

Community Ecology & Conservation

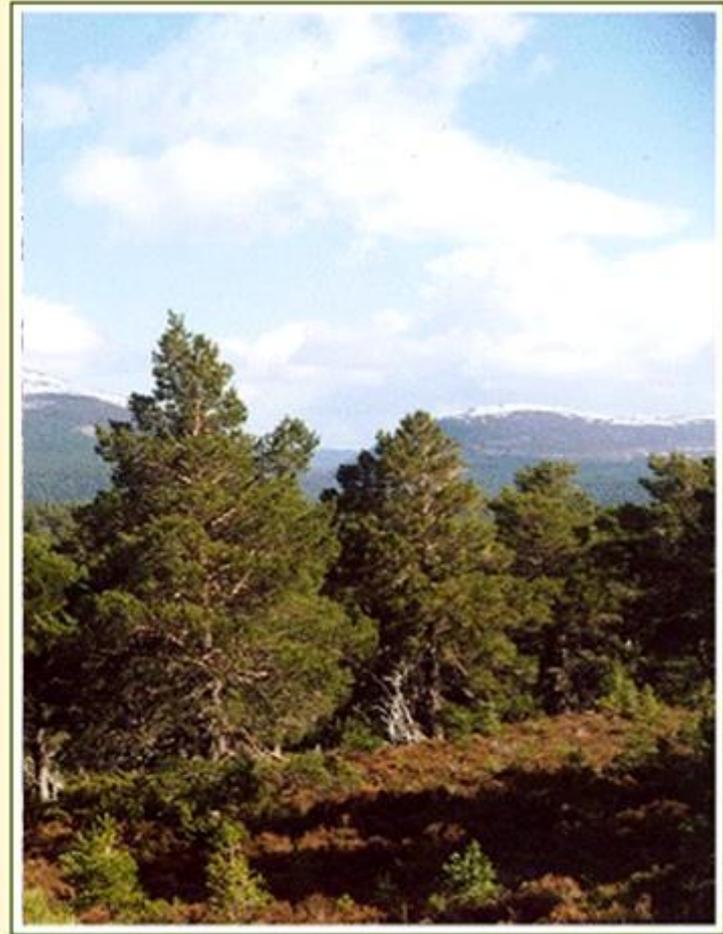
SCOTTISH PINEWOODS, some points to consider



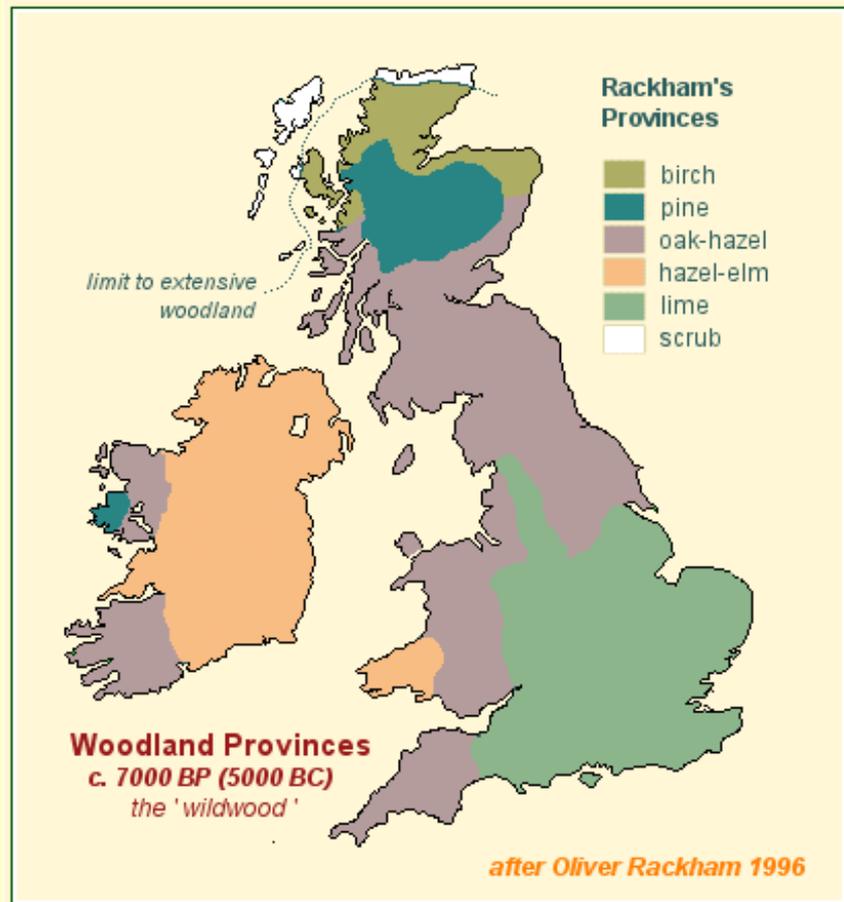
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SCOTTISH PINWOODS, some points to consider

However, before looking specifically at the native Pine Forests of the Highlands, it is instructive to consider too deciduous woodlands and their relationship across the British Isles and with coniferous forest both latitudinally and altitudinally.



WOODLAND relationships in the British Isles



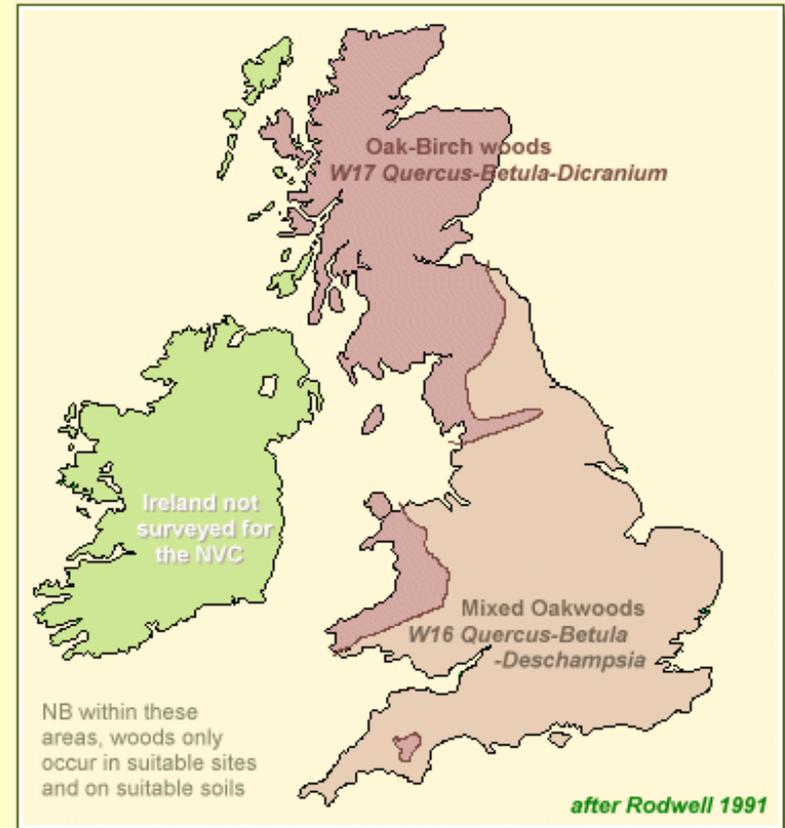
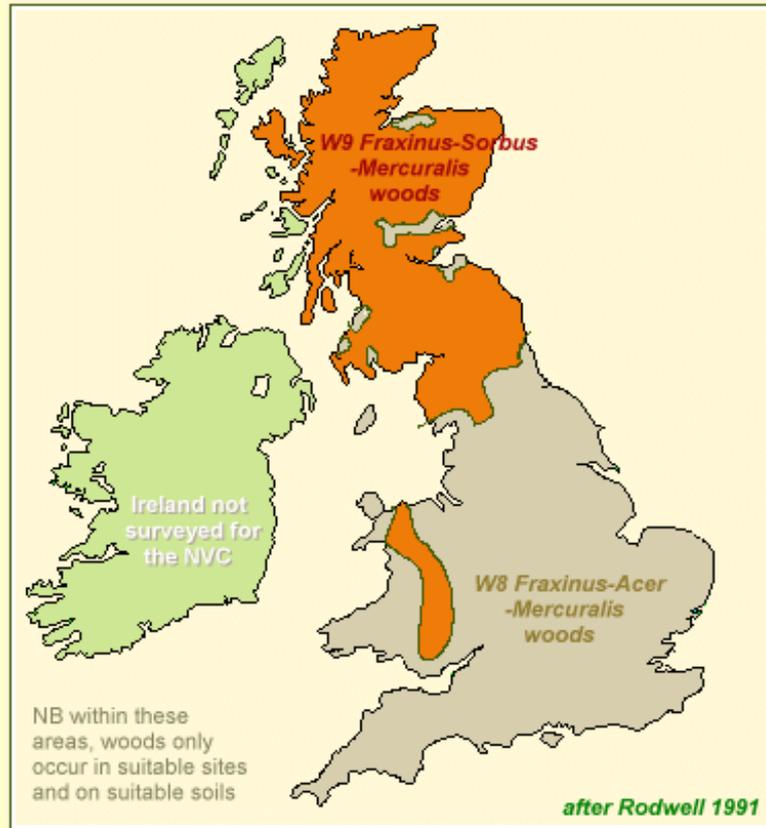
FORMER EXTENT

Everywhere in the British Isles where tree growth is not precluded by local ecological conditions, or by the altitudinal tree line the native vegetation cover would have been some form of mixed deciduous or coniferous forest.

