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Possible climatically driven, later prehistoric woodland decline on Ben Lomond, central Scotland

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Abstract

Later prehistoric woodland decline over most parts of Scotland is widely regarded as having been anthropogenic, *via* a range of mechanisms, to create farmland. Climatic causes are seen only to have driven the rapid expansion and then terminal decline of *Pinus sylvestris* around 2000 cal BC. Here we report radiocarbon dated analyses of pollen, microscopic charcoal, coprophilous fungal spores and peat humification from a small, water-shedding interfluve peat bog at 230 m elevation on the west-facing slope of the mountain Ben Lomond in west-central Scotland. The record spans the interval ca. 3450-200 cal BC. It shows marked and rapid changes in woodland composition before ca. 2600 cal BC, and from then to ca. 1940 cal BC a gradual decline of *Betula* woodland. This happened with no palaeoecological or archaeological evidence for anthropogenic activity. Woodland decline is interpreted at this site as climatically driven, perhaps through paludification or, more likely, exposure to wind, within a period of pronounced climatic deterioration. Anthropogenic activities are hinted at only after ca. 850 cal BC.

Keywords Scotland · Later prehistory · Pollen analyses · Climate change · Human impact

Introduction

Although spatially patchy, palynology is well advanced in Scotland (Edwards et al. 2019) and has been central to models of Holocene vegetation change (Pennington 1974; Birks 1977, 1988, 1989; Edwards 1988; Lowe 1993; Bennett 1989, 1994; Tipping 1994, 1996). In the mid-Holocene, deciduous *Quercus-Ulmus-Corylus* woods covered the lowlands and coastal hinterland, *Pinus* and *Pinus-Betula* woods grew on higher ground and on acid soils north of the Midland Valley, and more open *Betula-Corylus* woods in the far north. The upland and montane expanses have been defined as agriculturally marginal because of persistent climatic and pedological constraints (Parry 1978), and Scotland was sensitive to periods of climate change (Bond et al.1997; Gilbertson et al. 1999; Charman et al. 2006; Tipping et al. 2013; Baker et al.

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Richard Tipping r.tipping@stir.ac.uk 2015; Gallego-Sala et al. 2016; Stewart et al. 2017). Nevertheless, woodland decline and loss have almost always been interpreted as anthropogenic in origin because they were diachronous over short distances and small in scale until the late Iron Age ca. 300 cal BC. Woodland clearance was followed closely in time by the expansion of farmed land, through direct clearance of trees and seedling suppression by livestock grazing or vegetation burning. Until the late Iron Age, woodland decline was generally short-lived, followed by woodland regeneration (Turner 1965, 1975; Birks 1988; Buckland and Edwards 1984; Tipping 1994, 1997; Edwards and Whittington 2003; Edwards 2004; Edwards et al. 2019). Exposure to storminess has been used to explain woodland loss on islands around the northern mainland (Birks and Madsen 1979; Keatinge and Dickson 1979) but anthropogenic woodland loss is also argued for (Farrell 2015). Climatic changes related to abrupt hydrological shifts are more frequently asserted to have driven the abrupt expansion in range, and the equally abrupt contraction in range, of Pinus sylvestris woodland in the mountains and moors of central and northern Scotland between ca. 3400 and ca. 2200 cal BC (Bridge et al. 1990; Gear and Huntley 1991; Lowe 1993; Huntley et al. 1997).

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The Grampian Mountains are in central Scotland. They are sharply differentiated topographically, geologically and ecologically from the lowland trough of the Midland Valley to the south by the 'Highland line' (Whittow 1977; Fig. 1a, b). This division has resulted in significant long term agricultural and economic impoverishment of the Highlands (Forden 1380 in Smout 1969, p 39). In the west the fjord of Loch Lomond, close to sea level, pierces for 36 km into the Grampian Mountains, ringed to the west, north and east by hills rising above 600 m above sea level (a.s.l.) and formed of metamorphosed psammites and pelites. On its eastern side is Ben Lomond (974 m a.s.l.). Ramsay and Dickson (1997) summarised the vegetation history of central Scotland and described small-scale human impacts in lowland areas from ca. 2000 cal BC, becoming much more extensive. and often permanent, in the final centuries cal BC.

However, Stewart et al. (1984) described at Dubh Lochan on the shore of Loch Lomond, at the foot of Ben Lomond around 15 m a.s.l. (Fig. 1c) two pollen records, one from fen (DL) and one from lake sediment (DLM). They are strongly atypical of central–southern Scotland (Tipping 1994) in showing the persistence of deciduous woodland throughout the Holocene. The DLM core reflects changes in plant communities within several hundred metres of the lake (Stewart et al. 1984, p 538). From ca. 4000 cal BC until the BC/ AD boundary, *Alnus* and *Betula* values are unchanging at around 20 and 15% (total land pollen (TLP)), respectively. Abruptly higher *Quercus* percentages, reaching 25% TLP at ca. 3300 cal BC are followed by a consistent and gradual decline to around 10% TLP at the cal BC/AD boundary, a pattern reflected also in Coryloid (*Corylus avellana*-type) pollen. Careful work at the DL site showed, however, that as *Myrica* became established on the fen, *Corylus* contributed < 10% TLP after ca. 4000 cal BC. Poaceae values rose after ca. 1250 cal BC when *Plantago lanceolata* (ribwort plantain) was more frequently recorded, but the highest values of Poaceae are small. The interpretation was that "Iron Age man did not have a large long-lasting effect on the vegetation around the Dubh Lochan" (Stewart et al. 1984, p 544). Lowland woodland is, to an extent, extant (Tittensor and Steele 1971).

