* also thrive in these situations. Copper waste does not support many notable species in Snowdonia, but the uncommon lichen *Stereocaulon leucophaeopsis* has been recorded on copper-rich rocks near Snowdon, and the old Turf Copper Mine at Dolfrwynog in Coed-y-Brenin provides an unlikely setting for sea campion (*Silene uniflora*) and sea thrift (*Armeria maritima*). Prior to the exploitation of heavy metals, the above mentioned metaliferous plants were restricted to natural outcrops of metal rich ores and would have helped early miners to locate such sites.

**CONCLUSIONS**

Over the past 12,000 years, Snowdonia's landscape has moved from being completely dominated by physical processes, through one dominated by natural ecological processes, to one that has been greatly influenced by human activities. Nevertheless, over the past 10,000 years or so, plant life has made up much of the visible landscape and, today, includes a complex tapestry of vegetation types. The dominance of short grazed grassland communities in the uplands (due to heavy grazing pressures) is, however, unnatural and reduces the potentially wide diversity of vegetation that would otherwise characterise the area. Other concerns include recreation pressure, the possible effects of climate change, which could threaten the arctic-alpine communities if temperatures rose, and the ever-present threat of acidification. Despite all this, Snowdonia is still one of Britain's most important areas for plants, and other wildlife, and much of the area is of outstanding conservation interest, with some ninety Sites of Special Scientific Interest and sixteen National Nature Reserves. In addition, various habitats including alpine and sub-alpine heaths, alpine and boreal grasslands, acidic screes and rock crevice vegetation, oceanic woodlands and lakes are now recognised to be of international importance. Such recognition has resulted in improved measures to conserve and restore damaged habitats, including agri-environment schemes and biodiversity action plans for habitats and species. It is unlikely that Snowdonia could ever be returned to its natural state, but there is much scope for restoring the area's natural and semi-natural habitats. One recent positive development has been the removal of sheep from Cwm Idwal and, although it will take many years for the natural vegetation to be fully restored, this will, hopefully, be much appreciated by future generations.

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**REFERENCES**