DECIDUOUS FORESTS: SOURCES OF VARIATION

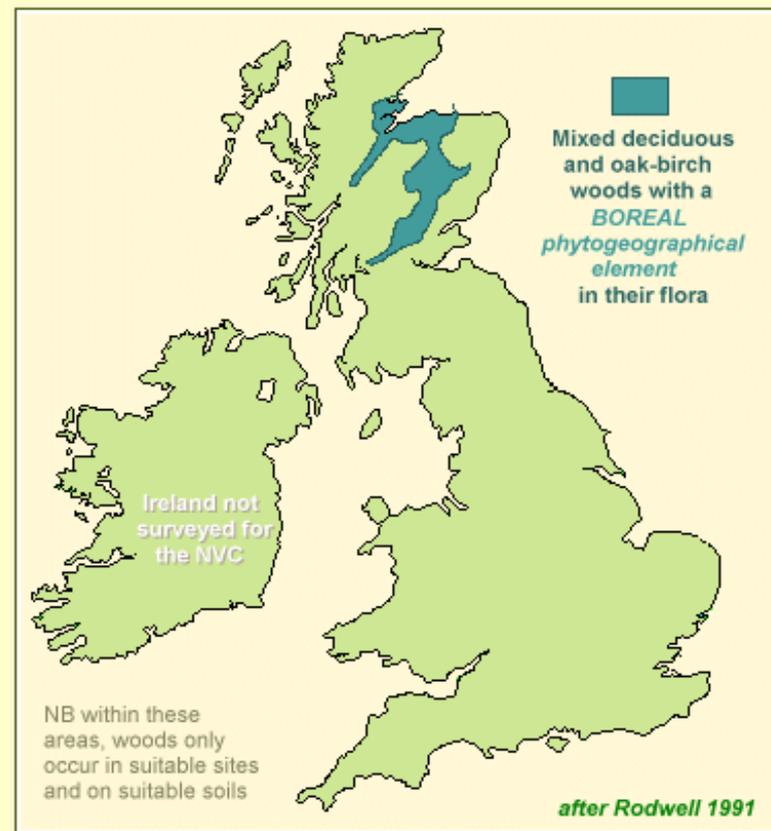
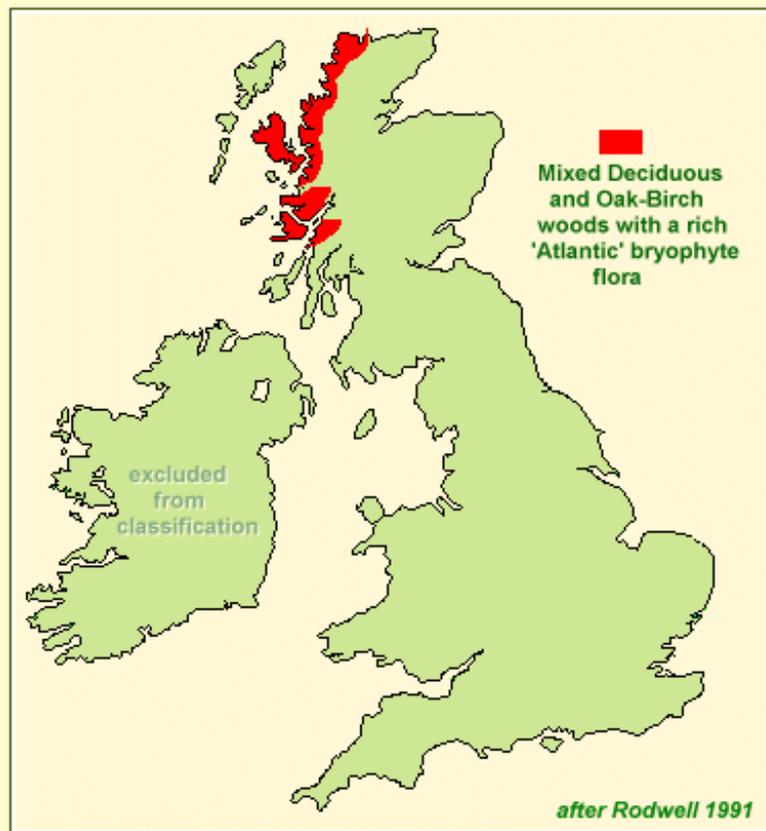
- Show two axes of variation, both are complex
 - **Geographical**, largely climatically determined
 - **Edaphic**, controlled by soil characteristics and drainage
- Both find expression in the floristic composition of the tree canopy, and the field layer or ground flora
- There is also an **historical** dimension to the geographical axis reflecting post-glacial or Holocene vegetation history

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- Geographical community pairs reflecting climatic trends and soil types

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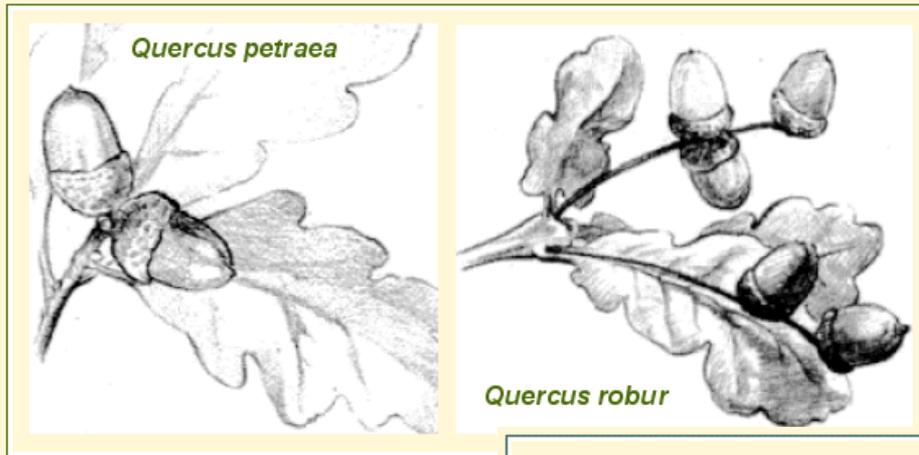
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- The second axis although explicable in terms of soil and drainage ...

		SOIL TYPE		
		<i>Calcaric and Eutric Cambisols</i>	<i>Dystric Cambisols and Luvisols</i>	<i>Leptosols Umbrisols and Podzols</i>
CLIMATE	<i>Cool & Wet Northwest Sub-Montane Zone</i>	<i>Fraxinus Sorbus Mercurialis</i> woodland	<i>Quercus Betula Oxalis</i> woodland	<i>Quercus Betula Dicranium</i> woodland
	<i>Warm & Dry Southeast Lowland Zone</i>	<i>Fraxinus Acer Mercurialis</i> woodland	<i>Quercus Pteridium Rubus</i> woodland	<i>Quercus Betula Deschampsia</i> woodland

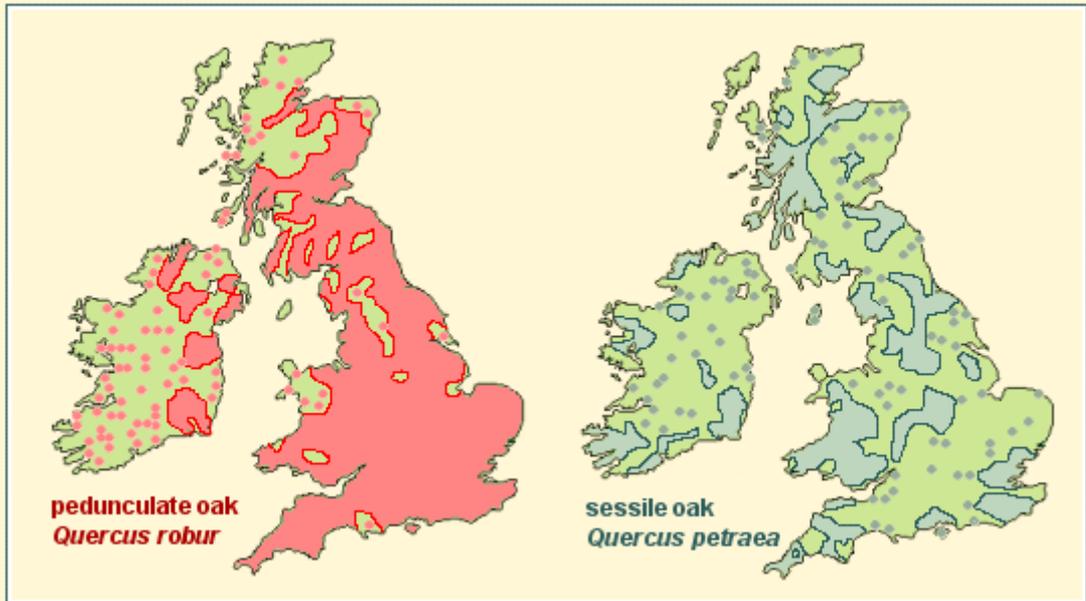
- can also be interpreted in terms of genetics and geneecology

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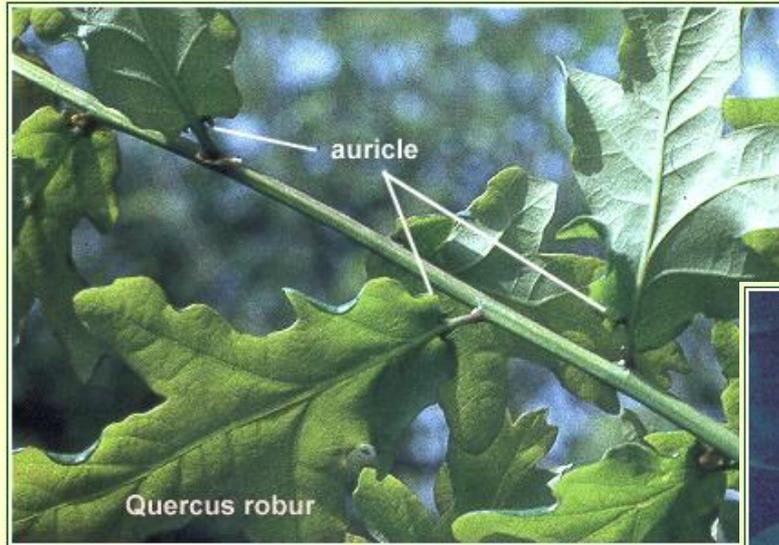


