How did this pine forest arrive here?

A chapter in: *Trees of the People*, by Alan R. Walker
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Many millions of years ago a small population of pine trees became separated from its main forest. Some chance of geography or climate could have been compounded by other chances of where the pine seeds were blown by gales. This new environment was different from that of the parent population, possibly more severe. Individual trees that reproduced well at the new site gradually, generation by generation, separated from their original. Individual trees that adapted to the new conditions persisted whilst those less fit for their new environment diminished in number. Eventually the genetic differences became so large that trees of this separate population could no longer interbreed with trees of their original main population. Pine trees of a new species came into existence somewhere centrally in the area that stretches between the seaboards of the Atlantic and Pacific Oceans. This new thing on Earth, this purposeful process as a population of individual trees, gradually spread across the vastness of Eurasia. Eventually, as the forests dominated by these trees came to live together with people also spreading in those lands, the people came to recognize this type of tree as not merely useful to them but as one of the most successful species of plant on Earth in terms of its distribution and enduring nature. One of those people, not that long ago, gave the formal scientific name to this species: *Pinus sylvestris* – simply 'pine of the forest'.

A new species of tree.
Carl Linnaeus invented the system of formal double names in Latin for species of plants, animals and fungi. He gave this apt name to a tree that became well known to people across much of Eurasia. Later these pines were carried to North America, New Zealand and other lands by early colonists from western Europe who included the seed with other agricultural stocks. Somehow the vernacular name Scots pine spread fast, with

variants as Scotch fir and similar, probably through the colonial spread of English language and little to do with the small isolated population of *Pinus sylvestris* remaining then in Scotland. Other vernacular names reflect the range of this pine species and the variety of people living there. Nevertheless, Scots pine is convenient for botanists and foresters to use, although people working in the timber (lumber) trade may call it Baltic pine, and planks cut from it as red deal, contrasted with white deal cut from spruce trees.

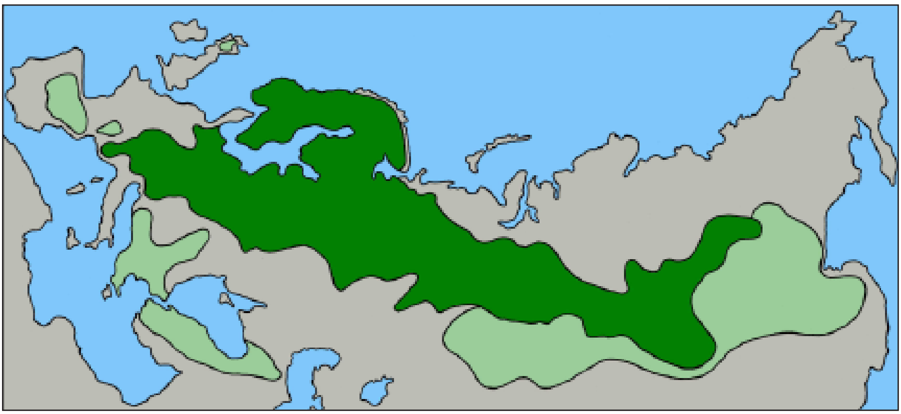
Scots pine forest in Scotland, growing around the lower slopes of granite mountains where the soil is sandy and nutrient poor, also where the climate higher up slope is too harsh for them to grow and reproduce.

The population of pines that *Pinus sylvestris* arose from could have evolved from some other unknown species of the genus *Pinus*, and from within the family of pines, the Pinaceae. These are typical cone bearing trees, in the functional group of plants known as gymnosperms. These plants, in common with the flowering plants, the angiosperms, all reproduce and disperse their offspring using seeds. They are seed plants within the group spermatophyta (see 'Reproduction' chapter). The pine family is a widespread species, two hundred and twenty in eleven genera, and *Pinus* alone has at least one hundred and twenty formally named species. As a branch of evolution's tree, the family Pinaceae grew strongly. They were becoming widespread about 130 million years ago, in the Cretaceous Period (see 'Fuelwood'). During those times *Pinus sylvestris* would have shared some of the northern parts of its range with mammoths. Evidence from mammoths semi-fossilized in permafrost indicates they fed mainly on the dense flora of herbs and bushes characteristic of these particular tundra lands, also known as mammoth steppe. Possibly the decline and extinction of mammoths was partly because of the advance of forests onto these lands as the climate warmed.

The western part of the natural distribution of Scots pine at time of the Last Glacial Maximum when this tree species was confined to isolated populations in refuge areas in the southern regions shown in **green**.

The species *Pinus sylvestris* probably originated by a common mechanism of evolution known as geographic speciation (also described as allopatric, or vicariant, speciation). A small population of some precursor species of pine tree became isolated by geographic forces: a new river system, mountains rising, or even of some massive storm spreading enough seed to create an outlying population. If the conditions of climate or soil were more severe, or milder, at the new site the trees would adapt by natural selection to grow and reproduce well in these new conditions. Possibly the genetic character of the trees in the isolated population just drifted to a new character by random events of mutation, as radiation particles from space collided with individual genes of the trees. As the isolated population changed in genetic character, then pollen from male cones of these trees could no longer fertilize the ovules in female cones of trees in the main population of pines. Also the other way round, pollen from the main population became infertile for the isolated population. The two populations became reproductively separated.

That is a simple definition of a species: it cannot interbreed with similar organisms of its original stock that it may come into contact with. The new species becomes fit for another environment. Sexual reproduction mechanisms of plants are complex and delicate. Small departures from the previous conditions and mechanisms are likely to have big consequences. This topic of how to define 'species' is difficult and fills entire books of discussion by academics. In nature a species flourishes or goes extinct depending on its vitality at the business of keeping the birth rate higher than the death rate.



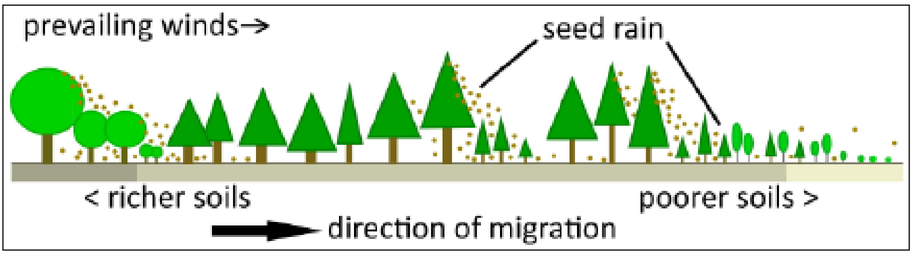
Distribution of natural populations of Scots pine; dark green showing the areas densely populated, pale green for areas with scattered populations. This distribution is mostly within the vegetation zones of taiga and temperate broadleaf forest. (derived from Critchfield & Little, 1966).

