Recent pine woodland dynamics in east Glen Affric, northern Scotland, from highly resolved palaeoecological analyses

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Summary

Glen Affric, a National Nature Reserve of international conservation importance for plant and animal communities associated with Scots pine (*Pinus sylvestris*) woodland is managed for nature conservation and woodland restoration at a landscape scale. Management plans have drawn on information on current stand structure and variation but have not used in any detailed way the analyses of past tree population changes from sources, such as pollen analyses. This paper reports the results of pollen analyses from three small peat hollows at the head of Loch Beinn a' Mheadhoin. The analyses demonstrate, first, that woods in the east of the reserve several centuries ago were different in species composition and were more varied than they are today and, second, that the currently patchy *Pinus* wood in the west of the reserve, at the head of Loch Beinn a' Mheadhoin, is the result of recent spread westward onto former heathland. This temporal and spatial variability in the recent past has implications for the future management of the woods because future woods may not develop with the characteristics of the current stands, and may not be stable over time.

Introduction

Caledonian Scots pine woodland is listed as an annex 1 habitat under the European Union Habitats Directive, requiring examples to be maintained or returned to favourable condition (UK Biodiversity Steering Group, 1995). The determination of favourable condition is made by reference to NVC classifications (Rodwell, 1991) and site classifications (Pyatt *et al.*, 2001). These classifications are based on extensive surveys in contemporary woodland, but have a limited temporal dimension. The methodology assumes that any restoration undertaken will provide a pine woodland that will be self-sustaining in perpetuity, or least over several generations. This assumption needs confirmation; if erroneous, it could have dramatic implications for future woodland management for sustainability.

A temporal dimension to woodland history can be provided through maps and documents (Rackham, 1980; Smout *et al.*, 2005), and through scientific techniques such as pollen analysis (e.g. Delcourt and Delcourt, 1991). In Scotland, archival analyses rarely give details beyond 400 years ago. Pollen analysis allows an examination of woodland dynamics over the whole Holocene epoch. It is the principal source for the description of a formerly widespread native woodland system throughout northern and western Scotland (Bennett, 1984, 1995; Tipping, 1994; Huntley *et al.*, 1997). However, these analyses have rarely been made in sufficient detail to give spatio-temporal patterning of woodland at the stand scale (Kerslake, 1982; Smith, 1998; Davies and Tipping, 2004). The detailed pattern of vegetation dynamics at small spatial scales, the density of previous woodland and its diversity and species patterning in space and time across a landscape are not fully understood (Bennett, 1995; Tipping *et al.*, 1999; Smout, 2000; Vera, 2000; Fenton, 2001). Delcourt *et al.* (1983, p. 157) suggest that a full understanding of vegetation process can only be obtained within a 'space–time hierarchy'. Studies are needed that bridge the gap between the analysis of Holocene vegetation dynamics at a coarse temporal scale and the precursors to present-day ecological variations at a fine spatial scale (Bennett, 1995).

Methods

Study sites

Glen Affric is celebrated as 'the jewel in Scotland's native woodland crown' (Forestry Commission, 2003). One of the largest areas of native forest in Scotland and one of the most important relicts of ancient Caledonian pinewood survives in the east of Glen Affric (Figure 1). Current plans are for regeneration of the native pinewood (Bell, 2003; Forestry Commission, 2003), with the assumption, not yet established, that its stability, variety