This genetic dimension to the **edaphic axis** is evident with the two species of oak preferring different sets of ecological conditions

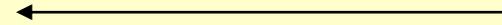
These species are the common or **pedunculate oak**, *Quercus robur*, of the heavier soils of the south east lowlands and the **sessile oak**, *Quercus petraea* of the more acid and freely draining soils of the north and west



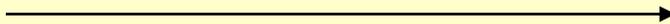
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- heavier soils of south and east



- acid soils of north and west



For this reason the oakwoods that occupy the valleys and straths in the Highlands are largely comprised of the sessile oak, *Quercus petraea*

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an **historical** dimension to the geographical axis reflects post-glacial or **Holocene** vegetation history, but has to be seen in the context of the place of trees and forest communities in the **Quaternary**

- pre-Quaternary northern hemisphere mid-latitude mixed forests

this circumglobal forest containing both deciduous, evergreen and coniferous species was progressively reorganised by the retreats, expansions and extinctions it suffered during the Quaternary

- Quaternary Temperate Stages:

these saw the re-establishment and retreat of climax forests by a complex interaction between vegetation migration driven by interglacial and interstadial climatic cycles and processes of ecological succession under ameliorating or deteriorating climates. The outcomes of these processes differed in each Interglacial and Interstadial

- the Holocene as an incomplete interglacial

the accepted wisdom is that the Holocene is an Interglacial cycle currently a little into the post-optimal part of the climatic cycle (though profoundly altered in its trajectory by the presence of man)

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an **historical** dimension to the geographical axis reflects post-glacial or Holocene vegetation history

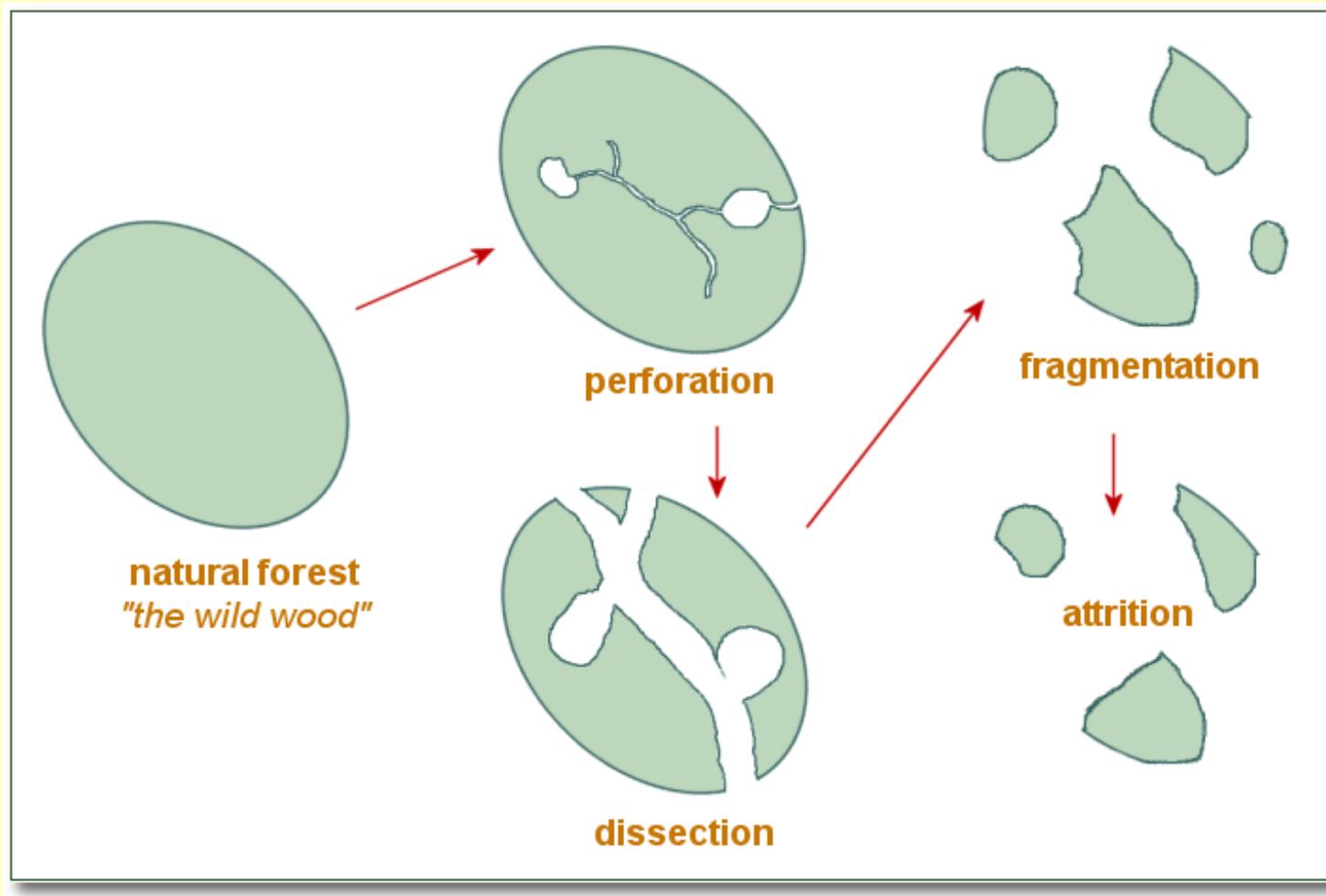
- the **late Devensian** precedes the opening of the **Holocene** as an interstadial wooded interval culminating in birchwood and scrub except in the extreme south where pine probably dominated. Following the final cold phase (**Loch Lomond Stadial**), climate amelioration and forest community assembly eventually led to the climatic optimum and an assembled climax forest (?). The question mark highlights the uncertainty that exists as to whether this process was completed or was altered by human intervention.
- the reasons for changes in Holocene forest composition may be climatic and environmental change as causal factors and/or anthropogenic factors and other causal factors during **the Neolithic, Bronze and Iron ages** through forest clearance and replacement
- if the latter is the case, as the evidence would suggest, the observed pattern of British forests and woodland has been effected profoundly by anthropogenic interference. Additionally, forest clearance has influenced the extension of what would have been non-climax open habitat vegetation like heath, grass and wetland during the Holocene

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Former extent of Forest of all types is now much reduced and the 'Wildwood' survives only as a legacy of fragmented remnants

- For Pine there has been some retreat from high altitudes and high latitudes which is apparently natural
- The remainder of the reduction in the extent of Pine is **anthropogenic** and is intimately associated with the **history of the Highlands**
- In the lowlands, in England, Wales, lowland Scotland and Ireland, deciduous forest underwent a longer and more complex process of reduction in area
- Here *George Peterken* recognises four stages, **perforation**, **dissection**, **shrinkage** and **attrition**
- Although more applicable to lowland England and Scotland these four stages also have some relevance to the **contraction of native Pine forest**

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- In the case of **PINE** the main periods of contraction occurred for the most part later than in the lowlands, while, their former geographical and ecological range is believed to be preserved in the distribution of surviving remnants
- However, doubts exist as to how natural the characteristics of these surviving pinewoods really are
 - a. uniformity of present field layer
 - b. pure PINE canopies and poorly developed shrub layer
 - c. lack of regeneration within existing remnants
 - d. the age structure of the tree populations of existing woods
 - e. apparent spatial dynamics of surviving patches
- Relationships with other woodland and shrub communities are still unclear

So **PINEWOODS POSE PROBLEMS** for **MANAGEMENT**

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- **Deciduous Woodlands** too probably preserve something close to the original geographical and ecological variation of the postglacial wildwood. though this is apparent in the nature of the **underwood** rather than the current **canopy**
- Indeed, the degree of departure, both in specific composition and in structural characteristics from any original climax forest ecosystem is probably greater in the mixed deciduous woodland remnants (ancient woodlands) than it is in native pinewoods

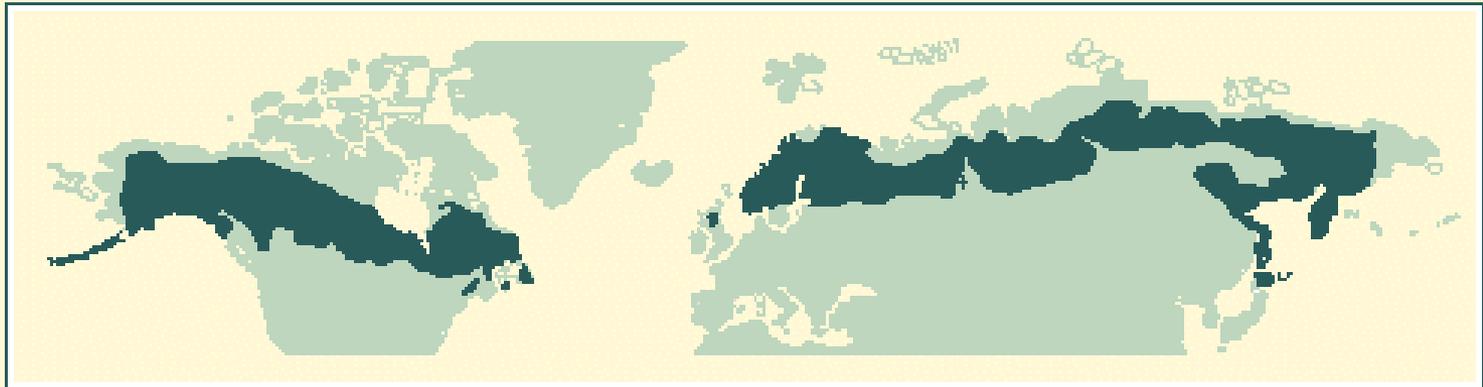
So **DECIDUOUS WOODLANDS** also **POSE PROBLEMS** for **MANAGEMENT**

- Nonetheless, both **native pinewoods**, and **ancient deciduous woods** provide habitats for several important species of plant and animal which are either restricted to them, or are rare in other habitats, and are of considerable interest in their own right

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SCOTTISH PINWOODS, some points to consider

The pine woodlands of the Scottish Highlands as a climax forest ecosystem must be considered as part of the Eurasian formation of **Northern Coniferous Forest**, or **Boreal Forest**. In Scandinavia the dominant tree of this formation, as far north as Lapland is the Norway spruce, *Picea abies*. Further north in Norwegian and Finnish Lapland this species is replaced by forests of pine, *Pinus sylvestris*, and then by birch, *Betula tortuosa*. The spruce, however, did not re-enter the British Isles in the **Flandrian**.