Directly above Dubh Lochan, the steep slopes of Ben Lomond are treeless save for exclosures and recent conifer forest. To contextualise the unusual pollen record at Dubh Lochan, we sought to understand woodland decline on these slopes, providing better data than Stewart's (1979) skeletal and undated pollen record at 500 m a.s.l. on Ben Lomond at Ptarmigan (NS 365 015; Fig. 1c). This paper reports new radiocarbon dated pollen, microscopic charcoal, fungal and humification data for an upland bog directly above Dubh Lochan and is designed to understand later Holocene vegetation dynamics and test the suggestion that prehistoric human impact was minimal on these slopes.

Coille Mhor Hill

Coille Mhor Hill is uphill and 2.5 km north of Dubh Lochan (Fig. 1c). It is a 30 ha rounded bedrock knoll on the western flank of Ben Lomond at 255 m a.s.l. East of Coille Mhor Hill rise the uniformly smooth and steep (18°) slopes of

Fig. 1 (a) The location of Scotland in north-west Europe, (b) the topography of Scotland (Robinson et al. 2014) marking the major divisions of the Grampian Mountains and the Midland Valley and the location of Fig. 1c; (c) the topography, drainage of central Loch Lomond (contour interval 10 m) and the pollen sites Coille Mhor Hill (this study), Dubh Lochan (Stewart et al. 1984) and Ptarmigan (Stewart 1979). Contains OS data © Crown copyright and database right (2021)



Beinn Urd (597 m a.s.l.). Two streams drain a col where peat has accumulated. The slopes around are formed in Ben Ledi Grit, an acid, nutrient poor metamorphosed sandstone. Soils are either skeletal, brown earths (brown forest soils in Scotland) or podsols (Tittensor and Steele 1971). They support, using Rodwell's (1992) classification, species-poor Nardus stricta-Galium saxatile (U5) and Pteridium aquilinum-Galium saxatile (U20) grassland with Trichophorum-Eriophorum germanicum sedge bog (M17) and Juncus-rich Carex echinata-Sphagnum poor fen (M6d) around flushes and mosaics of Vaccinium myrtillus-rich Trichophorum germanicum-Erica tetralix grass-heath (M15), Carex echinata-Sphagnum poor fen (M6), Juncus and moss-rich (M17c) on shallow peat. Mean maximum and minimum temperatures 1961-1990 are around 10.7 and 3.3 °C, respectively, and mean precipitation around 1,540 mm (Harrison 1997).

Reconnaissance on the broad interfluve between the two streams located a bog, < 0.1 ha in area, around 60 m long north-west to south-west and little more than 20 m wide, with >2 m deep peat at around 230 m a.s.l. (NS 37,432 99,068), draining south-east. The bog supports Erica tetralix-rich, Molinia caerulea-Potentilla erecta mire (M25). The pollen source area is hard to estimate. The basin is small and close to dryland soils, suggesting an extra-local pollen source area sensu Jacobson and Bradshaw (1981) but is at high altitude and barely sheltered from prevailing southwesterly winds such that the potential source of some pollen is best regarded as regional sensu Jacobson and Bradshaw (1981), and is increasingly so with woodland loss (cf. Bunting and Tipping 2004). It is assumed that woodland grew near and on the site when tree pollen (including Corylus avellana-type) reaches around 70% TLP (cf. Fossitt 1994) and that local plant communities contributed most pollen at these times.

The hillside has benefitted from detailed archaeological survey. Prehistoric structures are very rare, which contrasts with the frequent occurrence of Medieval and later farms and field systems, transhumant shielings and charcoal-burning iron-smelting sites (Boyle and MacInnes 2000). The bog is close to the generally accepted upper limit of sedentary prehistoric settlement in Scotland (Cowley 1998). Coille Mhor means 'big wood' in Gaelic, an early historic usage.

Sampling, materials and methods

After reconnaissance, survey and peat-stratigraphic description of the bog using a 1 m-long Eijelkamp peat gouge, the base of the bog was levelled by theodolite to an arbitrary datum to establish that the bog was free draining and sensitive to past water table fluctuations. A core was taken at the deepest point of the bog (259 cm) with a Russian-type corer of 1 m length and 6 cm internal diameter, placed in clean plastic guttering, wrapped, described in the laboratory and stored at 4 °C. The 32 samples taken for pollen and fungal analysis were each 5 mm thick. Subsamples were prepared by standard chemical methods (Moore et al. 1991). Mineral matter is absent above the basal sediment and hydrofluoric acid was not needed. Lycopodium spores (Stockmarr 1971) were added to calculate pollen concentrations and influx. Residues were embedded in silicone oil. Pollen identifications were made using an Olympus BX40 microscope. Counts were made at a magnification of ×400 with critical examinations and size measurements being made at a magnification of ×1,000 under oil immersion, sometimes using phase contrast. Pollen grains were identified with reference to Moore et al. (1991), the University of Stirling pollen reference collection, specialist keys and on-line images. Poaceae pollen grains with a-axes > 35 μ m were not encountered. Counts were to a minimum of 300 TLP excluding Cyperaceae. The pollen sum is % TLP-Cyperaceae, excluding aquatics and spores. Pollen nomenclature follows Bennett (1994) and plant nomenclature follows Stace (2010). Pollen preservation was recorded in five categories (Cushing 1967). Microscopic charcoal was quantified in five size classes of a-axis lengths 10-25, 25-50, 50-75, 75-100 and $>100 \mu m$. Six types of fungal spores were recorded from samples prepared for pollen analyses (cf. van Asperen et al. 2016) using photomicrographs in van Geel and Aptroot (2006) and van Geel et al. (2011). Values are given as % TLP+fungi. Most represent coprophilous (dung) fungi. Coniochaeta-type is found in both dung and wood, particularly Alnus and Fraxinus, Cercophora-type in both dung and wood, particularly Betula, and Gelasinospora-type is found in association with dung, charred wood and Vaccinium (Farr and Rossman 2009).

