

The Role of Grazing in Maintaining Open Landscapes in Temperate Regions



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Abstract

The concept of woodland being the climax community in temperate ecosystems has a long history but, where grazing animals play a major role in determining the vegetation pattern of a region, there are plausible ecological explanations of why this might not always be the case. If the carrying capacity of the vegetation for herbivores is significantly higher than the level of grazing necessary to allow the survival of young trees, then there is a low probability of woodland surviving in the landscape – unless the young trees are protected from grazing in some way. Where herbivores are naturally present, regeneration is only possible if young trees are protected by thorny shrubs, winter snow cover, rough topography, or the conditions are so optimal for young trees so that the probability of a proportion surviving browsing is high. The Scottish Highlands are presented as an example of an open moorland landscape where trees are no longer the climax vegetation because young trees have no natural protection from grazing; indeed, an open landscape is to be expected at this, the oligocratic phase of postglacial succession, where the evidence suggests a long period of natural woodland regression from a postglacial maximum. The moorland vegetation characteristic of the Scottish Highlands is more resilient than woodland over long time-scales because, to persist in the landscape, woodland always has a sensitive period when young trees have to out-compete the other vegetation without being browsed.

Keywords: Climax woodland; Open landscape; Woodland regression; Grazing; Trophic levels; Scottish Highlands

Introduction

This paper takes a theoretical perspective on the conditions under which woodland can persist in a landscape in the presence of large herbivores, using the trophic level approach to determine the expected size of the herbivore population. It is focussed on Europe but will have applicability to global ecosystems. Throughout the paper, the Scottish Highlands are used as a worked example of the theoretical principles identified. This area is referred to below as ‘the Highlands’ and its location shown in Figure 1. It is primarily an open, unwooded landscape of moorland, with most of the woodland shown on Figure 1 being post-1900 plantations. The moorland consists of a mosaic of unimproved acid grassland, dry heath, wet heath, peatland and marsh, with different plant communities dominant in different localities. For example, dry heath tends to be dominant in the east, wet heath in the west, peatland in the far northeast and montane communities at higher altitudes. A full description of the different vegetation types can be found in McVean and Ratcliffe [1], Burnett [2], Avenir et al. [3] and Lake et al. [4]. The climate is Atlantic maritime, the soils are generally acidic with a tendency to peat formation and the uplands are montane.

First Principles

Starting from first principles, the following statements are

relevant in relation to the expected distribution of woodland in climates supportive of tree growth.

- a) Trees are successful because their height means they can outcompete lower-growing competitors.
- b) At the seedling stage they have to successfully compete with the surrounding vegetation.
- c) Large herbivores are (or were) characteristic of the vast majority of European ecosystems.
- d) Regenerating trees are vulnerable until they are tall enough to be safe from browsing.

If trees cannot protect themselves from browsing, then an open landscape is the obvious outcome.

Using Trophic Levels to Determine Expected Herbivore Numbers

In natural ecosystems the amount of browsing is dependent on the population level of the indigenous herbivores, which leads to the question: ‘What is the expected natural population level?’

A standard model used in ecology is that of trophic levels, as first developed by Lindeman in 1942 [5]. At the bottom level is the primary production, i.e., the biomass of plants produced through photosynthesis. Plants are eaten by the primary consumers (herbivores) which themselves are eaten by the secondary consumers (carnivores); in some food chains there can also be tertiary (and higher) consumers. As a rule of thumb, only 10% of the energy (biomass = chemical energy) passes up to the next level. Thus for, example, in a given area, every 100 kg of plant material produced annually will support 10 kg of herbivores and 1kg of carnivores. Although a generalised and simplified model, this trophic level approach can be applied ecosystems.

The vegetation of the Scottish Highlands is here used as an example, as shown in Figure 2. The data come from various sources. The plant production figure comes from whole ecosystem production studies carried out at Moor House National Nature Reserve in the northern Pennines in the 1970s as part of the International Biological Programme [6]. This indicated net annual plant production averaged over a range of habitats as 635g dry wt $m^{-2}y^{-1}$, range 491-868. This equates to a photosynthetic efficiency of 1%, i.e., 1% of usable solar energy is converted to biomass. The study site is further south than Scotland, although at 550m altitude has a similar range of habitats. In Figure 2, a conservative value of 500g dry wt $m^{-2}y^{-1}$ has been used.

