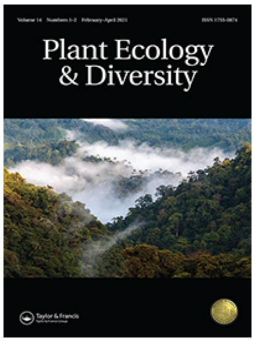

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Holocene expansion of the Caledonian pinewoods: spatial and temporal patterns at regional and landscape scales

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ABSTRACT

Background: To facilitate climatic change adaptation, landscape and conservation managers require understanding of spatio-temporal patterns of expansion of potential dominant species. Studying past expansions of canopy-dominant trees can contribute such understanding.
Aims: Test hypotheses about expansions of dominants using as a model the mid-Holocene expansion of forests dominated by *Pinus sylvestris* in the Scottish Highlands.
Methods: Pollen analysis and radiocarbon dating of Holocene sediments of a larger basin and several small hollows were performed in three landscapes along a north–south transect. A larger basin records expansion timing at landscape scale, whilst small hollows evidence within-landscape spatio-temporal patterns.
Results: Vegetation existing prior to the expansion of pinewoods influenced landscape-scale spatio-temporal expansion patterns of *P. sylvestris*. Open vegetation generally was invaded earlier and/or to a greater extent; invasion was often later, or did not occur, where woodland with a substantial temperate broadleaved tree and shrub component (e.g. *Corylus avellana, Quercus* spp.) was present. Most small hollows, not just those where pinewoods became locally established, recorded vegetation change during the expansion. Some present landscape-scale forest composition patterns were established at that time.
Conclusions: Studying past expansions of dominants provides evidence relevant to planning conservation and landscape management to facilitate ecological adaptation as species adjust their distributions and abundances in response to climatic change.

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KEYWORDS
Canopy-dominant tree; invasion pattern; Mid-Holocene; *Pinus sylvestris*; pollen analysis; Scottish Highlands; small hollows

Introduction

The objective of our study was to gain insight into the regional- and landscape-scale ecological impacts arising from range expansion of a dominant forest tree species. Potential future range expansions of such species have been projected in response to anthropogenic climatic change, e.g. *Fagus sylvatica* in northern Europe (Sykes et al. 1996), and it is important for landscape managers, especially if their aim is biodiversity conservation, to understand the likely ecological impacts of such range expansions. Although involving species native to the same wider biogeographical region, rather than alien species introduced from other biogeographical regions, such expansions of potential canopy dominant trees in response to climatic change will potentially lead to ecological regime shifts, paralleling such shifts following invasions by some alien species (Gaertner et al. 2014).

We chose to examine the previously documented Holocene expansion of *Pinus sylvestris* (Scots pine) (higher plant nomenclature follows Tutin et al. 1964, 1968, 1972, 1976, 1980) forests across the Scottish Highlands, because this provides a readily accessible model for such expansions that is amenable to investigation using palaeoecological methods. It is also likely that this expansion of pine-dominated forest was facilitated by the widespread but sparse presence of *P. sylvestris* prior to the expansion (Huntley et al. 1997; Froyd 2005), paralleling the present situation in many regions where potential canopy dominants (e.g. *Fagus sylvatica*) are already widely grown, either as ornamentals or as plantation trees.

Although only small fragments now remain (Steven and Carlisle 1959), the predominant forests throughout the Scottish Highlands from the mid-Holocene until the extensive forest clearances of the eighteenth to the twentieth centuries were the so-called Caledonian pinewoods. On the basis of the distribution of the remaining fragments (Figure 1), McVean and Ratcliffe (1962) have mapped the potential present extent of these pinewoods. They have shown them extending from sea-level to a potential treeline that reaches *ca.* 615 m a.s.l. in the Cairngorms (Pears 1967), and northwards from

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Supplemental data for this article can be accessed here.

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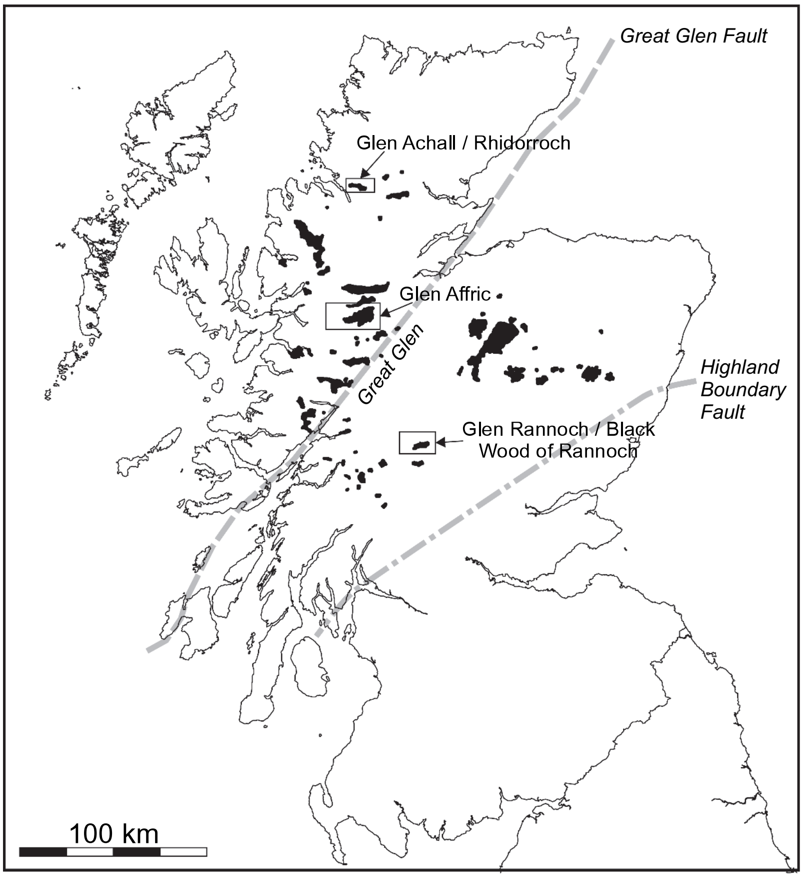

Figure 1. Remnant Caledonian pinewoods and landscapes examined, Scotland. Black shaded areas indicate remnant stands of Caledonian pinewoods as mapped by the Caledonian Pinewoods Inventory (Forestry Commission 1999) that investigated the remaining extent of native pinewoods listed by Steven and Carlisle (1959). Rectangles indicate the locations and approximate extents of the three landscapes examined, each of which is labelled to indicate the name used here for the landscape and the name used by Steven and Carlisle (1959) for the remnant native pinewoods in that landscape where that differs. Also shown are the approximate lines of the Great Glen Fault and the Highland Boundary Fault.

the Highland Boundary Fault, that marks the south-eastern boundary of the Scottish Highlands, to a northern limit in the south and east of the former county of Sutherland, although replaced by oak (*Quercus petraea*) woodlands in western coastal areas and along the Great Glen. The dominant canopy tree is *Pinus sylvestris*, although other tree species are often also present, especially *Betula pubescens, B. pendula* and *Sorbus aucuparia* (McVean and Ratcliffe 1962; Rodwell 1991, W18). *Juniperus communis* is the most characteristic understorey tall shrub, and is often abundant in central and eastern areas. The ground layer is most commonly dominated by the ericaceous dwarf shrubs *Calluna vulgaris, Vaccinium myrtillus* and/or *V. vitis-idaea*, usually with a continuous moss carpet dominated by *Hylocomium splendens, Rhytidiadelphus triquetrus, Ptilium cristacastrensis* and/or *Sphagnum* spp. (nomenclature for mosses follows Smith 1978).

Notwithstanding its essentially boreal character, palaeoecological evidence shows that this forest type was absent from Scotland during the early millennia of the Holocene, the areas it now occupies supporting scrub of *Juniperus communis* at the onset of the Holocene, quickly followed by woodland cover dominated by *Betula* spp., accompanied by *Sorbus aucuparia* and *Populus tremula*, and especially in the west by *Corylus avellana. Quercus* spp. and *Ulmus* spp. were also present; although neither was abundant generally, *Quercus* spp. were moderately abundant in some Eastern Highland glens, as well as dominating in western coastal areas (Birks 1977; Huntley et al. 1997). *Pinus* pollen increased in abundance first in the North-west Highlands *ca*. 8800 cal. yr BP, with *Pinus*-dominated forests subsequently expanding southwards, eastwards and, to a more limited extent, northwards over the following *ca*. 3000 years (Figure 2; Birks 1989). Thereafter, pinewoods were extensive throughout the Highlands, extending to the Northern Highlands after *ca*. 5500 cal. yr BP, and as far as north-west Sutherland by *ca*. 4800 cal. yr BP and Caithness by *ca*. 4300 cal. yr BP (Daniell 1997; Huntley et al. 1997). However, the pinewoods of the Northern

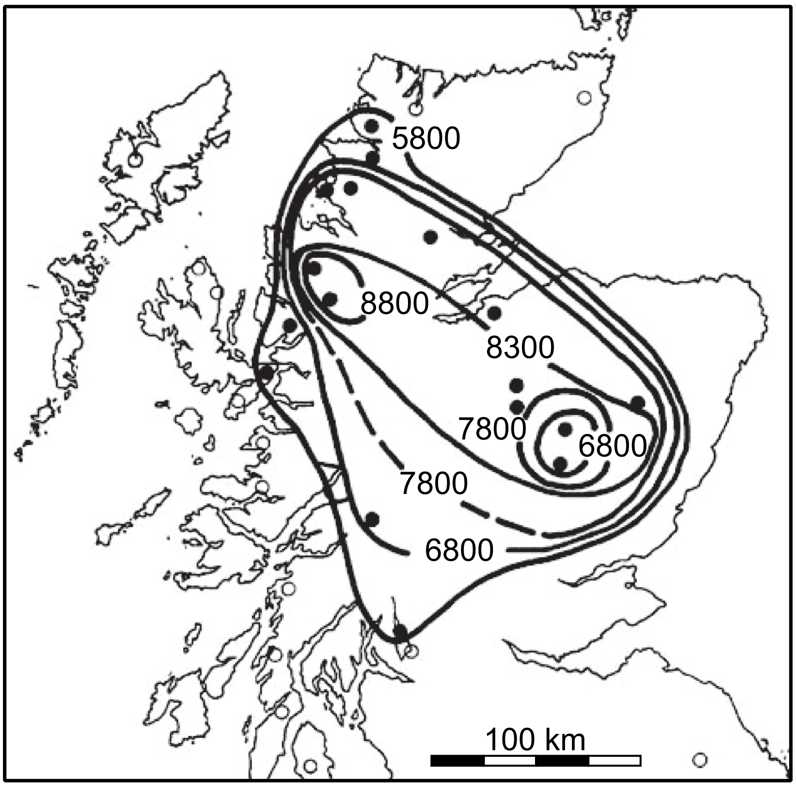

Figure 2. Isochrone map for *Pinus sylvestris* in Scotland. Isochrones (cal. yr BP) show the species' Holocene expansion as a forest dominant southward, eastward and, to a more limited extent, northwards across the Highlands of Scotland from an initial area of increase in the North-west Highlands (after Birks 1989, redrawn with modifications).

