

Article

Disturbance and Succession in Early to Mid-Holocene Northern English Forests: Palaeoecological Evidence for Disturbance of Woodland Ecosystems by Mesolithic Hunter-Gatherers

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Abstract: Forest succession can be monitored in the present, modelled for the future, but also reconstructed in the past on the records of forest history, including through the use of palaeoecological techniques. Longer-term records from pollen data can show changes over centennial and millennial timescales that are impacted by climate, migration or soil development. Having knowledge of previous phases of post-disturbance seral stages of woodland regeneration however, as after fire, can provide insights regarding successional process and function over short-term decadal timescales. The aim of this paper is to test the high-resolution pollen record as a source of new insights into processes of succession, assisted by the supplementary data of microscopic charcoal analyses. On short-term timescales, multiple phases of forest disturbance and then recovery have been identified in early to mid-Holocene peat records in northern England, many from the uplands but also from lowland areas. We identify and describe a typology of recovery patterns, including the composition and rate of recovery, and then test the processes and factors that impacted on different seral trajectories, concentrating on fire disturbance which might have had a natural origin, or might have been caused by pre-agricultural Mesolithic hunter-gatherers. Factors considered include the spatial location and intensity of the fire event, the duration of the disturbance phase, the structure and dynamics of the successional regeneration vegetation communities and the pre-disturbance tree cover. Data from examples of fire disturbance of woodland have been examined from both upland and lowland sites in northern England and indicate that they had different successional pathways after disturbance. Fire disturbances in the denser lowland forests were mostly single burn events followed by natural successions and regeneration to forest, whereas fire disturbances in the upland woods usually showed continued or repetitive fire pressure after the initial burning, arresting succession so that vegetation was maintained in a shrub phase, often dominated by *Corylus*, for an extended period of time until disturbance ceased. This creation of a kind of prolonged, almost plagioclimax, ‘fire-coppice’ hazel stage suggests controlled rather than natural successional pathways, and strongly suggests that Mesolithic foragers were the fire starters in the upland English woodlands where hazel was naturally common and could be maintained in abundance in later-stage successions, along with other edible plants, for human use. All post-fire seral stages would have been attractive to game animals, providing a reliable food source that would have been of great benefit to hunter-gatherer populations.



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1. Introduction

The concept of the Holocene temperate wildwood, postglacial primary forest that has developed over millennia through processes of immigration and autogenic succession until stability and equilibrium have been achieved, is one that has been fundamental in palaeoecology. This forest biome characterises the mesocratic and climatic optimum phase of an

interglacial [1–3], and has been shown by pollen analysis of Holocene sediments as well as those from several past interglacials [4,5] to comprise a rich arboreal community of broadleaf deciduous trees, with tree migration rates [6] and climatic tolerances [7] determining the timing and composition of the fully established climax forest, which represents the terminal stage of primary forest succession [8]. Coniferous boreal forests form the climax biome at higher latitudes. Climatic constraints rather than rate of migration appear to determine the composition of postglacial forests, so that latitude plays a major role regarding which trees become dominant [9], coupled with factors such as geology, altitude and edaphic conditions which might determine local tree populations and produce polyclimaxes which varied along environmental gradients [10]. Autogenic successions in established forest communities are slow to bring changes in biome components or abundance, because of the long lifespans of individual trees and the inherent stability and inertia of the forest ecosystem [11–13]. Exogenic factors, however, primarily disturbance impacts, might bring about rapid changes in forest composition [14], forcing ecosystem regeneration and often converting primary to secondary woodland and even deflecting post-disturbance seral successions towards plagioseres such as scrub, bog or heath when tree regeneration fails or is incomplete [15,16]. Natural disturbances would have occurred in the forest throughout the early and mid-Holocene [17,18] and these would have operated at various scales, from the death and fall of individual trees or populations of particular taxa through disease, changing edaphic factors or senescence, to widespread tree-throw due to major storm events [19–21]. The actions of large herbivores could also have impacted the forest [22], although probably to a lesser extent than in previous interglacials [23]. Natural fires would have occurred [24], particularly during drier climatic phases [25] and these would have been at differing intensities, from light surface or canopy fires to larger wildfire, although larger scale deforestation of large areas would have been rare [26]. Although impossible to prove, it is very likely that fire in the hands of Mesolithic hunter-gatherers was regularly and deliberately applied to the forest [27], particularly in the Late Mesolithic, reducing tree cover and setting in train vegetation successions that lasted several decades as the ecosystem reverted towards woodland. It would have had the effect of permanently changing forest structure and composition from its natural, undisturbed state and constructing new ecological niches and landscapes [28] which favoured the foragers by increasing food and other resources [29–32], in the same way that the earliest Neolithic agriculturalists during the Mesolithic–Neolithic transition would have impacted the forest by farming within it [33]. There is evidence [34] that Mesolithic groups employed woodland management techniques such as coppicing [32,35,36] that would have stalled or deflected natural forest succession. In this paper we consider some highly detailed palynological evidence for the nature of forest succession following four of these Late Mesolithic age, mid-Holocene disturbances in northern England, using fine interval sampling [37] to provide decadal or better time-series data [38]. Using indicator taxa [39,40] we compare the palaeoecology of these disturbances to the neoecology of post-disturbance community succession in deciduous forest, with the aim of elucidating the nature of the Mesolithic-age disturbances and informing the understanding of Late Mesolithic land use in different parts of the mid-Holocene forests.

2. Background

2.1. *The Natural Wildwood*

The nature of the primeval English mid-Holocene climax forest, or wildwood (Urwald), has been the subject of much debate. It is acknowledged that the forest would have had a mixed species composition and would have varied across the country under a range of influencing environmental factors, rather than being the same everywhere [41], as shown by pollen analyses [42]. Altitude was a regulating factor, and Birks [43] has estimated the percentage of tree cover on the summits of the highest uplands as being low. The greatest altitude at which macrofossil tree stumps are found, around 500 m in the Pennines of northern England for example [44], is well below the maximum altitude of that upland. Lower uplands such as the North York Moors, however, should have been fully tree covered but pollen analysis suggests an open woodland at most, so that some limiting factor was preventing

expansion of full forest cover to these upland summits. This prompted Simmons [45] to suggest the existence of a ‘hyper-forest’ zone above a tree line that was maintained by natural or anthropogenic factors, and which formed an ecotone between the highest ground and the woodland of lower altitudes. Over most of the landscape, however, where forest was the dominant vegetation, the accepted model has been one of a high forest structure [46–48], and this has been generally supported by landscape scale pollen-based reconstructions, e.g., [49,50]. There are opposing views, however, regarding the degree to which the forest canopy was naturally fully closed or partly open before any disturbance by human or other agency [51–54]. Knowledge of the natural composition and structure of the forest clearly must serve as the baseline upon which any study of post-disturbance succession must be based, and palynology remains the main technique by which prehistoric forest history and structure can be investigated in any detail [55,56], with intuitive reconstructions increasingly improved by pollen modelling techniques [49,57–59]. It can also occasionally be supplemented by macrofossil studies in the rare locations where a population of tree stumps and other large remains have been preserved [60–63], usually beneath peat deposits, revealing palaeo-woodland density and species composition. Other proxies such as molluscan or insect remains [64,65] can also be useful in the reconstruction of prehistoric forests. Vera’s [51] hypothesis is that the actions of large wild herbivores could have impacted on arboreal woodland vegetation and so created or maintained openings in the forest, and that the natural forest was therefore not closed canopy but a form of partly open parkland, or at least with large, open glades between individual trees. Although the megafauna of previous interglacials was not present in the Holocene, the aurochs and bison were active in the early and mid-Holocene forest, with red deer, and could have had an impact on natural tree density and successions [22,66,67]. Latałowa et al. [68], however, in the modern Białowieża Primeval Forest of eastern Europe, which contains bison and other large herbivores but no livestock, recorded a dense, closed-canopy structure with very few gaps, not supporting the Vera hypothesis. Grazing and browsing after woodland disturbance of whatever cause, however, can certainly prevent or at least retard natural tree regeneration and so maintain open areas and prolong herbivore activity [69], which should be visible in pollen diagrams [70], which should also provide information regarding the density of the pre-disturbance forest. Although a range of other causes of forest disturbance must have existed [17,71] including storms [20] and disease outbreaks [21], it is likely that the activities of Mesolithic hunter-gatherers, as suggested by Simmons [27] and other authors, e.g., [72–74] could have been a major cause of forest opening in the early and mid-Holocene in England, at least in some parts of the landscape.

2.2. Fire and Hunter-Gatherers

Study of the activities of recent hunter-gatherer societies has shown that the use of fire to modify temperate forest ecosystems was a common practice that was systematic, well planned and integral to their land-use and economic strategies [75,76], particularly in North America [77,78] but also elsewhere [79,80]. Indigenous burning was an important land management tool that could be set to open burned patches of various sizes and altered the forest to human advantage, often long-term [81]. In the same way, the similar benefits that would have accrued to Mesolithic hunter-gatherers in early and mid-Holocene England through the application of fire to diversify the forested landscape would have been considerable; the removal of dense undergrowth from the primary forest to increase visibility and mobility, the creation of a mosaic vegetation landscape with a range of resources and woodland products, and the increased productivity and concentration of plant and animal foods within the vegetation communities at various stages of the woodland regeneration cycle. Macroscopic charcoal layers are often present in Mesolithic-age sediments in both upland, e.g., [82,83] and lowland, e.g., [84,85] contexts, and the presence of microscopic charcoal [86–91] in many Mesolithic age peats suggests that fire was a regular occurrence in at least some areas of the early and mid-Holocene forest, in particular in the uplands and around wetlands. Natural fire from lightning would have occurred in these landscapes, although the English forests were not particularly prone to ignition and would not carry fire

well, particularly in the damp lowland forests [41,92,93]. Fire would, however, occasionally have escaped into the woodland from Mesolithic campfires and other domestic situations by accident [94] while the purposeful and frequent controlled application of fire to the forest by Mesolithic people seems very likely. While some parts of the landscape might have been selected for more intense or regular fire disturbance, such as the waterside or the uplands where the forest might have been naturally lighter, the palaeoecological evidence indicates that the English forest in the first half of the Holocene, whatever its natural density, was undergoing limited intensity but constant modification by fire in the hands of Mesolithic hunter-gatherers. The selection of more favourable sites for burning, such as upland spring-heads or lake margins where animals might naturally congregate, could mean that such sites were burned repeatedly [15,27], truncating successional pathways before regeneration could be completed and returning the site to its most economically productive state. As with some modern foragers, the burning might have had more than an economic purpose, perhaps a social or ritual cleansing role to maintain forest health, control it and make it less intimidating [95], although that can only be surmised.