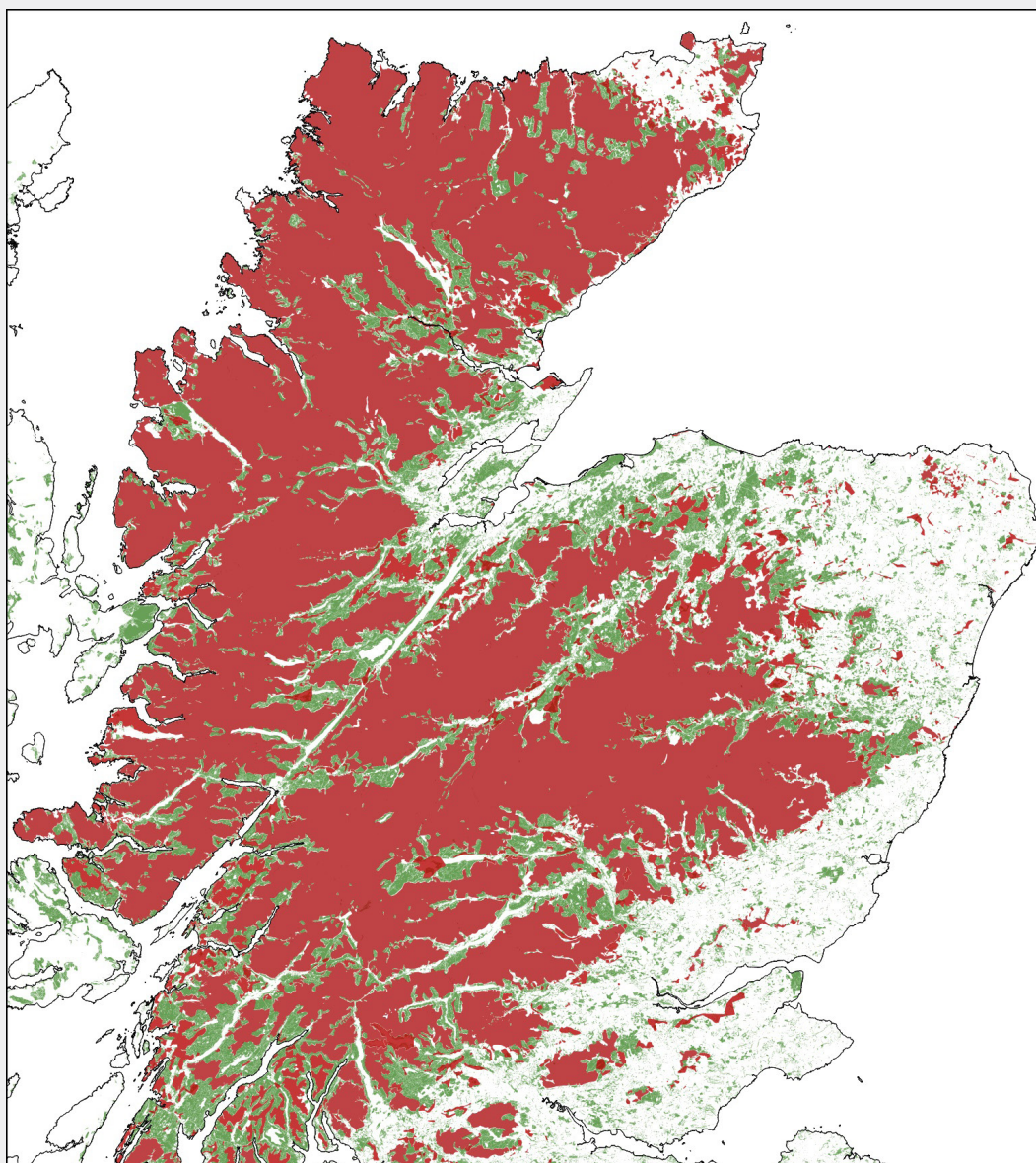


Figure 1: Distribution of unwooded moorland (red) and woodland (green) in mainland northern Scotland, the area here described as 'the Highlands'. Most of the mapped woodland consists of post-1900 plantations. Contains OS Data Crown Copyright 2018. Licensed under Open Government Licence v3.0. Produced on QGIS by James Fenton.

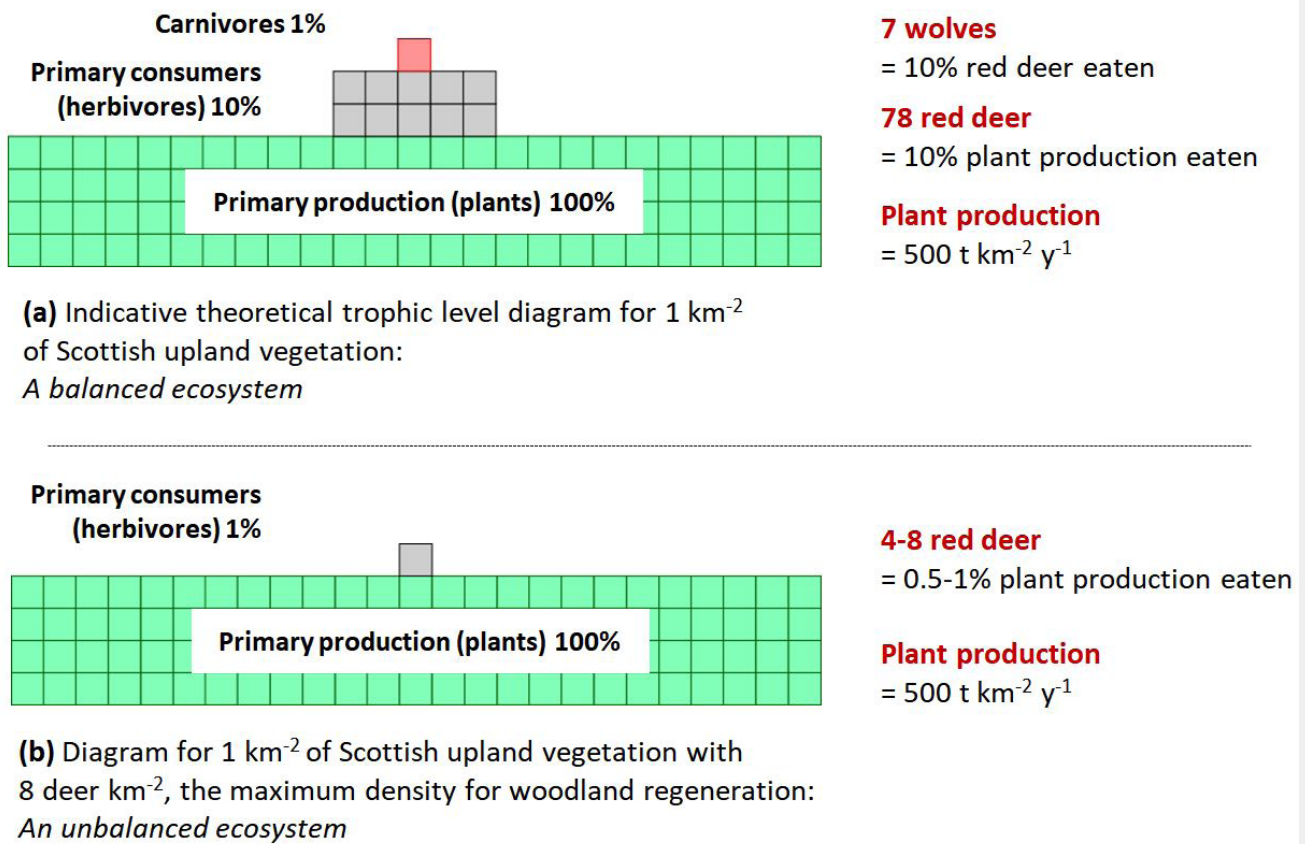


Figure 2: Trophic level diagrams for the Highlands, comparing the expected theoretical herbivore population with the level below which woodland regeneration is possible.

The dominant indigenous herbivore in the Highlands is the red deer (*Cervus elephas scoticus*). Armstrong [7] gives the daily food intake of red deer and an average value of 1.75kg dry matter per day has here been used. This figure gives a theoretical deer density of 78km⁻² assuming 10% of the plant production (biomass) passes to the primary consumers. This is a simplification in that it assumes that red deer are the only such consumer, whereas in practice there will be others dependent on location including roe deer (*Capreolus capreolus*), mountain hares (*Lepus timidus*), voles (*Clethrionomys glareolus*), red grouse (*Lagopus lagopus scotica*) and insects; in many areas, particularly in the locations of the north and west without domestic livestock, red deer are the only significant herbivore. However, Figure 2 does give an order of magnitude indication of the deer carrying capacity, which in practice will vary depending on the proportion and palatability of the actual vegetation types present. The same method indicates a carrying capacity of 131 blackface sheep, 23 Highland cows or 1,000 mountain hares based on the food intake data given by Armstrong [7]. The sheep figure equates well with St Kilda studies where the small Soay sheep in an unmanaged and unpredated environment have a varying density of 100-300km⁻² [8]. Additionally, King & Nicholson [9] show that in 1952 the densities of free-ranging sheep on upland farms in Scotland ranged from

>25km⁻² in the far north to 167km⁻² in the south of the area, with the majority of the area having a density of 50-100km⁻².