The pollen diagram is divided into six local pollen assemblage zones (LPAZ 1–6) with the aid of stratigraphically constrained cluster analysis (Grimm 1987). Humification by colorimetry was measured on contiguous 10 mm-thick sediment slices on a Jenway 6061 colorimeter at 540 nm (Blackford and Chambers 1993). Horizontally bedded, young, single entity roundwood samples from four depths were ¹⁴C dated by AMS. The ¹⁴C dates were calibrated using OxCal v4.3.2 r5 (Bronk Ramsey 2017) and the IntCal13 atmospheric curve (Reimer et al. 2013). An age-depth model of calibrated age estimates were generated using BACON v2.2 software (Blaauw and Christen 2011) with a step size of 5 cm.

Depth (cm)	Description
0–26	Dark brown herbaceous peat with common-many (40–80%) vertical coarse fleshy stems; gradual lower boundary to
26–68	Dark brown herbaceous peat with common (40–60%) vertical coarse fleshy stems; gradual lower boundary to
68–96	Dark brown herbaceous peat with few ($<10\%$) vertical coarse fleshy stems and few large wood fragments (75–78 cm), and few <2 mm-thick twigs (79–82 cm); gradual lower boundary to
96–251	Reddish-brown herbaceous peat with common–abun- dant (40–>80%) large wood fragments and small roundwood; sharp lower boundary to
251–259	Dark grey very poorly sorted mud with abundant mica- ceous angular-subangular fine gravel; bottomed on stone

Results

Table 1 describes the sediment stratigraphy at the sampled site. Table 2 lists the samples and depths from which AMS ¹⁴C assays were obtained. Figure 2 depicts the age-depth model generated by BACON. Linear regression through all depths has an r² value of 0.99, suggesting a more-orless constant peat accumulation rate of 12 ± 5 year cm⁻¹. In detail, however, peat accumulation falls from around 20 year cm^{-1} to 8 year cm^{-1} from the base to 125 cm depth and is constant at around 12 year cm^{-1} above 125 cm depth. All age estimates in the text are calibrated and, unless stated, are age ranges modelled in BACON. Figure 3 is the complete percentage-based pollen, microscopic charcoal, fungal and humification record, plotted against depth. There is no evidence from the humification data for a long-term trend in decay, so the data are not detrended. The mean percentage humification is $16.8 \pm 4.6\%$: higher percentages indicate less humified peat. The 1σ standard deviation around the mean (not plotted in Fig. 3 to retain clarity) is used to define significant changes in bog surface wetness. Figure 4a plots influx values (pollen accumulation rates) for major pollen taxa, used to infer local presence. Figure 4b presents the pollen data for major arboreal taxa on a % AP sum to allow direct comparison with the Dubh Lochan pollen record (Stewart et al. 1984). Figure 4c shows the percentages of well preserved (normal in Fig. 4c) and deteriorated pollen of four taxa common throughout the pollen record, calculated as % TLP. Pollen preservation is generally good. Interpretation focuses on fluctuations in proportions of corroded pollen because corrosion is closely linked to fluctuations in the peat water table (Havinga 1984).

Table 2	Details of ¹⁴ C	dates, pollen	profile Coille N	/hor Hill
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Depth	Material	Lab.code	¹⁴ C age	$\delta^{13}C$	cal
(cm)		(SUERC-)	$(BP \pm 1\sigma)$	(‰)	age BC
73	Unidenti- fied twig (20×5 mm); <10 yrs old	84,060	2,949±24	-28.8	1226– 1055
118.5	<i>Betula</i> twig (20×4 mm); <10 yrs old	84,064	3,432±22	-29.4	1871– 1665
203.5	<i>Betula</i> twig (30×20 mm); <20 yrs old	84,065	$3,959 \pm 22$	-27.9	2569– 2350
250.5	<i>Betula</i> twig (40×10 mm); <10 yrs old	76,331	4,690±24	-28.9	3625– 3372

LPAZ 1: 251 to 233 cm depth (3525 – 3104 to 3272 – 2786 cal BC)

A young twig lying horizontally at the base of the peat is ¹⁴C dated to 3625-3372 cal BC, modelled to 3525-3104 cal BC, i.e. the early-mid Neolithic of the British Isles (ca. 4000-3300 cal BC; Bradley 2007). Peat accumulation above this was around 20 year cm⁻¹. Peat was significantly less humified than the mean until 3259-2771 cal BC (232 cm depth; Fig. 3). Corroded and degraded pollen grains are common (Fig. 4c), suggesting that the peat in LPAZ 1 was an aerated organic soil. The high influx values of Alnus glutinosa, Betula, Corvlus avellana-type and Quercus in the basal pollen spectrum (Fig. 3) may include pollen from non-contemporary sources. Above this, Alnus pollen is recorded at percentages large enough to imply local presence before 3396 – 2924 cal BC (241 cm depth) (Tinsley and Smith 1974; Gearey and Gilbertson 1997) but influx values larger than 1,000 grains cm² yr⁻¹ indicate local presence throughout LPAZ 1 (Abraham et al. 2021). It is likely that Alnus colonised the basin when soil was paludified. Betula and Salix accompanied Alnus, influx values for Betula indicating local presence by 232 cm depth (Tinsley 2001; Abraham et al. 2021). Percentages of Salix pollen underrepresent the plant. The community was probably close to the Juncus effusus subcommunity of W4 Betula pubescens-Molinia caerulea woodland (Rodwell 1991) where Alnus can outnumber Betula trees and Salix bushes in an open canopy. Corvlus avellana-type pollen in this setting may more likely represent C. avellana but Myrica gale cannot be dismissed (Skene et al. 2000). If from Corylus, the low percentage representation and influx values < 2,000 grains cm² yr⁻¹ in mid-zone are taken to mean the tree was not common on the hillside (Tinsley and Smith 1974; Lisitsyna et al. 2011; Abraham et al. 2021). Quercus, from its low influx, may not