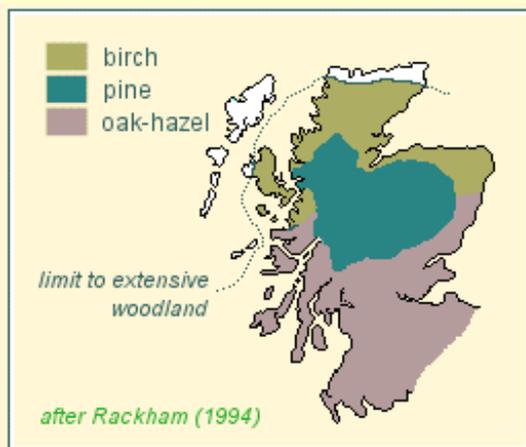


Distribution of Boreal Forest after Tamm (1976), Vasari (1977), and Pruitt (1978)

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SCOTTISH PINWOODS, some points to consider

- In the Highlands **Pine** appears to occupy an oceanic **ecotone** position relative to Boreal Forest or Taiga and transitional to **Oak** and or **Birch**



- Pine also occupies a considerable range of environmental variability within the highlands: **climatic, topographical, edaphic, latitudinal / altitudinal**

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In the early post-glacial, the **Pre-Boreal** and **Boreal**, forests of birch and pine spread across the country and invaded the uplands and highlands.

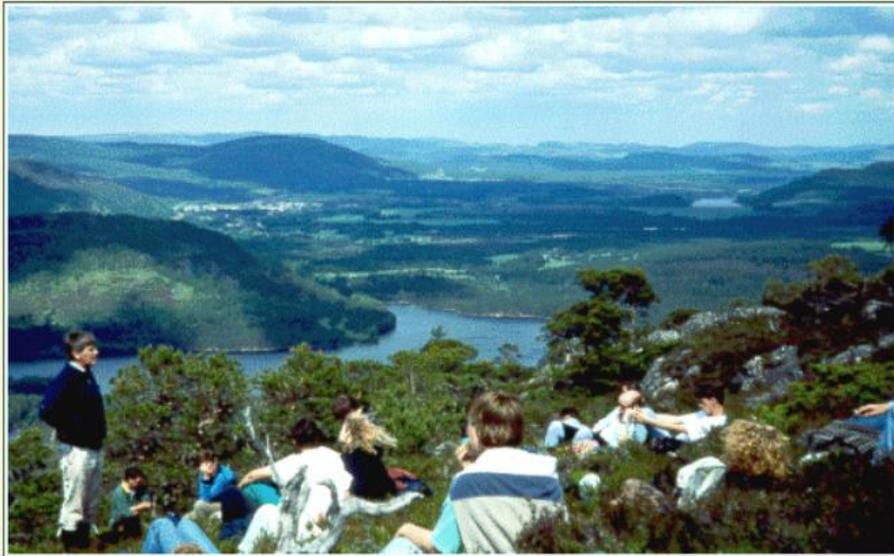
Towards the end of the Boreal and into the succeeding **Atlantic** (the climatic optimum) these trees were replaced in the south by a forest of oak, elm, and lime, which in turn extended northwards into the valleys and straths of upland Britain.

At the post glacial climatic optimum the woodlands of the Highlands form an extreme western, and hence highly maritime (high oceanicity) extension of the west European transition or *ecotone* from **Temperate Deciduous (Summer) Forest**, through **Boreal Coniferous Forest**, to **Boreal Deciduous Forest**.

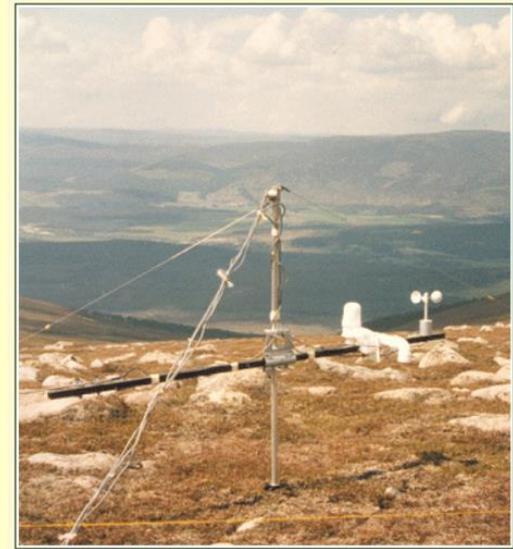
The latter was dominated by *Betula pubescens ssp. odorata*, believed to be the same variety of the birch as the Scandinavian *Betula tortuosa*.

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The traditional picture that emerges of the potential natural woodlands of the Highlands is one of **oak woodlands** flooring the valleys and glens up to perhaps 150m to 200m. Here on the mountain slopes, particularly in the east and central Highlands, they gave way to **forests of pine** which reached altitudes of over 700m, wherever soils and exposure permitted (the highest natural pines today are at 603m on Creag Fhiaclach in Glen Feshie in the Cairngorms). In the far north and west pine gave way to native birch woodland and scrub

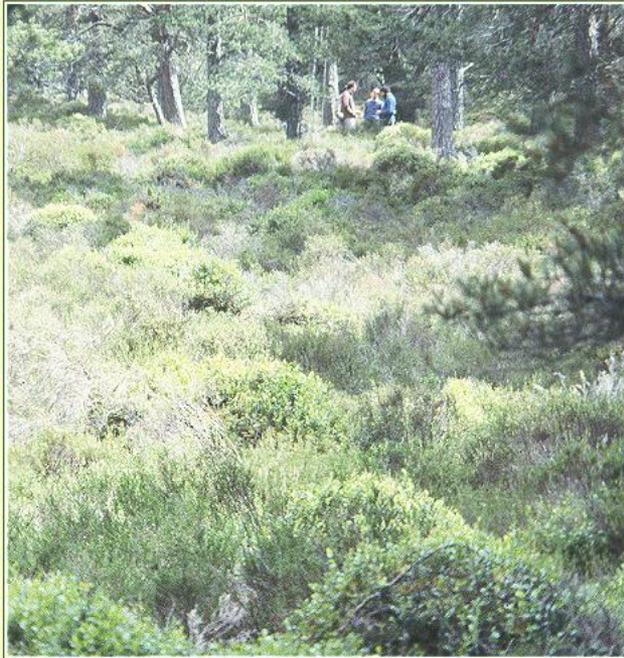


Pinus sylvestris: High climbing pines on the slopes of Creag Fhiaclach, Glen Feshie, Scotland. The pines here have become stunted in their growth, are often contorted or semi prostrate, while erect stems display a flag form or krummholz growth habit.



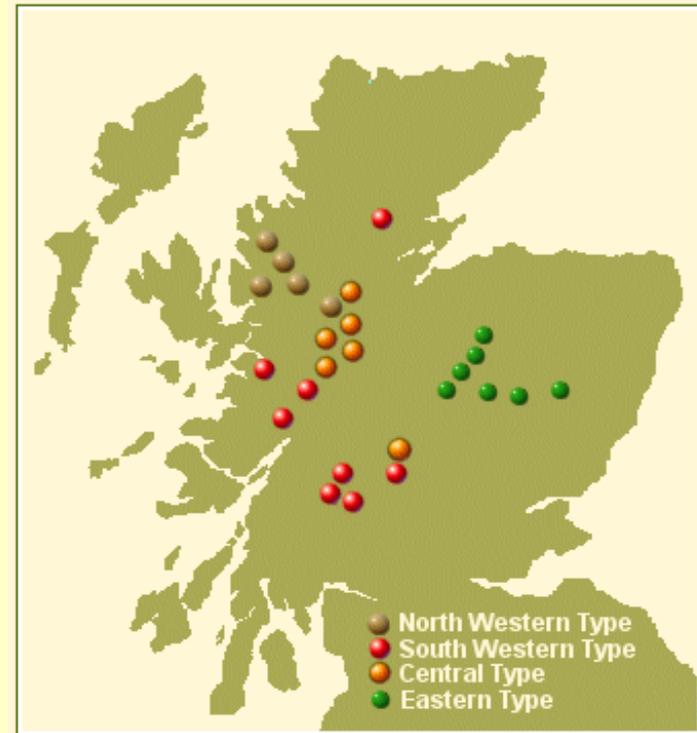
Climatic Limit of Pine: automatic weather station established above the treeline by John Grace to monitor the environment for tree growth at and beyond the potential natural treeline as preserved on Creag Fhiaclach, below and to the right