2.3. Palynology and Forest Successions

Scale is an all-important factor in the palynological reconstruction of past forest vegetation [59,96] and sediment sites should be selected for analysis on this basis [97]. The study of lakes or large peat bog deposits with big pollen source areas is appropriate for landscape-scale reconstructions over the long time periods of hundreds or even thousands of years at which climate-driven forest successions operate [98–101]. Large scale woodland removal caused by extreme tree clearance events such as major storms [20] will also be observable in such sediment archives. Small spatial scale analyses from sites within the forest, however, are required for the study of post-disturbance secondary forest successions which occur at the stand or patch scale [102,103], such as palaeoecological responses to localised fire events [104,105]. The study of site-specific forest successions therefore requires sediments from within forest stands, under the canopy in small hollows [1,106–108] or at spring heads [109], so that their pollen source area would have been limited [110,111], probably only from about 30 m around the site [96,112], although some research suggests a figure of over 50 m might be more realistic [113]. Consideration must also be made regarding the pollen productivity of different trees under forest stand conditions [1]. Several such studies have been undertaken and have provided spatially detailed data on longer-term forest succession [114–116]. Such sediments can be highly compact, but adjacent duplicate core analyses have shown that they contain a detailed and reproducible pollen record [117]. Fine temporal resolution is also required if the various seral stages which comprise the regeneration niche are to be understood, as these could represent vegetation growth of little more than a decade or so at most. This requires very fine sub-sampling intervals in the sediment so that each contiguous level analysed comprises only a few years' pollen accumulation and rapid ecological changes can be recorded [37,118], including the dynamics of the local forest stand canopy. The interpretation of such palaeoecological data in terms of post-disturbance seral plant communities requires close reference to each taxon's neoecology in analogous contemporary situations [119,120]. Several such high temporal resolution studies have been completed on mid-Holocene sediments, where sub-sampling intervals as low as one or two millimetres have been employed, depending upon the degree of humification of the sediment, and they have all provided highly detailed time-series records [38] of vegetation history and forest succession palaeoecology. Some have been aimed at investigating the Elm Decline and the Mesolithic–Neolithic Transition [121–125], while others have concentrated on either Early [126] or Late Mesolithic-age forest disturbances [127–130].

Such high-resolution pollen analyses, coupled with microcharcoal analyses, should be able to elucidate the scale and location of disturbance, as well as the rate, structure and pathways of post-disturbance successions, whether they were natural or controlled and whether there were differences in different parts of the landscape. A continuing literature search has revealed so far over a hundred sites in England with Mesolithic-age pollen diagrams

which contain evidence of woodland disturbance that set in train regeneration successions. A large majority of them include macro- and/or microscopic charcoal associated with the disturbance. Of those that do not, most are sites where charcoal analysis was not undertaken. It seems that fire was the main initiator of post-disturbance successions in Mesolithic times in England. Very few examples of disturbance have been examined using fine resolution sampling intervals, however, and in this paper we use fine sampling to examine in detail some of these phases of fire disturbance, to clarify the nature of the successions which followed fire, whether natural or human-induced, and see whether there are any differences among them that can assist interpretation of their source of ignition.

3. Materials and Methods

3.1. Methodology

For this study, four English pollen sites have been selected for examination, two from the lowlands and two from the uplands, where high-resolution pollen analyses have been carried out into Mesolithic age, early to mid-Holocene sediments. Pollen diagrams were produced for the entire profile at each site, but only the post-disturbance pollen data are presented here. Pollen analyses were undertaken following standard techniques, with preparation and identifications following Moore et al. [131] and nomenclature following Stace [132]. Pollen counts always exceeded 400 land pollen grains. Pollen diagrams were constructed using TILIA and TILIAGRAPH [133,134] and are presented as percentages of total tree pollen as forest history is the object of study [135]. The components of the tree pollen sum vary between sites as some trees, mainly *Betula* and *Alnus*, can be superabundant in the local pollen rain because of their wetland edge habitat. *Corylus* and all other taxa are excluded from the counting sum.

Microcharcoal particles were counted at each profile as a pollen/charcoal ratio according to the method described by Innes and Simmons [136]. Particles that passed through the 180 μm pollen preparation sieve were counted relative to the pollen count, with those around 30 μm in diameter regarded as the basic measurement unit, so that a piece of 90 μm would be counted as three units. All pieces smaller than 30 μm were aggregated to produce countable data. Separate curves for different size ranges are not produced as fragmentation of particles will occur during the laboratory preparation [137]. This consistent methodology allows direct comparison between profiles.

Well humified peat is required for viable fine resolution palynology [37] and the peat at all four sites meets this requirement. Full lithologies from the profiles are described in Supplementary Table S1 and the relevant numbered sedimentary units from Table S1 are shown in the lithology columns on the fine resolution diagrams.

3.2. Radiocarbon Dating

Radiocarbon ages are available for all of the four sites (Table 1) and prove the Late Mesolithic-age context of the finely sampled sections. They have been calibrated using OxCal4.4 and IntCal20 [138] and the mid-range calibrated yr. BC ages and laboratory codes are shown in the text after the radiocarbon date citation. The dates from Sniggery Wood were radiometric on bulk peat samples, whereas more recently obtained dates from Little Hawes Water, North Gill and Bonfield Gill Head are AMS dates.

Table 1. Radiocarbon dating at Sniggery Wood, Little Hawes Water (LHW), North Gill 7 and Bonfield Gill Head.

Site	Depth (cm)	Lab Code	^{14}C Date (yr BP)	Age Range (cal. BC)	Mean Age (cal. BC)
Sniggery Wood	11–13	SRR-2698	4510 \pm 50	3029–3363	3196 \pm 167
Sniggery Wood	171–174	SRR-2699	5770 \pm 50	4492–4726	4609 \pm 117
LHW ESE3	67–68	Wk-20078	6865 \pm 58	5644–5878	5761 \pm 117
North Gill 7	72	SRR-3654	4940 \pm 45	3641–3894	3767 \pm 126
North Gill 7	76	SRR-3655	5645 \pm 45	4360–4582	4471 \pm 111

Table 1. Cont.

Site	Depth (cm)	Lab Code	¹⁴ C Date (yr BP)	Age Range (cal. BC)	Mean Age (cal. BC)
North Gill 7	80	SRR-3656	6710 ± 50	5543–5715	5629 ± 86
North Gill 7	82	SRR-3657	6735 ± 45	5563–5723	5643 ± 80
Bonfield Gill Head	46	Wk-16273	4644 ± 43	3350–3623	3486 ± 136
Bonfield Gill Head	75	Wk-15152	5874 ± 44	4615–4844	4730 ± 115
Bonfield Gill Head	83	Wk-15154	6122 ± 46	4944–5211	5077 ± 133
Bonfield Gill Head	99	Wk-15745	6854 ± 46	5646–5841	5743 ± 97

Age range (2 σ) and mean derived from calibration results using Oxcal4.4 and IntCal20 [138].

4. Results

The four pollen sites that have been selected for examination are located on Figure 1, the two lowland sites being on the coastal plain of North West England and the two upland sites on the North York Moors upland in North East England. They provide a clear altitudinal contrast within northern England, a region that is known to have been heavily occupied and utilised by Late Mesolithic people [139–142].

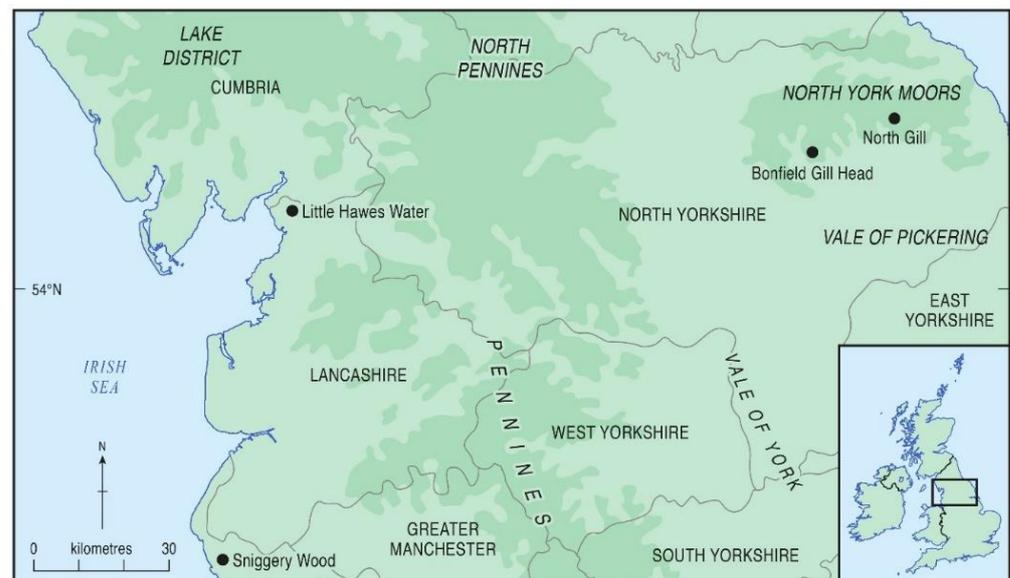


Figure 1. Location of the four sites studied in this paper. North Gill and Bonfield Gill Head are at about 350 m above sea level on the North York Moors in northeast North Yorkshire. Little Hawes Water and Sniggery Wood are lowland sites in North Lancashire and Merseyside, respectively. The dark green areas are land above 200 m altitude.

4.1. Sniggery Wood

The Sniggery Wood pollen profile (UK grid reference SD307015; lat. 53°30'20.2" N long. 3°02'46.8" W) lies in Merseyside near the coast of lowland northwest England (Figure 1) at a surface altitude of 6 m above sea level. Its pollen diagram was constructed at 4 cm intervals [143] and one level of Late Mesolithic age, dated soon after 5770 ± 50 BP [4609 ± 117 cal. BC; SRR-2699], showed evidence of woodland disturbance and regeneration, with ruderal weed grains, increased *Corylus* and other heliophyte tree percentages and then restoration of deciduous woodland cover. Subsequent pollen analyses of this phase at finer resolution intervals of 5 mm, shown in Figure 2, has clarified its disturbance and regeneration history.