The wolf (*Canis lupus*) figures of 7km⁻² are added for interest, based on an average daily meat consumption of 5.53kg per day (with a range 2.77-10.4) and 65% water content of the meat [10,11].

Figure 2 shows how the trophic levels would look, based on similar assumptions, when deer density is within the range 4-8km⁻², the level which is recommended for tree regeneration in the Highlands [12-15]. It illustrates an unbalanced ecosystem with a herbivore density such that one square kilometre of land would not provide enough deer to support a single wolf.

It also indicates that only 1% of the plant productivity is eaten, an order of magnitude less than would be expected from the theoretical model. This order of magnitude difference is one reason why it is so difficult to keep deer numbers low because there is enough food to support a much higher population; constant culling is needed to keep the population below the vegetation carrying capacity. The Figure 2(a) also illustrates that the presence of wolves amongst unmanaged red deer would not bring the density down to 4-8km⁻².

This trophic level model assumes that herbivore population levels are largely determined by food supply as suggested by Milner et al. [16]: the greater the vegetation productivity, then the greater the expected animal population. What little research there has been on this topic shows that unmanaged populations of red deer in Scotland are somewhere between the theoretical density of 78 deer km⁻² and the density of 4-8km⁻² necessary for woodland survival. Studies on the Letterewe Estate in the north west of Scotland and on the Isle of Rum indicate this density to be of the order of 16-18 red deer km⁻² [16,17]. The Letterewe study also indicates that a population level of 16-18 red deer km⁻² would result in 15% offtake of the vegetation biomass, a higher figure than the 10% of Figure 2, and yet resulting in a deer population level lower than the 78km⁻² calculated.

A recent review by Pedersen et al. [18] indicates that the offtake of vegetation by herbivores in the current natural areas of the world is of the order of 7% but would be expected to be nearer 13% if humans had not made many large herbivores extinct. This is very similar to the 15% of the Letterewe study [16] and of the same order as suggested by the trophic level model in Figure 2(a). The implications of this are that the Letterewe area at the time of the study in 2002 had a natural level of grazing because it had retained its population of indigenous herbivores, albeit at a level greater than that which would sustain woodland (1% offtake).

This discrepancy between the theoretical carrying capacity from Figure 2 and the actual population density can perhaps be explained by the seasonal nature of plant growth in the Highlands: most primary production takes place in the relatively short period of late spring and summer. Grazing at this time will be intense, with a high biomass offtake, as deer make up for their reserves lost over the winter and also have to support the current year's calves. The summer plant production will support a large number of animals, more than can survive the lean winter months: as Milner et al. have stated [16], it is the food availability during the unfavourable season which will be the ultimate determinant of herbivore populations and there is little palatable vegetation available during winter and early spring in the Highlands. This is reinforced by the conclusions of Pemberton & Kruuk [17] who state that in the absence of culling or supplementary feeding, the population density of red deer on the island of Rum is strictly dictated by the overwinter carrying capacity of the land. Therefore, it is not only the annual plant production which will determine the carrying capacity but also how much of this production the animals can store to maintain their metabolism through the unfavourable season.

Additionally, the trophic level approach averages the vegetation production across the whole altitudinal range and landscape and different vegetation types will have different palatability; also, significant tracts of land in the Highlands may have a lower productivity than that modelled, and hence would support a lower deer population. There have been few studies of

the overall vegetation productivity at the landscape scale across the Scottish Highlands and more research is needed on this topic. However, both the trophic level model and actual studies indicate that the vegetation is supporting a deer population significantly higher than that necessary to maintain woodland in the landscape.

These conclusions suggest that the indigenous herbivores of the Highlands are likely to keep the landscape open. It is a situation we are unfamiliar with in Europe as a whole because we have made most such species extinct or manage them to very low population levels [18]. For example, the environmental historian Kaplan says that removal of large animal species by humans has had effects on the landscape that are apparent almost everywhere: "A lot of land would be semi-open, kept partly open by these big herds of grazers and browsers and predators. It is important to keep in mind that landscape is also shaped by animals. These giant herds of bison would be trampling down little trees and keeping the landscape open [19]." Perhaps within Europe it is only the Scottish Highlands where free-ranging herds of indigenous large herbivores have been present throughout the postglacial period that we can observe their role in natural ecosystems.

Hence the Scottish hills are not treeless through 'over-grazing' which is the current opinion of many conservation organisations: the grazing level of 4-8 deer km⁻² necessary to maintain woodland in the landscape is a low grazing level according to the trophic level model. To quote Milner et al. [16] in reference to the Highlands: "Over-grazing is a controversial term ... Its precise definition is dependent on management objectives ... Over-grazing is not generally applied to natural ecosystems, even under heavy grazing pressure, because wild herbivores are regulated by their food supply during the unfavourable season ... For example, there is no evidence of habitat degradation on St Kilda or the North Block of Rum where herbivore populations are naturally regulated" [17].

Scenarios of Woodland Survival in the Presence of Grazing

In northwest Europe during interglacial periods there is recognised plant succession from an initial protocratic phase following ice retreat, through a mesocratic to an oligocratic phase as illustrated in Figure 3, taken from Birks and Birks [20]. This succession has taken place in previous interglacials in the absence of humans. The middle mesocratic phase is optimal for woodland with the highest percentage of the landscape covered with trees, a percentage which thereafter declines. The succession is brought about through long-term changes in both soil and climate, with the availability of soil nutrients, particularly phosphorus and nitrogen, reducing over time through leaching. In the past, the successional changes finished with a return to glacial conditions (the cryocratic phase), although anthropogenic global warming means that this is unlikely to be the case in the future.

For woodland to persist in the light of these long-term changes, conditions have to be permanently favourable for the survival of

seedlings and saplings. The next section lists the conditions under which woodland could persist in the European landscape (i.e., young trees can survive browsing) assuming indigenous large herbivores are present (and/or free-ranging domestic analogues) in accordance with the theory of trophic levels discussed above.

Woodland dominant or common in the landscape

Scenario A: Optimal soils/climate

In conditions favourable for tree growth with abundant production of viable seeds and seedlings, then there is a greater probability of woodland persisting in the landscape. It should be noted, though, that optimal conditions for trees are also likely to result in optimal conditions for the associated herbivores so it may not always be the case that optimal conditions for tree growth result in closed high forest without the help of the other factors (as discussed below). But with optimal conditions, there

will be a higher probability of at least some woods surviving in the landscape whatever the grazing level.