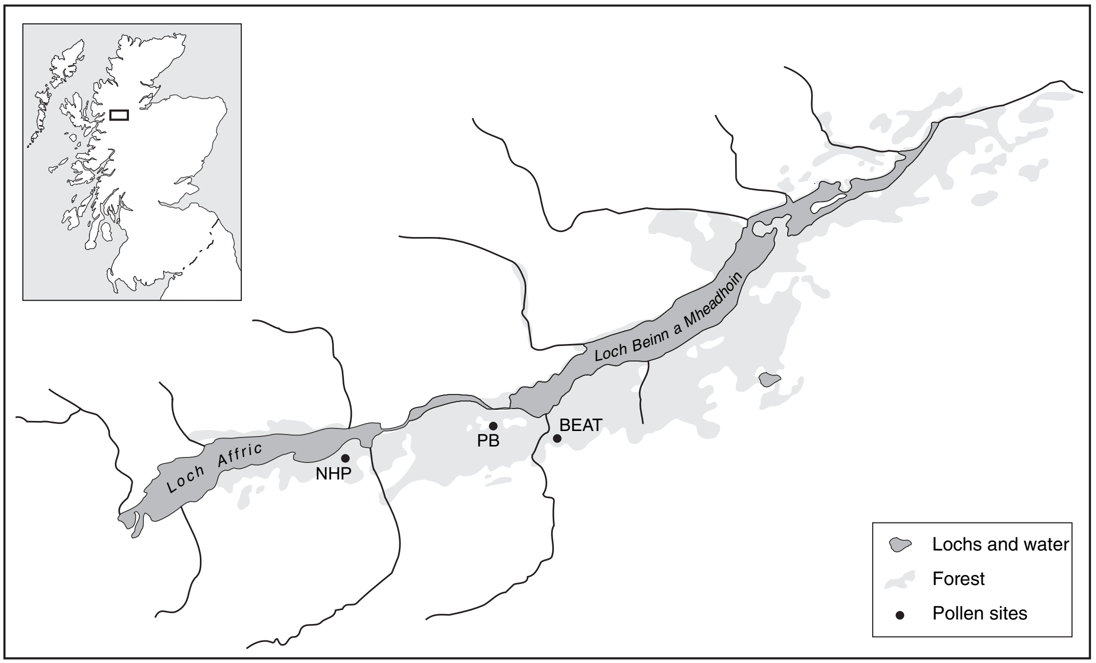

Figure 1. Loch Affric and the reservoir of Loch Beinn a' Mheadhoin in Glen Affric, showing the major streams draining the glen and the distribution of native woodland. The map shows the locations of the three pollen sites in this analysis.

and extent are inherited from former times. The past dynamics of these woods are still not fully understood. In east Glen Affric, Froyd (2002, this issue) demonstrates a strong signal for continuance of woodland from inception *c.* 8000 cal. BP (BP = before present, dates are expressed in calibrated (cal.) years throughout) to the present. This is in contrast to the absence of pine woodland west of Loch Affric over the last *c.* 4000 cal. years (Davies, 1999, 2003; Davies and Tipping, 2004).

Currently, the glen east of Loch Affric is predominantly wooded, while the west is almost treeless; the transition is at the head of Loch Beinn a' Mheadhoin and alongside Loch Affric (Figure 1) where trees and woodland begin to thin out into open heath. Steven and Carlisle (1959) noted a worrying lack of regeneration throughout the woodlands, attributed to deer grazing, and this assumption has led to the understanding that the trees in Glen Affric are part of a receding population. The pollen analyses presented here test this assumption and begin to explain in greater detail the shape and composition of the former woodland in the eastern glen. The results of three pollen diagrams forming the most westerly cluster of three in east Glen Affric (Figure 1) are presented in this paper with the aim of discussing the transition between the forested east and unforested west of the glen and testing whether the current pinewood was in retreat when Steven and Carlisle saw it. Teasing out the local detail of vegetation dynamics from the regional picture for time scales of relevance to trees can add to an understanding of these ecosystems and underpin conservation management strategies, biodiversity enhancement and long-term sustainability. Here some of these details are resolved by the use of a network of several interrelated pollen sites.

Peat coring and analysis

Peat cores were extracted from a network of sites in east Glen Affric: in this analysis, we use three of the eight analysed (Figure 1). The cores were taken from small (<20-m diameter) peat-filled basins. Data on pollen recruitment characteristics show that such small basins depict vegetation at the stand scale in fully wooded landscapes (Jacobson and Bradshaw, 1981; Jackson and Wong, 1994; Jackson and Kearsley, 1998). This assumption has been tested and confirmed in east Glen Affric by comparing surface pollen assemblages with surrounding vegetation at 30 sites (H. Shaw, unpublished data).