Sniggery Wood

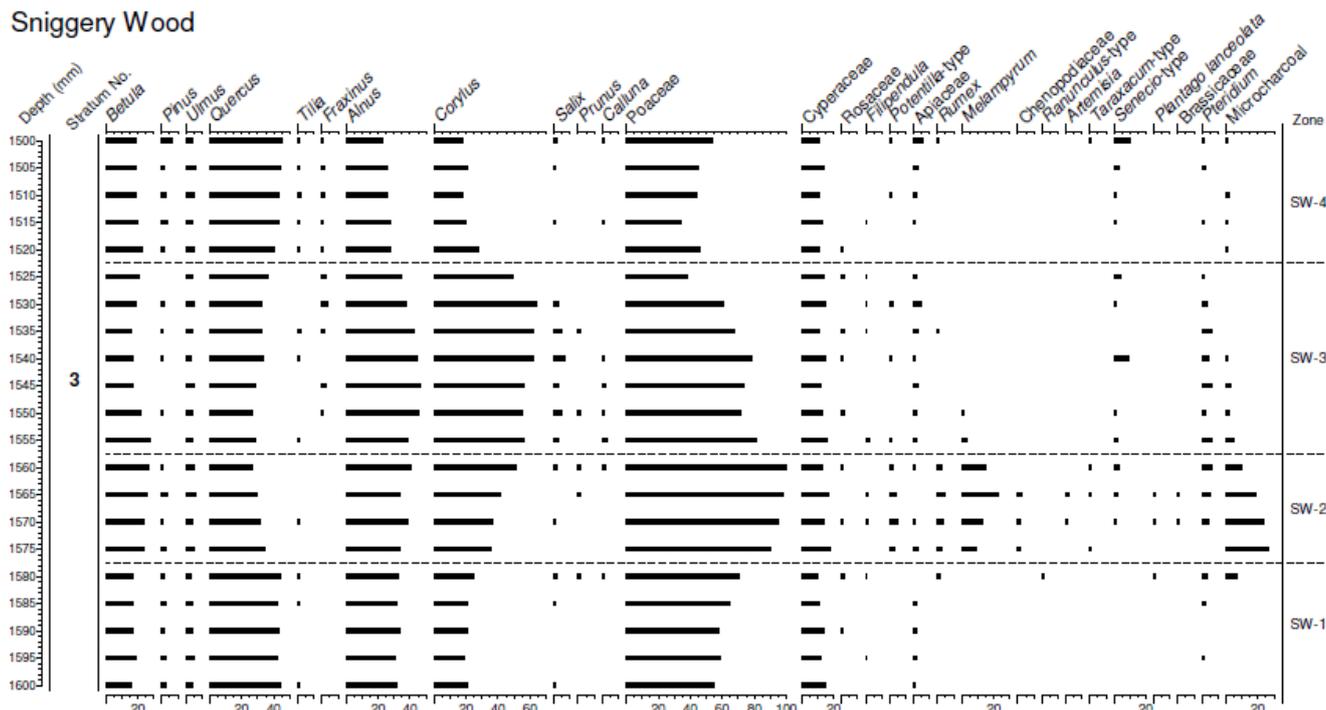


Figure 2. Selected taxa pollen diagram through a Mesolithic age disturbance phase at Sniggery Wood, Merseyside. Frequencies are calculated as percentages of total tree pollen, which comprises *Betula* to *Alnus* on the diagram.

4.1.1. Pollen Zones

The following four pollen zones are recognised.

SW-1

The lowermost zone has high levels of tree and shrub pollen, at almost 70% of total land pollen, although there are high *Poaceae* frequencies of almost 30%, probably caused by the site's near-coastal location, or by grasses growing on the wetland surface. *Quercus* and *Alnus* are the main tree taxa, with *Corylus* the main shrub. Herbaceous frequencies other than grasses are very low and are confined to wetland types. The local vegetation would have been woodland, probably open to some degree.

SW-2

This zone records a major decline in *Quercus* frequencies, *Alnus* being little affected, and a slight rise in *Corylus* percentages. Total trees and shrubs decline to about 50% of total land pollen. Microcharcoal frequencies rise to a peak at the start of the zone and decline thereafter. *Melampyrum* enters the assemblage, rising to a peak in mid-zone, while a wide range of open ground weeds is recorded, including ruderal types including *Artemisia*, *Taraxacum*-type, *Chenopodiaceae*, *Rumex* and *Senecio*-type. Grassland weeds like *Plantago lanceolata* and *Potentilla*-type increase, and *Poaceae* increases slightly. *Pteridium* is increased and some heliophyte shrubs occur late in the zone.

SW-3

In this zone *Quercus* values remain lowered, but *Alnus* is restored to its levels of zone SW-1. *Corylus* increases markedly to almost 30%, while *Salix*, *Fraxinus* and *Calluna* are consistently present. Total tree and shrub frequencies return to their zone SW-1 levels of about 70%, but with shrub pollen a more important component. *Poaceae* declines and the range of herb pollen is greatly reduced, with almost all of the open ground and ruderal taxa absent and wetland herbs as the main contributors. Microcharcoal and *Melampyrum* quickly fade from the assemblage. *Pteridium* remains present in low values.

SW-4

In the uppermost zone *Quercus* percentages are restored to at least the frequencies of zone SW-1, as are those of *Betula* and *Alnus*. *Tilia* becomes consistently present. *Corylus* percentages fall sharply to zone SW-1 levels. Heliophyte shrub pollen declines, although *Fraxinus* remains consistently present. Herb pollen contributes about 30%, again mainly by Poaceae. All herb taxa are now wetland types such as Apiaceae, with *Senecio*-type pollen, probably wetland members of the Asteraceae family. There are no dryland open ground weeds.

4.1.2. Diagram Interpretation

Ulmus percentages are low but consistent and there is a clear Elm Decline much higher in the profile at 56 cm, so this disturbance phase occurred in Mesolithic age times. Zone SW-1 had woodland vegetation, which was perhaps not closed canopy, depending on the origin of the grass pollen, which might have come from wetland communities rather than woodland glades. This oak/alder woodland was disturbed by the fire event recorded at the start of zone SW-2, which was nearby even though microcharcoal values are not very high, as pollen of many weeds was able to be transported to the sampling site. Fire-favoured *Melampyrum* is another signature of the burning [144], but some unstable open ground must have been created to account for the ruderal weed assemblage of zone SW-2, and the degree of *Quercus* decline suggests some significant recession of the local oakwood. Regeneration in zone SW-3 seems to have shaded out the open ground as the weed assemblage is absent in zone SW-3 and shrubs, mainly hazel but also ash and willow, appear to have occupied the scene of disturbance. Regeneration of woodland was completed in zone SW-4 with *Quercus*, and lesser *Betula* and *Alnus*, dominating the dryland vegetation. While woodland was restored to pre-disturbance levels, with hazel once again a minor component, its composition seems to have changed slightly with *Fraxinus* and *Tilia* now rare but consistent members. The pollen record indicates a single episode of fire disturbance of woodland, followed by the uninterrupted regeneration of woodland through ruderal, then *Corylus*-dominated shrub communities.

4.2. Little Hawes Water

The Little Hawes Water pollen profile (UK grid reference SD480768; lat. 54°11'03.6" N long. 2°47'53.9" W) lies in North Lancashire at a surface altitude of 7 m. above sea level (Figure 1) and is part of a basin peat deposit that surrounds a small lake [84] in a limestone catchment near the coast. The peat contains charcoal layers which record burning around the lake and one, at core ESE3, was selected for detailed study. Pollen analysis showed that vegetation disturbance was associated with the inwash of charcoal into the peat basin, caused by the fire event. The charcoal layer at 67–68 cm depth was dated (Table 1) to 6865 ± 58 BP [5761 ± 117 BC; Wk-20078], well within the Late Mesolithic period. Subsequent pollen analyses of this phase at finer resolution intervals of 2 mm, shown in Figure 3, have clarified its disturbance and regeneration history.

4.2.1. Pollen Zones

The following four pollen zones are recognised.

ESE3-1

This zone contains pre-disturbance assemblages. Microcharcoal frequencies are very low, although present, and the pollen assemblage is dominated by arboreal pollen, particularly *Quercus* and *Alnus*, as well as *Corylus* which together comprise almost 90% of total pollen. Herb pollen values are very low, with only Poaceae significant, although isolated grains of some ruderals, like *Plantago lanceolata* and *Ranunculus*-type, do occur.

ESE3-2

This zone records a fall in the frequencies of *Quercus* and *Alnus*, with total tree and shrub pollen reduced to 70% of the total assemblage, and tree pollen contributing only 50%. *Corylus* is not much increased until the end of the zone. Poaceae and other herbs mainly

benefit from the fire disturbance that the peak microcharcoal values represent. A wide range of ruderal weed taxa occurs, with *Artemisia*, *Potentilla*-type, *Rumex* and *Senecio*-type prominent, but *Melampyrum* shows peak values of almost 10% of total land pollen. *Pteridium* also increases and *Calluna* occurs late in the zone.

ESE3-3

Arboreal pollen frequencies remain at around 50% of total land pollen, with *Quercus* and *Alnus* showing no recovery, but *Corylus* is greatly increased. Light-demanding tall shrub/tree taxa *Fraxinus* and *Salix* are increased. While the number of herbaceous types recorded remains high, overall herb frequencies fall to a total of only 10% of total land pollen. *Melampyrum* and Poaceae in particular fall to low levels. *Pteridium* increases its frequencies while microcharcoal falls gradually through the zone.

ESE3-4

Only occasional microcharcoal counts are recorded, while *Quercus* and *Alnus* are restored to the pre-disturbance levels of zone ESE3-1. *Corylus* frequencies decline to those of pre-disturbance and total tree and shrub pollen again contributes 90% of the total assemblage. Most ruderal herb taxa cease to be recorded, with the remaining herbs more of wetland type than open ground. *Pteridium* is also reduced. Poaceae, with Cyperaceae, is the main herb type recorded.