As the current interglacial progressed in the wet climate of the Highlands, with its generally base-poor bedrock, continual leaching resulted in soils too acid for earthworms causing the formation of unmixed, stratified soils, often underlain by an impermeable ironpan. The presence of a thick humus layer together with the ironpan makes the soils liable to waterlogging. This indicates the natural succession from the mesocratic to the oligocratic phase (Figure 3). Thompson [21] states that such “a combination of very low soil nutrient availability and high soil moisture provides very unfavourable conditions for colonisation of birch (*Betula*), rowan (*Sorbus aucuparia*) and Scots pine (*Pinus sylvestris*)”. Hence the suitability of this landscape for regeneration of the native tree species declined as the interglacial progressed, a topic discussed in more detail by Fenton in 2008 [22].

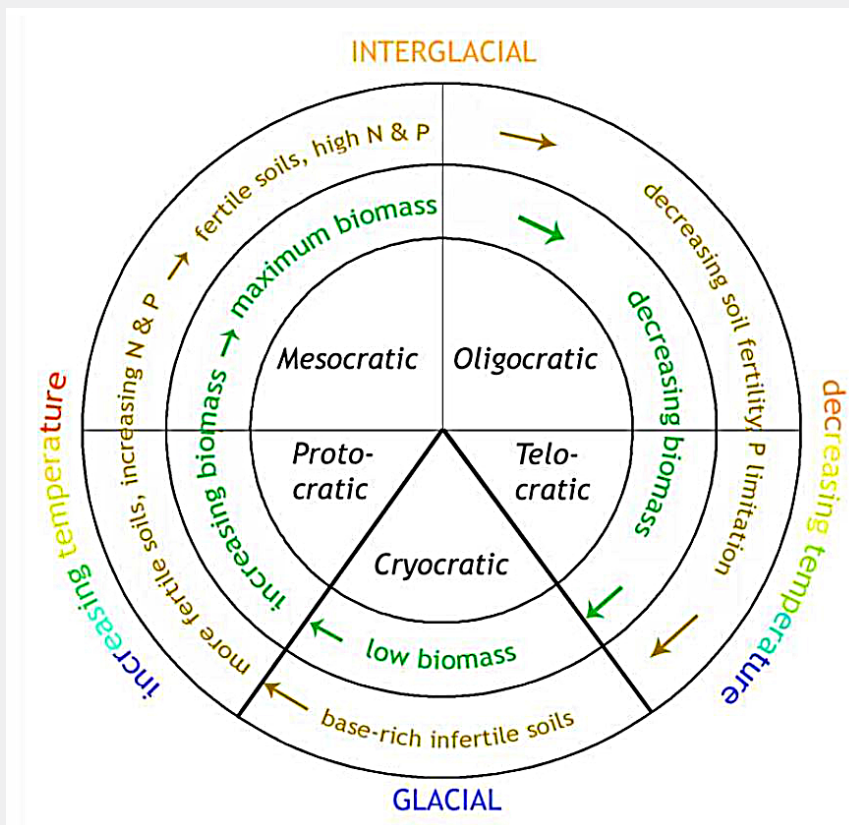
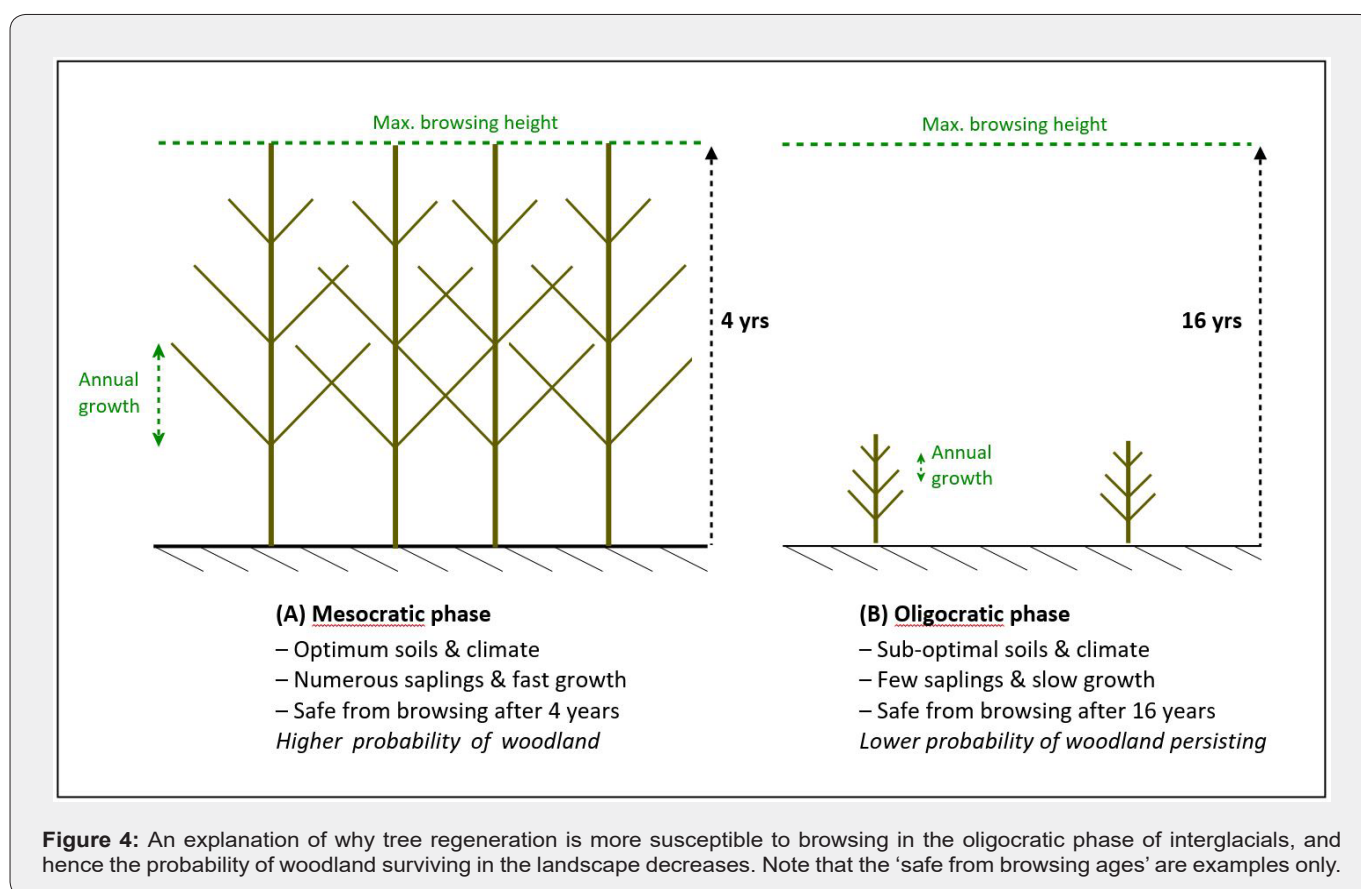


Figure 3: The interglacial cycle. Anthropogenic warming may mean that there is no return to a cryocratic phase. From Birks and Birks (2004) <https://doi.org/10.1126/science.1101357>. Reprinted with permission from AAAS.