After millions of years of expansion and migration this new species of tree retains high integrity as a species, with few or no sub-species, depending on the opinion of taxonomists. But there is a diverse and widely distributed range of genetic variants that can be recognized through analysis of molecular genetic codes. Such genetic distribution is aided by mechanisms for dispersing pollen and seed far away. Conifer trees disperse their pollen on the wind: these plants have no flowers adapted to attract pollinators. Scots pine is typical of most conifers in dispersing seeds on the wind, but some conifers have animal-dispersed seed.

Cones and seeds of Scots pine; these seeds are one of the smallest of genus *Pinus*, well adapted to dipersal over long distances by strong wind. See 'Reproduction' chapter for more about cones.

During the one hundred million years or so that Scots pine has existed, the Earth's climate has subjected it to huge changes in climate. These are caused by the complex way Earth circles around its Sun and how it interacts with the planets of our solar system. Also, Earth varies in tilt about its own axis – it slowly wobbles back and forth relative to being vertical through its poles. These changes are small and occur slowly during long cycles but have enormous effects on the amount of heat energy received from our Sun. They are the Milankovitch cycles (described in 'History') after the researcher who discovered their astronomical behaviour. Fluctuations in heat energy directly cause climate change at the level of ice ages interspersed with warm periods. Both stages are counted in thousands and millions of years periodicity. Ice sheets have formed, melted and formed again many times in polar regions, north and south, although much more extensively in the north because here there is far less buffering effect of relatively warm water in the Arctic Ocean compared with the Pacific Ocean around Antarctica. These ice sheets in the northern regions occupied by Scots pine spread deeply southward and the time relevant to this story was between 27,000 to 20,000 years ago, during the Last Glacial Maximum. Then the land was covered in ice sheets or was polar desert and steppe-tundra of minimal vegetation.

Mechanisms of pine migration.
Plants and animals, as populations of species, needed to migrate to escape these fatal conditions. How a population of trees, in the form of a forest, migrates depends on what happens at its outer margins, during the slow time scale of trees. A forest migrates as its seeds fall on patches of suitable ground short distances beyond the margins of where mature trees are rooted. As seedlings survived better on the southward facing margins of forests whilst seedlings on the northward margins survived less well, so forests migrated in retreat southward. Forests and species of trees migrate by the century, whilst birds migrate on the wing by yearly seasons. Both migrate to reproduce well: pairs of pines, or pairs of birds, doing what they evolved to do.



Scots pine migration. Deciduous species on richer soils out-compete the pine. Prevailing wind may also drive more seeds of the pines onto areas where pine has competitive advantages.

Researchers emphasize the dynamism of the various types of plant species in forests, from grasses and herbs to trees. The botanical history of North America, for example, is well described. As the ice retreated northward after the last major ice age, populations of trees migrated northward to occupy the newly bare lands. First came spruce, later tamarack, aspen, birch and balsam fir. Then came a preponderance of larger broad-leaf types: oaks, maple, ash and hornbeam. Eventually these forests came to include firs, cedars, pines, also beech and elm. The species of trees migrated by their individual routes: varied and indirect. They did not migrate as one broad phalanx of mixed forest. Some of these migrations continue as the end days of our current ice age pass, and are studied by botanists as forests expand their range beyond the taiga and onto the tundra regions around the coastlines of the Arctic Ocean. To define the term forest for a story about Scots pine this means mixed population of a few species of tree that will remain on a definable area of land, at time scales determined by the life spans of the trees and the ability of the forest to change in response to disturbances.

Semi-fossilized remains (bog-wood) of stem and roots of Scots pine that have been preserved for ~4000 years in acidic, anaerobic, peat-bog until exposed by recent erosion of the peat.

Forests of pine or spruce may be dominated by one species for long time-spans but always there will be other species expanding or contracting by their density of population as they exploit empty patches created by storm, fire and other major disturbances. To us restless humans trees seem the very opposite of dynamic – they just sit there, rooted, dropping branches or falling over. Scale and perspective are what matters here. Modern research, tree by stands of trees, and decade by century spans of data, now reveal ceaseless variation and movement of species within a forest, and the migrations of entire forests. Each tree species in the forest responds separately to disturbances: wind-storm, fire, disease, drought, rain-storm, that slowly leaches away nutrients from soil . . . Each species of tree works as a process as it lives by converting sunlight energy into woody material, as it reproduces, and as its genetic characteristics vary enabling adaptation to new environments.

Scots pine is well studied because it is a dominant forest tree of an enormous region. To discover how this tree responded to ice ages researchers gathered quantitative data from semi-fossilized remains in the form of tree stumps buried for millennia in peat bogs and of pollen grains, with their tough outer coats, buried in mud below mires and lakes. The usual reference point is the time of maximum extent of the ice sheets that spread from north polar regions southward: the Last Glacial Maximum of about 23,000 years ago. When these ice sheets over northern Eurasia reached about 55° south, Scots pine in its western forests had retreated to southerly lands now occupied by Portugal, Spain, southern France, Italy, and similarly south and east. Fossil evidence from regions to the south of the Pyrenees and Alps chains of high mountains reveal that Scots pine survived this glaciation in small areas of sufficient warmth in southerly areas that acted as refuges, or refugia, from the bleak climate northward.

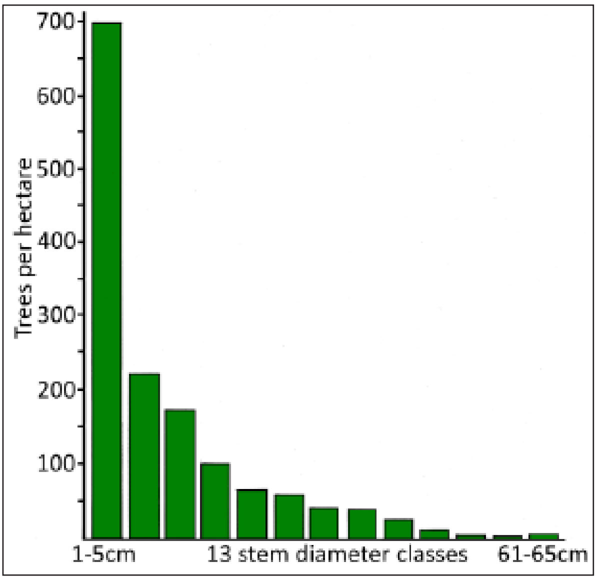
As the climate eventually warmed and ice sheets melted, so Scots pine migrated northward and westward into lands that had been scraped bare of all life. Well in advance of the trees were many types of lichen, mosses, grasses, and herbs. As described in 'History' and 'Roots' these plants, together with fungi below ground, slowly formed soil. This was potentially fertile because its mineral content was derived from rocks recently ground into small particles and had not been leached out by rainfall. Bushes such as those of the heather family, and pioneer trees such as birches (downy birch, *Betula pubescens* typically) were next to occupy these tundras. Scots pine was already adapted to grow well in cold climates and as it migrated northward its forests recolonized the wide empty lands they had been driven from by the sheets of ice.

UPPER. Gap formed by wind storm in a Scots pine wood at its stem exclusion phase. More light and space here provides opportunities for new trees.