Little Hawes Water ESE3

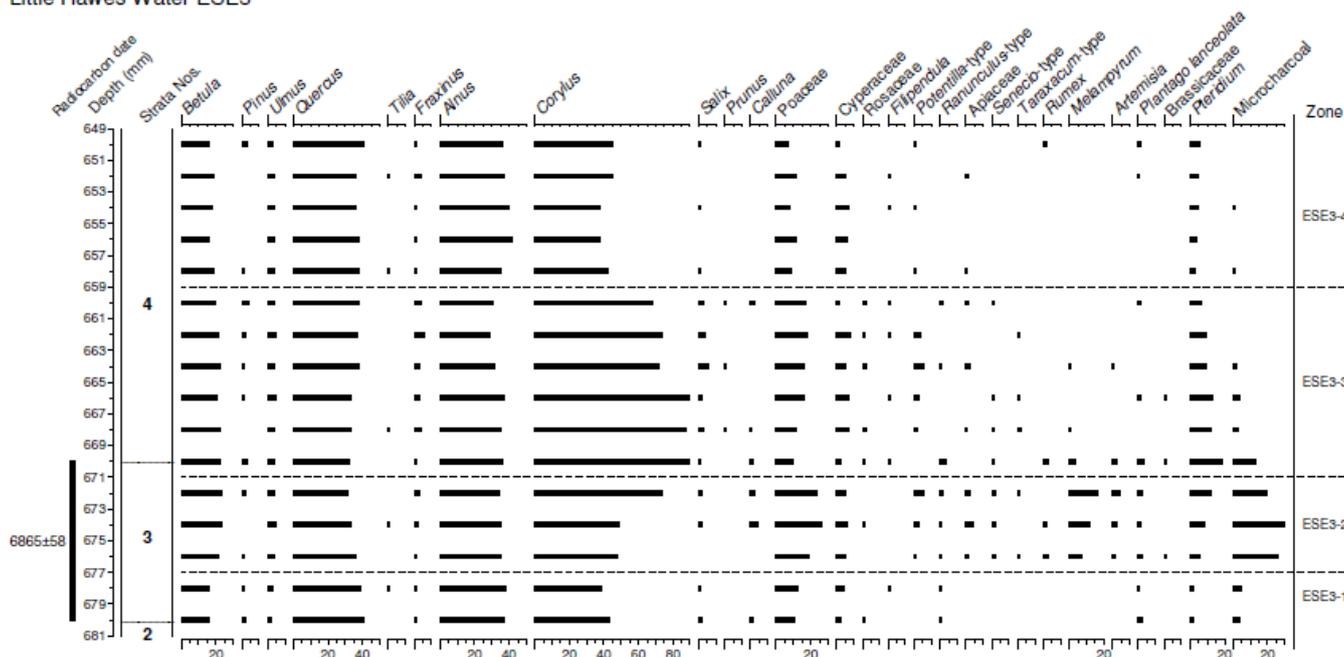


Figure 3. Selected taxa pollen diagram through a Mesolithic age disturbance phase at Little Hawes Water. Frequencies are calculated as percentages of total tree pollen, which comprises *Betula* to *Alnus* on the diagram.

4.2.2. Diagram Interpretation

Although not high, the substantial and consistent *Ulmus* pollen values throughout the diagram show it to be of Pre-*Ulmus* Decline age, confirming the Mesolithic-age radiocarbon date of 6865 ± 58 BP in the lower profile. The pollen record describes a disturbance event, initiated by a fire in the nearby catchment at the ESE3-1/ESE3-2 boundary, and the subsequent vegetation regeneration and recovery of woodland cover. As at Sniggery Wood and in many other mid-Holocene woodland disturbance pollen phases the pyrophyte *Melampyrum* is favoured in the initial phase of regeneration, along with ruderal colonisers of bare ground, such as *Artemisia*, *Taraxacum*-type and *Senecio*-type, and several weeds

which will have responded to the newly opened area. The second phase of regeneration, ESE-3, sees the increase in heliophyte shrub taxa as recovery continued, particularly *Corylus*. Although in greatly reduced frequencies, open ground herbs still occur, which might be because of the catchment’s limestone soils taking longer to stabilise than heavier soils might. The later stages of regeneration in ESE-3 records the expansion of tall shrubs and secondary trees on the site of disturbance as regeneration towards woodland continued and light levels reaching the ground fell. The final zone records the restoration of woodland cover, with vegetation communities returning almost exactly to the pre-disturbance state. At 90% of total land pollen, it must represent virtually closed canopy woodland, with hazel probably forming a canopy component on the limestone catchment soils. The Little Hawes Water evidence indicates a single episode of fire disturbance of closed woodland, followed by a unidirectional and uninterrupted regeneration of dense woodland through ruderal, tall herb and shrub communities.

4.3. North Gill

The North Gill pollen profile NG7 (UK grid reference NZ726008; lat. 54°23'51.0" N long. 0°52'59.8" W) lies within stream valley peat that has formed around a springhead at a surface altitude of 370 m above sea level near the summit plateau of the North York Moors (Figure 1) in North Yorkshire, North East England [109]. Bracketing radiocarbon dates (Table 1) of 6735 ± 45 BP [5643 ± 80 cal. BC; SRR-3657] at 82 cm and 5645 ± 45 BP [4471 ± 111 cal. BC; SRR-3655] at 76 cm show that the profile lies well within the Late Mesolithic period. Coarser interval palynology recorded fire disturbance phases, and subsequent pollen analyses of one of the phases at finer resolution intervals of 2 mm, shown in Figure 4, has clarified its disturbance history.

North Gill 7

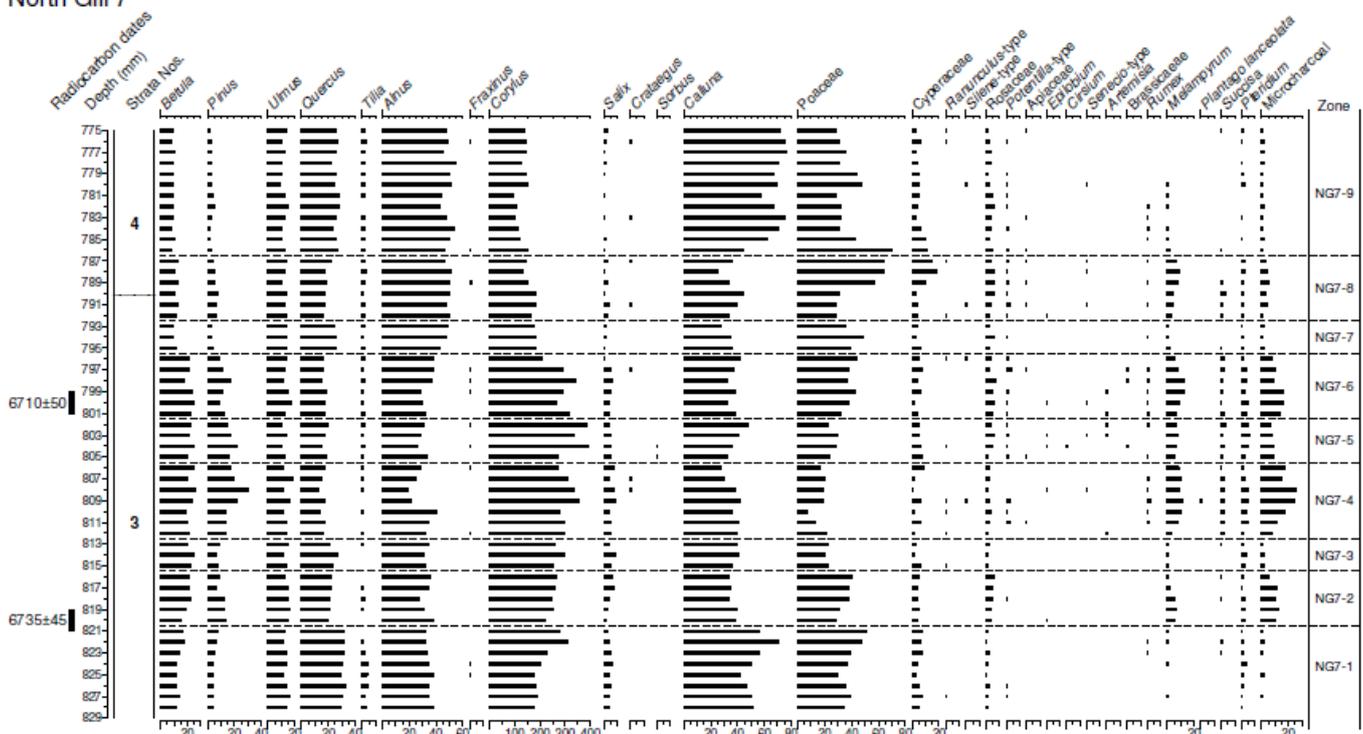


Figure 4. Selected taxa pollen diagram through a Mesolithic age disturbance phase at North Gill 7. Frequencies are calculated as percentages of total tree pollen, which comprises *Betula* to *Fraxinus* in the diagram.

4.3.1. Pollen Zones

The following nine pollen zones are recognised. The approximate ages of the boundaries of the phases of disturbance could be interpolated from the calibrated means of the bracketing date, although these can only be approximate given the ranges of uncertainty on the calibrations.

NG7-1

This zone shows no evidence of active disturbance, with microcharcoal frequencies very low and with only sporadic records of open ground herbs. Local vegetation was *Quercus-Alnus-Ulmus* woodland with some *Tilia*, although it must have been open, as there are substantial values for *Calluna*, Poaceae and *Corylus* all perhaps due to the high altitude or a legacy of earlier disturbance unless the heather and grasses were growing on the bog surface.

NG7-2

This zone records fire disturbance with microcharcoal showing peaks in frequency which are matched by the *Melampyrum* curve in the earlier part of the zone. *Pteridium* and Rosaceae also rise, but there are almost no ruderal weed indicators of newly bare ground, so that the disturbance will have been a little way from the sampling site. *Ulmus* and *Alnus* percentages are unaffected, but *Quercus* falls significantly, replaced by *Betula* and *Pinus*, showing a diversification of the local oakwood and increased pollen transport through the canopy.