Peat sub-samples *c.* 1 cm^3 in volume were taken from the top 1 m of each core at 2-cm intervals, each sub-sample being 0.3 mm thick to represent just a few years' peat accumulation. Pollen was extracted from the sub-samples by standard methods (Moore *et al.*, 1991) and counted using an Olympus BX40 microscope at ×400 magnification, with difficult grains identified under oil immersion at ×100 magnification. *Pinus* stomata were counted to assist with defining local *Pinus* presence (Parshall, 1999). Microscopic charcoal was counted on microscope slides as proportions of the pollen sum to provide evidence of vegetation burning. Pollen was identified with reference to Moore *et al.* (1991) and the pollen reference collection at the University of Stirling. A total land pollen sum of in excess of 500 grains per sample was counted. Pollen nomenclature follows Bennett (1994). Relative pollen percentage diagrams were produced using TILIA and TILIA.GRAPH (Grimm, 1991). Pollen diagrams were zoned using CONISS, a stratigraphically constrained cluster analysis (Grimm, 1987).

Samples from the top 20 cm of each core were dated by lead isotope (^{210}Pb) dating. ^{210}Pb age estimates were obtained from 15 to 20 dried, homogenized and pressed 1.0- or 2.0-cm peat slices: only the basal age defined by this technique for each core is given here. Two samples from each core were selected for AMS radiocarbon dating and the humic acid fractions of 0.5-cm peat slices assayed. Assays were calibrated using OxCal (Bronk Ramsey, 1995); age estimates are quoted in the text as the mid-point of the 2σ calibrated age range, rounded to the nearest 5 years. Numbers of spheroidal carbonaceous particles (Rose *et al.*, 1995) and of non-native, planted pollen types (mainly from *Picea*) were counted on the pollen slides to assist in age determination of the recent peat.

Results

Pollen diagram NHP (grid reference NH 174223: Figure 2)

This site is located on the south side of Loch Affric (Figure 1) in a putatively even-aged *Pinus*