Fig. 2 Age-depth model for the peat on Coille Mhor Hill generated by BACON, showing (**a**) the positions of the calibrated ¹⁴C assays, the 2σ age range constrained within black dotted lines, all probable age-depth models in grey, darker areas with increasing probability and the best model based on the weighted mean average by the red dotted line, (**b**) the number of MCMC iterations in the model; (**c**) prior (curve) and posterior (histogram) distributions for accumulation rate estimates and (**d**) the 'memory' in accumulation rate estimations

have been local (Tinsley 2001). *Ulmus* was rare if present. *P. sylvestris* was not present.

The wood may have been open, although total tree + shrub pollen percentages are very high, exceeding 80% TLP, or there were open areas. Less stable soils, perhaps gullied, supported plants producing *Ulex*-type pollen (probably *Ulex europaeus*). Proportions of Poaceae fluctuate, though average influx values around 5,000 grains cm² yr⁻¹ imply local presence (Abraham et al. 2021). Grassland herb taxa were common, though their proportions are low, with *Potentilla*type constant, two grains of *Rhinanthus*-type (perhaps *Euphrasia*), and *Ranunculus*, *Rumex acetosa*, Apiaceae and *Melampyrum*. Dwarf shrubs (Ericaceae, Empetraceae) were rare. Single spores of the coprophilous fungi *Podospora*and *Sordaria*-type are recorded. Microscopic charcoal is very rare.

LPAZ 2: 233 – 207 cm depth (3272 – 2786 to 2860 – 2452 cal BC)

Alnus influx values > 5,000 grains cm² yr⁻¹ continue to indicate its local abundance (Abraham et al. 2021) despite an abrupt fall in percentages at 233 cm depth (3272 - 2786 cal BC). Alnus may have been confined to the peat. Alnus was joined by Betula, probably rapidly in a few decades between 3388 - 2900 and 3312 - 2811 cal BC and later (225 cm depth; 3153 - 2657 cal BC) by an equally short-lived increase in Quercus values to around 50% TLP, and 25,000 grains $cm^2 yr^{-1}$ suggesting the tree was locally abundant (cf. Tinsley and Smith 1974; Tinsley 2001). A hiatus in deposition is not suggested by the highly resolved humification data. Although humification data suggest the peat surface became drier between 3259-2771 (232 cm depth) and 2924 - 2511 cal BC (212 cm depth) and was very dry (>1 σ) by 2951-2528 cal BC (214 cm depth), proportions of corroded pollen in major taxa fall, interpreted as meaning that reworked pollen grains from the organic soil were few. The shift in woodland trees is more likely to have been driven by the drying of the peat surface observed in the humification data (cf. McVean 1956a). In western Scotland today, the altitudinal limit of Quercus is around 150 m a.s.l. (McVean 1964) but Jones (1959, p 176) described *Q. petraea* woods up to 240 m a.s.l. in north Wales and, with Betula, in western Ireland up to 340 m a.s.l.

Corylus avellana-type pollen percentages remain comparatively low and unchanging. On very base-poor siliceous soils there can be few other canopy species with *Betula* and Quercus (McVean 1956b; McVean and Ratcliffe 1962; Steele 1974). The absence of Vaccinium-type pollen might indicate that Coille Mhor Hill was within the grass-rich Betula-herb nodum of Scottish Betula-Quercus woods (McVean and Ratcliffe 1962, p 16), or the species-poor W16 Quercus-Betula-Deschampsia flexuosa woodland of Rodwell (1991). Total tree+shrub pollen percentages are unchanging, and the woodland may have been closed. There are no other prominent palynological changes. Calluna (ling) is characteristic of upland and base-poor Betula-Quercus woodland but was rare at this time at Coille Mhor Hill. Coniochaetatype spores are recorded in all counts. Microscopic charcoal is very rare.

LPAZ 3: 207 – 176 cm depth (2860 – 2452 to 2473 – 2092 cal BC)

Humification data (Fig. 3) suggest the bog surface was significantly wetter than the mean in this LPAZ. Despite this, Alnus values (% and influx) do not increase. Corroded Betula pollen grains are fewer because of this hydrological shift but pollen of other taxa do not show this. A second abrupt increase of *Betula* to 65% TLP and > 40.000 grains $\text{cm}^2 \text{ vr}^{-1}$ occurred at 2860 – 2452 cal BC (207 cm depth), an influx that probably implies dense woodland at the pollen site (Tinsley 2001). Betula may have become the only tree taxon at and around the pollen site. The peak in *Betula* percentages at 204 cm depth (2822-2404 cal BC) was followed by a gradual, consistent decline but influx values indicate a more temporally confined expansion and fall centred on 190 cm depth (2638-2227 cal BC). *Quercus* representation fell to around 10% TLP and 2,500 grains cm² yr⁻¹, not necessarily indicative of local presence (Tinsley 2001; Abraham et al.

