The concept of woodland being the climax community in temperate ecosystems has a long history. However this can be difficult to reconcile with the fact that large herbivores which can browse trees are characteristic of the vast majority of ecosystems (or were before humans made them extinct).

This paper indicates eight scenarios which allow woodland to be the climax vegetation in the presence of browsing. Where herbivores are naturally present, regeneration is only possible if young trees are protected from grazing by thorny shrubs, winter snow cover, unpalatable leaves, rough topography, or regeneration conditions are optimal for young trees so the probability of some surviving browsing is high. If these conditions are not met then an open landscape is to be expected at this, the oligocrotic phase of postglacial succession.

The Scottish Highlands with its open landscape is a case in point: evidence suggests a long period of natural woodland regression from a postglacial maximum extent, with minimal anthropogenic input. The moorland vegetation characteristic of the area 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.

**SUMMARY**

The concept of woodland being the climax community in temperate ecosystems has a long history. However this can be difficult to reconcile with the fact that large herbivores which can browse trees are characteristic of the vast majority of ecosystems (or were before humans made them extinct).

This paper indicates eight scenarios which allow woodland to be the climax vegetation in the presence of browsing. Where herbivores are naturally present, regeneration is only possible if young trees are protected from grazing by thorny shrubs, winter snow cover, unpalatable leaves, rough topography, or regeneration conditions are optimal for young trees so the probability of some surviving browsing is high. If these conditions are not met then an open landscape is to be expected at this, the oligocrotic phase of postglacial succession.

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Introduction

In this paper the Scottish Highlands (here referred to as the Highlands) are used as an example of temperate ecosystems which have retained a population of large indigenous herbivores, the red deer (Cervus elephas), throughout the postglacial period. The landscape is largely unwooded (Figure 1) and Fenton (2008) has explained how its openness can be explained through natural causes. In summary, the ecological carrying capacity of the vegetation for the main indigenous large herbivore is an order of magnitude greater than that which would allow for persistence of woodland in the landscape in this, the oligocronic phase of an interglacial.

However in Scotland the dominant view amongst conservation organisations is that the open nature of the Highlands is anthropogenic: human activity has resulted in hills that are overgrazed – there are now too many deer and, in the past, too many sheep (see for example John Muir Trust 2019). The main justification for this view is the absence of trees in the upland landscape: the argument is along the lines ‘we know there are too many deer because there is too little woodland and grazing prevents regeneration.’ In practice this leads to a circular, self-fulfilling argument: ‘the reason we know there is too little woodland is because there are too many deer.’ This paper takes forward the arguments pursued in Fenton (2008) by addressing what should be the two more pertinent questions.

A. How many deer would you expect in a natural system? – addressed through trophic levels.

B. What is the expected natural distribution of woodland at this stage of the postglacial cycle, assuming herbivores are present at the natural level?

The paper identifies eight different scenarios which would allow woodland to persist in the presence of herbivores.

In the analysis which follows the following three statements are taken to be self-evidently true:

1. Trees are successful because their height means they can outcompete lower-growing competitors to form woods.
2. Regenerating trees are vulnerable until they are tall enough to be safe from browsing.
3. Large herbivores which can browse trees are characteristic of the vast majority of European ecosystems (or were before humans made them extinct).

The aim of this paper is to answer the two questions above and to analyse the implications of these three statements.

References


Figure 1. Distribution of unwooded moorland (red), woodland (green) and agricultural land (white) in mainland northern Scotland, the area here described as ‘the Highlands’.

This is the area used as an example in this paper.

Most of the mapped woodland consists of post-1900 plantations.

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 (1942). 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 1 kg of carnivores.

Although a generalised and simplified model, this trophic level approach can be applied to the vegetation of northern Scotland as shown in Figure 2(a). 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 (Heal et al. 1975). This indicated net annual plant production averaged over a range of habitats as 635 g 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 500 g dry wt m\(^{-2}\)y\(^{-1}\) has been used.