Highlands apparently persisted only for a few centuries (Gear and Huntley 1991; Daniell 1997; Huntley et al. 1997; Moir et al. 2010; Moir 2012) before the northern limit of pinewoods retreated once again to approximately that inferred and mapped by McVean and Ratcliffe (1962). Pinewoods also extended to higher elevations than today during the mid- and late-Holocene, macrofossil evidence of *P. sylvestris* dating from between *ca*. 4900 and 2600 cal. yr BP being found at 880 m a.s.l. in the Cairngorms (Huntley et al. 1997; Allen and Huntley 1999). Although the temporary expansion into the Northern Highlands is generally attributed to climatic variations (Gear and Huntley 1991; Moir et al. 2010), as are variations in treeline elevation (Huntley et al. 1997; Holtmeier and Broll 2005, 2020), there is no consensus with respect to the underlying cause of the mid-Holocene expansion of pinewoods across the Scottish Highlands, although changing climatic conditions seem most likely.

Although pine-dominatedwoodlands were predominant throughout the Highlands after the mid-Holocene, it is likely that, as indicated by the forest fragments that remain today, they were not uniformly dominant, but rather were the principal component of landscape-scale vegetation mosaics that included also various other forest and woodland types, as well as mires, heathlands and other open plant communities (Fyfe et al. 2013). Especially in glens (= valleys) that trend predominantly west–east, the remaining woodland fragments at lower elevations on the south facing slopes of the north sides of these glens are often composed primarily of *Quercus* spp., *C. avellana* and/or *Ulmus glabra* (B.H. personal observations). Such stands can be seen, for example, above the northern shores of Lochs Rannoch and Maree, whereas on the opposite north-facing slopes *P. sylvestris* dominates the woodlands down to the valley floor in both cases. Even within forest areas dominated today by *P. sylvestris* there is a mosaic, often associated with topographically-related variation in the degree of soil waterlogging, with areas of woodland dominated by *Betula* spp. on wetter soils and open areas of mire on the wettest soils. On riversides and stream banks *Alnus glutinosa* is often locally dominant, and clonal patches of *P. tremula* are also scattered within the overall forest area (B.H. personal observations). It is probable that at least some elements of these landscape-scale mosaics had already been established prior to the expansion of pinewoods across the Scottish Highlands.

Our study tested four hypotheses relating to spatial and temporal vegetation patterns prior to, during and after this expansion, at both regional and landscape scales, by performing a series of palaeoecological investigations designed to provide the required tests. These hypotheses were:

(1) Vegetation exhibited spatial patterns in structure and composition, at both regional and landscape scales, prior to pinewood expansion.
(2) Spatial and temporal patterns of pinewood expansion at the landscape scale reflected prior landscape-scale vegetation patterns.
(3) Vegetation changes occurred throughout the landscape at the time of pinewood expansion, not just in those landscape components invaded by *P. sylvestris*.
(4) Landscape-scale patterns of forest and woodland cover seen today have persisted since the expansion of pinewoods.

Pollen analyses and radiocarbon dating of the sediments of one larger basin and several small hollows were performed in three west–east trending glens located along a north–south transect through the Scottish Highlands. Dating and pollen analyses focused on the millennia preceding, during and following evidence of the expansion of pinewoods in each glen. Pollen data from the larger basins documented the landscape-scale expansion of pinewoods, as well as the overall composition and structure of vegetation at the landscape scale. Data from the small hollows provided evidence of the extent of within-landscape spatial and temporal patterning both of the pinewood expansion and of the vegetation composition and structure. The data obtained were used to test the four hypotheses.

Materials and methods

Landscape and site selection

In order to address spatial and temporal patterns at the regional scale of the Scottish Highlands as a whole, three landscapes were selected, one each approximately in the north, centre and south of the potential extant area of the Caledonian pinewoods (Figure 1). Of possible landscapes within each area, only those having a major west–east trending glen were considered. These offer contrasting north- and south-facing slopes, the microclimates of which potentially would favour different tree species now and in the past. Landscapes were also required to support extant stands, even if fragmentary, of Caledonian pinewoods. The three landscapes selected, hereafter referred to as (Glen) Achall (Figure 3), (Glen) Affric (Figure 4) and (Glen) Rannoch (Figure 5), host the remnant Caledonian pinewoods referred to by Steven and Carlisle (1959) as, respectively, Rhidorroch, Glen Affric and Black Wood of Rannoch.

In each landscape a series of sediment cores was collected. At least one was from a lochan (= small lake) or mire of sufficient size (100 to 300 m diameter, Jacobson and Bradshaw 1981) to provide a pollen record representing the palaeovegetation of the landscape as a whole (i.e. with dominance

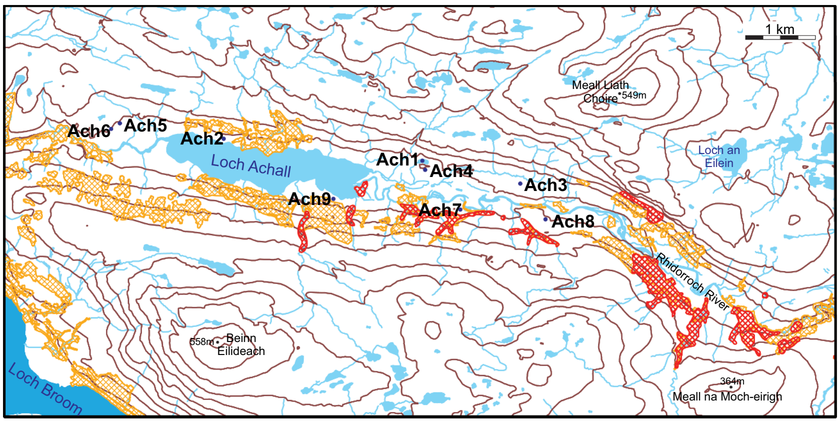

Figure 3. Remnant native woodland and coring sites in Glen Achall, Scotland. Orange cross-hatched areas indicate remnant stands of native woodland as mapped by the Native Woodland Survey of Scotland (Forestry Commission 2014); red cross-hatched areas indicate remnant stands of Caledonian pinewoods as mapped by the Caledonian Pinewoods Inventory (Forestry Commission 1999). Labelled dots indicate the locations (Ach1– Ach9) from which sediment cores were obtained. Contours at 50mintervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape11.879 km E – W by 5.860 km N – S; south-west and north-east corners at UK National Grid coordinates NH 13881 91551 and NH 25760 97411, respectively.

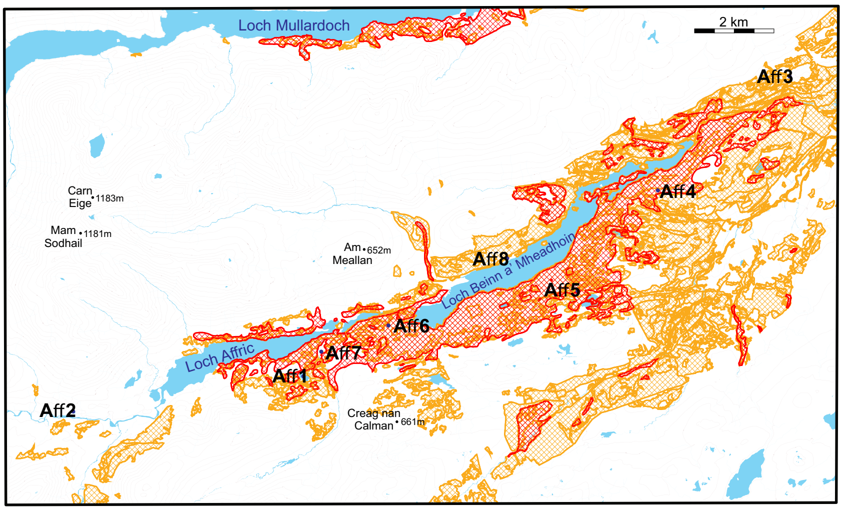

Figure 4. Remnant native woodland and coring sites in Glen Affric, Scotland. Orange cross-hatched areas indicate remnant stands of native woodland as mapped by the Native Woodland Survey of Scotland (Forestry Commission 2014); red cross-hatched areas indicate remnant stands of Caledonian pinewoods as mapped by the Caledonian Pinewoods Inventory (Forestry Commission 1999). Labelled dots indicate the locations (Aff1 – Aff8) from which sediment cores were obtained. Contours at 50 m intervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape 20.944 km E – W by12.517 km N – S; south-west and north-east corners at UK National Grid co-ordinates NH 10070 18454 and NH 31014 30971, respectively.

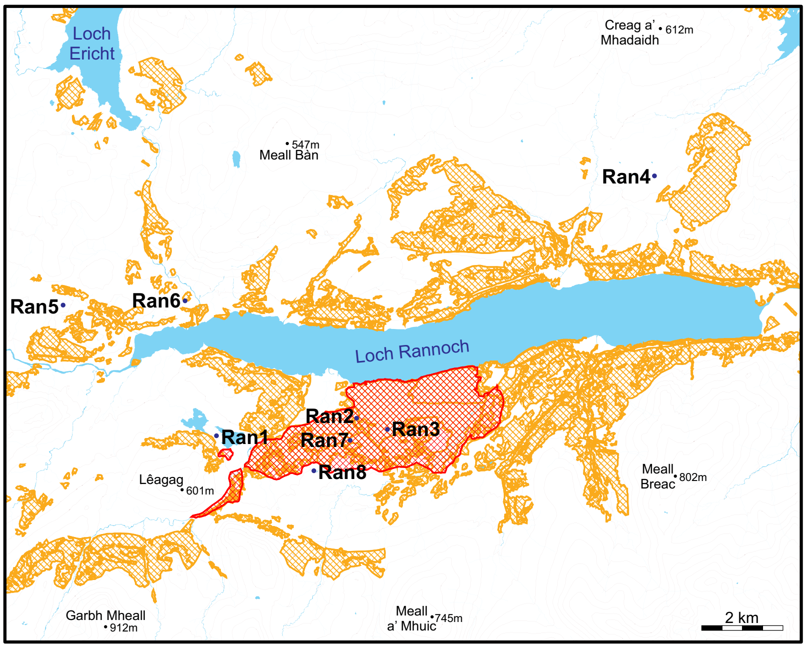

Figure 5. Remnant native woodland and coring sites in Glen Rannoch, Scotland. Orange cross-hatched areas indicate remnant stands of native woodland as mapped by the Native Woodland Survey of Scotland (Forestry Commission 2014); red cross-hatched areas indicate remnant stands of Caledonian pinewoods as mapped by the Caledonian Pinewoods Inventory (Forestry Commission 1999). Labelled dots indicate the locations (Ran1 – Ran8) from which sediment cores were obtained. Contours at 50 m intervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape 19.264 km E – W by15.367 km N – S; south-west and north-east corners at UK National Grid co-ordinates NN 47604 50228 and NN 66868 65595, respectively.

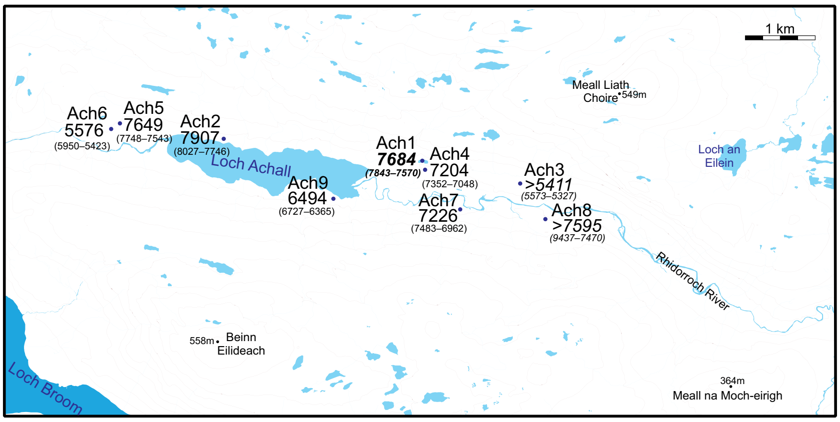

Figure 6. Local and landscape dates for pinewood expansion in Glen Achall, Scotland. Median ages and 95% age ranges (cal. yr BP) for local development of pinewoods adjacent to small basin sites and for general landscape pinewood expansion as recorded in the larger basin examined (bold-italic text). Minimum arrival dates (italic text) are indicated at two sites where *Pinus* pollen was already abundant in the earliest sediments. Contours at 50 m intervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape 11.879 km E – W by 5.860 km N – S; south-west and north-east corners at UK National Grid co-ordinates NH 13881 91551 and NH 25760 97411, respectively.