LOWER. Scots pine wood at left is at stem exclusion phase. Seed from these trees dispersed onto heather moor, centre and right, has produced a stand initiation phase of saplings. Here this new growth thrives because of a major cull of red deer.

UPPER. Scots pine wood in stem exclusion phase of mostly well developed trees but thinner ones are being shaded out by competing trees.
LOWER. Old-growth phase of Scots pines with two dead pine snags, also in the foreground is new stand initiation growth of about 30 pine saplings.

Scots pine seeds, small but winged, disperse as wind blows over the forest. Some will land on ground that is not dense with grass and herbs. Roots may rapidly establish with mycorrhizal fungi and sufficient water and minerals, whilst cotyledons turn sunlight and carbon dioxide into woody tissue. Space and light are crucial. A gap in the forest made by storm, fire or massive infestation of insects, may provide that. Seed and seedlings can *initiate a new stand* of potential new trees. After about fifty years these trees develop a closed canopy over the stand. Under this shade competition between the trees for light and nutrients intensifies. The more robust trees grow well. This is the phase of *stem exclusion*: the less robust trees remain spindly or die. After many more decades the stand will contain many trees that are past their reproductive prime, together with less robust trees shedding branches or dying on their feet as snags. This is the *old-growth* phase that may continue a long time. (Old-growth is not *ancient woodland*, which is a wood on land known to have been wooded at least thundreds of years ago.) As the stand becomes more decrepit gaps open up. Seed rain that falls here starts another phase of stand initiation. Dynamic change of a forest, driven by the growth and reproduction of each tree, gradually pushes the forest through time and into space where it can thrive.



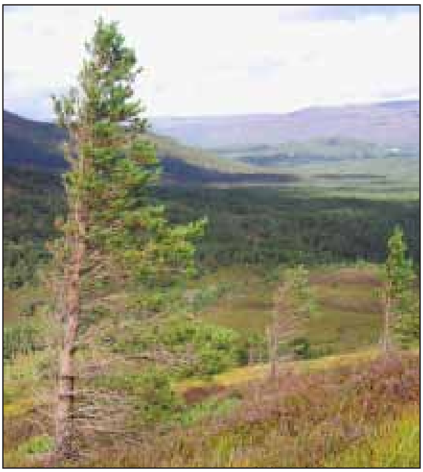
Sizes of Scots pines in near-natural stands shown as distribution of frequencies of stem diameters. This form of a frequency distribution is aggregated, with most trees of small size (data from Lilja & Kuuluvainen, 2005).

These phases of growth and change create a large scale pattern of patches within a forest. The ages and sizes of these trees in the patches are likely to be similar, dating from seedlings surviving well in the new space since the gap was created. However, the wide-scale distribution of sizes of trees in a natural forest tends toward a pattern of many small trees, few older trees, and fewer trees at their maximum size. A systematic survey of the sizes of trees in a large area of forest will probably reveal an asymmetric distribution when plotted on a chart, as shown here as frequency against size. Biologists call this an aggregated (or overdispersed) distribution, in contrast to another common pattern: the symmetrical distribution called normal. Ages of forest trees usually show an aggregated distribution. For plants and animals this is a common pattern but its cause can be obscure.

Scots pine is relatively safe from destruction by fire because of its thick bark resistant to low intensity fires. This species is not specifically adapted to fires as are some conifers that need fierce heat to trigger release of seeds from cones (serotinous cones). In the recorded history of Scots pine fires have been reported from Siberia and China that spread over many thousands of square kilometres. Scots pine is as broadly adapted to hot dry summer climates as it is to cool wet summer climates. But in regions with a continental climate of prolonged hot summers Scots pine seems to be as susceptible in Eurasia to fires as are the spruces and firs in the regions of North America with continental climates.

The standard terminology for developmental phases and patterns of a forest give an impression of regularity and predictability. Massive events of wind storm, fire, intense cold or heat, can be hundreds of years apart but for a species of tree that can be reproductively active at age of three hundred years or more it seems wise to be flexible in use of these formal descriptions of forest ecology.

Barriers to migration of Scots pine are conspicuous at tree-lines (timberlines) as a short zone up a mountain, or an elongated zone on a flat landscape of northerly latitudes. An altitudinal tree-line covers several hundred metres up hill where small, widely dispersed, trees grow (krummholz, or elfin forest). Air temperature reduces by ~1°C for every 100 metres of ascent. (Lapse rate of dry air is 9.8°C per 1000m.) Winds are strong, blasting ice crystals into the waxy waterproofing layer of leaves. Frozen soils togerther with strong sunlight cause a dehydration known as frost-drought. Tree-lines spreading many kilometres over taiga and tundra lands are caused by the same physical forces together with the rigours of longer winters.



Tree-line of Scots pine forest: upslope climate is harsh with strong wind and low temperature that stunts growth or produces a flagged form of growth away from the prevailing wind.

Most species of pines have seeds with a single wing to catch the air as the wind shakes seed from ripe cones. Scots pines have one of the smallest of such seeds, 10 to 15mm long including the wing, which being broad and membranous will increase the chance of wide dispersal. Small size will also decrease the chances of the seed establishing itself as a seedling. Its store of nutrients may not last whilst photosynthetic nutrition is being developed by the cotyledons (first needle-leaves) competing for sufficient light amongst grass and herbs.

Seeds that are blown far away from the edge of a forest may establish as reproducing trees. As isolated trees however, their reproductive success may be limited by the low density of pollen coming from the forest. Conifer forests produce pollen so prolifically during springtime ripening of the male cones that clouds appear like smoke from a fire within the forest. Much of these clouds of pollen fails to travel far from their parent trees, but each tiny grain is buoyant enough to travel many kilometres when caught in strong winds. The chances of such pollen cross fertilizing the female cones of a distant tree are exceedingly low, but as with so many factors in the workings of trees, repetition season after season compensates for low probability. There is evidence from the molecular genetics of far separated populations of Scots pine of wide dispersal of genetic potential and variants as pollen or seed is blown over the mountains of the European Alps.

> Some species of pines have seeds specifically adapted for dispersal by animals. Scots pine seeds are more typical of pines, adapted for dispersal on the wind, but some seed may also be dispersed by birds such crossbill and woodpeckers, species adapted for extracting seeds from cones. Also squirrels eat, cache, and forget pine seeds.