Svenning in 2002 suggested that “the ability of large herbivores to open up the vegetation would probably ... be stronger on poor soils” [23], but he does not state why. Figure 4 provides an explanation, indicating how, as the soils deteriorated in Scotland, the role of herbivores in opening up the landscape increased. In the early interglacial phases, conditions are optimal for tree regeneration and the probability of at least some saplings

surviving browsing and going on to develop high forest is high. However, as conditions later become sub-optimal, fewer seedlings are able to establish and the saplings take significantly longer to grow beyond the reach of herbivores: hence the probability of their being browsed becomes high with very few, if any, being able to go on to become mature trees.



The concept of climax, developed by Clements in 1916 [24], assumes that in a given location the vegetation goes through seral stages until it reaches a steady-state – the climax plant community. Clements saw this stable state as being brought about by the ability of the plants involved to retain dominance over time. However, Figure 4 illustrates that, in the presence of browsing animals, over long time-scales conditions can slowly change such that trees lose their ability to retain dominance. In other words, the mesocratic woodland is itself but a seral stage to a more stable climax of open-ground plant communities. Whether the moorland communities themselves remain as the climax vegetation in the Scottish Highlands depends on the long-term trajectory of climate change or, in the case of peatland, the long-term dynamics of the peat itself [25].

In summary, the climate and soils in the Highlands were more favourable for tree growth in the mesocratic phase of the interglacial so that the probability of some trees surviving to above browsing height was higher then. In the current conditions, the probability on most of the now impoverished soils is low so that woodland needs some protection from browsing to remain common. The exception to this is in sheltered coastal locations on the west coast where the favourable climate allows wintergreen vegetation to survive, enabling the herbivores in winter to eat this rather than young trees [22].

The following scenarios indicate the situations in which young trees can be protected from grazing.

Scenario B: Protection by thorny shrubs

Vera demonstrates how high forest can persist in the landscape of lowland Europe as one component of a mosaic of grassland, scrub and woodland [26]. Species of thorny scrub colonise open ground and thereafter protect seedlings and saplings from browsing. The saplings go on to develop high forest, which shade out the shrubs allowing large herbivores in which prevent *in situ* regeneration. When the trees eventually die, the cycle starts over again. Over long time-scales this results in an ever-changing mosaic of vegetation types rather than continuous high forest. Alexander *et al.* have reviewed the evidence for this in lowland Britain and conclude: “the post-glacial landscape exhibited a diverse mosaic of vegetation types, with open country very prominent ...” [27]. In other words, in lowland England (which might be representative of lowland temperate Europe as a whole), the lowland landscape would not consist of continuous climax forest.

The Vera model is predicated on thorny shrubs being present, which in Britain would comprise primarily bramble (*Rubus fruticosus*), blackthorn (*Prunus spinosa*) and hawthorn (*Crataegus monogyna*). However, these are all species characteristic of mesotrophic soils and do not occur in most locations across the

Scottish Highlands because, for reasons of soils and climate, the area is beyond their ecological range. The exception is coastal locations in the southwest Highlands where the climate is milder and the soils richer. In these locations, the Vera model can be seen to be operating as illustrated in Figure 5. However, over

most of the Highlands the Vera model will not apply, resulting in a greater probability of an open landscape. In recent years there has been an invasion of gorse (*Ulex europaeus*) into many parts of the Highlands, and it is possible that this species could in future protect young trees from browsing.



Figure 5: Scenario B: Blackthorn scrub invading grassland, with tree colonisation following the Vera model. A common situation in coastal Argyll which, unlike most of the Highlands, has richer soils suitable for hawthorn, blackthorn and brambles. In areas ecological unsuitable for such shrubs, an open landscape might be expected. (Photo: J. Fenton)

Scenario C: Protection by winter snow

In the parts of the world where winters are characterised by long periods of snow cover, then this snow protects any young trees from browsing as well as limiting the possible over-wintering herbivore population (Figure 6). Young trees are at their most vulnerable from browsing during winter and early spring when there is little other palatable food available other than nutritious buds. By the time of the snow melt, there is sufficient growth of other vegetation to dilute the impact of tree browsing. Note that damage to young trees by small rodents such as voles and lemmings (*Lemmus lemmus*) will not be affected by snow cover.

This winter snow cover explains the presence of woodland and scrub, often as the dominant community, in boreal, sub-arctic and sub-alpine locations across Europe in the absence of thorny shrubs. However upland Scotland has a montane climate, characterised by variable winter snow cover and hills of low enough altitude (maximum 1345m) for the indigenous herbivores (red deer) to easily migrate from the valleys to summits and back

in a day as the weather permits. Hence the high-altitude vegetation at the putative climatic tree line can be grazed at any time of the year, particularly because the montane grasslands on the steep hill slopes can provide better grazing than the acidic often peat-covered low ground and so draw the herbivores upwards.

This would explain the conclusion of Poore in relation to the Highlands that “there is little evidence that there was extensive scrub on the mountains within the current climatic period” [28]. Any small stands of existing sub-alpine/sub-arctic scrub in a few favoured locations are probably relicts from a colder period.

Scenario D: Tree morphology and toxicity

As discussed in scenario B above, thorny shrubs can resist browsing owing to their morphology and can colonise in the presence of herbivores. In contrast, the indigenous high forest trees of the Highlands (*Quercus petraea*, *Q. robur*, *Betula pubescens*, *B. pendula*, *Pinus sylvestris*, *Fraxinus excelsior*) are all browsable by herbivores to a level which can prevent regeneration.



Figure 6: Scenario C: Above Lillehammer, Norway. Winter snow cover in boreal climates both protects trees from grazing and prevents high over-wintering herbivore numbers. (Photo: J. Fenton).



Figure 7: Scenario D: Sitka spruce colonising moorland because its spiky needles are relatively resistant to grazing and establishment conditions are suitable for this species. (Photo: J. Fenton).