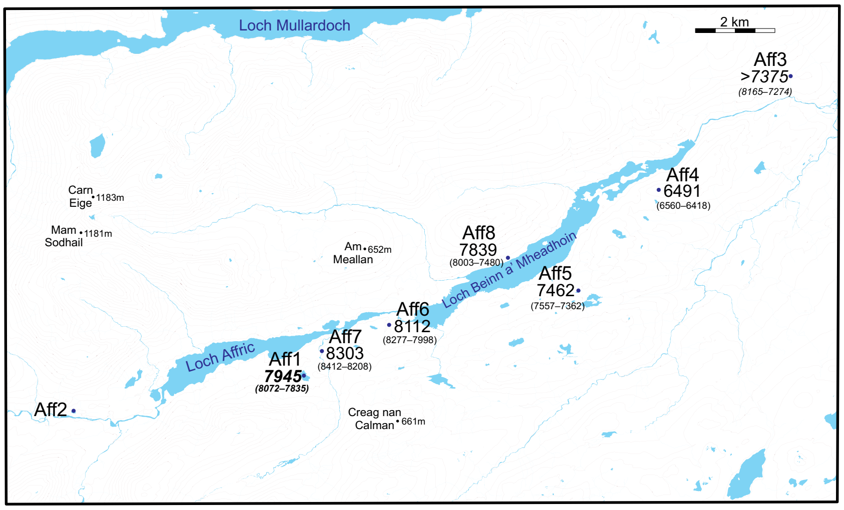

Figure 7. Local and landscape dates for pinewood expansion in Glen Affric, Scotland. Median ages and 95% age ranges (cal. yr BP) for local development of pinewoods adjacent to small basin sites and for general landscape pinewood expansion as recorded in the larger basin examined (bold-italic text). The minimum arrival date (italic text) is indicated at one site where *Pinus* pollen was already abundant in the earliest sediments. The record from the westernmost site, Aff2, extended only to *ca*. 2250 cal. yr BP and thus provided no relevant data. Contours at 50 m intervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape 20.944 km E – W by 12.517 km N – S; south-west and north-east corners at UK National Grid co-ordinates NH 10070 18454 and NH 31014 30971, respectively.

by extra-local pollen derived from between twenty and several hundred metres from the site margin). The remainder were from mires or small lochans within the area of present remnant, or potential past, woodlands and sufficiently small (<50 m diameter) that their pollen record would reflect the palaeovegetation of the immediately surrounding area (i.e. local pollen recruited from the surrounding 20 to 30 m predominated).

Sample collection

At lacustrine sites, sediment cores were collected in segments of up to 1 m in length using a 75 mm diameter Wright-modified square-rod piston corer (Wright 1967). The corer was operated from an inflatable boat moored using two ropes, approximately at right angles to one another and crossing at the deepest point of the lake. Plastic drainage pipe of 100 mm diameter was used as casing to enable the

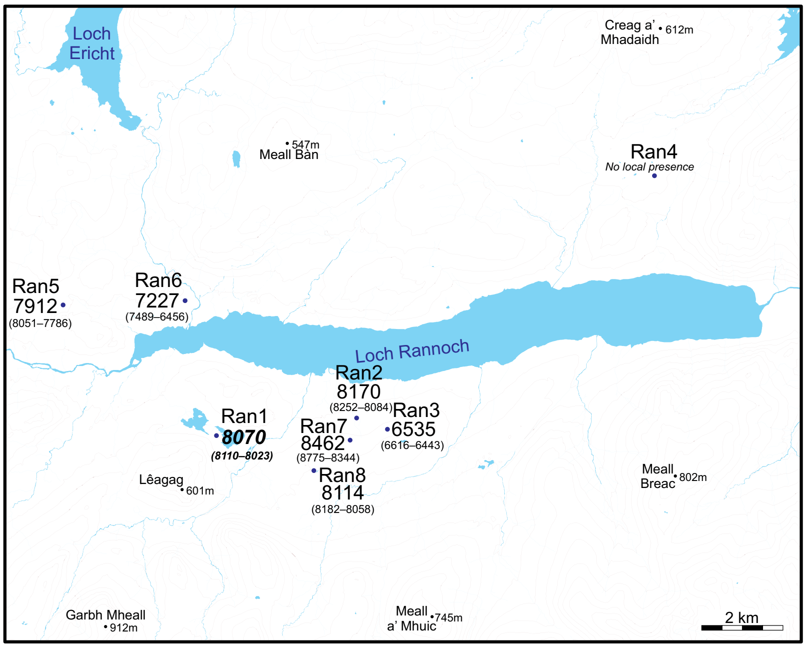

Figure 8. Local and landscape dates for pinewood expansion in Glen Rannoch, Scotland. Median ages and 95% age ranges (cal. yr BP) for local development of pinewoods adjacent to small basin sites and for general landscape pinewood expansion as recorded in the larger basin examined (bold-italic text). 'No local presence' is indicated at one site, Ran4, where *Pinus* pollen abundance never exceeded 15%, only approaching that value during the last two millennia. Contours at 50 m intervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape 19.264 km E – W by 15.367 km N – S; south-west and north-east corners at UK National Grid co-ordinates NN 47604 50228 and NN 66868 65595, respectively.

coring hole to be re-located as the sequence of core segments was collected. Two cores were collected from locations *ca.* 0.5 m apart, segments of the second being adjusted to ensure that segment breaks in the two cores did not coincide, thus ensuring a complete sediment column was provided by the two cores.

At mire sites the uppermost sediments, in most cases comprising relatively unhumified and very compressible peat, were sampled by collecting a monolith; a spade was used to dig a rectangular hole to a depth of 0.3 – 0.6 m and a bread knife then used to cut a monolith from one face of this hole. At Affric and Rannoch the 75 mm diameter Wright-modified square-rod piston corer was then used to collect cores of the sediment below the depth to which the monolith extended. At Achall a Wardenaar peat cutter (Wardenaar 1987) was first used to collect a rectangular sediment sample, 100 mm x 100 mm, extending to *ca.* 1 m below the depth reached by the monolith, the piston corer then being used to core the remainder of the sediment. As at lacustrine sites, two cores with overlapping segments were collected so as to ensure that the complete sediment column was obtained.

In all cases, coring was continued until either rock, or sediment too stiff for further penetration by the manually-operated piston corer, was encountered. Core segments were extruded from the coring tube in the field, supported by rainwater guttering. All sediment samples were wrapped in plastic film, to retain moisture, and aluminium foil, to exclude light, and after being transported back to Durham University they were stored at 4°C until required for sub-sampling.

Sites and sediment samples

Sediment samples were collected from a total of 25 sites, nine in the Achall landscape and eight each in the Affric and Rannoch landscapes (Figure 3–5). Sample collection took place between 13 and 25 April 2012 (Rannoch), 6 and 22 April 2013 (Rannoch and Affric) and 12 and 26 April 2014 (Achall). Site co-ordinates, altitudes and sediment depths recovered are given in Table 1.

Loch nan Eala (Ach1), a lochan of *ca.* 150 m x 40 m, was selected to provide a landscape-wide palaeovegetation record of the Achall landscape. At its deepest point the water depth was >3 m; coring extended from 3.5 m to a maximum depth of 12.91 m, 9.41 m of sediment thus being recovered. The other eight sites sampled in this landscape were all mires. None of the sites lay within

Table 1. Locations and sediment depths of sites from which sediment cores were collected.

Site	Name/'Informal name'	National Grid Reference	Longitude (W)	Latitude (N)	Elevation (m asl)	Sediment depth recovered (m)
Ach1	Loch nan Eala	NH 19881 95175	5° 2′ 30.5″	57° 54′ 34.4″	98	9.41
Ach2	'Terrace Hollow'	NH 16997 95468	5° 5′ 24.8″	57° 54′ 39.4″	90	2.76
Ach3	'above Cadubh'	NH 21319 94867	5° 1′ 2.9″	57° 54′ 24.6″	110	2.42
Ach4	'Sheepfold'	NH 19903 95058	5° 2′ 28.9″	57° 54′ 30.7″	97	2.67
Ach5	'West Achall Mire'	NH 15501 95662	5° 6′ 57.6″	57° 54′ 43.8″	96	7.07
Ach6	'West Achall Gorge'	NH 15428 95617	5° 7′ 1.9″	57° 54′ 42.4″	95	4.14
Ach7	'below Doir' a' Ghleannain'	NH 20443 94477	5° 1′ 54.6″	57° 54′ 12.7″	97	3.05
Ach8	Sanctuary Wood	NH 21578 94415	5° 0′ 45.6″	57° 54′ 12.4″	104	2.44
Ach9	'Eagle calling'	NH 18613 94642	5° 3′ 46.2″	57° 54′ 15.6″	93	3.02
Aff1	Loch Salach a' Ghiubhais	NH 17650 21625	5° 1′ 29.7″	57° 14′ 55.5″	288	3.15
Aff2	Loch an Fheadain	NH 11782 20810	5° 7′ 14.1″	57° 14′ 21.4″	246	4.0
Aff3	'Adit Track'	NH 29976 29272	4° 49′ 31.3″	57° 19′ 20.2″	254	2.9
Aff4	Loch an Amair	NH 26378 26111	4° 52′ 58.4″	57° 17′ 32.5″	325	5.7
Aff5	'above Loch an Eang'	NH 24408 23781	4° 54′ 49.7″	57° 16′ 16.3″	341	4.8
Aff6	'T-Junction'	NH 19766 23107	4° 59′ 24.7″	57° 15′ 47.0″	240	11.4
Aff7	'Cattle grid'	NH 17844 22199	5° 1′ 16.1″	57° 15′ 14.8″	264	7.6
Aff8	'Road below Beinn a' Mheadhoin'	NH 22693 24632	4° 56′ 34.1″	57° 16′ 40.4″	239	4.7
Ran1	'Finnart mire'	NN 52970 55145	4° 24′ 13.0″	56° 39′ 53.6″	286	6.13
Ran2	'Gunnar's Tree'	NN 56331 55513	4° 20′ 46.7″	56° 40′ 9.6″	284	4.6
Ran3	'No Aerial'	NN 57135 54951	4° 19′ 57.6″	56° 39′ 52.2″	379	3.0
Ran4	'Craiganour'	NN 63171 61262	4° 14′ 15.4″	56° 43′ 22.7″	382	5.3
Ran5	'Rannoch Forest'	NN 48971 58376	4° 28′ 3.9″	56° 41′ 33.7″	314	7.5
Ran6	'Camusericht'	NN 52049 58579	4° 25′ 3.5″	56° 41′ 43.8″	229	3.6
Ran7	'Black 4A'	NN 55903 54150	4° 21′ 8.3″	56° 39′ 25.0″	358	2.4
Ran8	'Log Canyon'	NN 54567 53210	4° 22′ 24.8″	56° 38′ 53.1″	369	3.9

a remnant stand of Caledonian pinewood, although one (Ach7) was adjacent to and two (Ach8 and Ach9) relatively close to such stands (Figure 3).