NG7-3

There is no evidence of local fire disturbance at the site in this zone, as the microcharcoal and *Melampyrum* curves fall to very low levels, although are still present. *Pteridium* still has a low curve but there are no weed taxa present. *Quercus* shows a small peak as it recovers some of its pre-disturbance frequencies, perhaps shading out some of the Poaceae pollen, which falls.

NG7-4

A more significant fire disturbance event occurs in this zone, with high peaks of microcharcoal and *Melampyrum*, and the presence of isolated ruderal and grassland weeds including *Potentilla*-type, *Rumex*, *Ranunculus*-type and *Plantago lanceolata*. *Pteridium* also shows elevated percentages. Poaceae frequencies are low. *Quercus* is again the tree mostly reduced, while *Alnus* values also decline late in the zone as *Corylus*, *Pinus* and *Salix* rise to peak values and *Crataegus*-type occurs.

NG7-5

Disturbance continues in this zone, although microcharcoal and *Melampyrum* percentages are reduced, and several weed taxa are recorded, notably *Potentilla*-type but also low values of ruderals such as *Epilobium* and *Artemisia*. *Pteridium* frequencies are high. *Quercus* percentages remain low, while *Corylus* and Rosaceae show peak frequencies, *Sorbus* occurs and *Calluna* also rises. Other tree taxa are unchanged.

NG7-6

Fire disturbance occurs near to the site as microcharcoal and *Melampyrum* frequencies rise to peaks, with the latter occurring slightly later. *Quercus* remains at low frequencies, and the percentages of other trees are also unchanged. *Corylus* remains in very high percentages relative to tree pollen, and *Salix* is also increased. *Pteridium* is still high, Poaceae frequencies rise and records of ruderal weed taxa, such as *Artemisia* and *Rumex*, occur.

NG7-7

In this zone there is little evidence of fire, although the microcharcoal and *Melampyrum* curves do not fade away completely. Percentages of *Pteridium* spores are much reduced. Pollen of open ground herbs is almost absent, and *Quercus* percentages rise markedly, as do those of *Alnus*. Frequencies of the shrubs *Corylus*, *Salix* and *Calluna* fall, and those of secondary tree regeneration, such as *Betula*, also fall.

NG7-8

In this zone both microcharcoal and *Melampyrum* frequencies increase, although rather less than in previous zones of disturbance. *Quercus* percentages are considerably reduced but other trees seem little affected, as is *Corylus* which does not respond to the renewed burning. Poaceae values rise strongly late in the zone but as this corresponds to a similar increase in Cyperaceae and a fall in *Calluna*, it is likely that changes in bog surface wetness account for these pollen shifts. Most of the herb pollen recorded in this zone could as easily be referable to wetland taxa as to open ground disturbance indicators.

NG7-9

The uppermost zone sees *Quercus* restored to higher values and with *Ulmus* and *Alnus* forming the main tree and shrub pollen contributors, *Corylus* being in low percentages. Microcharcoal is always present, but in very low frequencies indeed, and *Melampyrum* fades from the assemblage in mid-zone. Herb pollen, other than Poaceae, and *Pteridium* are almost absent. There is no evidence of disturbance in this zone. Only *Calluna* increases its percentages markedly and, as no other taxa vary significantly, could be associated with a drying of the bog surface after the cessation of disturbance.

4.3.2. Diagram Interpretation

The radiocarbon dates and the consistently high frequencies of *Ulmus* pollen show that the diagram is all of pre-*Ulmus* Decline, Mesolithic, age. The pre-disturbance woodland comprised *Quercus*, *Alnus* and *Ulmus* mainly, with lesser *Tilia* and *Betula*. Notable, however, is the very high proportion of *Corylus* pollen relative to the tree taxa, and hazel must have been an abundant component of an open woodland at this high altitude, perhaps naturally but also perhaps as a legacy of earlier disturbances. The diagram contains four phases of fire disturbance, in zones NG7-2, NG7-4, NG7-6 and NG7-8, of which NG7-4 and NG7-6 are two separate fires within a longer period of disturbance, in which NG7-5 saw some regeneration of tree cover as disturbance pressure was reduced somewhat, although was still present nearby, if not at this site. The first and fourth episodes of fire disturbance were of lower intensity or further away, having distinctly lower impacts on the woodland at the site. None of the fire phases seems to have created a lot of bare ground as ruderal frequencies and types are low throughout. *Quercus* was the tree most adversely affected in every case, and might be because oak, as *Quercus petraea*, tends to grow in single taxon stands in the northern English uplands. *Calluna* occurs in high values throughout the diagram and could form part of the long-term dryland regeneration community in the open woodland, like hazel, but its abundance might have been linked to hydrological changes on the wetland surface, as was most likely Poaceae, and so is difficult to interpret. The NG7 evidence, therefore, records multiple phases of fire at the same site within an open oak woodland which contained abundant hazel.

4.4. Bonfield Gill Head

The Bonfield Gill Head pollen profile (UK grid reference SE598558; lat. 54°21'15.3" N long. 1°04'53.1" W) also lies within stream valley peat that has formed around a spring-head at 346 m above sea level near the summit plateau of the North York Moors in North Yorkshire, North East England (Figure 1), on East Bilsdale Moor to the west of the North Gill site [145]. Bracketing radiocarbon dates (Table 1) of 6122 ± 46 BP [5077 ± 133 cal. BC; Wk-15154] at 83 cm and 5874 ± 44 BP [4730 ± 115 cal. BC; Wk-15152] at 75 cm show that most of the profile lies well within the Late Mesolithic period. Coarser interval palynology recorded fire disturbance phases of Mesolithic age, and subsequent pollen analyses of one of the phases at finer resolution intervals of 2 mm, shown in Figure 5, has clarified its disturbance history.

Bonfield Gill Head

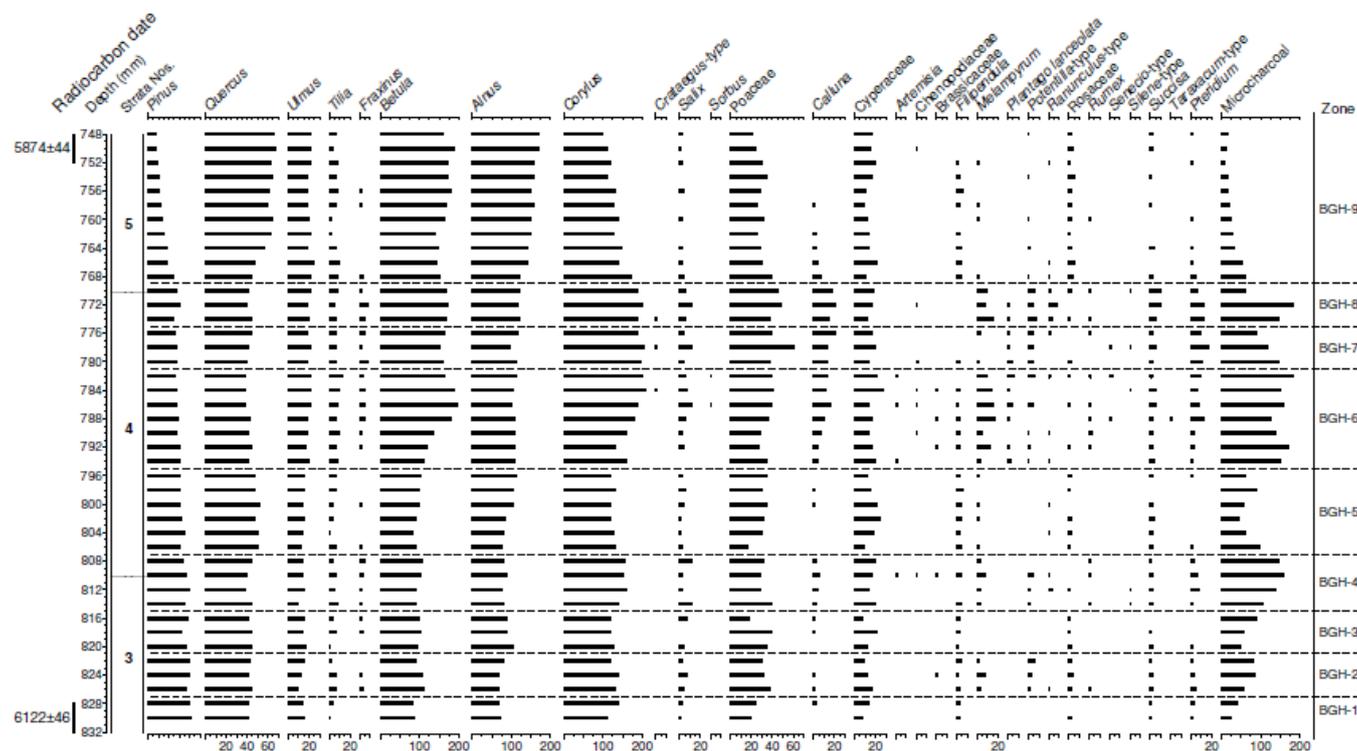


Figure 5. Selected taxa pollen diagram through a Mesolithic age disturbance phase at Bonfield Gill Head. Frequencies are calculated as percentages of total tree pollen, which comprises *Pinus* to *Fraxinus* in the diagram. *Betula* and *Alnus* are excluded because of local superabundance at this site.

4.4.1. Pollen Zones

The following nine pollen zones are recognised. The approximate ages of the boundaries of the phases of disturbance could be interpolated from the calibrated means of the bracketing dates, although can only be approximate given the ranges of uncertainty on the calibrations.

BGH-1

This zone contains no evidence of active disturbance, with microcharcoal frequencies low and no pollen records of herbs of disturbed and open ground. Herb pollen is contributed mainly by Poaceae, with some wetland types. The tree pollen assemblage is dominated by *Quercus* and *Pinus*, with substantial *Ulmus* values. *Betula* and *Alnus* are also present in high frequencies, while *Corylus* percentages are moderately high.

BGH-2

The second zone records a rise in microcharcoal frequencies to a peak of about 100% relative to the tree pollen sum. Herbaceous indicators of disturbance occur, although not in very high percentages, but include isolated records of Brassicaceae and *Rumex*, and peaks of *Melampyrum* and *Potentilla*-type. There is very little evidence of change in the arboreal pollen curves, although secondary trees and shrubs *Betula*, *Corylus* and *Salix* do increase slightly, and *Fraxinus* becomes present. This zone records fire disturbance, but either at low scale or at a distance from the sampling site.