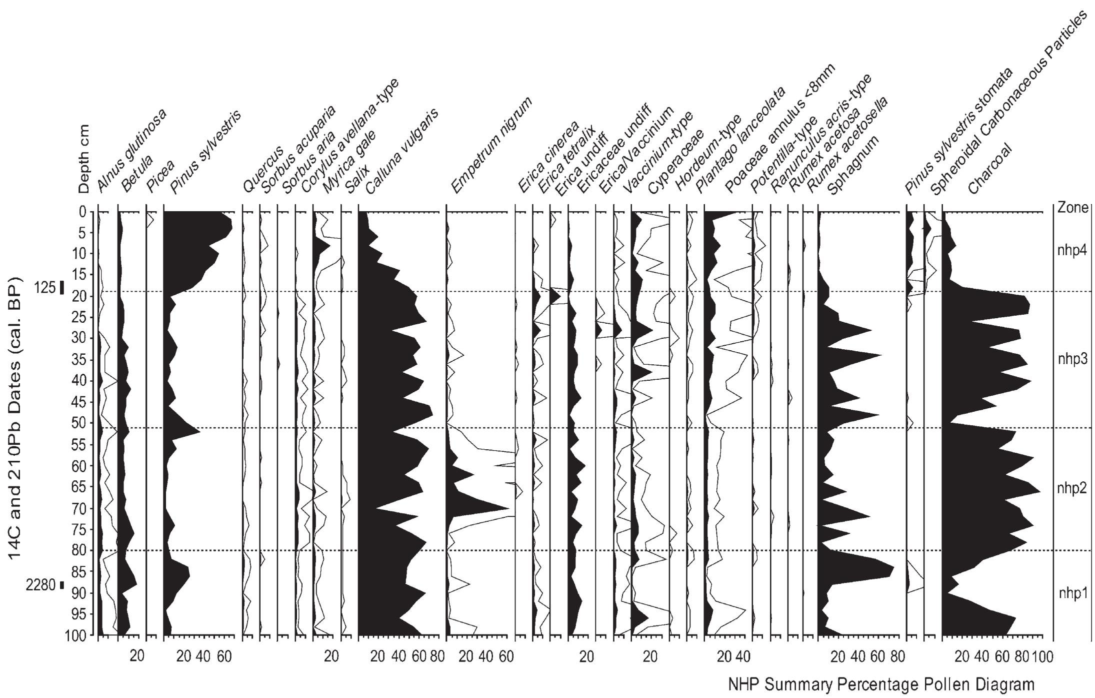

Figure 2. Percentages of selected pollen and spore taxa, and other microscopic particles, at NHP plotted against depth, showing the local pollen assemblage zonation applied. The depths of accepted dating controls are shown at the extreme left. Taxa from *Alnus* to *Rumex* inclusive are included within the tlp sum. Proportions of *Sphagnum* spores, *Pinus* stomata, spheroidal carbonaceous particles and microscopic charcoal fragments are calculated as percentages of themselves plus tlp.

stand. Species of Poaceae and Cyperaceae dominate the basin surface, with *Vaccinium* and *Calluna* on rocky outcrops above the basin. The topography slopes steeply towards the loch side.

^{210}Pb dating of this core suggests the depth increments of 18–20 cm to have an age of AD 1880 (125 years ago). The two ^{14}C assays (Table 1) are difficult to interpret because the lower sample is younger. The assay at 69 cm is here assumed to be inaccurate and is omitted from Figure 2. Few spheroidal carbonaceous particles were recorded but this curve (Figure 2) does not contradict the ^{210}Pb age estimate.

From 100 to 80 cm (zone nhp1: 2620–2000 cal. BP), the plant communities around and on the mire at NHP were dominated by a heath of *Calluna* and other Ericaceae. The occurrence of *Pinus* stomata between 92 and 82 cm (2370–2060 cal. BP) is the most assured evidence for some local *Pinus* trees. Percentage values for *Pinus* pollen of <20 per cent tlp need not represent trees local to the pollen site (Fossitt, 1996), and there may have been only a few pine trees close to the basin at NHP. Other trees and shrubs have probably not grown in this part of the glen in the last 2600 years.

The expansion of *Pinus* after 2370 cal. BP coincides with a decrease in charcoal and a very large increase in the proportions of *Sphagnum* moss on the bog surface. Zone nhp2 (80–52 cm: 2000–1140 cal. BP) is marked by a large increase and peak in *Empetrum* within the heath, and with the decline of *Sphagnum* in this zone, this is thought to indicate a sustained dry phase affecting water levels in the bog until 1360 cal. BP (Tallis, 1997).

Charcoal is present in high quantities throughout zone nhp2. The pollen of *Plantago lanceolata*

Table 1: Radiocarbon (^{14}C) dates and calibrated age ranges

Site	Laboratory code	Depth (cm)	Radiocarbon age BP (1σ)	Calibrated age range BP (2σ)	Mid-point (cal. BP)
NHP	SUERC-3955	69	2793 ± 26	2960–2790	2875
NHP	SUERC-3956	89	2299 ± 23	2360–2180	2270
PB	SUERC-3957	71	3773 ± 28	4240–4000	4120
PB	SUERC-3958	93	4384 ± 30	5050–4860	4955
BEAT	SUERC-3952	49	135	280–0	140
BEAT	SUERC-3953	67	242	320–0	160
BEAT	SUERC-3954	99	2042 ± 25	2110–1920	2015

is recorded in small amounts in the lower part of zone nhp2, but if indicative of grazing, these pressures were not significant. At the upper zone boundary at 52 cm (1140 cal. BP), charcoal values decrease sharply. There is a short-lived peak in *Pinus* pollen and *Pinus* stomata until 44 cm (895 cal. BP), indicating the re-establishment of a small local pine population for a single generation. This was lost in zone nhp3, and heathland continues to dominate and proportions of charcoal increase. Grazing pressures suggested by the proportions of *P. lanceolata* were low or negligible. Pollen grains of *Hordeum* type (barley type) are recorded after 600 cal. BP but these may represent species of wild grass. Open vegetation persists until zone nhp4 at 20 cm (*c.*150 cal. BP) when *Pinus* pollen and stomatal percentages rise. With the development of the current pine woodland, *Calluna* proportions decrease and values of Poaceae and Cyperaceae increase.