In the Affric landscape Loch Salach a' Ghiubhais (Aff1), a lochan of *ca.* 230 m x 120 m with two distinct sedimentary basins, was selected for the landscape-wide palaeovegetation record. The sediment core analysed was obtained from the southern basin, maximum water depth >6 m. Coring began at 6.25 m and the sediment recovered extended from 6.6 m to 9.75 m, a total of 3.15 m sediment thus being recovered. A second lacustrine site of *ca.* 110 m x 80 m was sampled in this landscape, Loch an Fheadain (Aff2), with a maximum water depth of *ca.* 4 m. Coring commenced at 4 m and extended to 8 m, at which depth coring was abandoned because, although the sediment was penetrable, it proved almost impossible to extract the corer without swamping the inflatable boat. Four of the sites sampled (Aff3, Aff6, Aff7 and Aff8) were mires, the remaining two (Aff4 and Aff5) being marginal mires of small lochans with shortest axes ≤ 50 m. Five of the sites sampled (Aff1, Aff4, Aff5, Aff6 and Aff7) were located within remnant stands of Caledonian pinewood (Figure 4).

All eight sites sampled in the Rannoch landscape were mires. 'Finnart mire' (Ran1), which lies between Loch Finnart and Loch Monaghan and has a shortest axis of *ca.* 270 m, was selected to provide the landscape-wide palaeovegetation record; 6.13 m of sediment was recovered from this site. The remainder were small mires, four of them partly wooded; one (Ran6) supported *Betula* spp. woodland and three (Ran2, Ran3 and Ran7) had scattered *P. sylvestris* on their surface. Three sites (Ran2, Ran3 and Ran7) lay within, and two (Ran1 and Ran8) were adjacent to the Black Wood of Rannoch remnant Caledonian pinewood (Figure 5).

Pollen analysis

Core segments were split longitudinally, using a 'cheese wire', the split surfaces photographed, and volumetric sub-samples of 0.5 cm^3 taken at intervals from the split surface of one half of the core using a cylindrical brass sampler. Prior to processing, a measured volume of a suspension of pollen of the exotic *Corymbia ficifolia* (formerly *Eucalyptus ficifolia*) was added to each sub-sample to enable calculation of pollen concentrations. Sub-samples for pollen and spore analysis were prepared as follows. Treatment with hydrochloric acid (10%) was followed by treatment with sodium hydroxide (10%), after which the sub-sample was passed through a 180 µm sieve to remove coarse material. Density separation of organic material followed, using a saturated solution of zinc chloride (specific gravity 2.0). The sub-sample was then washed with glacial acetic acid before acetolysis, using a 9:1 mixture of acetic anhydride and concentrated sulphuric acid. Residues were dehydrated by repeated washing with 2-methylpropan-2-ol before suspension in silicone oil (2000 cs viscosity). Sub-samples of the suspended residue were mounted on microscope slides for pollen counting, diluting with additional silicone oil as required.

Pollen and spores were examined and counted using a compound light microscope (Leica DM/LM); routine identifications and counting were performed at x400 magnification and critical identifications were made using x1000 magnification. Identifications were made using published monographs and keys (Erdtman et al. 1961; Moore et al. 1991; Beug 2004), supplemented by examination of specimens from the pollen reference slide collection of the Department of Biosciences, Durham University. Pollen and spore taxon nomenclature followed the conventions proposed by Birks (1973).

Given our aims, and our focus upon the vegetation history prior to, during and following the expansion of pinewoods in each landscape, widely spaced sub-samples were initially taken and preliminary pollen analyses undertaken, counting *ca.* 100 pollen grains, in order to determine the approximate depth at which the abundance of *Pinus* pollen increased. Further sub-sampling was then performed to refine the location of this increase, after which closely spaced sub-samples were taken spanning the relevant depth and subjected to full pollen analyses, with a minimum of 300 grains of terrestrial pollen taxa being counted from each sub-sample.

Pollen data were processed using Microsoft Excel®. Pollen diagrams were initially prepared using Tilia Version 2.0.41 and refined using CorelDraw®. Data are presented primarily as percentages, terrestrial pollen taxa being expressed as percentages of total terrestrial pollen (ΣTLP); other pollen taxa, *Sphagnum* and Pteridophyte spores are expressed as percentages of ΣTLP+ the relevant group sum. A consistent set of pollen taxa was included in all the diagrams and is presented in the same order, although some of these taxa were not recorded at some sites. Pollen concentration was calculated for each sample using the proportions of fossil pollen and *C. ficifolia* pollen counted in the sample.

Mapped summaries of vegetation patterns before, during and after the expansion of pinewoods in the three study landscapes were prepared for each study landscape and for the overall area spanned by the three landscapes. Pollen percentage values were interpolated to 100-year intervals and pie charts drawn showing mean relative abundances at each site, for 500-year spans, of pollen of six principal elements of the pollen spectra: (i) *Pinus*; (ii) Boreal trees and shrubs (BTS: sum of *Juniperus, Betula, Salix* and *Populus*); (iii) Temperate broadleaved trees and shrubs (TBLTS: sum of *Quercus, Ulmus* and *Corylus*-type, plus *Acer, Carpinus betulus, Fagus, Fraxinus, Prunus avium/P. spinosa, Sambucus, Sorbus*-type and *Tilia* at sites where these were present); (iv) *Alnus*; (v) Graminoids (sum of Cyperaceae and Gramineae); and (vi) Dwarf shrubs (sum of *Empetrum* and Ericaceae, including *Calluna vulgaris, Vaccinium*-type and Ericaceae undiff.).

Site chronologies

Site chronologies were determined using a total of 96 ^{14}C age measurements made upon identified terrestrial plant macrofossils extracted from 10 mm slices of sediment cores, washed in deionised water and dried at 80°C. All radiocarbon measurements were made by accelerator mass spectrometry at the Natural Environment Research Council radiocarbon facilities at Oxford and East Kilbride. The depths at which age measurements were made, and the nature of the material used, are given in Table S1. At sites where the Holocene increase in the abundance of *Pinus* pollen was identified, a series of ^{14}C age measurements was made on samples spanning this event; at sites where an increase in *Pinus* pollen abundance could not be identified a ^{14}C age measurement was obtained for the basal sediments sampled. Between three and seven age measurements were made at each of 20 sites, two age measurements at three sites, and only a basal age measurement at the remaining two sites.

All ^{14}C ages obtained were calibrated using Bchron (Parnell et al. 2008) and the INTCAL13 radiocarbon calibration curve (Reimer et al. 2013); calibrated ages are given in Table S1. At all sites where two or more age measurements were made the age–depth relationship was modelled for the dated section of the core using Bchron (see Figures S1–S23); the models obtained were used to estimate ages at the depths from which pollen samples were analysed.

Results

Palaeovegetation records

Palaeovegetation records were obtained from all 25 of the sites sampled. The number of sub-samples from which full pollen counts, of at least 300 grains, were made varied. Fewest sub-samples were counted for sites where the basal sediments had high relative abundances of *Pinus* pollen, whereas for sites where the increase in abundance of *Pinus* pollen was clearly evident larger numbers of samples were counted with the joint aims of characterising the progress of the increase and of refining the date at which it occurred. Pollen diagrams were prepared for all sites (see Figures S24–S48). Key features of the palaeovegetation record at each site, as illustrated by these pollen diagrams, are outlined in the Supplementary Information (see Supplementary Text – *Palaeovegetation Records*). Local presence of pinewoods in the immediate surroundings of small sites, and in the wider landscape around the larger sites, was inferred when *Pinus* pollen abundance exceeded 20%. This higher threshold value than that suggested by Lisitsyna et al. (2011) was used because we were not concerned to determine the local presence of *P. sylvestris* but of stands in which it was the dominant tree. At each site where *Pinus* pollen relative abundance values were initially low and subsequently increased markedly, the age for what we identified as the main increase was taken as the mean of the ages for the two pollen samples between which that increase occurred. Ages given in the text without qualification are median ages from the Bchron probability distribution function. When given, the 2.5% and 97.5% values follow in parentheses. The median date and 95% date range for the main *Pinus* increase are mapped for each landscape (Figure 6–8).

Palaeovegetation patterns before, during and after the Pinus *expansion*

Glen Achall

In addition to the landscape-wide record from Ach1, four of the sites examined in Glen Achall provide local records of the landscape-scale vegetation patterns for the half-millennium 8500–8000 cal yr BP (Figure 9) that preceded that during which the landscape-wide expansion of pinewoods occurred. BTS dominated the pollen spectra in all cases, accompanied landscape-wide by moderate abundance of TBLTS, although the latter were locally abundant only at Ach7. *Pinus* pollen was present at all sites, although in amounts insufficient to indicate local presence of pinewoods. *Alnus* pollen was essentially absent. At the sites east of Loch Achall, both graminoids and dwarf shrubs were present only in small amounts, indicating both

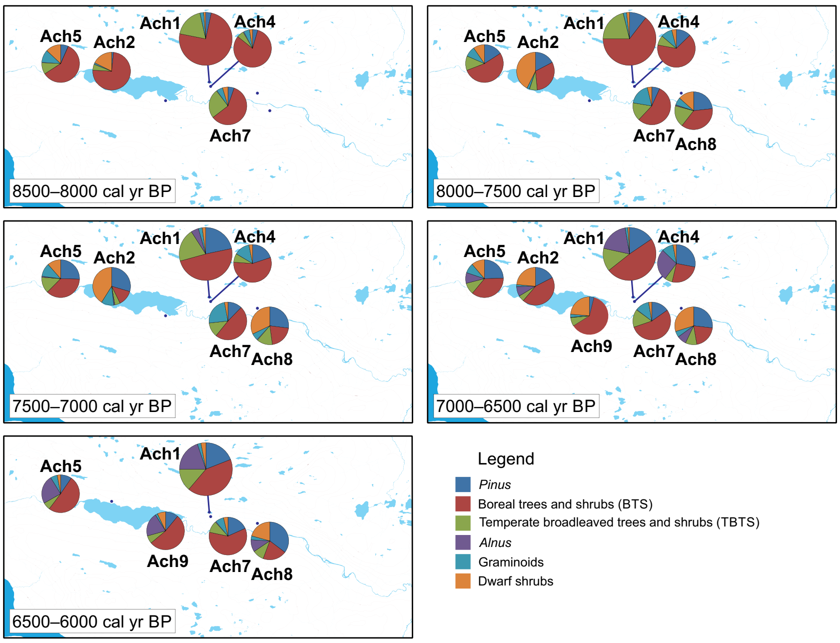

Figure 9. Local and landscape vegetation history 8500–6000 cal yr BP in Glen Achall, Scotland. Summary of the palaeovegetation patterns during five 500 yr intervals, before, during and after the landscape expansion of pinewoods. Pie charts show the mean relative abundances of pollen of *Pinus* and five other principal elements of the pollen assemblages during each interval. The larger pie chart is that for the site providing the landscape record. Contours at 50 m intervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape 11.879 km E – W by 5.860 km N – S; south-west and north-east corners at UK National Grid co-ordinates NH 13881 91551 and NH 25760 97411, respectively.

a relatively densely wooded landscape overall and locally dense woodland cover at Ach4 and Ach7. At Ach2, on the north shore of the loch, however, dwarf-shrub pollen was moderately abundant, indicating locally partially open vegetation of a heathland character, and at Ach5, west of the loch, dwarf shrubs and graminoids together accounted for about a quarter of the pollen spectra, again indicating locally partially open vegetation.