However non-indigenous trees, particularly Sitka spruce (*Picea sitchensis*), can often be seen colonising the Highland landscape because their spiky leaves result in minimal browsing and also because they are perhaps more suited to the prevailing

soil conditions than indigenous species (Figure 7). Similarly, the tall introduced shrub *Rhododendron ponticum* is colonising large tracts of the Highlands because of its toxicity to herbivores. It is therefore perhaps a matter of the chance of ecological

history whether a given landscape will be wooded or unwooded dependent on the characteristics of the trees or large shrubs which naturally colonised the area. This might explain the difference in characteristics of the wooded Pacific northwest coast of North America and the unwooded Scottish Highlands.

It is not that the Scottish Highlands are ecologically unsuited to all trees, just to the tree species that naturally colonised Scotland in the postglacial period. If soils are modified to reflect the early postglacial conditions by draining, ploughing and addition of fertiliser (particularly phosphate) then the indigenous trees grow well in locations not exposed to the strong winds characteristic of the area, as indicated by the numerous successful plantations of native trees.

Scenario E: Anthropogenic grazing reduction

Where humans have either eliminated grazing, or reduced it significantly from the expected natural level, then this can result in an increase in woodland cover, or allow woodland to persist where it otherwise might have declined or moved around the landscape (Figure 8). This has been a common situation within Europe in historical times where enclosed woodland blocks have been managed to provide a permanent supply of wood and timber, and perhaps also in less managed landscapes where there are no longer significant herbivore populations such as in parts of western Norway. It is also a common approach used in Scotland by organisations wishing to encourage the spread of native woodland.



Figure 8: Scenario E: An example of an ancient broadleaved woodland in England (Dorset) where enclosure and management has allowed it to persist in situ. (Photo: J. Fenton).

Woodland localised in the landscape

Scenario F: Geomorphological features

In many landscapes there are locations where the geomorphological features provide a natural barrier to large herbivores, resulting in no or reduced grazing (Figure 9). These are generally steep slopes or areas of rough topography. However, it should be noted that in wet climates steep slopes may also hold trees because the better drainage and mineral flushing results in soil conditions more suitable for trees. Hence the presence of trees in such places might be a result of a combination of both reduced

grazing and better soil conditions. There are also instances where dense vegetation such as tall *Calluna vulgaris* heath can provide some protection from grazing, allowing occasional trees to survive.

Scenario G: Episodic events

It is possible to envisage situations where episodic events provide a temporary reduction in grazing allowing some woodland regeneration. Examples could include an outbreak of disease or, as in tundra ecosystems harsh winters causing heavy herbivore mortality [29].

Scenario H: Predation hotspots

The trophic level model discussed above indicates that there has to be a significant herbivore population in order to support the presence of large carnivores, and that a population low enough to allow tree regeneration would not be large enough for a significant wolf population. Indeed, Warren concludes: "The evidence from Norway and America is that low numbers of large predators have little effect on deer numbers ... To have a significant impact on deer populations, a very large number of wolves would be needed, and there is unlikely to be enough space in Scotland (either ecologically, or socio-politically) for such large wolf populations" [30].

Large carnivores have become extinct over much of Europe so that it is hard to know what their impact in practice would be on both the population levels and distribution of large herbivores. In the Highlands, stalking (shooting) of red deer by humans causes the deer to move up to the higher slopes of the hills. This suggests that predation by wolves might also cause the deer to move up the hill, thus increasing the grazing level on the higher slopes and also preventing the growth of montane scrub.

Although both the climate and ecology are different, there has been much debate about the impact of the reintroduction of the wolf (*Canis lupus*) on the elk (*Cervus elaphus Canadensis*, a sub-species of red deer) population of Yellowstone Park in the

USA. However, MacNulty et al. conclude that "scientific consensus about the role of wolves in driving the dynamics of the northern herd has yet to emerge, despite 20 years of research by numerous federal, state, and academic investigators" [31].

A key point is that the wolf became extinct in Scotland in the eighteenth century, which is relatively recently in ecological terms, and that the woodland declined naturally over the previous millennia when wolves were present. This, together with the trophic level model, suggests that their reintroduction is unlikely to result in large scale recolonisation of the Highlands by trees. It is possible their presence might cause a reduction in grazing pressure in locations favoured by them and so promote localised woodland regeneration. However the only way to be sure of this is reintroduce the wolf and observe the result.

Application of the above scenarios to different areas of Europe

Table 1 summarises the above scenarios and applies them to three different areas of Europe. It should be noted that the situation can change with time. For example, in the Scottish Highlands conditions were better for tree regeneration in the mesocratic phase of the current postglacial period so that woodland was more common then, but the conditions for woodland survival have deteriorated in the current oligocratic phase.

Table 1: Theoretical probability of woodland in the landscape in three different areas of Europe.

Scenario of Woodland Protection	Lowland England (Lowland Europe)	Scottish Highlands	Boreal, Sub-arctic and Sub-alpine regions
Woodland Common			
A) Optimum soils/climate	✓	×	✓
B) Protection by thorny shrubs	✓	×	×
C) Protection by winter snow	×	×	✓
D) Tree morphology/toxicity	×	×	✓ (spruce)
E) Anthropogenic grazing reduction	✓	×	✓ (In some locations)
Localised Woodland			
F) Geomorphological features	✓	✓	✓
G) Episodic events	?	?	?
H) Predation hotspots	?	?	?
Expected Landscape	Woodland Common	Woodland Rare	Woodland Common

Discussion: The Scottish Highlands as an Example of a Naturally Open Landscape

Changing views of the scottish highlands

In spite of considerable forestry and woodland plantings over the past 100 years or so, the hill area of the Scottish Highlands

is dominated by open unwooded moorland vegetation of acid grassland, dry heath, wet heath, peatland and montane habitats (Figure 1). Views about whether this open ground represents the climatic climax vegetation or an anthropogenically determined biotic climax have changed over time.

In 1866 the eminent geologist, James Geikie, having studied numerous remains of old forests in peat bogs throughout Scotland, read a paper to the Royal Society of Edinburgh in which he concluded: "It can be shown that the destruction of our ancient forests has not been primarily due to man..." [32]. Moss in 1913 concluded that at least some areas of the open landscape of upland Britain could be natural in origin: "The conversion of woodland into scrub and of scrub into grassland, heath and moor is seen not only on the Pennines but in Wales, in the Lake District and in Scotland ... Such successions are not exceptional in this country but widespread and general; and whilst they are without doubt often due to artificial causes, it is at least conceivable that this is not always and wholly the case" [33]. This view is echoed by Pearsall who also recognised this succession across upland Britain, attributing it to a combination of anthropogenic and natural causes; however, he does go on to say that the landscapes of northern Scotland are "probably the least modified man-modified of our mountain or moorland areas" [34].