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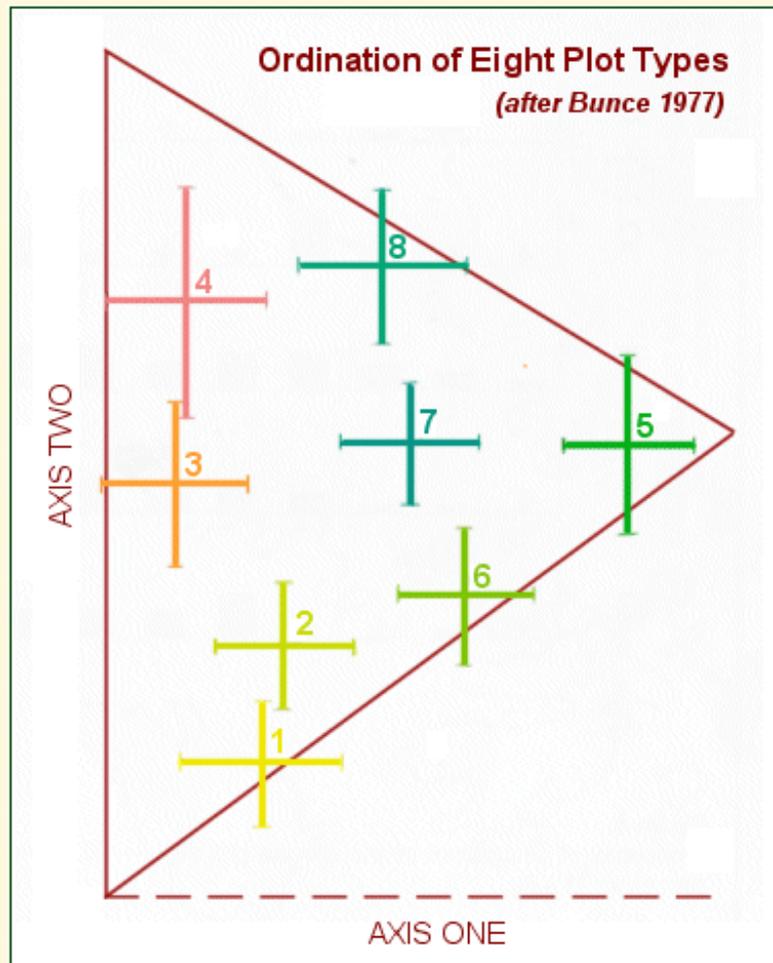


Here today's remnants of pinewoods are shown as the four distinct geographical types of pinewood into which they fall

SCOTTISH PINEWOODS,
some points to consider



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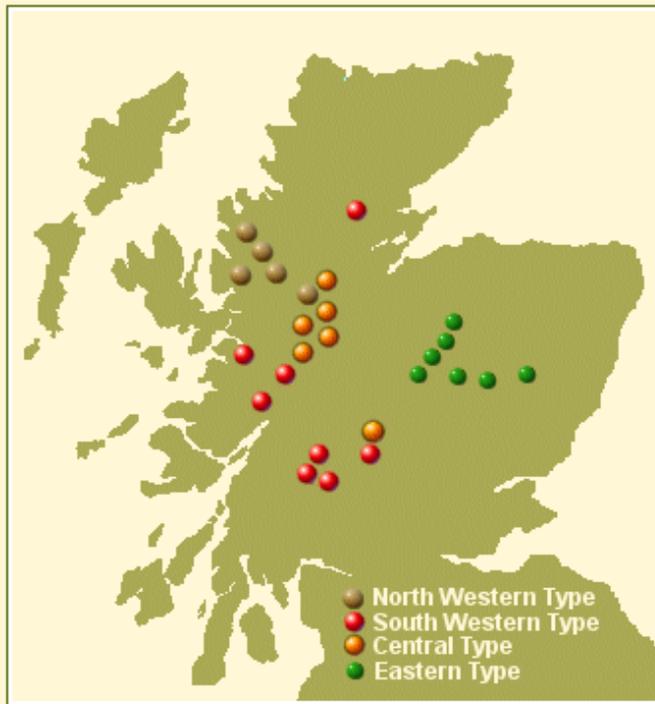
Here eight distinct pine plant communities (plot types) are placed relative to two axes:

axis one is a moisture or drainage axis from dry to wet.

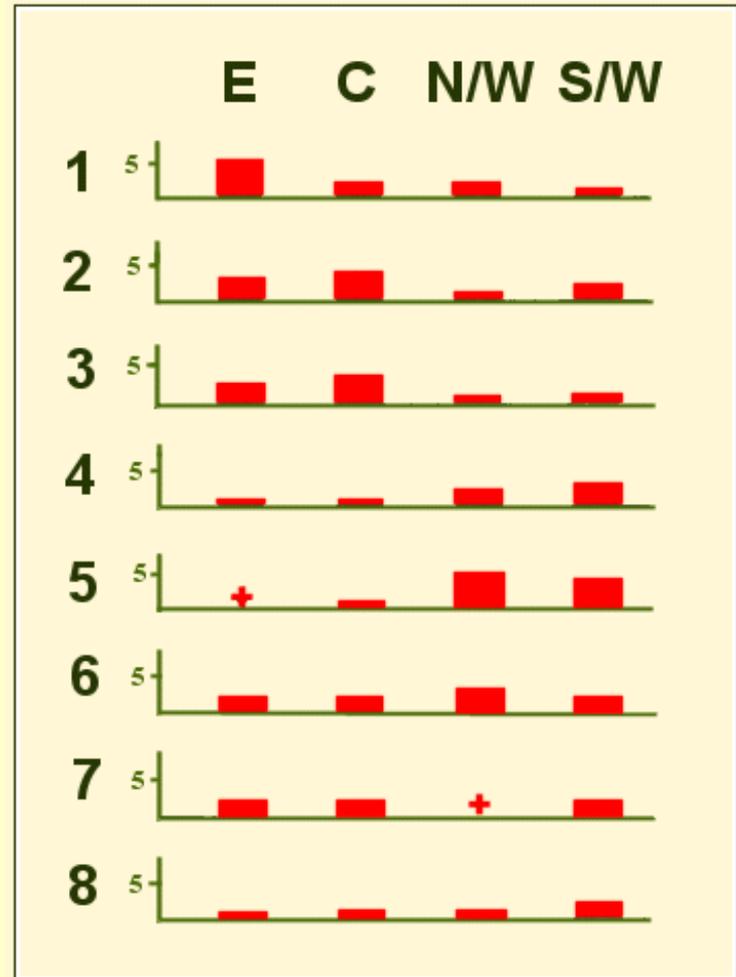
axis two on the other hand reflects soil nutrition or base status in the direction of increasing acidity.

the latter gradient is also one of decreasing species diversity from species rich to species poor.

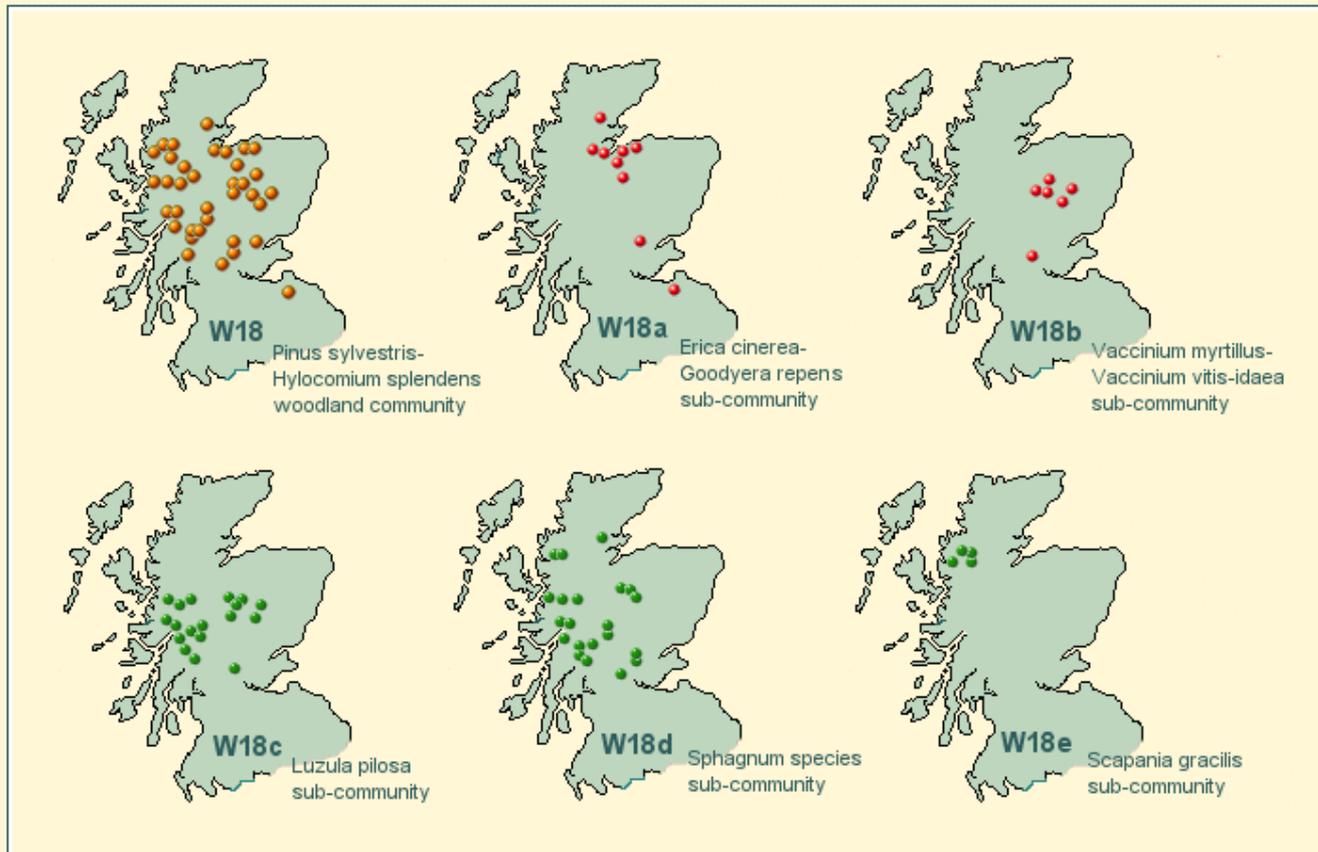
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Here eight distinct pine plant communities (plot types) from the previous slide are shown in relation to their relative importance in each of the four geographical types.