During the following half-millennium (8000–7500 cal yr BP), pinewoods began to expand across the landscape, being present locally at least around Ach8, the easternmost site. The landscape overall remained predominantly wooded, with BTS dominant but accompanied by moderate abundance of TBLTS. Locally around sites east of Loch Achall the vegetation was more open than before, with graminoids the principal low-growing component of the pollen spectrum at two of the sites (Ach7 and Ach4) and dwarf shrubs more abundant at the easternmost site (Ach8). At Ach2 the vegetation was locally much more open than previously, and also than at any of the other sites, with abundant dwarf shrubs and a very marked reduction in BTS.

By 7500–7000 cal yr BP pinewoods were locally present around at least three sites (Ach2, Ach5 and Ach8), consistent with the record from Ach1 indicating landscape-wide presence of such woodlands. Although BTS continued to dominate a largely wooded landscape, with moderate abundance of TBLTS, the vegetation was again locally at least partially open around Ach2, Ach5 and Ach8, with dwarf shrubs now more abundant than previously around the latter, indicating more open conditions there than before. The following half-millennium (7000–6500 cal yr BP) saw a rapid landscape-wide increase of *Alnus*, present previously only in small amounts in the landscape-wide record. In the landscape-wide record, *Alnus* pollen was now more abundant than that of *Pinus*; it was also locally abundant at Ach4, and to a lesser extent at Ach2, Ach5 and Ach8. Locally partially open vegetation continued to prevail at Ach8, with dwarf shrubs the principal low-growing vegetation component, whereas at Ach2 the degree of woodland cover had increased, largely as a result of an increased abundance of BTS.

The landscape remained predominantly wooded during the final half-millennium shown (6500–6000 cal yr BP). Dwarf-shrub pollen was less abundant than previously at Ach5 and Ach9, indicating locally more wooded conditions at these sites, but remained moderately abundant, albeit less so than previously, at Ach8, indicating a persistence of at least partially open vegetation at this site. *Pinus* was more abundant than before at Ach8, indicating increased extent of pinewoods at least around this site. Although its abundance had also increased landscape-wide, and at both Ach7 and Ach9, it had markedly decreased locally around Ach5. *Alnus* was moderately abundant landscape-wide, and had increased locally, especially at Ach5 and Ach9, less so at Ach8. BTS were the dominant component of pollen spectra at Ach5, Ach7 and Ach9, as well as landscape-wide, whereas TBLTS were less abundant overall than previously.

Glen Affric

In the landscape-wide record from Aff1, BTS dominated during the half-millennium 9000–8500 cal yr BP that preceded the increase of *Pinus* (Figure 10), although forest or woodland cover was discontinuous. Pollen of graminoids and dwarf shrubs was moderately abundant indicating a substantial fraction of open vegetation in the landscape. Forest cover was more continuous around Aff4, the easternmost site providing data for this half-millennium, and also much less dominated by BTS than in the landscape as a whole, with a more substantial fraction of TBLTS than at any of the other sites that provide local records. The other local records all had BTS as the dominant component of their pollen spectra, although its degree of dominance varied, being greatest at Aff8, on the north side of Loch Beinn a' Mheadhoin, and least at Aff7, south of Loch Affric. The extent of local forest cover also varied, being least around Aff5 and Aff7, although the predominant low-growing component of the pollen spectra was dwarf shrubs at the former and graminoids at the latter. *Pinus* pollen was present in the spectra from all sites, but at very low levels indicating that pinewoods were absent from the landscape at this time.

Although *Pinus* pollen abundance was greater at all sites during 8500–8000 cal yr BP than during the previous half-millennium, its abundance reached levels indicating local presence of pinewoods only at Aff7, on the south side of Loch Affric. At the other sites, and landscape-wide, BTS continued to be the dominant component of pollen spectra, with a smaller component of TBLTS as before that was

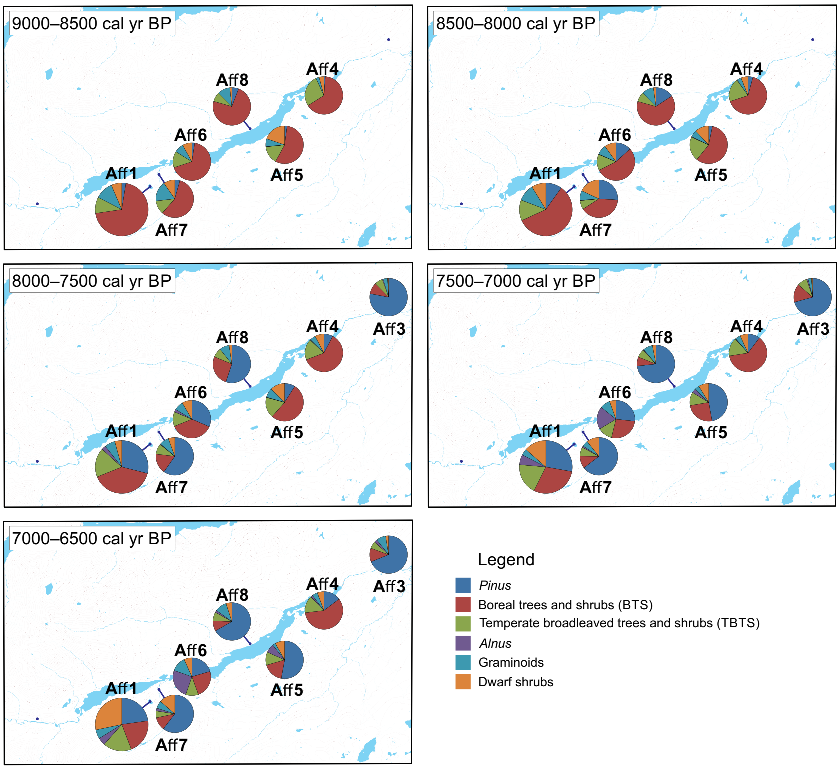

Figure 10. Local and landscape vegetation history 9000–6500 cal yr BP in Glen Affric, Scotland. Summary of the palaeovegetation patterns during five 500 yr intervals, before, during and after the landscape expansion of pinewoods. Pie charts show the mean relative abundances of pollen of *Pinus* and five other principal elements of the pollen assemblages during each interval. The larger pie chart is that for the site providing the landscape record. Contours at 50 m intervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape 20.944 km E – W by 12.517 km N – S; south-west and north-east corners at UK National Grid co-ordinates NH 10070 18454 and NH 31014 30971, respectively.

again greatest in the eastern sites of Aff4 and Aff5. Forest cover also remained discontinuous landscape-wide, with varied degrees of local openness that was again least at Aff4 and greatest at Aff7.

The subsequent half-millennium (8000–7500 cal yr BP) saw *Pinus* pollen abundance increase markedly to levels indicating local presence of pinewoods at four of six sites providing local records for this interval. The increased value at Aff1 also indicated that pinewoods were now present landscape-wide. Nonetheless, at Aff5 and Aff4, two sites to the south of Loch Beinn a' Mheadhoin, *Pinus* pollen abundance did not indicate local presence of such stands, whereas at Aff3, Aff7 and Aff8 *Pinus* now accounted for between half and three-quarters of the pollen spectrum, indicating local abundance of pinewoods. Landscape-wide, forest cover continued to be discontinuous, although, as before, the degree of openness varied, being least at Aff3 and greatest at Aff5. *Alnus* pollen was present at low abundance at a minority of sites, its presence in the record from Aff1 indicating that it was probably beginning to invade the landscape.

Pinewoods continued to be a landscape-wide component during 7500–7000 cal yr BP, and were now the dominant component of the local vegetation at four sites (Aff3, Aff5, Aff7 and Aff8). At Aff6, however, *Pinus* accounted for only slightly more than a quarter of the pollen spectrum, more or less equal in abundance to BTS, and thus mirroring the landscape-wide pattern, whilst at Aff4 BTS remained dominant and *Pinus* abundance remained at a level insufficient to indicate local presence of pinewoods. *Alnus* remained a minor component of pollen spectra generally, although its abundance had increased a little landscape-wide. Only at Aff6 did *Alnus* abundance increase markedly, reaching values sufficient to indicate its local presence. TBLTS persisted as a substantial component of the landscape-wide forest cover, although it achieved moderate abundance only in a minority of the local records, its greatest abundance being at Aff4 where pinewoods were probably not locally present.

Landscape-wide the most striking change in the subsequent half-millennium (7000–6500 cal yr BP) was a marked decrease in forest cover indicated by a substantial increase in abundance of dwarf-shrub pollen, this becoming the most abundant component of the pollen spectrum at Aff1. *Pinus* remained a major forest component around Aff3, Aff5, Aff7 and Aff8, whereas pinewoods continued to be locally absent around Aff4 where BTS once again dominated the pollen spectrum. *Alnus* was now locally a major woodland component at Aff6, had increased in abundance somewhat at Aff5, but remained no more than a minor component at the remaining sites.

Glen Rannoch

The record from Ran1 for the half-millennium 9000–8500 cal yr BP (Figure 11) indicates that landscape-wide the vegetation of Glen Rannoch was at that time markedly open, with pollen of low-growing taxa accounting for almost 40% of the spectrum, graminoids and dwarf shrubs being almost equally abundant. The local records clearly showed that the degree of openness of the vegetation varied across the landscape, with pollen of low-growing taxa accounting for slightly more than half the pollen spectrum at Ran8 but only *ca*. 11% at Ran6. The dominant low-growing component also varied, being predominantly dwarf shrubs at Ran8, dominantly graminoids at Ran2 and Ran6, and a mixture of the two at Ran5 and Ran7. Forested areas were of both BTS and TBLTS; although the former was a little more abundant landscape-wide, relative abundance of the two varied locally, BTS being markedly more abundant, for example, at Ran2, whereas the highest representation of TBLTS was at Ran5. *Pinus* pollen abundance was nowhere sufficient to indicate local presence of pinewoods.