Fraser considered much of the west coast open moorland of the Highlands to be climax vegetation [35]. More recently, Goodier and Bunce speculated that pine woods may be an endpoint "before return to open moorland as a result of soil degradation" [36].

There has been a lot of work carried out on pollen analysis in the Highlands, and the results are generally in keeping with the interglacial succession process as discussed above and supporting the views of Geikie, i.e., a natural regression of woodland from a postglacial maximum [32]. Paterson gives a good summary of this research in relation to indigenous pinewood: "In core areas, woodland is subject to fragmentation from as early as c. 7500cal BP; fragmentation is diachronous and is believed to have been earliest in the west. Human activity is sometimes implicated in woodland fragmentation but is more often cited as reinforcing the effects of a maritime climate preferentially affecting *Pinus* dominated woodlands ... Only in Speyside is human activity thought to initiate disintegration" [37].

Fyfe has reviewed the evidence from pollen analysis on the openness or otherwise of the British vegetation and concluded: "At the continental scale, western Atlantic Europe has for long been more open than other parts of the mainland. Britain and Ireland (especially western and northern regions) are particularly notable in this context and are different from much of inland continental Europe. This conclusion is replicated irrespective of which analytical method is applied to the pollen data" [38].

The above illustrates the pitfalls of generalisations across all of Britain and Europe. Ecologists have tended to see the north of Britain with the eyes of the south, unthinkingly transferring to the north what is valid understanding and or valid approaches further south with a rather simplistic assumption that the ecological characteristics should be the same across the UK. As an example, the phrase 'upland vegetation' is often used to describe vegetation

found at sea level in northwest Scotland: for example, Averis et al. [3] state that "an upland type of climate... descends to sea level in the cooler northwest" [3]. However, looked at objectively, if a vegetation type occurs at sea level it is, by definition, lowland vegetation and the climate is also lowland. Certainly, if you are brought up in England, vegetation found at sea level in northern Scotland is upland vegetation in, say, the English Pennines. But someone from the north of Scotland could equally question why this vegetation type is termed 'upland' in England – would it not make equal sense to call the Pennine moors 'lowland vegetation'?

It should be noted that palynologists have largely related changes in woodland cover over the millennia to changes in climate as, for example, in Clements' original review of plant succession [24], and the recent example of Paterson quoted above [37]. Although Svenning does suggest that herbivores might keep the landscape open on poor soils [23], Bradshaw and Mitchell conclude that "the role of past herbivore-vegetation interactions as a causal factor in determining plant community composition and dynamics has been largely ignored by palaeoecologists" [39] – an issue this paper is seeking to address.

In spite of the above contrary views, the current dominant view of the Highlands is that promoted by the ecologist Frank Fraser Darling who stated that the Highlands were 'a devastated countryside', the devastation brought about by anthropogenic woodland loss, the landscape kept open by artificially high populations of herbivores, domestic or wild [40]. This view is echoed by both McVean & Ratcliffe [1] and McVean who states "the destruction of the original forest cover of Scotland has been taking place since Neolithic times and is now virtually complete" [41].

Associated with the view of human-destroyed woodland is the concept of the Great Wood of Caledon as a forest which once clothed the Highlands but which humans have destroyed over the centuries. Although it is certainly the case that woodland was more common in the Highlands thousands of years ago, historians now conclude that the Great Wood of Caledon as a forest of historical times is a myth [42,43]. However the concept is popular in the public imagination and is one of the main driving forces behind woodland restoration schemes across the Highlands promoted by nature conservation organisations (Figure 10).

Impact of humans on woodland cover

In the popular literature, loss of woodland to the Highlands has often been attributed to human activity such as felling, burning, sheep grazing and encouragement of deer on sporting estates. However, examination of the military maps produced by General Roy and his team in the period 1747-52 exhibits the then rarity of woodland in the Highland landscape, with an example shown here in Figure 11. In addition to woodland, the Roy maps also illustrate areas of settlement and show that in many

instances there were woods and settlements in the same locality, whereas the uninhabited areas were unwooded: this could either be because both humans and trees have selected the optimum

sites, or that humans prevented complete woodland loss owing to the value of the trees [44].



Figure 9: Scenario F: Glen Coe in the Highlands showing persistence of woodland on steep slopes, cliffs and gorges where grazing is reduced or absent. (Photo: J. Fenton).



Figure 10: New native woodlands in the name of ecological restoration are being planted all over the Highlands, here a new Scots pine wood near Gairloch in Wester Ross planted on unwooded moorland. (Photo: J. Fenton).



Figure 11: An extract from the Roy maps 1747-52 of the Loch Monar area. Red arrows indicate woodland locations. The map indicates the area was largely unpopulated and unwooded. Reproduced with the permission of the National Library of Scotland.

The Roy maps illustrate the fact that woodland loss must have taken place in previous eras when large tracts of the Highlands, particularly away from the coast and main valleys were largely wild and unpopulated. To quote the historian Tom Devine: “Settlement in the western Highlands and Islands was mainly confined to very limited areas because of the challenging constraints of geology, climate and geography. Therefore, when modern visitors contemplate hills and glens which are empty of people, they should not assume they were inhabited in the past. Or that their present silence and loneliness were necessarily the consequence of later clearance and emigration” [45].

In fact large tracts of the Highlands were unused, apart from the localities of transhumance, i.e., used for the summer grazings of cattle (shielings); and such summer use is generally seen as beneficial to tree regeneration. Haldane states: “... not until sheep farming on a large scale became common in the Highlands [post 1750] were these upland areas put to fuller use than for the grazing of cattle from the shielings in summer and early autumn” [46].

Domestic stock before the eighteenth century probably would have consisted of the small, black Highland cattle, small breeds of sheep, goats and a few horses, although Steven and Carlisle conclude that “such records as there are indicate that the numbers are not large” [47]. Haldane adds that the cattle were taken off the shielings (summer pastures) by end of September and sheep

were wintered indoors. Large-scale sheep farming only came in after the wolf was extinct and the social structure changed from a clan-based system to landowner-based which was accelerated following the Battle of Culloden in 1746 [45] – by which time the woodland was long gone.

It should be noted that there were no roads through most of the Highlands before 1750, so access to timber and its extraction was impossible except in Strathspey where logs could be floated down the River Spey to the sea. Indeed, the Earl of Mar in 1618 bemoaned the fact that the indigenous pine woods on his land in the eastern Cairngorms were of no economic value to him because the timber could not be extracted [48].