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Again, this geographical variation in the composition of pine woodland communities is shown in relation to the distribution of the sub-communities recognised by the NVC (national vegetation classification)

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National Vegetation Classification		Equivalent in other classifications	
		Stevens & Carlisle (1959)	(a) McVean & Ratcliffe (1962) McVean (1964)
<i>Pinus sylvestris</i>- <i>Hylocomium splendens</i> woodland community	<i>Erica cinerea</i> - <i>Goodyera repens</i> sub-community	community 1	(a) <i>Pinetum Hylocomieto-Vaccinietum trinquetrosu</i> (b) Pinewood <i>Vaccinium</i> -moss association: <i>Hylocomium-Rhytidiadelphus</i> phase
	<i>Vaccinium myrtillus</i> <i>Vaccinium vitis-idaea</i> sub-community	community 3	(a) <i>Pinetum Hylocomieto-Vaccinietum myrtillosum</i> (b) Pinewood <i>Vaccinium</i> -moss association <i>Vaccinium</i> phase
	<i>Luzula pilosa</i> sub-community	communities 3,4,5	
	<i>Sphagnum species</i> * sub-community	communities 2,6,8,9	(a) <i>Pinetum-Vaccineto-Callunetum</i> (b) Pinewood <i>Vaccinium-Calluna</i> association
	<i>capania gracilis</i> sub-community	community 2	(a) <i>Pinetum-Vaccineto-Callunetum</i> (b) Pinewood <i>Vaccinium-Calluna</i> association

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- the distribution and community ecology of many other groups of organisms can be related to either the plot types, or to the site types.
- for example, *red squirrels* only seem to be associated with **plot types 1 & 3** and a **zone of transition** between them
- Furthermore, many of the species peculiarly associated with the pine like creeping lady's tresses, *Goodyera repens* do not appear in the classification, because they are not of sufficiently common occurrence,
- perhaps this is because in the Highlands the Scots pine is at the western extremity of its range.
- nevertheless, some of these typical and in some cases rare plants are worthy of comment

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Although common in Scandinavian woods the twin flower *Linnaea borealis* is rare in the native pinewoods of Scotland, though it does occur on Deeside, and near Inchriach on Speyside.



Linnaeus borealis : The twin flower is a prostrate dwarf shrub (woody chamaephyte lifeform) with slender pubescent stems which often form large mats. Pink often delicately marked flowers are borne in pairs on long bifurcating stems. It is a very local and rare plant, difficult to spot when not in flower and growing with low *Vaccinium* species under pine.

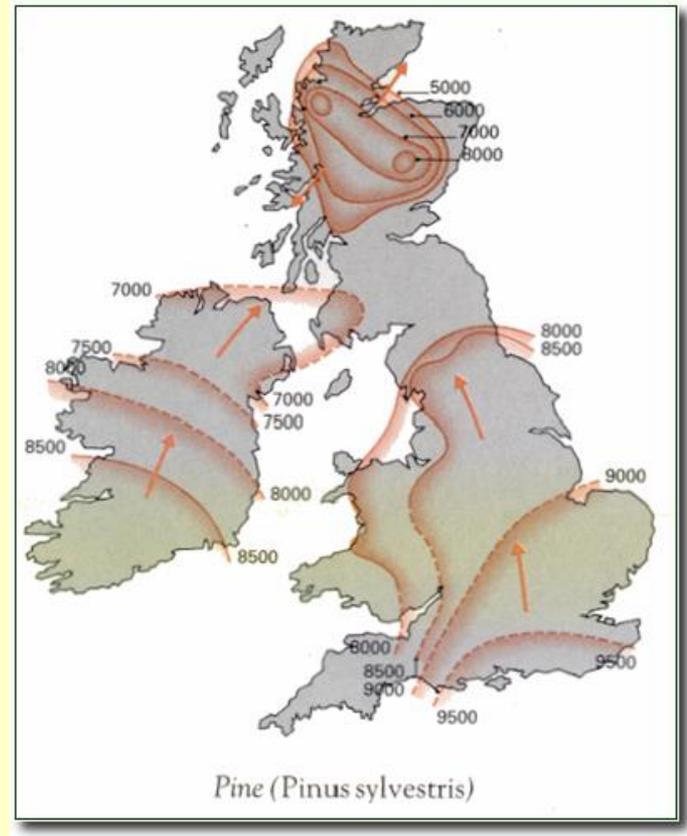
The chickweed wintergreen *Trientalis europaea* is commonest on Deeside, is scattered thinly through the woods of Speyside, does occur in the north, but is rarer in the south and west.



Trientalis europaeus: The chickweed wintergreen is a slender erect perennial which is characteristic of native pinewoods. It is locally common in northern and eastern woods in the Highlands, and usually grows on moss rooted in humus in the more grassy parts of the field layer.

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- Native pinewood in Scotland would appear to have a distinct origin and Flandrian history: a genetically distinct population derived from western refugia surviving the last or Devensian Glacial in refugia in Ireland or to the west on the then dry continental shelf.
- So, Scottish pines did not migrate back slowly through England from continental Europe, but reached the Highlands earlier in the Flandrian than might have been expected from westerly refugia



- So **NATIVE PINES & PINWOODLAND POSSESS SOME LARGELY UNIQUE** and **IMPORTANT GENETIC** and **ADAPTIVE CHARACTERISTICS** of ecological and conservation importance

Community Ecology & Conservation

- In its great range of adaptations to different environments the Pine displays considerable variation in morphology and probably in physiology
- Different geographical races, or subspecies of the Scots pine are recognised, even though in some cases the taxonomic justification may not be very sound.
- Some regard the native pines of Scotland as an endemic subspecies; *Pinus sylvestris ssp. scotica*, but Stevens and Carlisle prefer to regard it as a geographical variety *Pinus sylvestris L var. scotica Schott.* with close affinities with *var. septentrionalis Schott.* of southern Sweden.
- Pines currently growing in England and with southern origins are referred to yet another subspecies *Pinus sylvestris ssp. sylvatica* and remain more flat topped than *ssp. scotica*

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- whatever the justification for subspecies status, the reality of the morphological differences probably reflects the distinct Holocene origin of the current highland pine population.
- even within Scotland, however, the Scots pine shows great variability in growth habit, bark, cone size and leaf length, and in duration of leaf life, for example.
- some of these variations appear to be genetically controlled morphological differences which probably parallel physiological differences of adaptive significance.
- the preservation of the reservoir of genes reflected in these variations is not only of importance in terms of historical and ecological interest, but also of value in silviculture and commercial forestry..

Altitudinal Zonation of Vegetation and Climate:



- the theoretical datum line of such mountain *zonations* is the climatic **forest limit**, or **altitudinal treeline**
- actually two lines the forest limit, or **timberline**, and the **treeline**
- and a **zone of transition** or **ecotone** between them
- here trees thin out growing as small groups or as scattered individuals, often showing **dwarfed, semi-prostrate, flagform** or **krummholz** growth habits

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Although becoming smaller in stature with increasing altitude these pines are still showing a normal tree growth habit and are present at a normal forest density.

The altitude at which these characteristics cease to be present forms the **timberline**



High climbing pines on the slopes of Creag Fhiaclach, Glen Feshie, in the Cairngorms

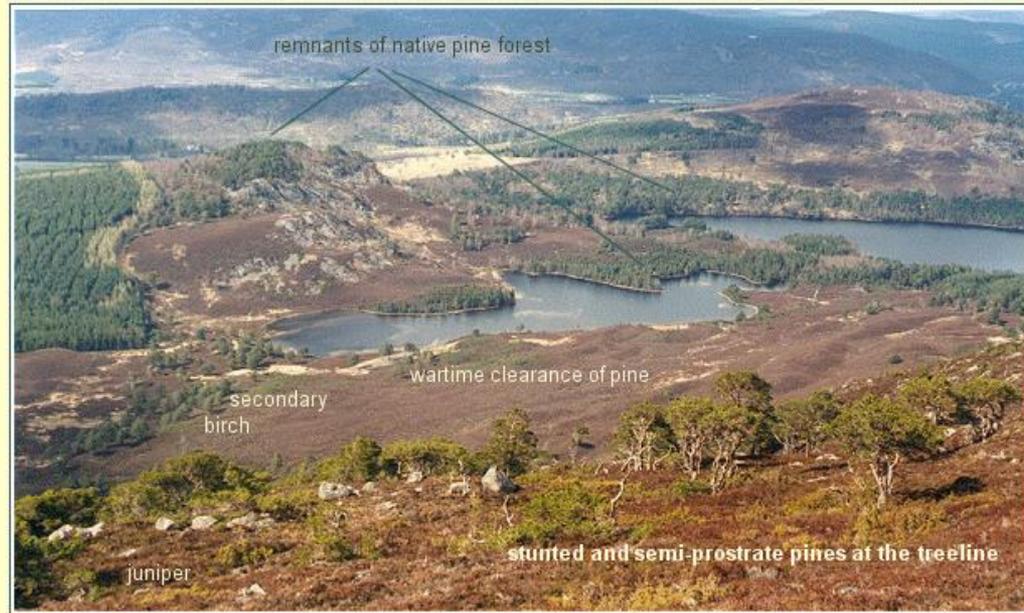
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- difficult to establish either the natural climatic forest limit, or the **potential treeline** in Scotland,
- forest has been cleared and where treelines exist they display none of the features of natural timber or treelines
- they occur at lower altitudes than would be the case under natural conditions because of anthropogenic interference