By the following half-millennium (8500–8000 cal yr BP), *Pinus* pollen was sufficiently abundant at Ran2 and Ran7 to indicate local presence of pinewoods, interestingly in what remains today the core of the Black Wood of Rannoch Caledonian

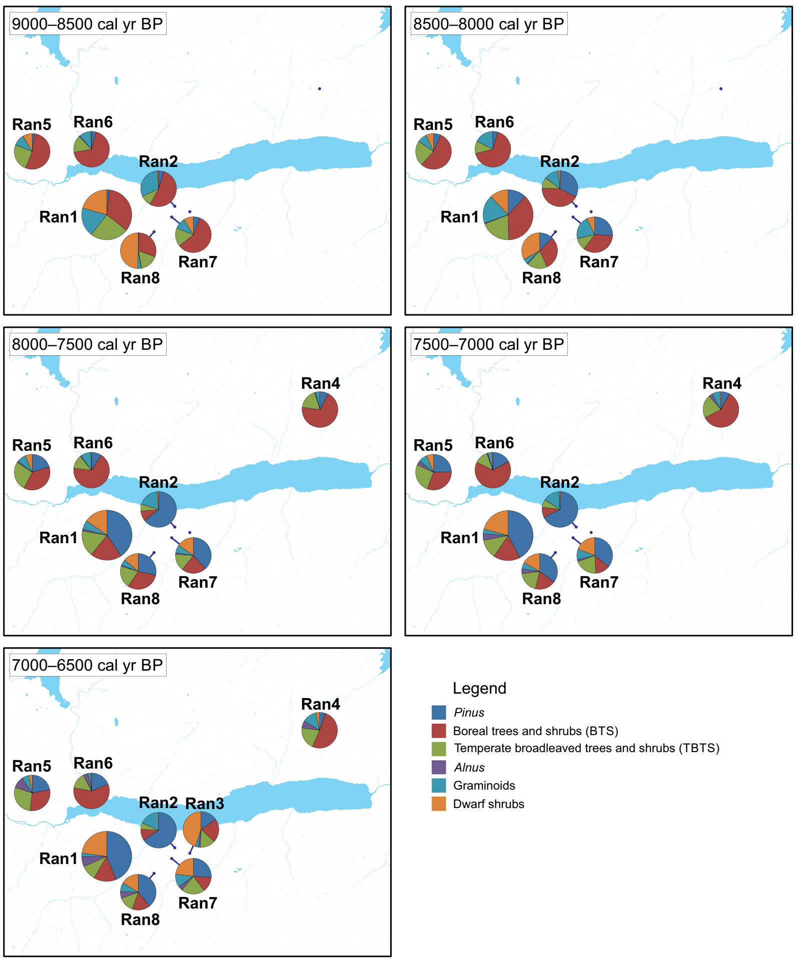

Figure 11. Local and landscape vegetation history 9000–6500 cal yr BP in Glen Rannoch, Scotland. Summary of the palaeovegetation patterns during five 500 yr intervals, before, during and after the landscape expansion of pinewoods. Pie charts show the mean relative abundances of pollen of *Pinus* and five other principal elements of the pollen assemblages during each interval. The larger pie chart is that for the site providing the landscape record. Contours at 50 m intervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape 19.264 km E – W by 15.367 km N – S; south-west and north-east corners at UK National Grid co-ordinates NN 47604 50228 and NN 66868 65595, respectively.

pinewood. Local presence at these sites is reflected by an increase in the abundance of *Pinus* pollen at Ran1, although its abundance there is insufficient to indicate extensive landscape-wide presence of pinewoods. This inference is reinforced by *Pinus* abundance values at Ran5, Ran6 and Ran8 insufficient to indicate local presence of pinewoods at any of these localities. The dominant component of the forested fractions of the landscape continued to be BTS, with lesser amounts of TBLTS. Much of the landscape, however, remained open, with *ca*. 30% of the pollen spectrum at Ran1 accounted for by graminoids and dwarf shrubs, the former now noticeably more abundant than the latter, although as before the relative proportions of these components varied locally across the landscape.

The subsequent half-millennium (8000–7500 cal yr BP) saw *Pinus* become a major forest component landscape-wide, although its presence was far from ubiquitous. BTS and TBLTS continued to form substantial components of the forest where present, with dwarf shrubs the dominant low-growing taxa, their pollen abundance again indicating a substantial degree of openness of the landscape. *Pinus* pollen abundance at Ran2, Ran7 and Ran8, south of Loch Rannoch, was sufficient to indicate local presence of pinewoods at these sites, with local dominance of such forest at Ran2. At Ran4 and Ran6, however, *Pinus* pollen was present only in small amounts and BTS was the dominant forest component, accompanied by a small component of TBLTS. Forest cover was also more continuous around these sites north of Loch Rannoch than at the others, their pollen spectra having only a small component of pollen of graminoids and almost none of dwarf shrubs. At Ran5, although the abundance of *Pinus* pollen was greater than at Ran4 or Ran6, and at *ca*. 20% is sufficient to indicate likely local presence of pinewoods, BTS continued to dominate, although with a substantial component of TBLTS, the two together accounting for the majority of the pollen spectrum.

The situation during the half-millennium 7500–7000 cal yr BP was very similar to that during the preceding half-millennium. *Pinus* pollen at Ran5, however, was now sufficiently abundant to indicate that pinewoods were locally present at this site, although such stands remained locally absent at Ran4 and probably also at Ran6. *Alnus* pollen was now present in small amounts at some sites, and was likely present widely but sparsely landscape-wide.

The final half-millennium illustrated (7000–6500 cal yr BP) again showed only limited changes from the preceding half-millennium. *Alnus* pollen was now present in small but noticeable quantities at five of the sites providing local records; along with its increased but still low abundance at Ran1 this indicates sparse but widespread occurrence of *Alnus* landscape-wide. *Pinus* continued to be a major, and in some cases the dominant, forest component at sites south of Loch Rannoch, whereas BTS and TBLTS remained important components, and together the dominant component, of forests north of Loch Rannoch. Increased abundance of dwarf-shrub pollen at Ran1 indicates an increase in heathland vegetation landscape-wide, reflected also by increased abundance of this pollen component at Ran7 and its dominance of the pollen spectrum at Ran3, a site where the record begins only during this interval.

Regional-scale transect

The sites in each study landscape recording the landscape-wide palaeovegetation composition form a north–south transect across the region formerly occupied by the Caledonian pinewoods. Their pollen spectra illustrate the changing regional patterns in landscape-wide vegetation as pinewoods expanded their range and dominance (Figure 12). 9000–8500 cal yr BP the Glen Rannoch landscape was much more open than the other landscapes, with the Glen Achall landscape the most forest covered. In Glen Rannoch and Glen Affric, pollen of low-growing taxa, both graminoids and dwarf shrubs, indicates the presence in these landscapes of both heathlands and grasslands, both being extensive in Glen Rannoch. As might be expected, BTS dominated the forest cover in the northernmost study area, Glen Achall. They were also dominant in Glen Affric, but in the southernmost study area, Glen Rannoch, they shared dominance with TBLTS. Unexpectedly, TBLTS formed a larger component of the forest cover in Glen Achall than in Glen Affric, although the contrasting position of these study areas with respect to the principal mountain backbone north of the Great Glen may account for this, with Glen Achall west of this divide and thus more exposed to the warming influence of the Atlantic. *Pinus* pollen was present only sparsely at this time, indicating that pinewoods were probably absent from all three study areas.

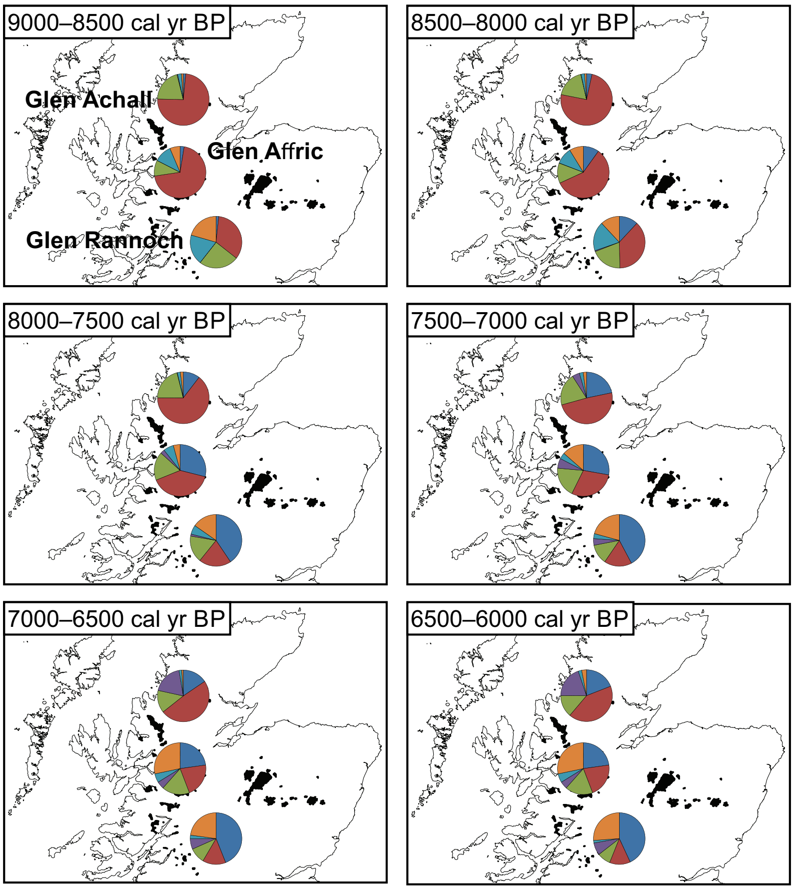

Figure 12. Landscape vegetation history of the three study areas, Scotland, 9000–6000 cal yr BP. Summary of the landscape-scale palaeovegetation composition in each study area during six 500 yr intervals, before, during and after the expansion of pinewoods across the Highlands. Pie charts show the mean relative abundances of pollen of *Pinus* and five other principal elements of the pollen assemblages during each interval. For key to pie charts see Figure 9–11.

The subsequent half-millennium saw increases in abundance of *Pinus* pollen in both Glen Rannoch and Glen Affric, but only a marginal increase in Glen Achall. Aside from this, the composition of the pollen spectra, and hence of the landscape vegetation mosaics, showed little change in any of the landscapes. In contrast, the following half-millennium (8000–7500 cal yr BP) saw striking changes in both Glen Affric and Glen Rannoch, although in Glen Achall change was limited to a modest increase in abundance of *Pinus* pollen and a small decrease in the predominance of BTS. *Pinus* pollen was now the largest component of the pollen spectrum in Glen Rannoch, where the proportion of BTS had markedly decreased and that of graminoids had also decreased substantially. In Glen Affric, the proportion of *Pinus* pollen had also increased substantially and that of BTS decreased markedly. Here too the proportion of pollen of low-growing taxa had decreased, indicating a generally more forested landscape than previously, although TBLTS had increased somewhat in abundance. *Alnus* pollen was now present, albeit in low abundance, in both Glen Affric and Glen Rannoch.

Half a millennium later (7500–7000 cal yr BP) *Alnus* was present in increased amounts in all three landscapes, and *Pinus* had increased in abundance in Glen Achall where BTS were now less abundant than previously. BTS had also decreased in abundance in Glen Affric, where the landscape was markedly more open, with an increase in dwarf-shrub pollen indicating an expansion of heathlands. Glen Rannoch also had more open vegetation than before, with heathland the dominant non-forest vegetation. By this time *Pinus* was a prominent component of forest vegetation in all three landscapes, although there was a clear gradient in its abundance from south to north, more or less complemented by a north–south gradient in abundance of BTS.

These general complementary patterns in the abundance of *Pinus* and BTS persisted in the subsequent half-millennium (7000–6500 cal yr BP). The most striking change was a marked increase in *Alnus* pollen abundance in Glen Achall, where this tree must by this time have become a substantial component of the forest cover, perhaps especially on the relatively flat valley floor to the east of Loch Achall across which the River Achall today meanders. There was also a more or less twofold increase in the proportion of pollen of dwarf shrubs in Glen Affric, indicating a marked increase in vegetation openness with expansion of heathland. The final half-millennium shown (6500–6000 cal yr BP) saw little further change in any of the three study areas, although a marginal increase in abundance of pollen of low-growing taxa in Glen Achall indicates some opening of the vegetation there, although to nothing like the extent seen in the other two study areas even in the earliest half-millennium illustrated.