BGH-3

There is no evidence of disturbance in this zone, with microcharcoal frequencies falling and no records of any weeds of open ground. *Melampyrum* and *Pteridium* are absent. Little change occurs in the arboreal and shrub taxa, other than *Alnus* increases slightly and *Corylus* is reduced.

BGH-4

Evidence of fire disturbance returns to the assemblage in this zone, with microcharcoal rising to peak frequencies and a wide range of ruderal and open ground weeds recognised, including *Artemisia*, *Chenopodiaceae*, *Ranunculus*-type and *Rumex*. Peaks of *Melampyrum*, *Potentilla*-type and *Pteridium* occur. *Quercus* falls slightly and increases occur in *Corylus*, *Salix* and *Fraxinus*, with *Calluna* significant for the first time. Despite the evidence of disturbance, the tree pollen curves are not greatly affected and the disturbance, while creating open ground, seems not to have caused a significant recession of tree cover.

BGH-5

Quercus and *Alnus* pollen percentages increase while *Corylus*, *Salix* and the secondary tree *Betula* decline in value. *Fraxinus* and *Calluna* are hardly represented. Herbaceous pollen frequencies are very low, with almost no records of disturbance indicators, with *Melampyrum* and *Pteridium* almost absent. Microcharcoal frequencies have declined sharply although are consistent in their lower values.

BGH-6

Microcharcoal frequencies rise sharply to high peaks, mirrored by peak values of *Melampyrum* at over 20% of tree pollen and, later in the zone, *Pteridium*. A wide range of ruderal and grassland herbs is recorded, including for the first time *Plantago lanceolata*, which is consistently high later in the zone. *Corylus* rises throughout the zone, achieving peak frequencies at its end, as do *Betula*, *Salix* and *Calluna*. *Quercus* declines slowly through the zone, while *Tilia* and *Fraxinus* increase. Although no major tree recession occurs, this is a substantial phase of fire disturbance, which must have occurred quite close to the site.

BGH-7

The tree pollen assemblage does not change greatly, although *Quercus* does recover somewhat and *Tilia* and *Fraxinus* remain important. Microcharcoal frequencies are reduced, but still quite high, and there are fewer ruderal herb types recorded, although *Plantago lanceolata* remains present throughout. *Melampyrum* is scarcely recorded, suggesting no new burning at the site. *Pteridium* and *Calluna* maintain their increased percentages, and *Corylus* remains high. This zone seems to reflect a degree of local regeneration and maintained openness, while disturbance might have continued at a greater distance from the site.

BGH-8

Renewed fire disturbance occurs in this zone, with microcharcoal frequencies rising sharply to high peaks, while *Melampyrum*, *Pteridium*, *Potentilla*-type and *Ranunculus*-type are all present in peak percentages and *Plantago lanceolata* is consistently present. *Calluna* and *Corylus* frequencies are also very high, while *Fraxinus* and *Salix* show peaks. *Quercus* values decline slightly but all other tree and shrub percentages are maintained. Although evidence for fire disturbance is clear, it seems to have had only a small impact on the forest.

BGH-9

The uppermost zone records the end of fire disturbance as *Quercus* and *Alnus* percentages rise significantly and *Corylus* frequencies are greatly reduced. *Pinus* frequencies also fall. Microcharcoal percentages become very low and disturbance indicators *Melampyrum*, *Pteridium*, *Potentilla*-type, *Calluna* and *Fraxinus* fade from the assemblage. There are very few herb counts, almost all contributed by wetland types, and tree pollen dominates as the recovery of the forest is completed.

4.4.2. Diagram Interpretation

The consistently high *Ulmus* pollen curve confirms the two radiocarbon dates that bracket the high-resolution diagram in showing Figure 5 to be entirely of Late Mesolithic age. The pre-disturbance woodland was quite mixed and although *Quercus* and *Ulmus* were important, there were major components of *Betula*, *Alnus* and *Corylus*, as well as a

surprisingly high proportion of *Pinus*. This might be due to local geology and soils, with sandstone ridges in the vicinity of Bilsdale Moor. The woodland was closed, there being little pollen other than that of trees and tall shrubs. The diagram contains four phases of fire disturbance, in zones BGH-2, BGH-4, BGH-6 and BGH-8. The earlier two zones saw the introduction of open areas, or at least significant breaks in the canopy, as ruderal herbs and pyrophyte taxa are prominent. The increases in *Corylus* are not great but do indicate more heliophyte conditions, with *Quercus* most affected. The intervening zones are periods of regeneration of the woodland canopy. The major changes to the woodland occur in zones BGH-6 and BGH-8, with much greater creation of ruderal and open ground habitats and the major increase in *Corylus*, and also *Betula*, which is maintained in the reduced disturbance of zone BGH-7, suggesting a more long-lasting diversification of the woodland. These three later zones indicate a more effective disturbance, either of greater intensity or closer to the site, which made real changes to the local woodland. At the end of this sequence of disturbances, in zone BGH-9, a woodland composed of *Quercus*, *Alnus*, *Betula* and *Ulmus* became established, with *Corylus* and *Pinus* much less important members. The BGH evidence records four phases of fire disturbance of a resilient, closed, mixed woodland, with increasingly severe impacts until the final disturbances brought significant and lasting woodland community change.

5. Discussion

Observations of contemporary temperate deciduous woodland [120] allow an understanding of both longer-term autogenic processes of change within the tree community [146–148] and the several, relatively dynamic stages of vegetation change caused by disturbance, opening and then regeneration of the woodland matrix [8,149]. Depending on the size and nature of the gap created [150], disturbances within mature woodland are the main process for the creation and maintenance of diversity within that ecosystem [147,151], both in plant species and community structure [152,153], and the neocology of woodland disturbance and the regeneration niche has been the subject of considerable study [154–156]. Fire clearly has a major environmental impact in forested ecosystems [157–160] and the fire disturbances present in the four profiles shown in this paper, and in many less detailed published examples, allow an understanding of prehistoric woodland disturbance ecology [161,162], spatial patterning of vegetation [163] and the encouragement of islands of plant diversity in woodland ecosystems [164,165] which would otherwise have been generally closed-canopy [52] and homogeneous.

5.1. Distribution of the Evidence for Mesolithic Disturbance

This is not the place for a comprehensive review of the palynological evidence for Mesolithic age forest disturbance in northern England and beyond. It is, however, important to consider how widespread the occurrences of disturbance were in pre-Neolithic times, particularly in the mid-Holocene, Late Mesolithic forests that are the main focus of this paper, and therefore to establish how representative the four examples in this paper are of the overall Mesolithic disturbance evidence. The distribution of the evidence will inevitably reflect the distribution of the research effort, yielding more examples in areas more closely studied, particularly in places where the analysis of such evidence has been the research aim, such as in the uplands of the North York Moors, and parts of the Pennine Hills in northern England [15,44,164,166]. The authors, however, have accumulated a database that extends into the hundreds of sites of Mesolithic age disturbance, and, given that earlier palynological studies often did not record microcharcoal data, it is clear that burning in the Mesolithic forest was very commonplace indeed, causing significant changes in forest dynamics, although its linkage with a hunter-gatherer origin is inevitably circumstantial. Evidence of such disturbance, usually involving fire, occurs almost everywhere in Britain and Ireland where research has been undertaken, for example in South West England [74], Scotland [32,167,168], Wales [82], the Isle of Man [169] and Ireland [30]. Fire disturbance of vegetation in Mesolithic times was clearly very widespread. Of particular interest are

those cases where fire disturbance coincided with major changes in forest structure and dynamics. The initial rise of *Corylus* pollen percentages in the earlier Holocene might have been promoted by fire in the hands of hunter-gatherers [170]. There are also over forty instances where the mid-Holocene *Alnus* rise, a major pollen-stratigraphic event and pollen zone boundary, was probably assisted by fire as it coincided with macro- or microcharcoal peaks, e.g., [82,171,172].

While Britain has most of the published evidence for Late Mesolithic fire disturbance of woodland ecosystems, there is a considerable body of evidence from mainland Europe suggesting that the same type of fire-management of forests might well have been practiced across that much larger area, in both the Early and Late Mesolithic, and in both lowland and upland locations. Pollen evidence of woodland canopy opening in western Europe has long been reported [173] but more recently higher resolution palynology has revealed many examples of forest burning, some of which have been attributed to deliberate burning and management [174] and have stimulated discussion of fire and forager-landscape relationships similar to that in Britain [175–182], often with a similar focus on the encouragement of *Corylus* and its value as a food resource [179,183–188], and even the transformation of the forest to hazel ‘plantations’ [188]. While some examples of fire disturbance have been reported from southern Europe [189–191] and from Scandinavia [192–194] it is in central and northern Europe that most examples occur, in particular in woodland and marshes around wetlands in the North European Plain of The Netherlands, Germany, Poland and the Baltic States [180,195–203] situations that were unlikely to have supported natural wildfires during the early to mid-Holocene. These northern European sites resemble the record at the lowland sites of northern England discussed in this paper, usually being single or long interval burn events, although some repeated burning did occur [186]. The widespread occurrence of fire disturbance in the Mesolithic of Britain and many parts of Europe indicates that the ecological successions that followed burning must be taken into account when reconstructing early and mid-Holocene forest structure and dynamics, at least at regional, and perhaps at wider, scales.