The dominant indigenous herbivore in the Highlands is the red deer (Cervus elephas scoticus). Armstrong (1996) gives the daily food intake of red deer and an average value of 1.75 kg dry matter per day has here been used. This figure gives a theoretical deer density of 78 km\(^{-2}\) 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 scoticus) 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 it 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 in Armstrong (1996). 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 100-300 km\(^{-2}\) (Clutton-Brock and Pemberton 2004). Additionally, King and Nicholson (1964) show that in 1952 the densities of free-ranging sheep on upland farms in Scotland ranged from >25 km\(^{-2}\) in the far north to 167 km\(^{-2}\) in the south of the area, with the majority of the area having a density of 50-100 km\(^{-2}\).

References


The wolf (*Canis lupus*) figures of 7 km\(^{-2}\) are added for interest, based on an average daily meat consumption of 5.53 kg per day (Glowaciński and Profus (1997), Stahler *et al.* (2006) indicate a range 2.77-10.4) and 65% water content of the meat.

**Figure 2(b)** shows how the trophic levels would look, based on similar assumptions, when deer density is within the range 4-8 km\(^{-2}\), the level which is recommended for tree regeneration in the Scottish Highlands (Beaumont *et al.* 1995, Staines 1995, Staines *et al.* 1995, Milne *et al.* 1998). 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. It also indicates that the presence of wolves amongst unmanaged red deer would not bring the density down to 4-8 km\(^{-2}\).

This trophic level model also assumes that herbivore population levels are largely determined by food supply as suggested by Milner *et al.* (2002): 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 4-8 km\(^{-2}\) 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\(^{-2}\) (Milner *et al.* 2002; Pemberton & Kruuk 2015). 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 78 km\(^{-2}\) calculated.

This discrepancy between the theoretical carrying capacity 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.* (2002) point out, 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 and Kruuk (2015) 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.

**References**


**Primary production (plants) 100%**

**Primary consumers (herbivores) 1%**

0 wolves

4-8 red deer
Additionally, the trophic level approach averages the vegetation production across the whole altitudinal range and landscape, and in practice significant tracts of land in the Highlands may have a lower productivity than that modelled, and hence would support a lower deer population than that modelled. 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 the key point is that 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. 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 (Kaplan 2013).”

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 ‘overgrazing’ 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. (2002) in reference to the Highlands:

“Overgrazing is a controversial term ... Its precise definition is dependent on management objectives ... Overgrazing 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.”

2) What is the expected natural distribution of woodland at this stage of the postglacial cycle?

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 as illustrated in Figure 3 (Birks & Birks 2004). 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.

**Scenarios of woodland survival**

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. Given below is a list of conditions which would enable woodland to 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.

**Looked at logically from first principles, woodland will remain or become common in the landscape if:**

A. Optimal soils/climate allows numerous seedlings to germinate and grow so fast that the probability of some surviving browsing is high: *e.g.* mesocratic phase (and also likely to be the case in the tropics).

B. Young trees are protected from browsing by thorny shrubs: temperate forest – the Vera hypothesis (Vera 2000).

C. Young trees are protected by snow in winter and early spring, the period when seedlings and saplings are most vulnerable: *e.g.* boreal & sub-alpine forests, sub-alpine & sub-arctic scrub.

D. Tree morphology or toxicity reduces browsing: *e.g.* spiky needles of spruce, *Rhododendron ponticum*.

E. The anthropogenic activities of removal or reduction of grazing: *e.g.* compartmentalised broadleaved woodland (browsing animals significantly reduced or excluded).

**Woodland may remain localised in the landscape:**

F. Where young trees are protected from grazing by natural features such as cliffs, boulder fields, gullies, or, occasionally, dense vegetation such as tall *Calluna vulgaris*.

G. Episodically, owing to temporary reduction in grazing through extreme weather or disease events.

H. Locations commonly visited by predators.

Each of these eight scenarios is now discussed in more detail.

**Reference**

Woodland dominant or common in the landscape

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 (Figure 4a). 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 Scottish 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 and has resulted in the large-scale development of blanket peat on land with a gentle gradient. This characterises the natural succession from the mesocratic to the oligocratic phase (Figure 3). Thompson (2004) 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 in Fenton (2008).

Svenning (2002) suggests that ‘the ability of large herbivores to open up the vegetation would probably ... be stronger on poor soils’, but he does not state why. Figure 4b 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. Figure 5 shows a location where trees can only regenerate in a localised area with optimal conditions, here a well-drained stream-side at low altitude.