Discussion

Testing our hypotheses

Spatial vegetation patterns were exhibited, at regional and landscape scales, prior to pinewood expansion

In all three landscapes, our results support this hypothesis (Figure 9–11). In Glen Achall, both the local relative abundance of BTS and TBLTS, and the degree of vegetation openness, varied considerably in the half-millennium prior to the expansion of pinewoods, with greatest abundance of TBLTS at the easternmost site represented (Ach7) and greater openness at the two westernmost sites (Ach2 and Ach5). Similar patterning was seen in Glen Affric, with greatest abundance of TBLTS at the easternmost site represented (Aff4), greatest abundance of BTS at the site on the north side of Loch Beinn a' Mheadhoin (Aff8) and varying degrees both of vegetation openness and of the dominant component of pollen representing low-growing taxa. In Glen Rannoch, the strongest patterning was in relation to the degree of vegetation openness, with dwarf shrubs accounting for almost half of the pollen spectrum at the southernmost site (Ran8), graminoids about one-third of the spectrum at Ran2, but much less openness at some other sites, notably the westernmost site (Ran5), where TBLTS also had their greatest abundance, contrasting with the nearby Ran6 where BTS strongly dominated the pollen spectrum.

Across the Highlands overall, our results also support the hypothesis (Figure 12). Once again, the main contrasts relate to the degree of vegetation openness, which was greatest in Glen Rannoch and least in Glen Achall, and to the relative proportions of pollen of BTS, which was greatest in the north at Glen Achall, and TBLTS, which was greatest in the south in Glen Rannoch, although almost as abundant in Glen Achall where pollen of low-growing taxa was markedly less abundant than in either of the other two landscapes.

Spatial and temporal patterns of pinewood expansion at the landscape scale reflected prior landscape-scale vegetation patterns

In Glen Achall, pinewoods apparently became locally established first at sites where the pre-existing vegetation was more open (Ach2, Ach5 and Ach8), subsequently establishing at Ach4 where the degree of openness was less. There is also an indication that they established locally later, or even not at all, at the site with the greatest abundance of TBLTS in the pre-existing local vegetation (Ach7). The earliest local establishment of pinewoods in Glen Affric was also at a site with a high degree of openness of the pre-existing vegetation (Aff7), followed in the next half-millennium by local establishment at a second previously relatively open site (Aff6), but also at a site where forest or woodland, dominated by BTS, had previously been relatively more closed (Aff8). Local establishment of pinewoods was even later at Aff5, a site with previously relatively open local vegetation but with a higher proportion of TBLTS than most other sites, whilst pinewoods apparently did not become established locally around Aff4 where once again TBLTS were a relatively higher proportion of the forest cover than at most sites examined and the degree of openness remained lower than across the landscape as a whole. In Glen Rannoch the first two sites at which pinewoods became locally established (Ran2 and Ran7) once again had a relatively high degree of openness of the pre-existing vegetation, although local establishment at Ran8, where local openness was initially greater than at any other site, occurred somewhat later. Local establishment of pinewoods was later still at Ran5, where TBLTS was more abundant in the pre-existing vegetation than at any of the other sites examined, whilst it is possible that pinewoods never established locally at Ran6, where BTS was persistently dominant. At Ran4, on the south-facing slopes north of Loch Rannoch, pinewoods did not become locally established during the period examined; forest cover predominantly of BTS, but with a substantial component of TBLTS, was initially largely closed, although some progressive opening occurred, albeit without any local establishment of pinewoods.

In all three landscapes examined there are strong indications that the establishment of pinewoods was favoured by locally more open vegetation, as well as by situations in the landscape less favourable to the generally more thermophilous TBLTS. Both findings are consistent with the ecology of *P. sylvestris*. The seedlings of this species require unshaded conditions and an absence of competition if they are to thrive, establishing best after a catastrophic disturbance such as that caused by wildfire (Steven and Carlisle 1959). The tree is also predominantly boreal in distribution, growing successfully in cooler climates than trees of the TBLTS, although it is also able to grow under the climatic conditions that favour TBLTS taxa, but is then generally restricted to soils that are either relatively infertile, more acid and/or subject to greater seasonal moisture deficiency.

Our results thus support our hypothesis, showing that both the spatial pattern and the timing of local establishment of pinewoods in different parts of the landscapes examined was related to the pre-existing vegetation patterns in the landscape.

Vegetation changes occurred throughout the landscape at the time of pinewood expansion, not just in those landscape components invaded by P. sylvestris

This hypothesis can be addressed both at the level of the individual local palaeovegetation records, and using the records from the larger basins that represent the landscape-wide palaeovegetation. In Glen Achall, the landscape-wide record indicates that expansion of pinewoods in the landscape was principally at the expense of BTS stands, with little overall change in the proportion of the landscape occupied by TBLTS nor in the general degree of vegetation openness. This record also shows *Alnus* invading the landscape during the millennium following the initial expansion of pinewoods, with *Alnus* woodlands becoming relatively extensive, probably on the relatively flat valley floor east of Loch Achall. The individual records of local palaeovegetation show a greater or lesser degree of vegetation change during the period of pinewood expansion, some of which, such as the changing degree of local openness, likely reflect patch-scale vegetation dynamics associated with natural disturbances, whereas systematic shifts in relative abundance of BTS and TBLTS seen at some sites probably reflect long-term changes in climatic conditions.

In Glen Affric, the landscape-wide record again shows pinewoods expanding mainly at the expense of BTS stands, with TBLTS also modestly increasing during the period of pinewood expansion. Overall openness of the landscape-wide vegetation fluctuates somewhat, although it increases markedly after pinewood expansion, and there is also a marked shift towards a much greater proportion of dwarf shrubs in the fraction of pollen of low-growing plants in the pollen record. Both the increased openness and the greater abundance of dwarf shrubs are probably a consequence of the pinewood expansion. Pinewoods are generally more prone to patch-scale disturbance by wildfire than are forests dominated by broadleaved trees, whether BTS or TBLTS, leading to an overall greater degree of landscape openness at any given time. Pinewoods also tend to generate soils characterised by mor humus, and hence more often have an understorey dominated by dwarf shrubs tolerant of such acid soils. Broadleaved woodlands, especially those dominated by *Betula*, the predominant taxon of the BTS component of the pollen spectra, more often generate mull humus, and hence support an understorey dominated by grasses and forbs. Changes in the local vegetation during the period of pinewood expansion are seen at all but one of the sites providing local records. The one exception is Aff4, which shows very limited local changes throughout the period, with forest cover of BTS, accompanied by a lesser but nonetheless substantial component of TBLTS, dominating, and only a limited degree of vegetation openness. Froyd and Bennett (2006) analysed a core from the centre of the lochan and reported a similar palaeovegetation history, although their date of 8220 cal. yr BP for the main increase in *Pinus* pollen is about 1700 years earlier than that of 6491 cal. yr BP that we obtained. This apparent discrepancy may in part reflect their ^{14}C age measurements being made on bulk sediment; it has been shown that such measurements potentially can give age over-estimates of this magnitude (Grimm et al. 2009). However, this discrepancy more likely reflects principally the difference in pollen catchment between our marginal core and their mid-lake core, the lochan having a diameter of *ca*. 100 m. Thus, the main increase in *Pinus* in our marginal core reflects the time of development of pinewoods locally close to the lochan, whereas the *Pinus* increase in their mid-lake core reflects the development of pinewoods across the wider landscape, and corresponds well in age to our inferred age for this development based on our data from Aff1. This hypothesis is supported by the observation that in our record from Aff4 the main increase in *Pinus* pollen abundance coincides with that in *Alnus*, whereas in the record of Froyd and Bennett (2006) the *Pinus* pollen increase pre-dates that of *Alnus*, the timing of the latter more or less corresponding with that in our record.

The landscape-wide record from Glen Rannoch shows pinewoods expanding mainly at the expense of dwarf-shrub communities in the second half-millennium of the expansion period, but thereafter principally at the expense of BTS-dominated woodlands. There is also an overall trend towards less vegetation openness, and a strong shift from more or less equal representation of the low-growing dwarf-shrub and graminoid taxa to a predominance of dwarf-shrub taxa. As noted above, the shift towards dwarf shrubs is consistent with a shift from BTS woodlands, dominated by *Betula*, to pinewoods. The decrease in landscape-wide openness contrasts with what was seen in Glen Affric and suggests that here pinewood expansion took place preferentially into areas of pre-existing open vegetation, hence leading to an overall increase in the extent of forest cover in the landscape. This inference is supported by the local records that, as discussed above, show pinewoods expanding first at sites where the pre-existing vegetation generally was more open. As in the other two landscapes, local but varied changes in vegetation were recorded by all of the sites providing local records, with some sites recording changes of opposite sign to those seen landscape-wide; Ran4, for example, records increasing, albeit limited, openness whereas the landscape-wide picture is one of initially decreasing, and later a stable, degree of openness.

Once again, our results support our hypothesis, showing that vegetation change occurred across most, or even all, of each study landscape during the period of expansion of pinewoods, although the nature of the changes varied both within and between the three study landscapes.

Landscape-scale patterns of forest and woodland cover seen today have persisted since the expansion of pinewoods

The present cover of native forest and woodland, including Caledonian pinewoods, in Glen Achall is generally discontinuous (Figure 3), a large proportion of the landscape being occupied by open heathland and blanket mire, or by grasslands on the valley floor, with grazing by domestic stock, both sheep and cattle, as well as by red deer (*Cervus elaphus*). Regeneration of *P. sylvestris* is rare except in areas from which an effort has been made to exclude large herbivores by the erection of deer fences (e.g. Sanctuary Wood, B. H. personal observations), and some at least of the relict pine stands are on steep craggy slopes in the narrower upper part of the valley that offer some degree of relief from grazing pressure. The remaining Caledonian pinewood stands are mainly east of Loch Achall, with woodlands alongside and west of the loch mainly of deciduous trees, and dominated by *Betula* spp. The westernmost woodlands in the valley are probably best regarded as a fragment of Corylo-Fraxinetum (Birse 1980), having a component of TBLTS, including *Fraxinus excelsior* and *Corylus avellana*, that is absent further east, perhaps mainly because this western area overlies calcareous dolostone bedrock of the Eilean Dubh and Ghrudaidh formations, whereas the remainder of the glen is dominated by acidic psammite of the Altnaharra Psammite Formation, variously overlain by superficial deposits of Quaternary age (British Geological Survey, cartographer 2013). Although the greater local abundance of *Pinus* at sites east of Loch Achall by the end of the period of pinewood expansion (Figure 9) broadly corresponds to the present pattern of occurrence of relict stands of Caledonian pinewoods in the same part of the glen, the greater component of TBLTS in the westernmost woods today is not apparent in the palaeovegetation records, probably because none of these falls in the area of dolostone where peat cover is thin or absent and no suitable sites of sediment accumulation could be located for investigation.

Caledonian pinewoods remain extensive in Glen Affric, especially on the north-facing slopes of the south side of the glen (Figure 4). The other remaining native woodlands, which also are extensive principally to the south of the glen, as well as on the lower slopes of the north side of the glen, are principally comprised of *Betula* spp., although *Quercus* spp., *C. avellana* and *Ulmus glabra* all occur sparsely on steep south-facing slopes of the glen in the easternmost part of the study area (B. H. personal observation). The remainder of the landscape is occupied principally by heathland and blanket mire. The pattern of forest and woodland cover shows some correspondence to the pattern of local vegetation recorded following the expansion of pinewoods across the landscape, but with some marked discrepancies. Notably, Aff3 and Aff8, both of which had local vegetation dominated by *P. sylvestris* by the end of the period of pinewood expansion, today fall outside the remaining areas of Caledonian pinewoods, although they do both fall within areas that remain wooded, albeit principally by *Betula* spp. It is likely that the loss of pinewoods at these sites results from anthropogenic activities, from prehistoric times onwards; at Aff8 the pollen diagram (Figure S40) shows a long-term decrease in *Pinus* abundance beginning shortly after local pinewood expansion and persisting until *ca.* 3000 cal. yr BP, albeit that the sparse sampling may mask fluctuations about this trend. In contrast, Aff4, which retained local dominance by BTS at the end of the pinewood expansion period, today lies within the area of Caledonian pinewoods, albeit at relatively high elevation (325 m) and close to their boundary with other native woodland mostly of *Betula* spp.