Habitat: soil fungi and minerals.
Individual Scots pines form close relationships with fungi that live mainly in the soil. Here the fine roots of the tree interact with a network of threads that are the main mass of a complete fungus. The above ground mushrooms of fungi are the fruiting bodies, the sporocarps, that

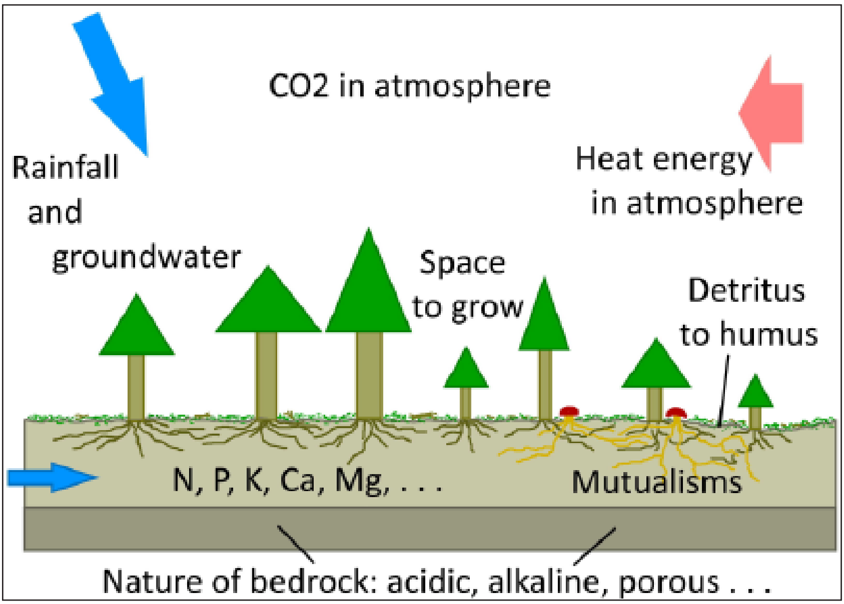
produce huge numbers of minute spores for dispersal. Most of such a fungus is below ground, where it branches out to extract all the nutrients and water it needs to live.

The relationship between plant and fungus is of benefit to both organisms. This is a mutualism: a form of symbiosis, but symbiosis simply means living together. Symbiosis also includes parasitism and many species of fungi are parasitic on plants and animals (see ‘Roots’ chapter for much more about mycorrhizas).

Seedling of Scots pine with a mycorrhizal fungus on its roots at right.
Top line: a rhizomorph of fungus. Lower line: an ectomycorrhizal sheath.

The fungi relevant here are called ectomycorrhizal, their hyphae come close to cells of roots for exchange of nutrients but do not penetrate the cells. The mycelium contacts mineral grains and from them extract, by enzymic activity, nutrient minerals that contain nitrogen, phosphorus and other elements of value to both fungus and tree.

As ice sheets retreated they left behind wastelands of boulders, gravel, sand and silt. This is glacial till: remains mountains ground down by mass and movement of the ice. We can see similar terrain wherever a mountain glacier is accessible. Mounds of till pile up as moraines whilst a short distance downhill herbs, bushes and tree seedlings advance up hill. This rocky material, unweathered and devoid of organic matter was barely able to support a full range of plant life. Organic soil able to support a full range of plant life developed slowly as lichens and small plants lived, died and decomposed for many generations. Their remains became the amorphous brown material called humus, containing most of the nutrients they had extracted directly from the rocky ground. As trees grow on these early soils they produce continually a litter-fall of leaves and dead branches. The fine roots of the trees grow, work, and die rapidly, so adding to the organic content of the soil.

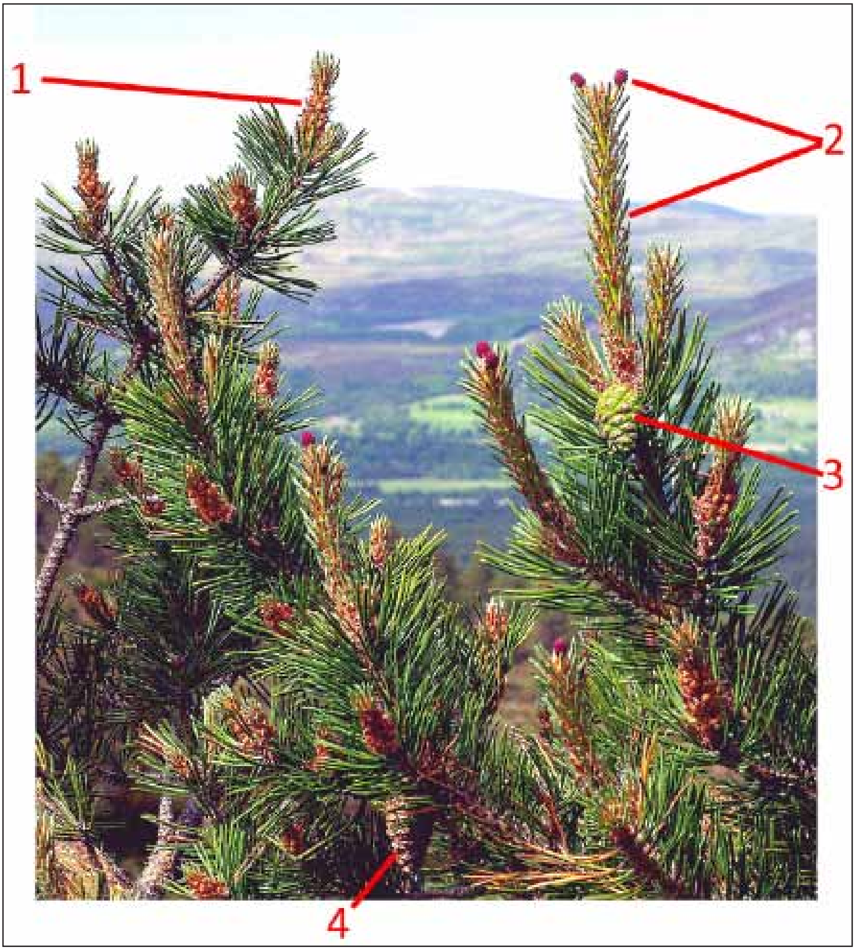


Resources for growth of forest trees; not including sunlight but including ambient heat energy and resources such as mycorrhizal fungi and other soil organisms that make available nutrient materials.

All trees are deciduous, broad-leaf and needle-leaf. Most species of conifer make use of each of their needle-leaves or scale-leaves for several to tens of years rather than just one annual season as with broad-leaf trees (see 'Leaf-fall'). Addition of organic material to soil from this litter-fall, of all plants, is enormous. Trees provide the majority of it and each entire tree is eventually rotted down into humus by saprophytic fungi and many other minute soil organisms that feed this way. As the organic content of early soils slowly accumulated the mineral content first increased as weathering by rainwater and the action of freeze-thaw leached mineral compounds out from the rocky material. Young soils of this origin are often at their maximum fertility. As these soils age the leaching of minerals by much rainfall reduces the fertility of upper layers of soil and is likely to create a layer lower down that becomes impermeable. The soil forms a hard-pan of grains of silt cemented together. These are soils of the podzol type. On better drained soils with much gravel and sand content that form over rocks such as sandstone or granite a hard-pan is less likely, and the soil will develop a slightly acidic character.