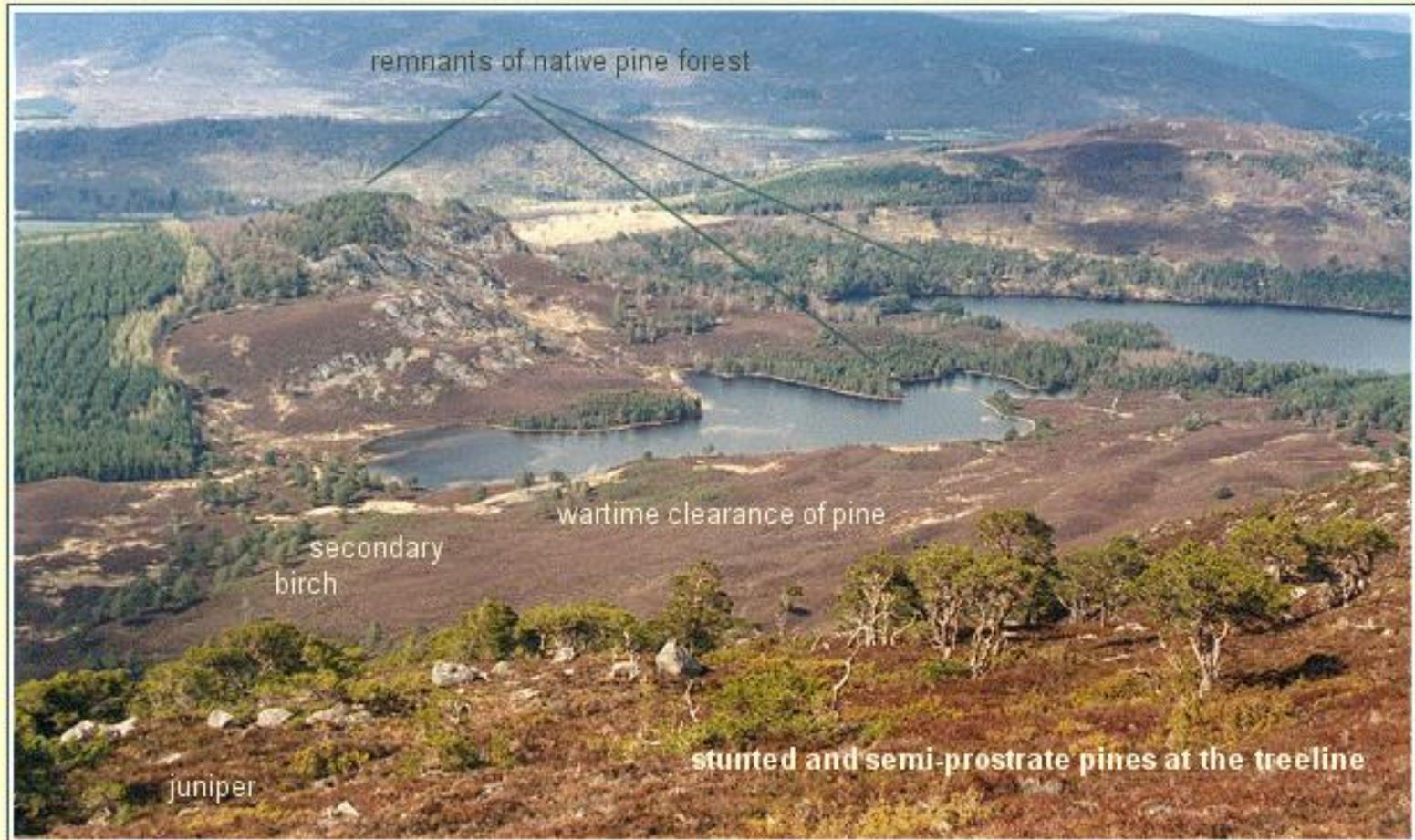
- An example of an artificial “treeline” on the slopes of Cairngorm

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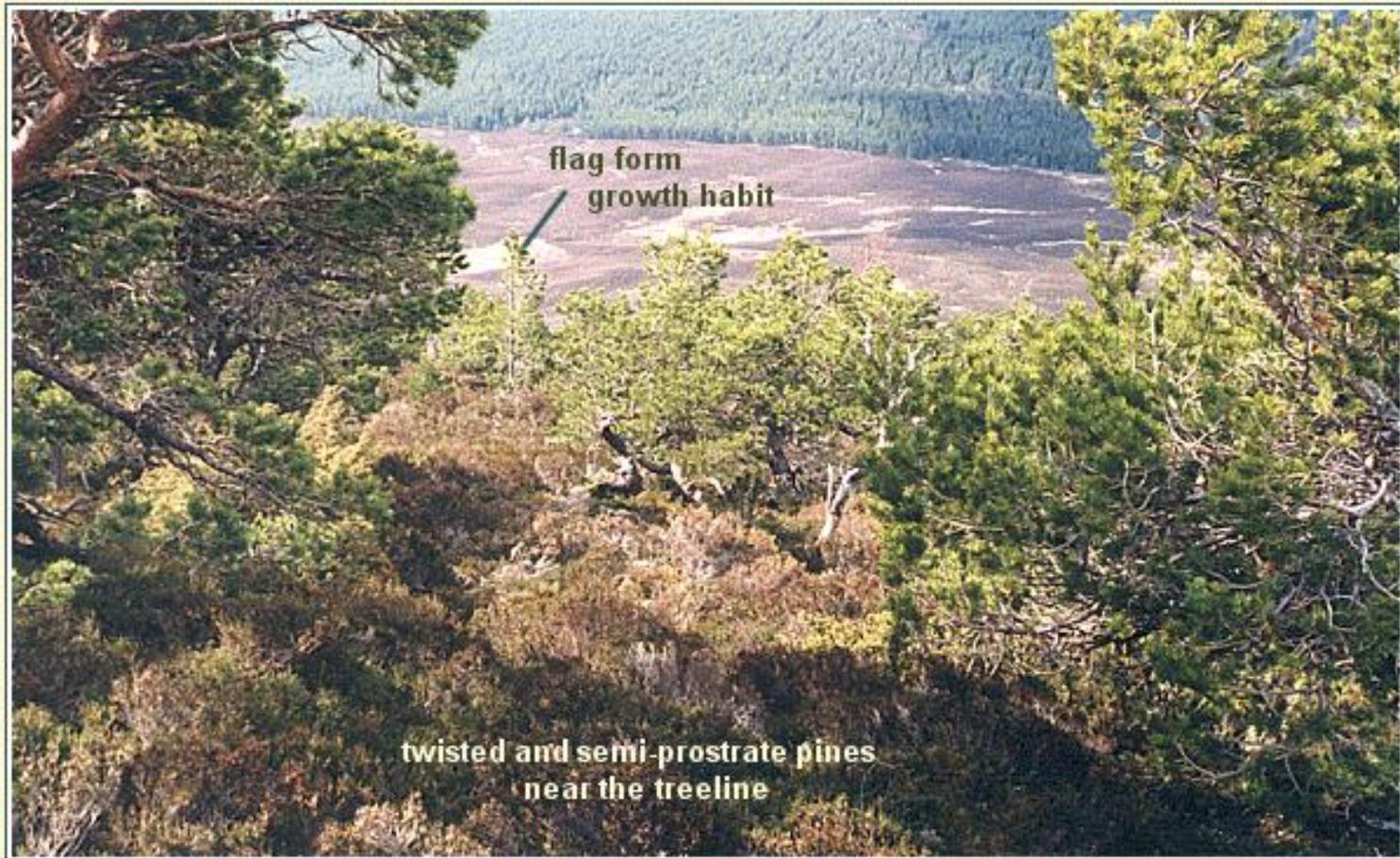


- the only really natural treeline in the Highlands occurs at c. 640m at **Creag Fhiaclach** in the Cairngorms
- beyond is a distinct **Sub-Alpine Zone** of juniper scrub that appears to have escaped the burning that presumably destroyed it elsewhere

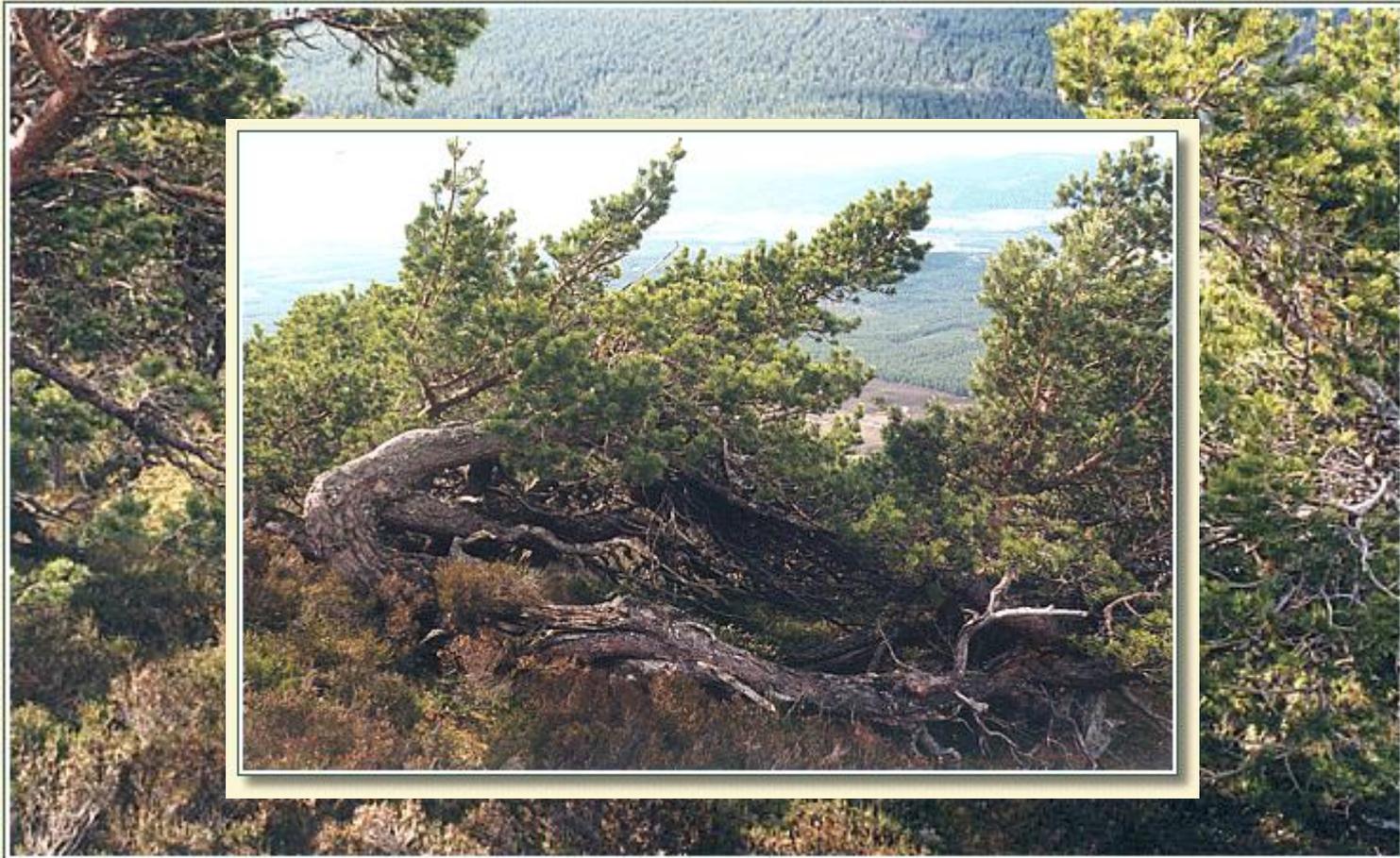
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Sub-Alpine Shrub Zone in Scotland