Pollen diagram Pollan Buidhe (grid reference NH 198230: Figure 3)

This site is located on the south side and at the head of Loch Beinn a' Mheadhoin (Figure 1). The vegetation covering the basin surface is dominated by tall, mature *Calluna* heath, with mature *Pinus* trees on the surrounding higher ground.

The Pollan Buidhe (PB) core consists of very compact peat, and the pollen record extends to *c.* 5300 cal. BP, although the ^{210}Pb age estimate at 11.0 cm of *c.* AD 1895 suggests that recent peat growth has been more rapid (Table 1).

Zone pb1 (100–74 cm: 5350–4250 cal. BP) is dominated by *Pinus* and *Betula*. *Pinus* stomata are constantly present during this period, demonstrating a strong local presence of the species. The woodland composition was mixed, and included *Alnus*, *Quercus* and *Corylus*. The understorey was mainly a *Calluna* heath, with small proportions of Cyperaceae and Poaceae. Microscopic charcoal amounts are generally low. Zone pb2 is divided into three sub-zones on the abundance of *Calluna* pollen. It begins (sub-zone pb2a) with a decline in *Pinus* pollen to below 20 per cent between 74 and 56 cm (4250–2720 cal. BP) and a shift to open vegetation, maintained until 22 cm (370 cal. BP). This is supported by the absence of *Pinus* stomata. The initial decline in *Pinus* abundance at this site corresponds in age with the regional *Pinus* decline (Bennett, 1995; Tipping *et al.*, this issue). *Calluna* pollen percentages increase during this phase, with an increase in *Empetrum* at the start of sub-zone pb2a (4250–4000 cal. BP), suggesting some drying of the peat surface. *Sphagnum* representation is low throughout zone pb2a. A mosaic of heath with Poaceae developed, the latter rich in *Potentilla*.

By sub-zone pb2b, tree presence was limited, and *Pinus* and *Betula* percentages less than 20 per cent probably represent pollen dispersed from trees some distance from the site. Charcoal values remain high during the period of low woodland cover but there is no palynological indication of human influence. From 20 cm (230 cal. BP) to the present day, woodland increased and the growth of *Pinus* trees local to the site is supported by the occurrence of *Pinus* stomata. This present woodland lacks the arboreal diversity of the mid-Holocene woodland.

Pollen diagram BEAT (grid reference NH 212227: Figure 4)

This site is located on the south side to the western end of Loch Beinn a' Mheadhoin (Figure 1).