To grow into a mature tree, a seedling will need many more nutrient elements than just carbon. The plant will need about twenty essential minerals as chemical compounds to provide: nitrogen, phosphorus, potassium, calcium, and so on. These are essential for the inner processes of cells with their soft membranes and arrays of enzymes. Scots pines produce in their first year long roots that penetrate deep and wide in search of sufficient water and nutrients. Later the lateral roots may become more important as roots encounter a hard-pan or the bed-rock. A dense network of fine roots develops and on them are minute root hairs through which the water is absorbed.

The water taken up by the roots carries nutrients through xylem tubes up and out to the furthest branch tip and into every needle-leaf. This prodigious process is passive for the tree, it requires no energy other than that going into construction of the plumbing tubes running from roots to leaves. As water evaporates from veins and tissues of each leaf and exits as vapour via stomata out to open air, a negative pressure is created within each leaf. By the physical properties of water, specially its high surface tension when confined to narrow tubes, negative pressure in the foliage pulls up soil water from the deepest roots. The process is called transpiration. Water transpired from the trees then re-joins the normal water cycle of the atmosphere and soil to fall as rain somewhere, possibly back onto the same ground, possibly far away. The form in which all land plants are constructed, from cellular to whole plant level, evolved around this fundamental need to transport water from root to leaf.



Scots pine at midsummer. 1: Male cone. 2: Female cones developing on a new shoot. 3. Green, year 2 cone. 4: Brown, maturing year 3 cone.

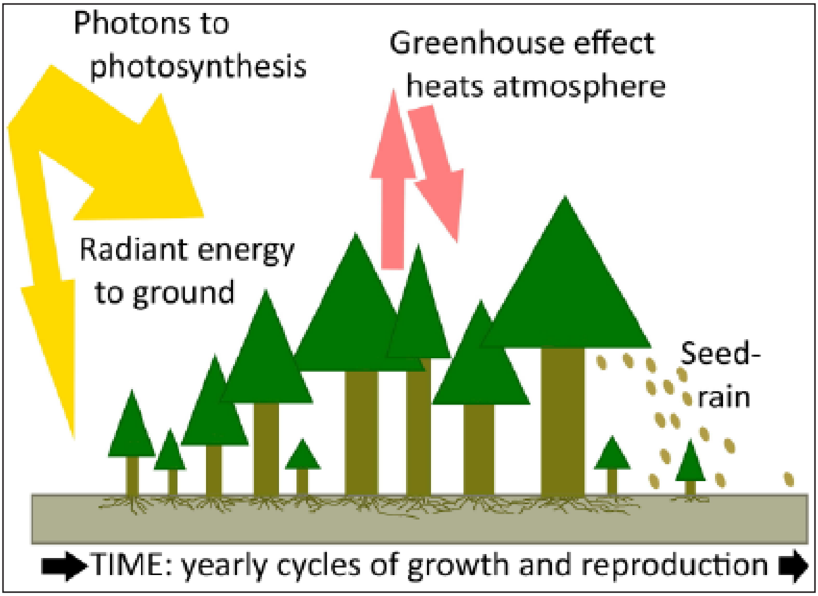
Scots pine is a species that thrives in the cool wet climates typical of northern Eurasia but is also well enough adapted for warm dry climates of the lands bordering the Mediterranean Sea. Scots pine has a high capacity for photosynthesis compared to many other conifers, and like them can continue photosynthesis beyond the growing season of the stem and roots. Reserves of carbohydrate are diverted to the stem and roots for storage, to support later the next early seasonal growth of male and female cone buds. Photosynthesis continues into winter, unless the air temperature and low angle of sunlight slows photosynthesis to the point where the enzyme activity of this process slows to a halt.

Growth needs sufficient heat energy because it depends on complex chemical reactions and enzyme activity of the process of respiration. Here oxygen combines with the carbon of sugars for a type of cold combustion that releases energy for the plant's use and gives off carbon dioxide and water as waste gases. This biochemical oxidation, a burning process, is slow and requires plenty of time to work for plants. Foresters study the combination of temperature and time a tree needs to complete each year of growth. This is termed *growing degree-days* at above the 5°C threshold for growth. A study of Scots pine populations in Russia revealed at the most northerly and southerly sample sites, with mean annual temperatures of -0.7°C and 7.5°C respectively, degree-days available for growth of the pines were 665 and 2536. Scots pine grows in climates of varied average temperature but at margins of its range a miss-match with seasonal pattern of temperature may lead to reproductive failure.

Energy drives growth.

The prime source of energy for plants with green leaves arrives as light from our Sun. This energy shines on Earth as discrete packets called photons, and these can also be measured as waves of energy. Sunlight powers directly the biochemical process of photosynthesis that works in the leaves (see 'Photosynthesis'). Power in this context is defined precisely as the rate of doing work. That is the rate at which the high energy of photons is used by photosynthesis per unit of time and does work by synthesizing sugars for the plant.

> This power is measured as joules per second, usually expressed more simply as watts. A domestic light bulb is rated at several watts and an electricity generator at kilowatts or megawatts. To a physicist a watt is a watt wherever and however it does work, and work is also defined precisely. These laws and definitions of physics apply to living things exactly as they do to man-made machines.

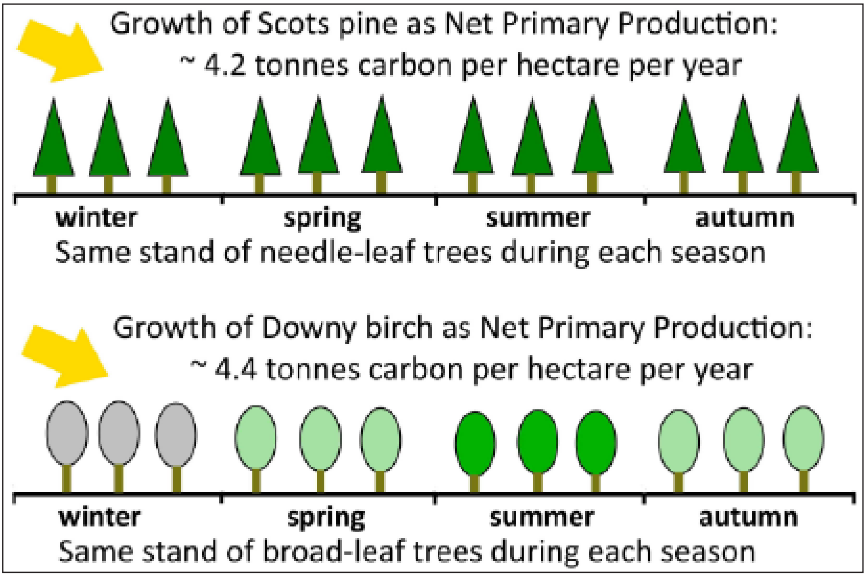


Energy drivers of the progress of a conifer forest through its yearly cycles of growth and reproduction. The main driver is radiant energy used by photosynthesis, also heat energy of the atmosphere through the greenhouse effect provides conditions for biochemical reactions of photosynthesis and respiration.