Fig. 3 Peat humification and percentage-based (% TLP) diagram at Coille Mhor Hill as follows: (**a**) pollen and spores (% TLP+spores), (**b**) coprophilous fungal spores (% TLP+fungi) and (**c**) microscopic charcoal (% TLP+charcoal), plotted against depth



2021). *Quercus* may have persisted locally or elsewhere on the hillside or in the region; much of its pollen in this and later zones may have been regional in origin (cf. Lisitsyna et al. 2011) so that the woodland on Coille Mhor Hill may have remained floristically similar to that in LPAZ 2. *Betula* and *Quercus* are ordinarily intimately associated (McVean and Ratcliffe 1962, p 16) but Jermy et al. (1978, p 10.22) noted that *Betula* displaces *Quercus* through edaphic controls on steep slopes on thin, increasingly base poor, degraded brown

earth soils that become with time more acid and increasingly podzolic. *Quercus* prefers deeper soils with accumulating nutrients at the base of slopes. *Betula* improves the base status of very poor soils (Miles 1981) but there are no changes in representation of *C. avellana*-type pollen to suggest that base status increased in soils on Coille Mhor Hill. Probably because of a dense cover of *Betula*, pollen of *Ulmus*, *Calluna*, *Ranunculus*-type, Rosaceae, *Rumex acetosa*, Apiaceae and *Melampyrum* (also Polypodiaceae, i.e. undifferentiated





fern spores) are only infrequently recorded, as is *Sphagnum* even though it probably grew on the peat. *Coniochaeta*-type spores are recorded in all counts. Dung fungi are present, including *Sordaria*-type and *Podospora*-type. Microscopic charcoal is very rare.

LPAZ 4: 176-118 cm depth (2473 – 2092 to 1829 – 1625 cal BC)

From being wetter than the mean at 2473 - 2092 cal BC (176 cm depth), the humification data suggest that the bog surface, became very dry by 1853 - 1652 cal BC (120 cm depth) for around 50 years, and then continued to be drier than the mean. After 2527 - 2143 cal BC (180 cm depth), *Betula* and *Alnus* pollen grains are more corroded, particularly so between 2315 - 1943 (160 cm depth) and

1972 - 1718 cal BC (130 cm depth), supporting the interpretation of the humification data. Wood fragments in the peat are few above 140 cm depth (2097 - 1784 cal BC). *Betula* percentages continue a sustained fall to around 20% TLP by 140 cm depth (2097 - 1784 cal BC) and influx data show a decline after 140 cm depth. Both represent declining woodland extent, thinning of the canopy or pollen productivity, after which proportions and influx values are unchanged. Nevertheless, *Betula* persisted locally (cf. Tinsley 2001; Abraham et al. 2021). Percentages of *Betula* remain much higher than in surface pollen studies in Scotland where *Betula* is of long-distant origin (Gearey and Gilbertson 1997; Bunting 2002; Fossitt 1994).

Quercus pollen is slightly better represented, at around 15% TLP, except for a few decades in mid-zone (145 - 141 cm depth: 2156 - 1821 to 2106 - 1794 cal BC)where it is > 20% TLP, Influx values around 2,500 grains cm² yr⁻¹ probably imply local presence (cf. Tinsley and Smith 1974; Tinsley 2001). An increasingly open canopy may have permitted the more consistent representation of trees of regional origin such as Pinus and perhaps Fraxinus. Salix pollen grains are slightly better represented. Cyperaceae are better represented at the upper zone boundary. Filipendula was probably more common after 145 cm depth (ca. 2000 cal BC), in moist grassland, and so probably was Rumex acetosa. P. lanceolata is recorded for the first time at 131 cm depth (1982 - 1728 cal BC), at the end of the phase of sustained woodland decline but at values no more than 1% TLP. P. lanceolata pollen is over-representative of the plant (Tinsley and Smith 1974; Hjelle 1998; Shaw and Whyte 2020) and its rarity in the pollen record at Coille Mhor Hill suggests its rarity also in plant communities. It is absent in acidic soils in uplands (Sagar and Harper 1964) and rare at pH < 4.5 (Grime et al. 1988, p 438). There are very few other grazing indicator herbs. Although percentages of Poaceae increase, influx values do not. Dung fungi (Sordaria-type, Podospora-type) continue to be represented, as is Cercophora-type above 150 cm depth (1859-2203 cal BC). Coniochaeta-type is less well represented. Microscopic charcoal is slightly more common.

Melampyrum pollen is markedly more common above 145 cm depth (2156 – 1821 cal BC). The high proportion at 121 cm depth (1862 – 1661 cal BC) may be due to incorporation in the pollen sample of an anther, but it nevertheless attests to local presence, as do the comparatively high pollen percentages (Moore et al. 1986). The pollen cannot be identified to species but either *M. pratense* or *M. sylvaticum*, or both, are possible from current distributions (Tippett 1974; Lee 1933; Rich et al. 1998). Both inhabit upland open *Betula* woodland (>30% shade) and woodland edges of herb-rich W11/W17 *Quercus petraea-Betula pubescens* woodland (Rodwell 1991), as well as heaths and upland moors on shallow, often skeletal, acid (pH 3.9–4.7), continually moist free-draining soils Dalrymple 2007; Rich et al. 1998, p 34) comment that *M. sylvaticum* plants are "usually found in the same precise spots each year" despite being an annual plant and, for this reason, *Melampyrum* species are sometimes regarded as ancient woodland indicators (Rackham 2003, p 54; Miles 1988: see also 'Discussion' below). It became a persistent feature on Coille Mhor Hill into LPAZ 5, until at least 90 cm depth (1533 – 1222 cal BC).