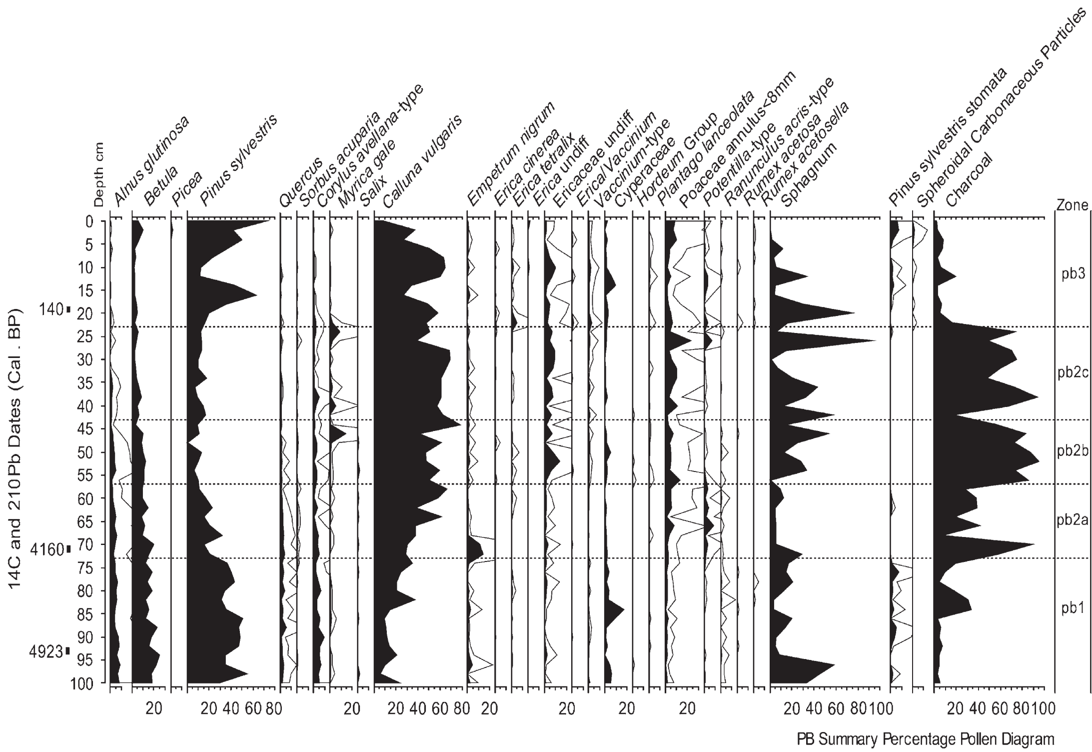

Figure 3. Percentages of selected pollen and spore taxa, and other microscopic particles, at PB plotted against depth, showing the local pollen assemblage zonation applied. The depths of accepted dating controls are shown at the extreme left. Taxa from *Alnus* to *Rumex* inclusive are included within the tlp sum. Proportions of *Sphagnum* spores, *Pinus* stomata, spheroidal carbonaceous particles and microscopic charcoal fragments are calculated as percentages of themselves plus tlp.

Steep slopes with rocky outcrops and boggy flushes surround a basin of *Sphagnum* and Cyperaceae within *Calluna* heath and a mature *Pinus* and *Betula* woodland canopy.

Although chronology construction is currently uncertain, for this publication, the interpretation assumes a linear slope between the oldest ^{210}Pb assay and the ^{14}C assay at 99 cm (SUERC-3954: Table 1).

From 100 to 66 cm (2020–1150 cal. BP), the pollen record depicts a wood dominated by *Betula* with some *Alnus*, *Quercus* and *Corylus*. *Pinus* pollen percentages are low, and there are no *Pinus* stomata. At 66 cm (1150 cal. BP), there was a rapid change to more open conditions, with a reduction in *Betula*, *Alnus* and *Quercus*. There is an increase in Cyperaceae pollen percentages, together with an increase in total numbers of diatoms (undifferentiated to species and not depicted on Figure 4) which together could indicate a shift to a wetter climate or a raising of the water level within the basin through disturbance to the surrounding vegetation. *Hordeum*-type pollen grains persist throughout this phase, but these are thought to be from wild grass species such as *Glyceria* rather than from cultivated cereals.

In zone beat2a from 66 to 56 cm (1150–900 cal. BP), *Pinus* pollen values rise gradually, accompanied by the appearance of *Pinus* stomata, indicating the spread of *Pinus* trees nearer to the site. From 56 cm (900 cal. BP), *Pinus* proportions increased further, evidenced by both *Pinus* stomata and pollen, stomatal values peaking at 50 cm.