Energy from sunlight also becomes available to plants as heat energy, which is simply the degree of movement of the atoms and molecules that comprise all materials. Hot water has its molecules of H_2O jiggering about faster than they move in cold water. Plants need water to be to be liquid and they need air temperature at least 4 to 5°C for photosynthesis to work, but at 40°C it shuts down. Earth's atmosphere is warmed by the greenhouse effect. Light energy reflected from the surface of the Earth has a longer wavelength than light direct from the Sun and energy of longer wavelength is readily absorbed by gases in the atmosphere. Most of this heat is trapped by the same water vapour that forms rain-clouds. Carbon dioxide, methane and others exert a smaller but important effect. (These three main greenhouse gases are in the atmosphere naturally; what is unnatural is the additional amount of carbon dioxide and methane from our technological lives powered by fossil fuels.)

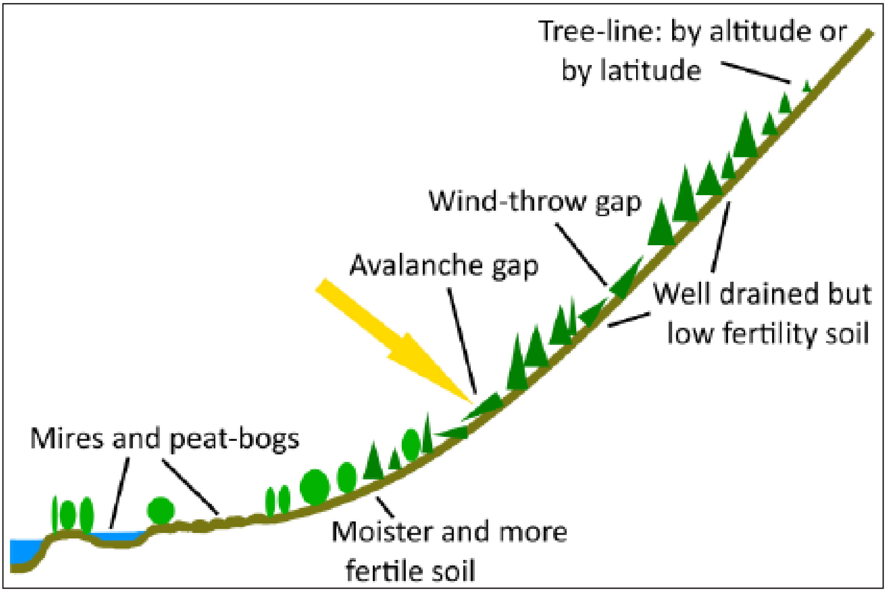
Photosynthesis can seem like a miracle: energy pouring in from the Sun in vast amounts is turned into plants as useful to us as grasses and herbs for food and trees for fuel and timber. But as the chapter 'Photosynthesis' showed, this process is highly inefficient viewed from the perspective of our familiarity with machines. A diesel engine burning oil appears to be efficient: a machine of intense power using little fuel, but where did the concentrated energy of the oil come from?

Space in which to grow.



Comparison of growth rates Scots pine and Downy birch in Finland. (Data from Mälkönen 1974,1977. In: Cannell 1989, converted to tonnes of carbon from tonnes of dry stemwood + bark.)

A stand of trees can receive sunlight energy at about 9.5 megajoules per square metre of tree canopy per day. Then, during the process of photosynthesis, energy left available for the processes of respiration, growth and maintenance, is reduced to 0.05MJ per square metre per day. Nevertheless, keeping alive and growing naturally as a tree in a forest can operate at a greatly slower or less powerful pace because there is much energy available as sunlight and much time for reproduction



Space for pines to grow. In lower wetter and more nutrient rich areas pines are out-competed by broad-leaf trees or mosses forming peat. On well drained low fertility soils pines flourish. New growth of pine seedlings is aided by gaps created by wind-throw or avalanche. Growth at high altitude or high latitude is limited by harsh climate, creating tree-lines.

A forest that started as a new species in one small area millions of years ago, then expanded across a continent, required much work as it maintained and reproduced itself. As long as the rate of renewal of individual trees exceeds the rate decline of trees toward infertility, the forest lives on. For a population of a species of tree to increase slowly in numbers of trees, its birth rate of individual trees must exceed their death rate. These two rates provide the net reproduction rate when expressed as a ratio called *R zero* (R_0). For the population to increase this needs to be greater than 1.0, say 1.1 for example. This ratio is calculated from the number of individuals in one generation against those in the next generation. A definition of how long a generation lasts is needed. For trees this will be many decades and is difficult to measure within a forest.

Red deer hind. Credit: Wikimedia, Charles J. Sharp. Similar predators upon conifer trees in the range of Scots pine include roe deer and moose.

Scots pine seedling after losing its apical meristem to predation by deer. Its growth will permanently be stunted.

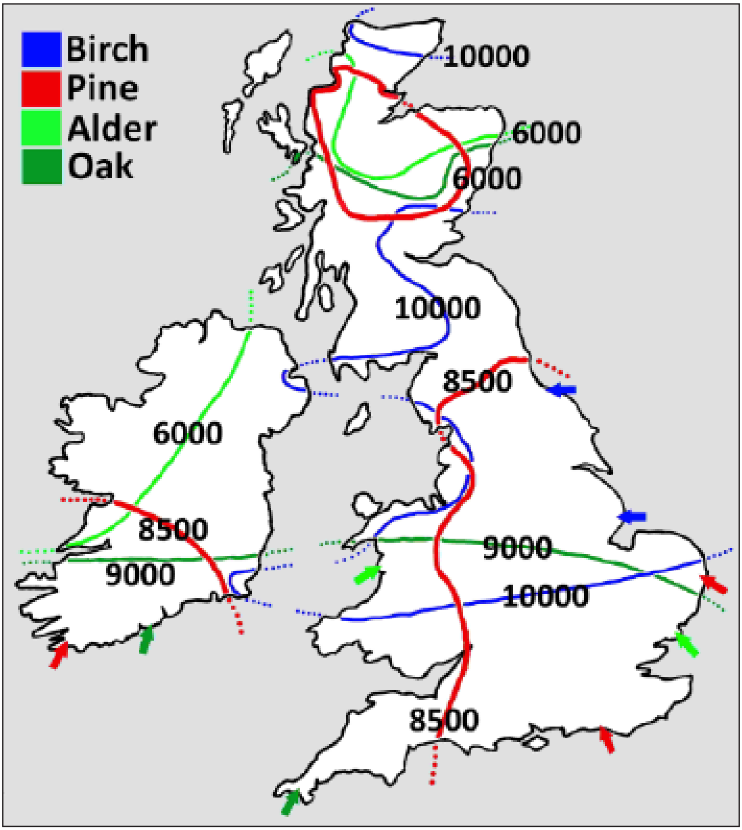
Scots pine and oak trees, mainly as pedunculate oak, *Quercus robur*, have lived for millennia in the same geographic and biological area of taiga and temperate broad-leaf forest. These needle-leaf and broad-leaf species are potential competitors. The ability of Scots pine to grow, in terms of tonnes of woody biomass per hectare of forest, is fundamental to how it migrates and establishes new populations in an environment it shares with broad-leaf species such as oak, elm, ash, and beech. Data from one study of this done in Belgium provides a simple comparison of a stand of *Quercus robur* close to a stand of *Pinus sylvestris*, measured for standing biomass, and for Net Primary Productivity (NPP, see 'History'). Standing biomass of the oaks was 177 tonnes per hectare, and of the pines was 169 tonnes per hectare. On the same ground, sharing the same soil and climate, broad-leaf trees are likely to thrive better than needle-leaf trees, particularly if the soil is rich in nutrients.