LPAZ 5: 118-6 6 cm depth (2473 – 2092 to 1234 – 948 cal BC)

According to the peat humification data, the bog surface remained from dry or very dry, although *Salix*, Cyperaceae and *Equisetum*, and falling proportions of corroded *Alnus* and *Betula* pollen, suggest wetter conditions. Proportions of tree genera suggest no significant changes to the partly open *Betula* woodland. This zone sees the establishment above 111 cm depth (1752 – 1488 cal BC) of *Calluna*. Other dwarf shrubs like *Empetrum* (crowberry), *Erica* (heaths) and Ericales (undifferentiated Ericaceae or Empetraceae) are not recorded until 91 cm depth (1541 – 1235 cal BC). Microscopic charcoal was recorded more frequently, probably because heather species were more common. *P. lanceolata* is the only anthropogenic indicator, occurring mostly as single grains. All fungal spore taxa are absent above the basal spectrum save single occurrences of *Sordaria*-type.

LPAZ 6: 66 – 0 cm depth (1234 – 948 to 739 – 38 cal BC)

Modelled age ranges are increasingly imprecise above the youngest ¹⁴C assay at 73 cm depth. Extrapolation of the peat accumulation rate (~15 year cm^{-1}) above 73 cm depth suggests that the peat surface has an age of ca. 2400 cal BC. The peat has been truncated above this, probably by peat cutting. Quercus percentages abruptly fall to a mean 2.5% TLP at 66 cm depth (1234 – 948 cal BC); influx values are unchanging. Alnus, probably not common on the peat at Coille Mhor Hill above LPAZ 2 (above), declined to values < 5% TLP by 11 cm depth (821 – 187 cal BC). Betula proportions were maintained. Influx values increased to > 5,000 grains cm² yr⁻¹, indicating the persistence of *Bet*ula near the pollen site. Salix is unrecorded between 91 and 51 cm depth (1541 - 1235 cal BC to 1127 - 730 cal BC) and above 51 cm depth was not common, if present. Calluna would have gained an advantage in grassland communities and under the open Betula wood. Vaccinium-type pollen is recorded consistently for the first time, and considerable diversity in heath taxa is indicated by consistent records of Ericales and Erica, and above 31 cm depth (974-445 cal

BC) by *Empetrum*. Humification data indicate the bog surface became wetter, after 1049 - 566 cal BC (40 cm depth), and after 974 - 474 cal BC (31 cm depth), so do increases in *Sphagnum* and Cyperaceae percentages. However, proportions of corroded pollen do not reflect this. Local growth of *Melampyrum* may have ceased because of this hydrological shift. Charcoal fragments < 50 µm are abundant but it is not clear from these whether fires were local. Dung fungi (*Sordaria*- and *Sporormiella*-type for the first time) are found sporadically.

Discussion

Peat inception at Coille Mhor Hill at 3625–3372 cal BC coincided with evidence in southern Scotland for increased effective precipitation (Langdon et al. 2003, 2012). It may have been that peat initiation was climatically induced. *Alnus* colonised lowland soils along Loch Lomond around 4800 cal BC (Dickson et al. 1978; Stewart et al. 1984). It grew locally at Coille Mhor Hill from peat inception. On the slopes of Ptarmigan, Stewart (1979) recorded *Alnus* pollen in proportions high enough to suggest that the tree grew at much higher altitudes than is commonly recognised (McVean 1953).

Climatic factors may have resulted in partial losses of Alnus at Coille Mhor Hill at 3272-2786 cal BC when the bog surface became increasingly dry, approaching very dry at 3128-2647 cal BC. This shift may reflect the end of a wetter and stormier climate centred on ca. 3200 cal BC (Magny and Haas 2004; Caseldine et al. 2005; Magny et al. 2006; Leuschner et al. 2007; Moir et al. 2010; Roland et al. 2015; Stewart et al. 2017). As the bog surface and surrounding soils became drier, Alnus lost competitive advantage, although the numbers of *Coniochaeta*-type fungal spores, often associated with Alnus, suggest its presence at Coille Hhor Hill until LPAZ 5 at 2473-2092 cal BC. Alnus did not, however, respond when bog surface wetness increased between 2951-2528 and 2848-2435 cal BC, perhaps because seed sources were by then distant. Among tree taxa, Betula seems to have responded first to the loss of Alnus. Open Betula woodland already grew at Ptarmigan (Stewart 1979). The low proportions of C. avellana-type pollen at Coille Mhor Hill are explained by nutrient impoverishment of soils (Godwin 1975, p 272; Theuerkauf et al. 2014).

Pinus sylvestris woodland spread south from the Grampian Mountains (Fig. 1b) after ca. 3650-3350 cal BC (Bridge et al. 1990), into the deciduous woodland north and north-west of Loch Lomond after ca. 2900-2750 cal BC (Dickson et al. 1978; Stewart 1979; Wylie and Dickson 1998), less than 15 km north of Ben Lomond. This was part of a short-lived expansion of range in *Pinus* from core areas in the Scottish Highlands. Expansion has long been seen in Scotland as climatically driven (Bridge et al. 1990; Gear and Huntley 1991) as *Pinus* colonised peat surfaces made drier through lowered water tables. *Pinus* did not invade the *Quercus* woodland at Dubh Lochan (Stewart et al. 1984) or the *Betula* woodland on Coille Mhor Hill, or on Ptarmigan (Stewart 1979), at least sufficiently to be palynologically detected. Deciduous trees continued to out-compete *Pinus*.