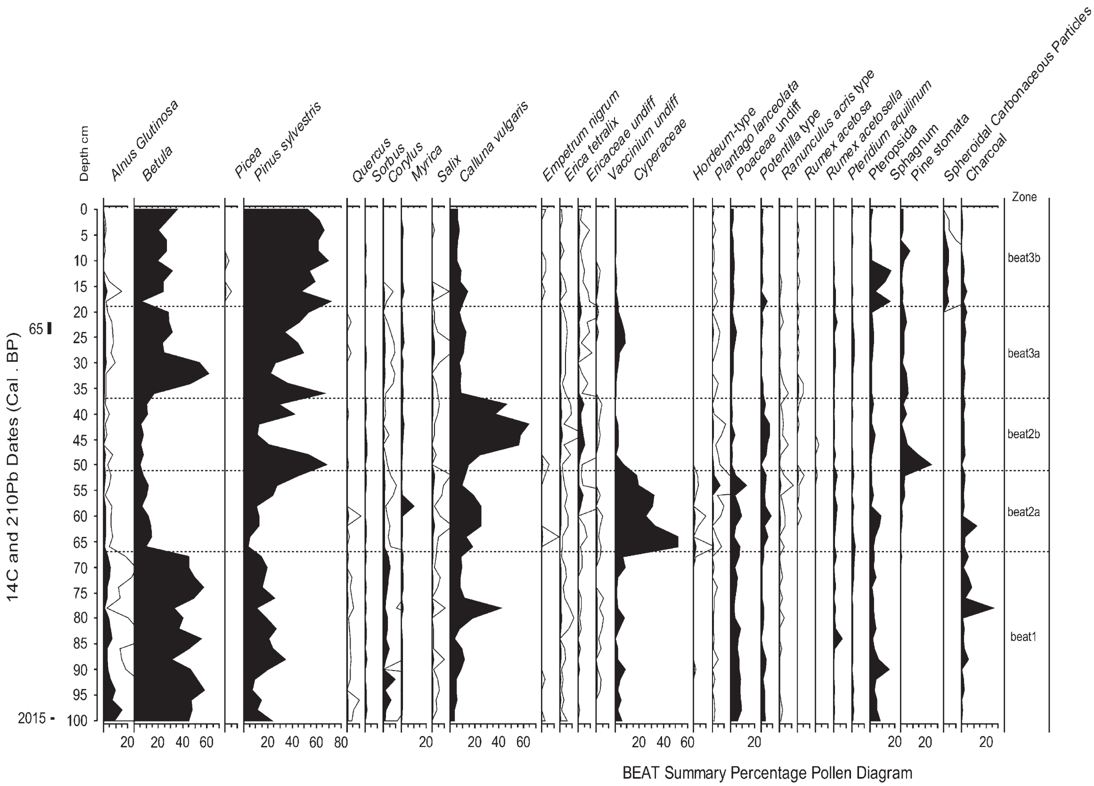

Figure 4. Percentages of selected pollen and spore taxa, and other microscopic particles, at BEAT plotted against depth, showing the local pollen assemblage zonation applied. The depths of accepted dating controls are shown at the extreme left. Taxa from *Alnus* to *Rumex* inclusive are included within the tlp sum. Proportions of *Sphagnum* spores, *Pinus* stomata, spheroidal carbonaceous particles and microscopic charcoal fragments are calculated as percentages of themselves plus tlp.

From 50 to 36 cm (zone beat2b: *c*. 750–390 cal. BP), *Calluna* pollen percentages increase as those of Cyperaceae and *Pinus* decrease. Some local *Pinus* trees persisted, determined by the presence of stomata. The decreasing percentages of *Pinus* to <20 per cent at 42–46 cm, with high levels of heathland pollen, indicate a generally open environment throughout most of this zone with the stomatal presence depicting a few *Pinus* trees, perhaps situated on the surrounding rocky outcrops. *Calluna* dominance lasts until 36 cm when *Pinus* begins to increase with *Betula* in zone beat3a and the current stand structure develops. From 36 to 0 cm (*c*. 390–0 cal. BP), although woodland dominates the vegetation once more, the stand structure is less diverse than the previous woodland with *Pinus* and *Betula* dominating and additional woodland components such as *Quercus*, *Alnus* and *Corylus* disappearing from the locality.