Industrial exploitation of timber largely started after 1750 when woodland was already rare in the landscape but there is little evidence that this exploitation resulted in significant woodland loss. To quote Lindsay: “The largest and longest-lived of the [ironworks], The Bonawe Furnace in Argyll, needed 10,000 acres of oak coppice to keep going, and left the woods in at least as extensive condition when it closed in 1876 as when it opened in 1753” [49]. Smout adds that “the same could be said of the much more widespread users of oak coppice, the tanbarkers, who operated throughout Argyll, Perthshire, Dunbartonshire, and Stirlingshire” [43].

The Roy Maps indicate that only about 4% of the Highland landscape was wooded in 1750 so that most woodland loss must

have taken place before then. Sometimes anthropogenic woodland loss is pushed back in time to the earliest inhabitants of Scotland, but this itself raises a host of ecological questions:

1) Which particular areas are we talking about as is improbable that much of the mid to high altitude ground was ever inhabited? What percentage of the landscape would have been involved? It is extremely improbable that large tracts were ever farmed. Why did the trees not regenerate after felling? Why would a relatively small human population have needed so much wood?

2) Early peoples were unlikely to cut down or burn all the trees at once in a given locality, allowing plenty of time for cut/burnt woodland to regenerate, so why did it not regenerate? We know today that clearfell sites provide optimum regeneration conditions.

3) The presence of wolves would have prevented early populations having large free-ranging populations of grazing animals. Is it not possible also that early colonisers killed and ate deer, hence reducing their numbers and encouraging trees? Indeed, it is possible that the hunting of deer over the millennia has resulted in less deer than would occur naturally, thus encouraging woodland rather than destroying it.

4) People came and went, with a loss of population in periods of climate deterioration, allowing plenty of time for woodland to recover. So why did it not?

5) It has been suggested that early felling caused an ecological tipping point from woodland to moorland, human activity pushing the ecosystem to a new non-woodland dynamic.

But to be the case, it would have to have been over the whole landscape, and the fact that the landscape also opened-up in interglacials without humans (Birks and Birks 2004) suggests that the transitions would have happened in any case.

6) The sheer abundance of open moorland across all of Scotland indicates that successional trends are pointing in this direction because it is more resilient than woodland: to persist in the landscape, woodland always has a sensitive period when young trees have to out-compete the other vegetation without being browsed. It could be the case, that in some localities, human activity did accelerate a natural decline, but the endpoint would be the same.

A point which is often missed is that, come 1750, 96% of the Highland landscape would have been open moorland, so that, taking a wide strategic overview, any woodland loss subsequent to this becomes largely irrelevant. In practice, though, because woodland is rare in the landscape, and because rarity is a criterium indicating nature conservation importance [50], most conservation effort has been focussed on the remaining woodland. This strong focus on one rare and declining habitat type has tended to skew the nature conservation effort: no value is ascribed to that which is common.

However, if you stand back and view the Highlands from an international perspective, then that which is locally common (temperate moorland) is seen to be globally rare, and that which is locally rare (temperate woodland) is globally common. Indeed, many of the open moorland habitats are recognised as being of international importance under the EU Habitats Directive.



Figure 12: A natural open landscape in Wester Ross, NW Scotland, with woodland localised and rare. (Photo: J. Fenton).

Conclusion

Evidence suggests that, away from settlements, the open nature of Highland landscape is largely natural in origin (Figure 12). Such open moorland with only isolated woodlands is the key characteristic of the terrestrial biodiversity of the Highlands. Indeed, this perhaps represents one of the most natural vegetation patterns remaining in Europe.

The Highlands are different from most of Europe in that the human population over most of history has been low, with some areas, particularly away from the coast and the main valleys, uninhabited. This makes the Scottish Highlands unique in that the continuing processes of postglacial plant succession can be observed in a location of minimal human impact. The analysis here makes it improbable that humans have been a major cause of deforestation of the landscape as a whole, and supports the successional process of natural regression of forests in this, the oligocratic phase of an interglacial, from a postglacial maximum as described by Birks and Birks [20]. Related to this is the fact that much of the level and gently sloping ground of the Highlands is peat covered, which supports the view of Klinger that peat bogs can be the end point of succession in many parts of the world [51].

Hence the mainstream view that the Highlands are a once-forested landscape, the forest destroyed by anthropogenic activity, needs revision, as it does for other naturally open landscapes in the world. Veldman et al. [52] state: "The WRI [World Resources' Institute] erroneously assumes that non-forest areas where climate could theoretically permit forest development are 'deforested', an assumption rooted in outdated ideas about potential vegetation and the roles of fire and herbivores in natural systems" [52].

The open landscape of the Highlands is caused by the discrepancy between the herbivore carrying capacity and the lower density required to ensure woodland survival, combined with a lack any natural mechanism to prevent young trees from browsing which is found in other areas of Europe, such as the presence of thorny shrubs or persistent winter snow cover. The dominance of acidic, waterlogged soils, resulting in sub-optimal soils for tree regeneration, is also a major contributing factor, resulting in both a lower probability of seeding establishment and a higher probability of seedlings and saplings being eaten.

It should be noted, though, that across the Highland landscape as a whole all three models of woodland dynamics [22] can be observed: 'woodland as climax' in a few optimal coastal locations and in those naturally protected from grazing by topography; 'the cyclical model' as proposed by Vera [26] on the better soils and more favourable climate of lowland, coastal Argyll in the southwest Highlands; and 'natural decline', the dominant model over most of the landscape.

The trophic level model as applied here, combined with

an understanding of the ecological mechanisms which deter browsing, can provide a sufficient prediction of whether a given natural landscape will be wooded or not; although it should be noted that where the availability of palatable biomass is highly seasonal, the trophic level model is likely to over-estimate the expected herbivore population. It should also be noted that the model is predicated on herbivores being a natural part of the ecosystem. There are a few areas of Europe, particularly islands such as Iceland and the Faeroes, which large mammalian herbivores never colonised. In this case the natural woodland and scrub, which was once more common, has been largely destroyed by the introduction of domestic livestock, particularly sheep. However, in the Highlands, where sheep were introduced on a large scale in the eighteenth century, their presence has probably made little difference to the overall tree cover owing to the pre-existence of populations of the indigenous red deer.

In conclusion, the hypothesis here is that, in temperate ecosystems, high forest is not always the pre-determined climax vegetation. An alternative model of an ever-changing mosaic of vegetation instead of a stable Clementsian climax, as proposed by Vera [26] is supported by recent evidence for lowland Britain [27] but will not apply to most of the Scottish Highlands where the end result of succession appears to be various types of resilient moorland plant communities.

With climate change causing a reduction in consistent winter snow cover in parts of Europe, and also the possibility of it encouraging the spread of temperate thorny shrubs, then there is possibility of both woodland loss and woodland expansion in different regions if natural processes are allowed to determine the direction of ecological change.

Conflict of Interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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