Irrespective of soil and climate conditions, needle-leaf (wintergreen) trees have the considerable advantage of being able to grow for much longer each year, as long as the temperature and light conditions are sufficient to maintain a minimal level of photosynthesis. There are many studies of the growth rate of trees, comparing different species by their NPP, measured by increase in volume, or by weight as tonnes of carbon, accumulated per hectare of forest per year. Needle-leaf trees have NPP similar to that of broad-leaf trees. The data in the comparison diagram here are one example from a pair of studies by one researcher using the same method in Finland. Numerous studies show that the needle-leaf and broad-leaf adaptations for growth are similarly effective.

History of Scots pine in Ireland and Scotland.
This peripheral region of the range of Scots pine has been studied in detail, it has only this one indigenous pine species, thus is a simple example for this species. (More on this topic is in the chapter 'Deforestation'.)

By the time when the area now occupied by the islands of Ireland and of Britain was released from ice-sheets Scots pine forests migrated to the north, west and east. This land was tundra. In the far west of this migration there were lands that would later be cut off from mainland Europe by rising sea level. The conifers of *Pinus* and *Picea* genera tended to be in the vanguard of this widespread tree migration northward through Europe, but it was only Scots pine that colonized southern areas of Ireland

and Britain. They migrated onto most of the lands newly freed of ice along with broad-leaf species adapted to young undeveloped soils and cold climate; species such as birches, willows and hazel. The only conifers other than *Pinus sylvestris* that became native to these new lands are the common yew, *Taxus baccata,* and juniper, *Juniperus communis*.



Migration of trees into Ireland and Britain from 10,000 to 8,000 years ago. Arrows indicate likely directions of advances onto these new lands. Northerly population of Scots pine (top red line) indicates the original area it dominated 6,000 to 5,000 years ago. (Data from Birks, 1989).

Behind the conifers in this slow migration came larger species of broadleaf hardwood trees: oaks, elm, ash, lime and others that flourished on the developing soils of increasing fertility. The geology of these island is complexly varied and the mild, moist climate that results from the warm oceanic current of the Gulf-stream accelerated the development of soils typically rich in mineral nutrients.

Broad-leaf trees such as oak and beech out-competed the Scots pine. These species did so by reproducing with seeds well stocked with food reserves: acorns, beech nuts, hazel nuts. Some of the annual crop of seeds are dispersed far by birds and small mammals in various specific mutualistic adaptations of both partner species. The seedlings have cotyledons that either store the food reserve, or are leaf-like and produce the first photosynthesized food for the seedling. The mature trees create dense shade when in leaf, strongly inhibiting colonization of the area by many forms of vegetation, including seedlings of Scots pine. Any pine that does manage to establish and mature in a canopy gap will suffer lack of sufficient light if surrounded by oak or beech trees.

Scots pines eventually, between about 6000 to 5000 years ago, established a relatively stable population on the uplands of Scotland, having arrived there by routes through what is now England and Wales, and also from Ireland at some stage. This population grew in the valleys and lower slopes of minor mountains situated north of the geologic rift known as the Great Glen. The leading edge of this slowly migrating population found less competition from large broad-leaf trees on the poorer soils and colder climate here, whilst the trailing edge continued to be out competed, by oak in particular, wherever the soils were richer. The map of tree migration here shows approximately the Scots pine travelling 300 km from its position at 8500 years ago to its final destination at 6000 years: a rate of 120 metres each year. The forest moved whilst each tree remained rooted. This rapid speed remains a puzzle, named 'Reid's paradox' after the researcher who estimated rates of forest migration.

Despite this migration to lands they could dominate, Scots pine in Scotland declined in both spread and density of their population. After the maximum extent of the Scots pine forest that had migrated here about 6000 years ago, the southern edge of its distribution became defined by the effects of oak and alder woodlands. Much later, about 2400 years ago, a contraction of the range of the forest at its northern and western margins occurred rapidly, during several hundred years. This reduction, the *pine-decline* as it is known to ecologists, can in a sense still be experienced by us. The bog-wood we can see during a walk in these uplands is a poignant reminder of how well these lands were forested long ago.

A Scots pine wood in Scotland showing effects of long term grazing by a dense population of red deer: no young pine trees except on the small island in the river. Many of these trees have spread their branches wide when unconstrained by other trees growing as a dense stand at its stem exclusion phase.

This pine-decline is considered to have occurred through natural causes, not by human activity. It has been studied by comparative pollen counts covering large spans of time, together with the evidence from these semi-fossilized trees by counting tree rings (dendrochronology). When data from these sources are compared with archaeological data, a correlation is indicated between a prolonged increase in rainfall around 2500 to 2400 years ago. A frequently proposed explanation for what might have happened is that mosses thrived in these wet conditions, growing so fast and tall above the mineral soils that pine seedlings could not establish roots into sufficient source of nutrients. Some of these wide peatlands remain naturally treeless in northern areas of Scotland.

Despite much research there is insufficient evidence for any single explanation for this decline. A combination of causes seems likely.

Scots pine as a plantation of timber trees growing densely in a favourable climate for this species, in Poland. Credit Wikimedia.

Human influence on the forest: decline then regeneration.
Humans had also migrated into these lands. They continued northward, reaching the wide natural area of Scots pine here about 9,500 years ago. They searched for better hunting grounds and less competition from other people for space and resources. They continued migrating in every direction, depending greatly on woodlands and open grassy areas between for fuelwood, construction timber, tools, grazing land for their livestock, and animals to hunt for food.

First the newly arrived people used stone axes to cut and harvest wood. Later came the times of bronze tools, then iron tools and implements such as nails to join construction timbers. People cleared land to grow crops. Their sheep, goats and cattle grazing within the woodlands reduced the survival of seedlings, but for thousands of years these people had little overall impact on the high level of tree cover, broad-leaf and needle-leaf, in Britain. By about two thousand years ago people of these islands equipped themselves with axes adequate for felling trees to provide the wood to convert to charcoal. This charcoal in turn was used to smelt copper and iron from ores that were increasingly exploited in these islands rich with mineral deposits.

For centuries after establishment of settlements of people in the area occupied by this forest, the impact of human use of the same land would have been slight because of the sparse human population. People's need for firewood and construction timber would have been slight relative to the size of the natural resource.