5.2. The Original Forest and Natural Succession in the Study Area

Pollen evidence from the four sites examined above suggests that they all supported mixed deciduous forest, with a high-forest full canopy in the lowland examples, in the years before the occurrence of disturbance. *Tilia* and *Ulmus* were common where edaphic conditions permitted [120], and *Quercus* and *Alnus* were most important in other areas, as well as more generally in the uplands. As in the case of the two upland examples, the upland oakwoods of northern England would have naturally contained a lot of *Corylus* [204]. In places, particularly at higher altitudes, they might well have been less dense and included trees of secondary type like *Betula* and *Fraxinus*, perhaps a legacy of earlier disturbance combined with higher altitude and more acid soils. Tree stumps and trunks at high altitudes [60,62,205] indicate that all but the highest uplands would have been able to support mature broadleaf woodland before any disturbance and after it ceased, with woodland composition determined primarily by geology and topography. Pollen-based reconstructions of the upland northern English woodlands would generally support this, e.g., [44,74,205–209], with relatively high arboreal pollen levels during undisturbed periods. The presence of several tree stumps of various taxa, including *Quercus* and *Betula*, at the highest altitudes at Bonfield Gill Head and elsewhere on the North York Moors immediately before the *Ulmus* Decline and the start of the Neolithic indicates the potential for full woodland cover, forest not just scrub. That the recolonisation of the upland summit plateaux by mature deciduous woodland coincided with the end of the Mesolithic and the end of the microcharcoal curve in pollen diagrams [60,210] is compelling evidence that burning and suppression of the upper forest limit was a function of Late Mesolithic land use. Without disturbance, the Mesolithic age woodland seems to have been stable, with consistent arboreal curves in pollen diagrams, particularly once the full suite of broadleaf trees had been assembled after the rise of *Alnus* in the centuries around 7000 radiocarbon

years ago. The inertia of the forest [11,13,211], in Boreal times, but particularly in the mid-Holocene Atlantic climatic phase, meant that natural within-forest successions [212] were slow and limited to replacement of individual trees by same-taxon individuals or as a community to the slow pace of soil development and gradual climate change [101].

5.3. Post-Disturbance Recolonisation

There is a variety of secondary successional pathways following fire disturbance of woodland [213,214], depending greatly on the type and intensity of the burn, canopy or ground, and which plants survive the burning on site as ‘legacy’ species [215]. In the case of Mesolithic-age fire disturbances, unless the fire was intense it is unlikely that all trees in the burned area would have been killed, but some would have remained standing as ‘standard’ trees amongst the regeneration community, and so would have continued to contribute to the local pollen rain. Canopy fires would have allowed penetration of light to the ground flora field layer understorey [216] but would not have devegetated the site entirely and caused bare ground. The pollen data from the four diagrams, however, indicates ground rather than canopy fire as the pollen of pioneer recolonising taxa is common. In general, the earliest successional, pioneer communities are dominated by annual herbaceous weed species for the first few years after disturbance, although these are then displaced by perennial herbaceous species, and then shrubs in later regeneration stages [153], as each successional community is replaced in turn. This process of taxa replacement [217] continues until seral regeneration is complete and a self-replacing woodland community is re-established. Several regeneration stages are apparent in the four pollen diagrams.

5.3.1. Ruderals

Several of the disturbance phases in the four pollen diagrams contain ruderal weed pollen that indicate broken ground and almost devegetated conditions [39,40], suggesting that the disturbances were of significant scale and intensity to create a clearing in the forest and initiate regeneration from its earliest stage, with bare ground conditions attractive to pioneer colonisers. A major, although localised, ground fire is suggested. Zones SW-2 and ESE3-2 in the lowlands, and zones NG7-4 and 5, and BGH-6 to 8 in the upland examples, contain a wide ruderal assemblage with weeds in quite substantial frequencies. *Artemisia* is commonly present in these assemblages and reflects disturbed soils, but several other ruderals occur also. The presence of grassland herbs, most commonly the perennials *Potentilla*-type and *Plantago lanceolata*, in these disturbance pollen assemblages suggests the effects of trampling and grazing by ungulates [218], presumably the game that the burning was designed to attract. That ruderal pollen is present throughout the disturbance phases will reflect the continued soil disturbance that the game animals would cause as succession progressed [69]. That some of the disturbance phases in the upland diagrams do not have pollen of this ruderal stage might mean that these were lighter, perhaps crown fires which allowed enhanced light penetration to the ground, but is more likely to mean that they were similar ground fires but at a distance from the pollen site, but within its pollen source area, most ruderal pollen being unable to be transported to the pollen site and therefore unrecorded.

5.3.2. Pyrophytes

Melampyrum (particularly *pratense* and *sylvaticum*) is an early successional field layer taxon characteristic of disturbed woodland glades and edges [216,219,220], particularly in upland woodland on acidic soils [221], which immediately invades burned areas after fire [222,223]. This explains the near synchronicity of the microcharcoal and *Melampyrum* curves on all of the site examples in this paper, and their co-occurrence in many other fire disturbance episodes in pollen diagrams of Late Mesolithic age in northern England, e.g., [122,224–226] and elsewhere, e.g., [82,144,227,228] often in high peaks of over 20% of tree pollen. It also shows increased values, however, in some disturbances of Neolithic age and later [145,229,230]. The palaeoecological data thus confirms the neoecological status of *Melampyrum* as a pyrophyte indicator of the field layer of burned woodland [223,231]. That it is resistant to trampling [232]

and is thus favoured by grazing in the recently fire-disturbed areas is another reason why it appears so regularly in post-fire woodland assemblages, the magnitude of its frequencies likely regulated by the proximity of the burned area to the pollen sampling site, as modern pollen rain studies show that high percentages tend to be recorded close to *Melampyrum* plants [220]. It is almost ubiquitous in fire disturbance phases, whereas some ruderal types fail to be recorded, however, suggesting that its small pollen grains might be capable of wind transport [233], so that if microcharcoal is capable of transportation from some distance away to a sampling site, so can *Melampyrum*. *Pteridium* is also regarded as being able to regenerate from its rhizomes rapidly after fire [184,234–236], and the *Pteridium* curve in the four diagrams, often mirroring the *Melampyrum* and microcharcoal curves, confirms its pyrophyte nature. Shrubs, including *Corylus*, can sprout from surviving burned bushes [237] and so can also be favoured by fire and figure strongly in forest stand replacement [238], and burning also favours the spread of the dwarf shrub *Calluna vulgaris* [239], which agrees with the behaviour of the heather curve in the four pollen diagrams.

5.3.3. Tall Forb and Heath Communities

The four pollen diagrams are alike in showing evidence for succession passing through a phase of tall herbs and low heath shrubs as they displaced the shorter pioneer ruderal weeds and grasses through competition for light and space [240]. Taxa diversity in the pollen diagrams falls after the initial recolonisation phase as many pioneer types cannot survive in the tall herb phase, being rapidly removed by strong competition from taxa like *Pteridium*, thus reducing floristic richness [222,241]. The pollen diagrams suggest that *Filipendula* and *Rumex* were important in the tall herb phase but that grazing pressure on the ground flora [242], as animals were attracted to the dynamic early successions in the opened areas, tended to allow less palatable taxa like *Pteridium* and *Calluna*, bracken being particularly effective in invading pioneer communities [235,236], to become common and suppress herbaceous vegetation through shade and litter. *Pteridium* can provide food for humans after appropriate treatment [243] and its importance in Mesolithic subsistence can be overlooked [244]. Peaks of *Pteridium* and *Calluna* in the pollen diagrams suggest that this bracken and heather community was an important, and sometimes prolonged, intermediate phase before regeneration of woody vegetation in the disturbed area.

5.3.4. Mantle Vegetation

One purpose of much of the Late Mesolithic anthropogenic disturbance in northern England was to break the homogeneity of the forest by reducing the amount of biomass locked up in mature trees and to increase the proportion of fringing forest-edge and mantle shrub vegetation in the landscape's woodland cover [245]. This ecotone transitional vegetation which naturally occurred at the edge of mature woodland, and which could be quite wide, was dominated by lower stature, heliophyte shrubs which were particularly productive in terms of nuts and fruits [162,168,243,246,247], as well as important wood products for tools and structures [248]. Its area would have been greatly increased by human disturbance activity which created open areas within the forest, probably producing a patchy woodland cover [102], and therefore more woodland-edge, mantle vegetation in the later stages of regeneration. *Corylus* was naturally common in early and mid-Holocene English woodlands, usually as understorey but it might well have been abundant and even a canopy component in areas of favourable edaphic and other factors [249]. It would have been a member of any forest margin community, both outside and within the forest. Increases in *Corylus* pollen in the mid- to later stages of regeneration in all four study profiles, first sprouting from surviving understorey bushes and then from colonisation of the opened area, illustrates the importance of this woodland edge community, which would have spread from the disturbance margins to occupy the whole of the opened area. The pollen data from many sites of Mesolithic-age fires in Britain [27] and elsewhere, e.g., [250] show clearly that *Corylus* typically spread to occupy the burned site after forest fires. This was probably one of the objectives of the burning, and as well as the dominant hazel, the

four pollen diagrams show that other shrubs were part of this later stage regeneration shrub community, including *Prunus*, *Sorbus*, *Crataegus* and other Rosaceous taxa, all of which would have provided food for Mesolithic foragers. The bushes of this regeneration stage are important for the re-establishment of woodland as they provide shelter for the younger saplings of the primary forest trees and which eventually will overtop and shade out the mantle community, despite the considerable inertia of the dense *Corylus* vegetation, some of which would have survived into the restored woodland as understorey, a role to which the shade tolerant *Corylus* is well adapted [251,252].

5.3.5. Restored Closed Woodland

After disturbance, forests might have never fully recovered to their pre-disturbance state and some increased diversity in the tree community might be expected [148]. The creation of a clearing might well provide opportunities for taxa to join the forest matrix during regeneration and then to persist as part of the new stabilised order when regeneration was completed [253], even if a closed woodland canopy was restored. *Betula* and *Fraxinus* might be expected to be prominent in any 'secondary' type woodland, although birch does find it difficult to penetrate dense *Corylus* shrub thickets as seem to have formed in the later stages of regeneration, and is outcompeted by hazel generally [254]. These two fairly short-lived trees should be considered as 'gap-phase' species [98,255] which would persist in the canopy for a few decades until replaced by longer-lived canopy dominants, which is what can be observed in the pollen diagrams. At Sniggery Wood, while the trees present before disturbance resumed their earlier pollen frequencies almost exactly when regeneration finished, *Tilia* and *Fraxinus* became consistent members of the restored woodland community, perhaps occupying some areas previously carrying *Alnus*. Diversity would therefore have been introduced to the woodland composition over a range of timescales [256] by the disturbance, particularly if the incidence of fire was high with a short return interval [190] as in the upland examples in this paper. Elsewhere, while composition remained the same, the proportions of the original trees often changed because of the changes in soils and other environmental factors caused by disturbance, such as the replacement of *Betula* by *Alnus* at Bonfield Gill Head, presumably due to edaphic changes and paludification within the burned area. In all four cases in this paper, however, it appears that woodland was able to recover to its pre-disturbance levels, whether that was dense in the lowlands or more open in the uplands. In both areas, however, even though it was the tree that the pollen data says was most affected by fire-disturbance, it is *Quercus* that dominated the restored forest community, partly because it was the major forest component before disturbance, but also because oak is fire-resilient, has shade-tolerant seedlings, regenerates well in open areas in woodland, can outcompete the more light-demanding secondary trees when the regeneration succession gets to the canopy-closure stage, and trees that survived the burning tend to produce more acorns in the years following fire [257–259]. Like *Pteridium* in the earlier stages of post-fire succession, after treatment acorns could present a useful addition to the plant foods encouraged by the fire disturbance [259].