Of the three landscapes examined, Glen Rannoch has the most discrete and generally continuous area of remaining Caledonian pinewoods, the so-called Black Wood of Rannoch that lies on the slopes to the south of Loch Rannoch (Figure 5). There are also extensive stands of other native woodlands, mostly dominated by *Betula* spp., especially on the north-facing slopes, but with *Quercus* spp., *C. avellana* and *U. glabra* all present in the remnant native woodland stands on the lower parts of the south-facing slopes north of Loch Rannoch. *Alnus glutinosa* occurs along the lake shore as well as on riversides. Extensive areas of the lower slopes on both sides of the glen have been afforested with exotic conifers and/or *P. sylvestris*, mostly during the twentieth century. Where such plantations are absent, however, heathland and blanket mire cover large areas, the latter especially on the less steep slopes north and west of Ran4. Eroding peat in the blanket mires of the latter area reveals buried stumps of *P. sylvestris* that must, from their stratigraphic position, date from at least several millennia ago, perhaps from the period around 5000 cal yr BP when *P. sylvestris* temporarily spread widely onto peatlands in the Scottish Highlands (Huntley et al. 1997). By the end of the period of pinewood expansion, *P. sylvestris* was a major or even dominant local forest component at all but one of the sites within the Black Wood of Rannoch (Figure 11), the exception being Ran3 where heathland dominated locally at that time. However, as the pollen diagram from this site (Figure S43) shows, *Pinus* pollen abundance increased rapidly after 6500 cal. yr BP, indicating a slightly delayed local pinewood expansion at this site, but a shift to local dominance of pinewoods nonetheless. At Ran6, where BTS remained the dominant component during and after the period of pinewood expansion (Figure S46), and *Pinus* pollen abundance decreased rapidly to low levels after 6500 cal. yr BP, the dominance of *Betula* pollen corresponds to the present woodland composition around the site that is dominated by *Betula* spp. Similarly, *Pinus* was never abundant at Ran4, BTS being the dominant forest component. This site today is surrounded by heathland, but the relict woodlands nearby are dominated by *Betula* spp. Only at Ran 5 is a clear discrepancy apparent between the present vegetation and that at the end of the pinewood expansion period. The TBLTS that shared dominance with the BTS at that time are now absent around the site; instead it is surrounded mostly by heathland, with the nearest remaining woodland stands being dominated by *Betula* spp.

Our records thus provide some support for the hypothesis being examined, but this is not universal, with some clear evidence that forest and woodland composition has continued to change, either as a result of anthropogenic activities or in response to continuing climatic changes, since the end of the period of pinewood expansion.

Wider context and general conclusions

Although the potential of palaeoecological studies of the sediments accumulated in small woodland basins, and of mor humus profiles, to provide records of the history of individual forest stands has long been recognised (Bradshaw 1981, 1988; Bradshaw and Miller 1988; Mitchell 1988; Bradshaw and Zackrisson 1990; Davis et al. 1998), very few of the previous studies using this approach are directly comparable to our study, most being focused upon documenting the history of only a single, or a small number of, forest stands (e.g. Mitchell 1988; Bradshaw and Hannon 1992). Bradshaw and Zackrisson (1990), however, studied a mor humus profile from a small island in a Swedish lake, exploring the disturbance history of the forest stand on the island. They examined how disturbance episodes related to shifts in forest composition and, in particular, to the invasion by *Picea abies*. They have shown that this invasion had followed episodes of local disturbance, and also that different plant taxa benefitted according to the nature of the disturbance, as had been discussed by Davis (1987). They have also shown that local invasion of the island forest was not synchronous with invasion by *P. abies* of the forest 4 km to the northwest on the mainland, but instead lagged by more than a millennium. Such a patchy invasion history, with lags of up to a millennium between different parts of a landscape, parallels our findings in relation to the mid-Holocene expansion of pinewoods in the Scottish Highlands.

Davis and colleagues (Davis et al. 1992, 1994, 1998; Frelich et al. 1993) have used a series of pollen diagrams from small forest hollows to explore the invasion by *Tsuga canadensis* of the forests of the Sylvania Wilderness in the upper peninsula of Michigan in the Great Lakes Region. They have also used their results to examine the extent to which *T. canadensis* invasion occurred preferentially into stands of different pre-existing composition, and to explore when the present pattern of stands dominated either by *T. canadensis* or by *Acer saccharum* and *Tilia americana* developed. They have shown that at the time of invasion by *T. canadensis*, stands of *Pinus strobus* were preferentially invaded, whereas stands dominated by hardwoods, mostly *Quercus* spp. and/or *Acer saccharum*, generally were not invaded. In contrast to the findings of Bradshaw and Zackrisson (1990) with respect to the invasion of Swedish forests by *Picea abies*, however, Davis et al. (1998) found no evidence that disturbance was required to facilitate forest invasion by *T. canadensis*. They did find clear evidence, however, that the present mosaic of stands dominated by *T. canadensis* or by *A. saccharum* and *T. americana* was largely established at the time of the invasion by *T. canadensis*. *Tsuga* stands, in particular, have persisted, albeit that the initial mixed stands of *T. canadensis* and *Pinus strobus*, the stand dominant prior to the invasion, have become much more dominated by *T. canadensis*.

The results from these earlier studies thus concur generally with our results and lead to several key conclusions, notably:

(1) That a landscape-scale vegetation mosaic existed prior to expansion of the potential new forest dominant taxon.
(2) That the invasion by the newly arrived potential forest dominant taxon of individual stands within a landscape exhibited spatial and temporal patterns, including preferential invasion of more open, perhaps recently disturbed, stands and later invasion of, or even a failure to invade, stands with a high proportion of alternative forest dominant taxa.
(3) That changes in stand composition were not restricted only to invaded stands but also occurred more generally across the landscape.
(4) That some, at least, of the pattern of forest stands of differing composition seen in the landscape today corresponds to the initial pattern established at the time of invasion.

These conclusions have some generality, not just across the three landscapes that we examined, but also when invasions by other potential canopy-dominant tree taxa are examined, and are thus relevant to considerations about the potential impacts of current and ongoing climatic change. Many studies have predicted that species, including potential forest-dominant tree taxa (Huntley 1995; Huntley et al. 1995; Sykes et al. 1996), will respond to projected climatic changes by shifting their geographical distributions. Such range shifts inevitably involve projected expansions into regions where the species are currently absent. In the case of the Caledonian pinewoods, we have shown previously, using a vegetation modelling approach, that the relict stands in the landscapes we have studied are already out of equilibrium with the present climate as a result of the climatic changes that have taken place over the past two centuries, the period since most of the current canopy-forming individuals became established (Huntley et al. 2018). Species distribution models have been used to project that by the end of the twenty-first century climatic conditions in Scotland may no longer be suitable for the development of any extensive forests dominated by *Pinus sylvestris* (Huntley 1995), and that climatic conditions by then will permit *Fagus sylvatica* potentially to have invaded, and possibly come to dominate, forests throughout much of Great

Britain, including much of Scotland (Huntley 1995; Sykes et al. 1996). Given that *F. sylvatica* is already widely planted, and often naturalised, in Great Britain, including Scotland where it occurs north to Caithness and Orkney Mainland (Preston et al. 2002), a widespread seed source is available from which invasion, fuelled by climatic change, can be expected to take place, and potentially to do so rapidly.

Even if measures are successfully taken to limit mean global warming to 1.5 or 2.0 K, conservation of the Caledonian pinewoods, and their associated fauna and flora, is likely to face severe challenges. The reduced ability of *P. sylvestris* successfully to regenerate, and hence sustain the *Pinus*-dominated canopy of these woodlands, in many of the locations today occupied by relict Caledonian pinewood stands (Huntley et al. 2018), as a consequence of the climatic changes that already have taken place, will render these stands vulnerable to invasion by other canopy-dominant tree species. The shift to climatic conditions favourable for the development of forests dominated by broadleaved trees, including *F. sylvatica*, the considerable shade tolerance of seedlings of this species, and the regular dispersal of its seeds over distances of ≥1 km by the Jay (*Garrulus glandarius*), likely will enable it to achieve invasion of relict *Pinus* stands, especially as their canopies open. The seedlings of *F. sylvatica* also out-compete those of *Quercus petraea*, by achieving greater height growth across much of the light-availability gradient (Ligot et al. 2013), whilst *F. sylvatica* is as tolerant of soil waterlogging as *Quercus robur*, although more sensitive to summer drought (Scharnweber et al. 2013). Given that the central projection of future summer precipitation in the Scottish Highlands is of only a modest (0–20%) reduction (Murphy et al. 2018), summer drought is likely to remain a relatively rare occurrence in this part of Great Britain. The ecological attributes of *F. sylvatica*, along with evidence from past invasions by canopy-dominant trees, thus lead us to suggest that this species has the potential to invade not just relict stands of *P. sylvestris*, but most currently wooded sites, and many unwooded sites, below the potential treeline in the Scottish Highlands. The principal factor preventing both this invasion and the establishment of *P. sylvestris* stands on parts of the landscape where conditions still favour this species' growth, is the combined grazing pressure of domesticated stock, principally sheep, and of native Red Deer, as well as of introduced Roe Deer (*Capreolus capreolus*) and Sika Deer (*Cervus nippon*).

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Notes on contributors

Brian Huntley is Emeritus Professor of Biosciences. He trained as a botanist and palaeoecologist, and has research interests in ecology, palaeoecology, biogeography, conservation biology and global change. He has undertaken research widely in Europe, from the Arctic to the Mediterranean, as well as in New Zealand and South Africa, and has worked

with many international collaborators. In addition to studying plants and vegetation, he has worked on butterflies and birds, as well as on Pleistocene and Holocene palaeoecology and palaeoenvironments. His research uses a combination of field and laboratory data collection, field and laboratory experiments, data analysis and modelling. He has published numerous scientific journal papers and edited volume chapters, has co-edited two books and has co-authored two further volumes.

Judith R.M. Allen retired from her post as Research Fellow in Palaaeoecology in 2018, but maintains research links with Brian Huntley. Trained initially as a zoologist, her interests in palaeoecology and palynology developed during her early career. Working with numerous international colleagues, she has undertaken palaeoecological research in northern and southern Europe, and in China, collecting material from field sites, and preparing and analysing palynological samples. She has co-published many scientific journal papers and co-edited one book.

Authors' contributions

The research project was initiated and the study designed by B.H., who also led the three field expeditions, prepared the various maps used as figures, and wrote the first draft of the paper. J.R.M.A. organised the logistics and permissions for, and participated in, the field expeditions, described and sampled the cores, carried out the pollen analyses, prepared and submitted samples for radiocarbon dating, prepared the pollen diagrams and computed the age–depth relationships, as well as reading and commenting upon the first draft and approving the final submitted version of the paper.

Data availability statement

The pollen data and radiocarbon measurements, as well as the age–depth models used, have all been deposited in, and are available from, the Neotoma Palaeoecology Database (http://www.neotomadb.org).

Geolocation information

Table 1 provides the longitudes and latitudes, as well as the UK National Grid Reference, for each of the 25 individual basins studied.

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