Quercus replaced, for a time, a single generation of Betula (upland Betula may live for around 200 years (Kirby 1984)), though most die when less than a century old (Rackham 2003). If local to the peat at Coille Mhor Hill, which is likely, the establishment of Quercus occurred at a higher altitude than can be observed in western Scotland at the present day (150 m a.s.l.: McVean and Ratcliffe 1962, p 16; Stewart 1979), probably explained by warmer temperatures 5,000 years ago (Davis et al. 2003). The loss of Quercus on Coille Mhor Hill after 2860-2452 cal BC, perhaps again of a single generation of trees, may have a locale-specific explanation such as soil acidification, operating at altitudes and on slopes where Quercus had anyway a tenuous foothold (Miles 1985; Jermy et al. 1978). This change is not seen in the pollen 'rain' of the region (Dickson et al. 1978; Ramsay and Dickson 1997; Fyfe et al. 2013).

Because Quercus did not later regain a foothold around Coille Mhor Hill, edaphic factors (Leuschner et al. 2002; Wardle et al. 2004) are unlikely to have induced its decline. There is no evidence in the Coille Mhor Hill record from (a) anthropogenic indicator pollen taxa developed for northwest Europe (Behre 1981; cf. Deza-Araujo et al. 2020), (b) microscopic charcoal or (c) coprophilous fungi for anthropogenic activities to have changed woodland composition or caused the demise of locally growing Quercus (cf. Hellman et al. 2009) on Coille Mhor Hill. Indicator taxa are almost absent, and not all, like *P. lanceolata*, are poorly represented on acid soils. The only moderate increases in grassland communities at Coille Mhor Hill may have been within open Betula woodland. Melampyrum is often seen to be indicative of anthropogenic disturbance (Tinsley 1975; Moore et al. 1986; Mitchell 1988; Innes et al. 2013) but Tittensor and Steele (1971) found M. pratense most commonly in the undisturbed island oakwoods of Loch Lomond, and Dalrymple (2007) regarded M. sylvaticum as sensitive to grazing pressure. Fire, sometimes associated with Melampyrum (Innes and Simmons 2000, though see Moore et al. 1986, p 215 and Blackford et al. 2006, p 198), is not indicated at Coille Mhor Hill because proportions of microscopic charcoal are very low. Other forms of disturbance such as hydroseral change on bog surfaces can favour the plant (Pilcher 1973; Birks 1975). *Melampyrum* became established on Coille Mhor Hill from ca. 2000 cal BC when humification data show the bog surface became very wet. It then persisted for around 650 years, to at least ca. 1350 cal BC. Its persistence is taken to indicate a lack of disturbance of grassland communities near or on the peat surface. It is possible that the later, more prolonged phase of dry bog surface after 1606 - 1307 cal BC adversely affected its growth. Numbers of *Cercophora*-type fungal spores, associated with *Betula* wood, track the representation of *Melampyrum* for reasons that are unclear, but which might also imply a lack of vegetation disturbance. They are absent after LPAZ 4, after the decline of *Betula*.

Dung fungi were comparatively abundant when the woodland was locally present, but they decline to absence from ca. 1600 cal BC with *Betula* woodland decline, when this vegetation change would have favoured fungal spore dispersal. This pattern is unexpected had grazing animals been the cause of, or gained from, woodland decline (Blackford and Innes 2006; Cugny et al. 2010). It is not explained by changes in sample preparation methods, pollen preservation or change in sediment type, and although an absence of evidence, for which there are many explanations (cf. van Asperen et al. 2020), the simplest interpretation is that grazing animals did not have a role in woodland change or decline.

Anthropogenic disturbance is also hard to identify when Betula pollen percentages declined in LPAZ 3 between 2822 - 2404 and 2097 - 1784 cal BC. Interpretation is complicated because, as local woodland declined, arboreal pollen became increasingly regional in origin (above), but in the region Betula pollen percentages increased at this time (Dickson et al. 1978; Fyfe et al. 2013). It is likely, then, that the pollen record at Coille Mhor Hill describes a local decline. The linear decline in Betula pollen percentages between ca. 2600 and ca. 1950 cal BC ($r^2 = 0.98$: n = 8) might, in its consistency, reflect natural change rather than anthropogenic interference. The period when *Betula* woodland declined at Coille Mhor Hill was one of major hemispheric scale climate change (Bond et al. 1997; Karlen and Larsson 2007; Walker et al. 2012). The tolerance of both Betula pendula and B. pubescens to very large temperature variations (Atkinson 1992) suggests that thermal change (McDermott et al. 2001; Taylor et al. 2018; McKeown et al. 2019) would not have affected upland Betula woodland at 230 m a.s.l. in western Scotland. The Betula woodland decline at Coille Mhor Hill occurred in a period of predominantly high local bog surface wetness 2909-2429 to 1955-1713 cal BC. The bog surface wetness record at Coille Mhor Hill need not relate to climate change because the peat receives, as well as sheds, water, but there is good agreement with data from raised mosses in central Scotland that bog surfaces became wetter from around 2000 cal BC and were very wet ca. 1850 cal BC (Charman et al. 2006). Although Swindles et al. (2013) and Roland et al. (2014) argued that there is little consistent peat-stratigraphic evidence in the Irish Sea region for major hydrological change, Barber et al. (1994) in north-west England regarded this deterioration as the most significant in the Holocene. Bog and soil surface wetness may have become inimical for a time to the growth of Betula (Crawford et al. 2003), as it did for Pinus populations further north in Scotland (Bridge et al. 1990; Gear and Huntley 1991; Lowe 1993; Huntley et al. 1997), but such an effect could be expected to have been recognised by earlier workers. Attrition by exposure to high winds on this west facing slope is perhaps more likely (Lamb 1964; Allen 1992; Quine and White 1994; Paus 1995). Ecological data on how winds affect Betula are few, but Atkinson (1992) drew on the northern limits of B. pubescens in Greenland and Iceland in indicating its vulnerability to cold and dry winds. Our study area lies on one of the principal Atlantic cyclone tracks (Lozano et al. 2004). Increased aeolian activity is commonly recorded in ¹⁴C-dated dune construction along the north-eastern Atlantic facade between 2500 and 2000 cal BC Gilbertson et al. 1999; Wilson et al. 2001, 2004; Sommerville et al. 2007; de Jong et al. 2009; Orme et al. 2015; Ballin-Smith 2018, p 19; Goslin et al. 2019), and Olsen et al. (2012) identified from a palaeo-limnological record in Greenland a strong, positive North Atlantic Oscillation before ca. 2350 cal BC.