The concept of climax, developed by Clements (1916), 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 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 depends on the long term trajectory of climate change or, in the case of peatland, the long-term dynamics of the peat itself.

References


In summary, the climate and soils were more favourable for tree growth in the mesocraic 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.

B) Protection by thorny shrubs

Vera (2000) shows how high forest can persist in the landscape of lowland Europe as one component of a mosaic of grassland, scrub and woodland. 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. (2018) have reviewed the evidence for this in lowland Britain and concluded: ‘the post-glacial landscape exhibited a diverse mosaic of vegetation types, with open country very prominent.’ 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 Rubus fruticosus, Prunus spinosa and 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 this area observation suggest that the commonest habitat for woodland regeneration is within a Rubus fruticosus/Pteridium aquilinum matrix, and, less commonly, in Prunus spinosa. In these locations, the Vera model can be seen to be operating as illustrated in Figure 6. However, over most of the Highlands the Vera model will not apply, resulting in a greater probability of an open landscape.

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 7). Young trees are at their most vulnerable from browsing during winter and early spring when there is little other palatable food available 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, arctic/sub-arctic and alpine/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 1345 m) for the indigenous herbivores (red deer) to easily migrate from the

References


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 (1997) in relation to the Highlands that ‘there is little evidence that there was extensive scrub on the mountains within the current climatic period.’ Any small stands of existing sub-alpine/arctic in a few favoured locations are probably relics from a colder period.

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, Betula, Pinus, Fraxinus) are all browsable by herbivores to a level which can prevent regeneration.

However non-indigenous trees, particularly Sitka spruce (Picea sitchensis), can often be seen colonising the Highland landscape because its spiky leaves result in minimal browsing and also because it is perhaps more suited to the prevailing soil conditions than indigenous species (Figure 8). Similarly the tall introduced shrub Rhododendron ponticum is colonising large tranches 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.

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 9). 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 large scale landscapes such as western Norway where in the past humans have made large herbivores functionally extinct.

Figure 8. Scenario D: Picea sitchensis colonising moorland in the central Highlands because its spiky needles are relatively resistant to grazing and establishment conditions are suitable for this species. Hence it is better able to regenerate and grow in the Highlands than native tree species.

Figure 9. Scenario E: An example of an ancient broadleaved woodland in England (Dorset) where enclosure, grazing exclusion and management has allowed it to persist in situ.

Reference
Woodland localised in the landscape

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 10). 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 can provide some protection from grazing, allowing occasional trees to survive.

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 (Ims and Fueglei 2009).

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 sufficient to allow tree regeneration would not be large enough to allow for a significant wolf population at the local level. Indeed, Warren (2002) 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.”

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. (2016) conclude:

“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.”

References


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 the presence of wolves might cause a reduction in grazing pressure in locations favoured by them and so promote localised woodland regeneration; but 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

The above analysis indicates that in northwest Europe different geographical regions might be expected to possess different percentages of woodland cover. As an example, Table 1 summarises the above scenarios and applies them to three different areas of Europe.

Discussion in relation to the Highlands of Scotland

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 original views of Geikie (1867) who stated ‘It can be shown that the destruction of our ancient forests has not been primarily due to man’; i.e. a natural regression of woodland from a postglacial maximum. Paterson (2011) gives a good summary of this research in relation to indigenous pine woodland:

“In core areas, woodland is subject to fragmentation from as early as c. 7500 cal 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.”

Fyfe (2018) has recently 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.”

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 (National Library of Scotland 2019) 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

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

<table>
<thead>
<tr>
<th>SCENARIO OF WOODLAND PROTECTION</th>
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<th>Scottish Highlands</th>
<th>Boreal Europe, alpine/arctic, sub-alpine/arctic</th>
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<td>B) Protection by thorny shrubs</td>
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<td>C) Protection by winter snow</td>
<td>x</td>
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<td>D) Tree morphology/toxicity</td>
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<tr>
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</tbody>
</table>

**Woodland common**

**Localised woodland**

| F) Geomorphological features   | ✓               | ✓                  | ✓                                             |
| G) Episodic events             | ?               | ?                  | ?                                             |
| H) Predation hotspots          | ?               | ?                  | ?                                             |

**Expected landscape**

<table>
<thead>
<tr>
<th>Woodland common</th>
<th>Woodland rare</th>
<th>Woodland common</th>
</tr>
</thead>
</table>

References


humans and trees have selected the optimum sites, or that humans prevented complete woodland loss owing to the value of the trees. It would be interesting to undertake a full analysis of the Roy maps to assess the distribution of woodland in relation to settlements.