- juniper scrub on the well drained acid hills of the east and central Highlands.
- willows (*Salix lanata*, *S. lapponum*, *S. myrsinites*, *S. aurita* *S. repens*) on wetter and more eutrophic soils. nb. good example of such willow scrub on Durness Limestone in Inchnadamph.
- dwarf juniper scrub (*Juniperus communis spp nana*) on the Torridonian sandstone, Cambrian Quartzites, and granites of the west and north.
- the dwarf birch, *Betula nana*, may have been an important constituent of the scrub growing on bogs in this **Sub-Alpine Zone**

Pine Regeneration & Conservation

- The highly **segregated woodland remnants** of the Highlands is now regarded as partially, at least, artificial.
- Segregation into virtually pure pine, oak, and birch woods (nb. birch occurs with both oak and pine but is often apparently secondary) is thought to reflect in part **climatic gradients**, but particularly **edaphic conditions**
- It is largely an **edaphic/climatic segregation** of tree dominants.
- It may, however, owe much more to **human interference** and **selective exploitation** than was hitherto supposed.

Pine Regeneration & Conservation

- Pollen (**palynological**) studies of Abernethy forest have shown that the forest formerly contained more birch and other deciduous species such as:
 - willow, alder, poplar, wild cherry and rowan; very different from the present pine dominated wood with its large expanses of heather.
- Initial expansion of this heathland in the forest began about 400 AD. associated with the felling, grazing, and burning activities of Pictish Dark Age settlements in the area;
- It continued through the medieval period eliminating many deciduous pioneer species and encouraging a change towards:
 - a pine and dwarf shrub community with soil impoverishment and the build up of MOR humus.

Pine Regeneration & Conservation

- suggests that the forests of the Highlands were formerly more **mixed in composition** than they now
- at least some deciduous trees growing with the conifer (and presumably vice versa).
- shrub and ground flora layers too would have been more mixed, and hence more **species rich**,
- with **MULL forming herbs** present in significant quantities, thereby modifying **humus and soil conditions**.
- such mixed woods are comparatively rare today, but they could have great significance in terms of the **dynamics of the forest** and for its **regeneration**.

Pine Regeneration & Conservation

- **fire** may also have played an important role in **forest dynamics** with patches of pure pine being related to areas affected by natural forest fire
- being in effect transient **pyroclimax communities** dependant on fire as a natural ecological factor.
- Indeed pine is often said to be fire adapted.
- because of the seedling's shade sensitivity (Prentice and Lehman 1990) the gap left by an individual pine may be too small to sustain regeneration,
- leaving it dependent on natural events like **large storm damage**, or **natural fires** to open larger gaps.

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Storm events have frequently led to destructive floods which themselves create areas of open habitat promoting bursts of regeneration. Here two flood deposits are separated by a buried soil



Pine Regeneration & Conservation

- Free regeneration is rarely observed in pine forest today, inspite of the fact that **ample seed** is produced every 3-6 yrs.
- The most common stands of young pine occur colonising heathland, usually after burning, but even here regeneration is not easy, and may be delayed for two years or so.
- There appear to be three main reasons for regeneration failure:

Pine Regeneration & Conservation

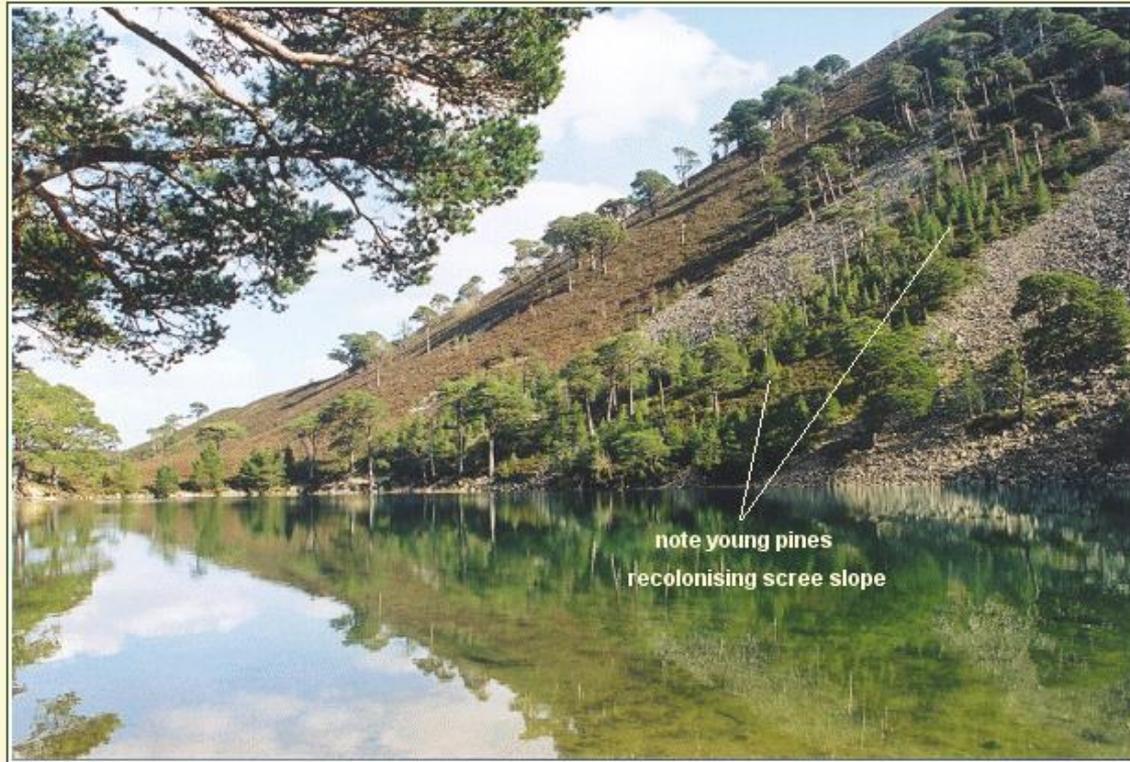
- There appear to be three main reasons for regeneration failure:
 - Pine seedlings have relatively high light requirements and under the often relatively evenaged stands that exist today the canopy density is too great to allow regeneration
 - Grazing and browsing is ubiquitous in native woods, particularly by deer.
 - and

Pine Regeneration & Conservation

- The characteristics of the vegetation and soils within and surrounding pinewoods, particularly the **depth of the moss mat**, **litter layer**, and the **biological inactivity** of the **raw acid humus (MOR)** militate against successful regeneration.

Seedlings established in this moss mat and litter layer are liable to **dessication** in only mild spring droughts, while a growing season slightly wetter than average can result in the **asphyxiation** of the roots of the seedling in *Sphagnum* mats and dense fibrous humus or peat.

Pine Regeneration & Conservation



- disturbed, or bare soil seems vital for successful seedling development, except at high altitudes.

Pine Regeneration & Conservation

- Repeated burning of forest and moorland, coupled with extensive and uncontrolled grazing has produced
... a vegetation completely dominated by **MOR humus forming species** adding acute **nitrogen deficiency** to the intrinsic **lack of phosphorus** in the soil parent material.
- Mineral deficiency **checks seedling growth** and renders them more susceptible to **competition** and **shading** from more vigorously herbaceous and shrubby species,
... and more liable to succumb to the **defoliation by grazing herbivores.**

Pine Regeneration & Conservation

- Grazing by wild and domesticated animals is a **prime control** on successful regeneration.
- A **seedling mortality rate** of 99% is stated for birch by Kinnaird (1971), while
- Miller (1971, & et al 1982a & b), having planted seedlings of birch, juniper, and pine in Glen Feshie found that 57% had died, **32% were damaged by grazing or trampling**, and only 11% were undamaged.
- Pears, in his investigation of seedling establishment above the present treeline found that of 101 pine seedlings, although 55 seedlings exhibited climatically induced dieback **87 had lost their terminal growth point due to grazing** - mainly by deer.

Pine Regeneration & Conservation

The effect of deer grazing in pine seedling density is clearly shown here.

A deer proof fence excluding grazing has a profound effect on regeneration