Discussion

The two pollen diagrams furthest to the west, NHP and PB, record a sustained lack of tree cover around these sites for several thousand years until the present tree cohort developed. The site at PB extends sufficiently far in time to demonstrate that *Pinus* woodland loss began at the classic *Pinus* decline at *c*. 4000 cal. BP. The pattern from these two sites, particularly from PB, is similar to that at Torran Beithe (Davies, 2003; Tipping *et al.*, this issue) a few kilometres west at the head of Loch Affric. The current open and patchy woodland stand structure along the side of Loch Affric (Figure 1) is likely to be invasive into a former, stable heath community.

The interpretation of the tree cover over the last *c.* 2000 years at the site at BEAT is more consistent with analyses to the east by Froyd (2002, this issue) which show a continuous woodland cover since *c.* 8000 cal. BP. Open phases at BEAT, as from 66 to 36 cm (1150–390 cal. BP), were probably less extensive or long-lived than at sites further west. There may be several explanations for the persistence of woodland along the south side of Loch Beinn a' Mheadhoin (Figure 1). The steeper, more free-draining valley sides may support less blanket peat, and the greater abundance of mineral soils may encourage woodland growth. The steeper slopes may also have discouraged human activities in the glen, although these appear not to have been significant around the pollen sites of NHP and PB. Finally, it may be that a marked climatic gradient throughout the glen has existed through the later Holocene, inhibiting tree growth to the west and allowing it to persist in the east.

The variation in woodland composition in former times is also of note. This observation validates and supports an approach to future woodland restoration which includes the encouragement of broadleaved species. *Quercus* and *Corylus* are currently restricted to the east of the glen. It is difficult to understand whether the present limited range of these trees is due to former human exploitation, pedogenic constraints or some climatic influence.

In the contrasts between pollen sites in the frequency or intensity of burning, seen in the microscopic charcoal records at NHP, PB and BEAT, there may be suggestions that west and east Glen Affric supported different land use strategies in the past.

Given the palynological evidence for arable agriculture to have been confined to alluvial valley floors (Davies, 1999, 2003), it may have been that gentle slopes above these were used for grazing, while the steeper slopes, such as along Loch Beinn a' Mheadhoin, were reserved for woodland.

The removal of farming communities from the glen during the nineteenth century 'clearances' might, then, explain the new and steady progression westward of the *Pinus* woodland. This expansion may then have been checked by the increase in deer numbers after the mid-nineteenth century (Steven and Carlisle, 1959; Watson, 1983), but there is little evidence at these three pollen sites for deer to have decimated the woodland.

In addressing the management objectives of expanding the natural pine woodland (Bell, 2003), the data from this paper can be considered in terms of two possible models. The first is that the current scarcity of trees to the west of Loch Affric is a result of sustained human impact on the landscape, from later prehistory, with the recent expansion of woodland demonstrated at NHP and PB being the result of tree regeneration released from anthropogenic pressures in the nineteenth century. The second posits that the boundary between woodland and heath represents a natural, shifting ecotone defined by climatic and topographic gradients (cf. Tipping *et al.*, this issue), with the recent westward woodland expansion being only the latest response to climate change.

These two models cannot be separated on current data but need to be considered when restoring or creating woodland into the west of the glen. Although social constructs may make woodland desirable, the past expansive pine woodland here was lost several thousand years ago (Tipping *et al.*, this issue). It may be that tree populations in the future will be inherently unstable. Long-term sustainability of the more westerly woodland may be questionable unless continued intervention is considered. In more easterly areas, tree regeneration following the exclusion of deer probably also means that the current woodland is denser in structure than in the past; an open and fluctuating woodland structure inferred from the pollen data may be important for the maintenance of understorey biodiversity.

Two final points emerge. First, landscape-scale woodland restoration is important in maintaining the open structure of the woodland, with gaps and open areas, while maintaining a core of woodland from which to preserve the genetic integrity of the *Pinus* stands. Second, the sometimes rapid changes in woodland structure and episodes of woodland decline recognized in the pollen analyses perhaps imply that if expansion of woodland is to be maintained over several generations, we need to accept and not constrain some surprising changes in species composition and woodland structure.

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