These maps illustrate the fact that woodland loss in the Highlands from its postglacial maximum 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 Devine (2018):

“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.”

In the centuries preceding 1750 large tracts of the Highlands were unused, apart from the localities of transhumance, i.e. the areas used for the summer grazings of cattle (shielings) – Figure 12; and such summer use is generally seen as beneficial to tree regeneration. Haldane (1952) 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.”

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 ‘such records as there are indicate that the numbers are not large’ (Steven & Carlisle 1959). Haldane states 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 became extinct around 1700 and the social structure changed from a clan-based system to landowner-based which was accelerated following the Battle of Culloden in 1746 (Devine 2018) – by which time woodland cover was about 5%.

It should be noted that there were no roads through most of the Highlands before 1750, so away from settlements 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 (Taylor 1618).

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 (1975):

“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.”

References


Smout (2000) 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.”

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.

The sheer abundance of open moorland across all of Scotland (Figure 1) 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 may well be the case, that in some localities, human activity did accelerate a natural decline, but the endpoint would be the same. It is also worth pointing out that most woodland must have taken place when wolves were present in the landscape.

References


Recent conservation effort in the Highlands

A point which is often missed is that, come 1750, 95% 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 criterion indicating nature conservation importance (Ratcliffe 1977), a significant amount of conservation effort has been focussed on the woodland habitat: whether encouraging tree regeneration or on creating new woodland of indigenous species on open moorland. (Figure 13). This strong focus on one rare and declining habitat type has tended to skew the nature conservation effort: no value is ascribed to the common open ground habitats – with the exception of peatland.

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.

It should also be noted that reintroducing the wolves, although introducing more balance to the ecosystems (Figure 2a), is unlikely to cause a significant increase in woodland cover: postglacial woodland expansion and decline occurred during the 10,000 year period when wolves were present in the landscape.

Conclusions

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; and that indigenous large mammalian herbivores (the red deer) have been present throughout the postglacial period. 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, particularly away from the coasts where population has tended to be more sparse.

The analysis here shows how the open nature of the landscape can be explained through natural processes, and demonstrates the successional process of natural regression of forests in this, the oligocrotic phase of an interglacial, from a postglacial maximum as described by Birks and Birks (2004). 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 (1996) that peat bogs can be the end point of succession in many parts of the world.

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. (2015) state:

“The WRI [World Resources’ Institute] erroneously assumes that nonforest 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.”

References


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 (Fenton 2008) can be observed: 'woodland as climax' in the few locations with better soils naturally protected from grazing by topography; 'the cyclical model' as proposed be Vera (2000) on the better soils and more favourable climate of 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 where the availability of palatable biomass is highly seasonal, the trophic level model is likely to over-estimate the expected herbivore population.

It should be noted that the ecology would be expected to be different in ecosystems which have never had indigenous mammalian herbivores, such as Iceland: in these situations the probability of native wood and/or scrub being a natural component is increased (although in Iceland introduced livestock have since destroyed most of the woodland).

The hypothesis presented here is that, in temperate ecosystems able to support trees, 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 (2000) is supported by recent evidence for lowland Britain (Alexander et al. 2018), 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. The current conservation practice of converting these areas to woodlands composed of indigenous trees therefore reduces the naturalness and biodiversity value of the Highlands.

The current natural vegetation of the Highlands (Figure 14), comprising a range of open moorland plant communities, appears to have become dominant owing to its greater resilience than woodland over time. This suggests that with continuing climate change it will remain dominant. With climate change causing a reduction in consistent winter snow cover in parts of Europe, this could increase the potential for over-wintering herbivores and hence lead to woodland loss. However, it could also encourage the spread of temperate thorny shrubs, allowing woodland expansion. Hence 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.

This paper, which has gone back to first principles, will hopefully result in a wider recognition of the role of herbivores in the landscape – and of the fact that open landscapes can occur naturally in locations climatically suitable for trees.

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References