5.4. The Lowland Disturbances and Succession

The two examples of Mesolithic age fire disturbance shown in this paper are alike in showing a single burning event, followed by a 'progressive' succession with a unidirectional, 'seral' series of stages of regeneration, moving from pioneer vegetation through increasingly taller communities until the re-establishment of an internally stable, mature woodland [260], very similar to the pre-disturbance forest. Almost all the coarser resolution lowland examples of such disturbance contain a record of continuous regeneration to woodland, e.g., [261–263], with no indication of multiple fires at the same site, nor an arrested succession, and it must be assumed to be the norm for lowland examples. The few lowland examples with multiple charcoal horizons, e.g., [84,264] are usually around places like small lakes where long-term occupation might be expected, and with significant intervals between fires, e.g., [265]. It might be that the lowland examples in northern Eng-

land actually represent natural fires from lightning strike, which are most likely to occur during periods of dry and warm climate [266], a correlation noted elsewhere [160,267], with no human ignition involved, although the dense and damp mid-Holocene lowland forests would not have burned easily [92,268]. Alternatively, they could have been caused by human ignition [269,270] as an isolated event which would have been temporarily economically advantageous for people given the productive successional communities that followed disturbance, but not as part of any land-use strategy that altered the local woodland vegetation structure long term. The greater density and arboreal composition of the lowland forest might not have been conducive to any such prolonged form of landscape management, although hunter-gatherers could have utilised it to their advantage in a low intensity way [271].

5.5. The Upland Disturbances and Succession

The successive post-fire vegetation communities would have contained several species that provided Mesolithic foragers with plant food [243,246,272–274] during the earlier seral stages, but it is the role of *Corylus* that was probably the most important. Mid-Holocene pollen data from most of the English uplands indicate that these Late Mesolithic age upland areas naturally carried a lot of *Corylus*, hazel often having the highest frequencies among the dryland tree and shrub taxa, e.g., [163,275], only matched by *Alnus* at wetland margins under specialist edaphic conditions. *Corylus avellana* was a very important component of the English postglacial woodland after its initial immigration in the centuries around 9000 radiocarbon years ago [42], a process which was asynchronous as it was regulated by local ecology, climate, immigration rate and competition [249,276,277]. It was, however, apparently often triggered by fire breaking the inertia of the woodland, e.g., [99,151,278,279] and providing hazel with an opportunity to colonise disturbed areas, judging by the many examples of macro- or microcharcoal coinciding with the initial and also later rises of *Corylus* frequencies in northern English pollen diagrams, e.g., [136,166,264,280]. It has been suggested [170,176] that this fire evidence shows that Mesolithic people were instrumental in promoting the early Holocene initial *Corylus* rise, its rational limit on pollen diagrams. Some pollen diagrams with the *Corylus* rational limit do not record coincident charcoal [281], however, and it is probable that the natural factors listed above [249] controlled the immigration of *Corylus*, as with the other tree taxa, with fire having an influence and triggering hazel immigration at individual sites [267,280]. In the later Mesolithic, however, after *Corylus* was well established in the forest, fire might have been the main force that controlled its abundance. In the later Mesolithic lowlands, as in the examples shown above, fire disturbance was a single event at particular sites which set in train natural successions that went through seral stages until woodland was restored. In contrast, the evidence in the examples of upland fire-disturbance presented above suggests that in the uplands a fire-disturbance regime operated in which fire continued to be applied to individual sites on multiple occasions after the initial burn, promoting the longer-term abundance of hazel by holding succession at the shrub mantle phase and preventing regeneration of the taller woodland trees and their eventual shading out of hazel. Such repeated burning of a site leads to reduced taxa diversity in the ecosystem, and concentrates nutrient resources in a few species, in this case mainly *Corylus*, and delays the regeneration of 'climax' species [222,241,282]. This would amount to the creation of a new ecological niche [29,32,168,179,181] through the concentration of food-producing plants into accessible stands [29,31] by Mesolithic foragers. *Corylus avellana* can sprout naturally in coppice form and thus persist in the plant community [237,283,284] including after fire, a stage which would be the most productive for hazel nuts which would have been produced in abundance [285,286], as well as useful wood products. Fire-management of the upland woods by Mesolithic people would therefore have maintained a stable, reliable food resource [185,187,246,247,287] at individual sites for long periods of time, perhaps for several decades [288], presumably in favoured, selected locations to which people could return regularly [289]. Although only broad approximations, interpolated ages for the duration of the four disturbances at

North Gill suggest that disturbance/regeneration phases lasted about a century and so it seems that the regenerating areas were available for exploitation for about four generations of foragers. Phases at Bonfield Gill Head appear to have been shorter, of only about two generations, although the disturbance signal might have faded from the assemblage more quickly if the burns were further from the sampling site. These short intervals between fires indicate strongly that they were very probably the result of human agency.

The upland woods would have been transformed into a dynamic mosaic of patches recovering from disturbance [102,290] so that an overall equilibrium in the proportion of various successional and restored woodland communities would have been maintained [14,255,291]. Late Mesolithic coppice wood has been found [36,292,293] and early hazel coppicing has been inferred from palynological data [226,294], while the presence of abundant hazelnut shells on many Mesolithic archaeological sites, e.g., [202,295] reflects the importance of this food source to hunter-gatherers. The regenerating patches of successional vegetation would have been attractive to deer [296], the most important quarry for Mesolithic people, and would have concentrated the animals in predictable locations, making them easier to find and exploit. The presence of high dung fungi concentrations during one such mid-Holocene disturbance and regeneration event, particularly in its early stages, indicates that such increased concentrations of game animals did occur within the regenerating area [297]. Such partial control of upland deer populations, added to the enhanced hazel resource [244,298], could well have been a major element of the Late Mesolithic economy [299,300]. It is likely that while some patches in the forest regeneration mosaic were being actively burned to attract game to the dynamic earlier stages of succession, other patches more advanced in regeneration were being cropped for hazel nuts until further burning was required to delay forest re-establishment. In the northern English uplands even when forest cover was restored, it was dominated by *Quercus*, which itself had the potential to be of value to foragers as oaks regenerated after fire often produce an enhanced acorn crop, itself a source of food for humans [259].

6. Conclusions

It is well documented that many fires occurred during the Late Mesolithic period in the forests of northern England, in both lowland and upland contexts, deduced from charcoal in peat sediments and confirmed by evidence of woodland recession as recorded in pollen diagrams. Microscopic charcoal particles in the microfossil assemblages provide a more spatial record of the presence and magnitude of fire in the forest environment. At coarse resolution sampling these fire disturbances seem to be evidence of single forest fires. Fine resolution palynology, however, provides a much more detailed understanding of these fire disturbances, allowing a reconstruction of their scale and internal structure. It ensures that all stages in the regeneration process are preserved in the pollen data, with no gaps in the record, and has shown that in some cases these disturbances were not single burning events but composite, involving a succession of fires around the same site.

The two lowland examples presented in this paper are very similar. A single burning event, which might have been natural or anthropogenic, caused substantial tree recession or at least major canopy opening, allowing ruderal and pyrophytic herbs to colonise the open areas created between the trees. The range of weeds recorded suggests that these open areas were substantial. Plant succession ensued, with the removal of open ground weeds from the pollen record, replaced by the pollen of shrubs, from the increased flowering of understorey woodland edge shrubs, from individuals that persisted in the burned area and from those that recolonised the affected area, mainly *Corylus*, which was eventually joined by secondary trees. Regeneration culminated in the re-establishment of the original deciduous forest as the clearing closed completely. There was only one burning event, followed by seral succession and successful forest regeneration.

The two upland examples were very different from the lowland examples. Seral succession after the initial burn continued into the *Corylus* shrub phase of regeneration as in the lowland examples. When this phase was mature and canopy closure was beginning as

trees began to recolonise the opened area, however, a further burning event occurred which reopened the clearing and made succession revert to an earlier stage. At the upland sites three or four such fires occurred at short intervals during a protracted phase of disturbance until restoration of woodland was allowed to occur. Estimation of the active disturbance duration suggests one to five generations. Moreover, that microcharcoal continued to be present in low values between the fire events suggests that some burning was continuing in the vicinity but not at these sample sites.

The multi-burn nature of the upland examples, with frequent recurring fires around the same site, is unlikely to record natural fire. It is much more likely to represent a controlled human agency for the burning, and it would have maintained the upland woods in a patchy state of late succession, maximising the populations of early-succession plant foods, then fruit-bearing shrubs, primarily *Corylus* and its nut yield. This form of continued ‘coppicing’ of the upland woods would have had other economic benefits in the attraction and control of ungulate game and would have been a central element of Late Mesolithic economy and land-use. The greater frequency of burning episodes in the uplands, if of human agency, must reflect a preference of Mesolithic people for hunting and foraging in these areas. The uplands would have naturally carried lighter woodland with a greater *Corylus* component on lighter soils, compared to the denser, wetter lowland forest. The uplands would also have been home to greater numbers of game animals, especially deer and particularly in the summer when the cooler, drier uplands with better browsing enabled animals to escape the flies infesting the heavily forested damp lowland. Presumably summer was the Mesolithic hunting season when setting fires would be easier and hunting bands would have the best chance of success. Whether the lowland fires were also ignited by foragers is possible but perhaps less likely, with single burns or long intervals between fires, and natural ignition can be considered as a cause. The location of many lowland burning events in Britain and Europe in wetlands around lakes, however, might make natural ignition less likely, and hunter-gatherer activity a more probable cause. More fine resolution studies of fire disturbances in both lowland and upland contexts are needed to address this question.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14040719/s1>. Table S1. Full stratigraphic descriptions and interpretations of the four sediment profiles discussed in this paper: Sniggery Wood, Little Hawes Water ESE3, North Gill 7 and Bonfield Gill.

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