The forest was already under natural grazing pressure from small animals such as the field vole (*Microtus agrestis*) that will damage any tree in its first year of growth. Mountain hares (*Lepus timidus*) inhabit heather moorlands but they will feed on tree seedlings at the edge of a forest. Deer, both red (*Cervas elaphus*) and roe (*Capreolus capreolus*) were then the herbivores exerting the greatest grazing and browsing pressure on the vegetation of the forest. That pressure includes seedlings as a single mouthful through to young trees that have not yet grown stems thick enough to resist gnawing by deer for nutrients from the bark.

Any account of plant-eating pests of pine trees should include moose (*Alces alces*) and insect pests such as the leaf-eating larvae of the pine-tree lappet moth, *Dendrolimus pini* and similar moths of the same genus. This general topic is covered in chapter 'Herbivore'.

Official records indicate that the last wolf in Scotland was killed in 1680, probably as the end of a long campaign to eradicate them to protect farmer's livestock. Without this top predator, and with insufficient hunting of deer by people, numbers of deer in these forest areas increased more rapidly.

From the mid-1700s through to 1850s livestock rearing in the Highlands changed radically. Formerly the farmers in the forested areas kept herds of cattle that grazed on the uplands, generally away from croplands but where there was sufficient grass amongst the heather. If cattle also grazed in the forest their method of feeding, with teeth only on their lower mandible working against their flat upper mandible, tended to be less damaging to seedlings than that of sheep or deer. These have two sets of front teeth and more precisely selective feeding behaviour.

At this period of the history of Scots pine here the story becomes too complex for this account, with its politics and economics of a region feeling the forces of the industrial revolution thriving in central Scotland and much of the rest of Britain. There were massive social and economic upheavals in the way land was managed for livestock grazing and the fates of the people living there, along with the forests. Two sources of much information about these turbulent times are by Smout and co-authors, 2003, also 2005; see **References and notes**.

Scots pine produces good quality timber and has been used that way for as long as the people living here had axes sufficient to cut branches and fell trees. The resin that can be extracted from live trees would have been used for many purposes. Even without cutting tools the pine forest contained fallen branches and cones useful as wood-fuel for cooking. When managed as protected plantations some areas of Scots pine forest became important for commercial timber production and processing. These trees became an economic resource that could be extracted, transported and traded. Little use was made of Scots pine for making charcoal: the resinous wood of this species provided poor quality charcoal in comparison with oak wood. Coppice oakwoods situated and managed nearer the iron smelters were more efficient economically.

By the time industrialized timber extraction was made possible by efficient tools and transport on roads or by floating down rivers Scots pine had become greatly valued for use in ship building. Here it was used for both planks and masts, and the demand for shipbuilding timber was strong, specially for naval warships. Then as mining for coal rapidly increased, leading to the industrial revolution active in central Scotland, Scots pine became much used for pit-props.

Scots pines in the Cairngorms National Park naturally regenerating from stands formerly much reduced by red deer but now managed by the landowner by rigorously culling the deer.

Plantations of Scots pines were developed to continue for this demand, but it was never easy to transport the timber from these relatively remote, upland forested areas to the shipyards, either by road or river. Similar conifer timber had for long been available, imported from countries around the Baltic Sea. The reputation of this timber, known in the trade as Baltic pine, was high because the trees, variously Scots pine, Norway spruce (*Picea abies*) and some larch (*Larix*), grow slowly in those colder regions and thus become finely grained, strong and ideal for construction work and fine joinery.

When this original natural forest of pines in Scotland was at a stable population size, at between six and five thousand years ago it was distributed within a broadly **L** shaped area of approximately 3,000,000 hectares, as shown on the map here. That was not all stands of pines, which probably occupied only half that area. The rest of the area comprised: mountain tops; peatlands; lochs rivers and mires; heather and grassy moorlands. A calculation in 1998 by the Forestry Commission in Scotland showed the entire population then covered 17,900 hectares of natural and mixed-origin Scots pines, distributed as eighty-four discrete populations of greatly varying sizes.

How that diminution came about cannot be explained by any one predominant factor because multiple causes have operated for so long. The continuing threats to the size and health of these woods are centred around continuing grazing and browsing pressure from deer. It is generally agreed by ecologists that the population of red deer in Scotland is more than double what is healthy for the environment of trees and moorlands they inhabit.

Forests have their own momentum through time, taking far longer to change than we do with perspectives we develop during our short working lives. How these scraps of forest that remain in Scotland will fare is substantially within our own ability to generate and influence. There has been for decades now a growing determination to nurture the existing woods and forests of this land, for many reasons. We plant trees to draw down carbon dioxide from the atmosphere and store it in trees varying from large new plantations of exotic conifers to small patches of native broad-leaf trees in urban areas. We plant trees to regenerate woods that have not existed on upland areas for hundreds of years whilst that land was pasture for livestock. We make laws, regulations and specifications for areas of land that can be protected for nature reserves.

Current economic policies and regulations aimed at mitigating climate change are causing a major change in land-ownership patterns of these lands. Purchases of Highland estates by private individuals and business are now less likely to be bought and sold as hunting estates and more likely to be converted for commercial advantages of owning land on which many trees can be planted to store carbon (a financial mechanism called *carbon offsetting*). As 'Regeneration' chapter described, this regenerated forest will take a long time to become similar with what was there hundreds of year ago. When established, several centuries hence, the forest will resemble the original and there will be many people within it: tending the trees, watching birds, cycling for fun . . .

Open-air nursery of pines and birches for regeneration of woodland as part of the Cairngorms Connect project.

National parks of areas relatively large for a small country are now established and for the native area of Scots pine, the Cairngorms National Park is a key factor in the plans for regeneration. These parks are on land privately and variedly owned and managed. The role of the park authority is in regulated planning of land use. An ambition is now active here with a project named *Cairngorms Connect*. This aims to regenerate Scots pine forest around the western periphery of the Cairngorms massif of uplands, hills and mountains. The formal plans of this project extend for two hundred years – growing trees is a slow business.

This story of a forest started with an ice-age a long time ago. These huge changes in our climate repeat in slow cycles over many thousands of years. The changes are variable because of subtle complexity in the causative interactions, so future changes are not precisely predictable. Other influences on our long-term climate are from movements of the crust of the Earth as tectonic plates, massive volcanoes and collisions with asteroids. What is predicted with confidence is that this ice-age of our current period of Earth's history, will end when the ice-sheet on Greenland disappears because of these long-term climate changes. Then the next ice age will start gradually to form. Climatologists recognise the most regular of these cycles to repeat about every 41,000 years and from that they predict the start of our next ice age in ten to twelve thousand years from now.

This life-form, this process, this tree we call *Pinus sylvestris*, has a good future ahead of it to judge by its past performance. Scots pine looks like a survivor with its broad bulk of gnarly roughness topped with a dense mass of shining greeness. Its enduring presence comforts us. So our current contribution to the continuing good fortunes of this beautiful and iconic tree is no whistling into the winds of inevitable change. We people can help it on its way.

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