After ca. 1950 cal BC the stresses imposed on *Betula* regeneration at Coille Mhor Hill appear to have eased. *Betula* pollen proportions do not decline further. *Cercophora*-type spores, if associated here with *Betula*, are not recorded after 1745 - 1464 cal BC, suggesting that the *Betula* record contains much long-distant pollen. The bog surface became very dry by 1853 - 1652 cal BC, then dry until 1606 - 1307 cal BC, before becoming wetter at 1533 - 1222 cal BC, tracking closely comparable changes in raised mosses in the region (Charman et al. 2006), and storminess subsided Wilson et al. 2001, 2004; de Jong et al. 2009; Orme et al. 2015).

Increases in Poaceae pollen in the region from ca. 1850 cal BC (Dickson et al. 1978; Fyfe et al. 2013) arise from the atmospheric mixing of pollen from many small and temporary anthropogenic activities that led to localised woodland clearance and settlement, and grazing-driven woodland losses (Turner 1965; Tipping 1994; Ramsay and Dickson 1997). Around Dubh Lochan at the foot of Ben Lomond, woodland decline on dry soils appears limited to Quercus, gradually from ca. 3300 cal BC and ceasing by the cal BC/ AD boundary (Stewart et al. 1984). Further vegetation disturbance is seen at Coille Mhor Hill after 1054 – 580 cal BC, resulting in P. lanceolata being a component, though not common, of grassland. Betula pollen declines to values that suggest trees were not growing locally. Some dung fungi reappear sporadically after ca. 960 cal BC. If from domestic livestock, this is the first clear evidence in the pollen record

at Coille Mhor Hill of human activity. It is not precisely dated but, as around Dubh Lochan (Stewart et al. 1984), later prehistoric people appear to have had little impact. There is a scarcity along Loch Lomond of archaeological sites from this period (Harding 2004; Alexander 2015; Lock and Ralston 2017). There is no indication that human activities at Coille Mhor Hill became more intense or extensive before truncation of the peat at ca. 2400 cal BC. The impact of Iron Age farming communities after ca. 500 cal BC elsewhere in central and southern Scotland, from similar anthropogenic indicator pollen taxa, was extraordinary (Turner 1965, 1979, 1981, 1983; Dumayne 1993a, b; Ramsay 1995; Ramsay and Dickson 1997; Tipping 1997, 2010; Dumayne-Peaty 1998, 1999; Dark 2000; Tipping and Tisdall 2006) as woodland clearance changed from small and temporary to large and, at some places, permanent, continuing into the period of Roman occupation after cal AD 80. Along the eastern shore of Loch Lomond, the palaeoecological data at Dubh Lochan (Stewart et al. 1984) and Coille Mhor Hill suggest agrarian impact was negligible.

Radiocarbon dated pollen records immediately north of Loch Lomond are few. In the Grampians, Bridge et al. (1990) describe *Pinus*-rich woodland which yielded in later prehistory to extensive paludification, blanket peat and wet heath spread with no evidence that these changes involved human impact. It is possible that the 'Highland line', a fundamental economic boundary in Scottish history, defined by sharply contrasting potentials for agricultural productivity through geological and climatic controls, had considerable significance for human ecology in later prehistory.

Conclusions

A ¹⁴C dated pollen, microscopic charcoal and coprophilous (dung) fungal record, supported by humification data, is described from a water-shedding peat, Coille Mhor Hill, on Ben Lomond, the most southerly slopes of the Grampian Mountains. The site is around 230 m a.s.l., on a steep and exposed west-facing slope. Mineral soils are very acid and nutrient poor. Analyses were developed to test the suggestion from Stewart et al. (1984) that later prehistoric people had almost no impact on the vegetation cover. Whilst later prehistoric human activities in southern Scotland are almost universally seen to have been causal in later Holocene woodland loss (Miles 1988; Tipping 1994; Edwards and Whittington 2003), we found that woodland decline on Coille Mhor Hill probably occurred without anthropogenic impacts. Because of this limited evidence for human interference, it has been necessary to explore in detail ecological and edaphic processes and relations, and to draw on palaeoclimatic data. We suggest that exposure to intense North Atlantic winds during climatic deterioration reduced the exposed west facing *Betula* wood at Coille Mhor Hill. How common this was in the uplands of Scotland needs to be explored. This interpretation does not replace the general model for central and southern Scotland of anthropogenic woodland decline (Tipping 1994; Edwards and Whittington 2003; Edwards et al. 2019); climatic impacts may have been restricted in extent. One implication, however, is that there may have been other areas of the Grampian Mountains that were almost empty of people in later prehistory. Another might be that the aphorism that "The crucial feature of upland vegetation within the natural forest zone in Britain is that it is largely man-made" (Miles 1988, p 57) needs to be re-visited.

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Availability of data on request.

Declarations

Conflicts of interest/competing interests: none.

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