Palynology and the study of the Mesolithic-Neolithic Transition in the British Isles

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Abstract

The transition from Mesolithic hunter-gatherers to Neolithic agriculturalists was one of the most important turning points in human history. The economic base, material culture, population levels, settlement patterns and world-views were transformed, along with significant changes in the ways in which people interacted with the landscape, including impacts upon the vegetation cover. The rate and process by which Mesolithic economies and societies were replaced by Neolithic ones in Britain's mid-Holocene forested landscape is difficult to discover by archaeological methods, unless it involved the rapid immigration of high numbers of fully-Neolithic farmers. Before the transformation was completed and Neolithic societies were established everywhere, there could well have been an extended period of time during which early settlers introduced domesticated animals and other elements of Neolithic-style economy and land use. Mesolithic groups could well have co-existed with these pioneer agro-pastoralists and continued with their foraging strategies as the transition progressed, until finally supplanted. Such early agriculturalists might be hardly visible in the archaeological record, but as vegetation is a sensitive indicator of environmental change, the introduction of new land-use techniques and their impacts should be discernable in the pollen and spore record. In this paper we examine the ways in which palynology has been used in Britain to investigate the transition from forager to farmer, illustrated by examples from three sites in North-East Yorkshire. Palynological methodologies and problems are evaluated. Evidence suggests that late Mesolithic people were using fire to manipulate woodland and improve its food resources. The cultivation of cereals might have been an early agricultural introduction. There was a phase of forest farming in the later transition in which the woodland was managed and utilized rather than opened significantly. Woodland clearance and more intensive farming occur after the transition was completed.

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The Mesolithic-Neolithic transition involved the replacement of foraging societies, that relied upon hunting of game and collecting of wild plant foods, by agriculturalists who produced food through the cultivation and husbandry of domesticated plants and animals (Zvelebil and Rowley-Conwy 1984, 1986; Williams 1989; Armit and Finlayson 1996; Whittle and Cummings 2007; Milner 2010). The differences between the lives of Mesolithic foragers and Neolithic farmers were clearly very great, with not only the economic base being different (Richards et al. 2003; Schulting et al. 2004), although elements such as hunting would have continued (Cummings and Harris 2011), but also material culture, social organization, settlement patterns and belief systems (Whittle 1996). The two cultures had starkly contrasting ways of viewing the world, and different ways of organizing themselves within the landscape and utilizing its resources. This transition is therefore of critical importance, being one of the major turning points in human history, but it remains one of the least well understood, and even in the limited context of the British Isles has been the subject of considerable research effort and debate (Thomas 2004). Occurring at different times between the start of the Postglacial c. 12,000 BP and the late Holocene (c. 100 BP) in different parts of the world (Mannion 1999), local social and environmental factors and the availability of suitable plant and animal domesticates meant that the transition had different complexions wherever it occurred. While the fully developed Neolithic is most likely to have been achieved by migrating populations (Collard et al. 2010; Cassidy et al. 2016) and should be easily recognizable, the early stages of the transition might be much less visible in the archaeological record. In places, the transition may have occurred swiftly, with the rapid replacement of the forager population by an incoming well-developed Neolithic (Rowley-Conwy 2004; Whitehouse et al. 2014). Alternatively, it has been suggested there might have been an extended period during which low numbers of pioneer Neolithic settlers arrived, bringing basic elements of a farming culture which indigenous foragers may have adopted (Monk 1993; Zvelebil 1986; Price 1987). Continued immigration of Neolithic settlers would have then gradually supplanted, or possibly absorbed, the indigenous foragers (Innes et al. 2009; Warren 2013; Sørensen and Karg 2014) until the transition was complete. A combination of immigration and acculturation might therefore have been a likely occurrence in the British Isles (Cooney 2007; Garrow and Sturt 2011). In this case, on the heavily forested north-western fringes of Europe, with low population densities, the earlier stages of the transition may be invisible archaeologically, and the social and philosophical elements of the Neolithic

world view would remain intangible. 'Initial Neolithic' presence may be recognizable only through changes in human ecology, in land use and relations with the landscape, small-scale and subtle. As the Mesolithic-Neolithic transition progressed, however, it brought about major transformations of landscapes, ecosystems and land-use niches (Welinder 1983; Finlayson and Warren 2010; Rowley-Conwy and Layton 2011). One way of investigating the transition, therefore, should be through the interpretation of palaeoenvironmental evidence (Edwards 1988, 1989a; Innes et al. 2003a; Innes and Blackford 2009), as palaeoecology records human relations with the biophysical environment. In this paper we explore the value of palynology as a medium for reconstructing vegetation patterns across the transition in Britain, as a proxy for human activity, land use and culture change.

The value of Palynology

Vegetation is a highly sensitive indicator of environmental conditions, with plant communities influenced by a wide range of factors that include autogenic changes within the ecosystem, edaphic factors of soils and hydrology, and external allogenic stimuli such as climatic parameters and disturbance, all of which will impact vegetation development (Tipping 2004). Disturbance due to human impact (Edwards 1989a, 1998; Edwards and MacDonald 1991) was an increasingly significant factor as the Holocene progressed, with different types and intensities of human activity changing natural vegetation into culturally created and managed communities, which increasingly included artificially promoted and even non-native taxa which can be used as indicators of human agency (Edwards and MacDonald 1991; Edwards et al. 2015). Pollen analysis enables us to reconstruct these past plant communities (Odgaard 1999; Bradshaw and Hannon 2004), with knowledge of pollen production and transport allowing the definition of pollen source areas so that a spatial view of the vegetation cover can be gained (Fyfe et al. 2013) and modelled (Caseldine and Fyfe 2006). The degree to which the landscape is wooded or supports open vegetation, and the spatial distribution of those elements, can be inferred and to an extent modelled (Sugita 1994; Sugita et al. 1999; Gaillard et al. 2008). This is very important when studying human activity and impact within mid-Holocene woodland, which should naturally be closed-canopy high-forest (Birks 2005; Mitchell 2005) where patches of open ground may have been few and of limited extent. Such open areas would therefore be oases of vegetation diversity and of great ecological importance (Svenning 2002; Fyfe 2007). Disturbance

of plant communities can be revealed particularly clearly. For example, the creation of an opening in closed woodland can be seen by abrupt reductions in tree pollen frequencies, coinciding with the increased abundance of open habitat taxa, usually followed by the gradual regeneration of woodland through successional plant communities dominated by heliophyte shrubs until the tree canopy closes again. In the case of hunter-gatherers and early farmers in wooded north-west Europe, it is tempting to interpret evidence of disturbance as recording human activity, and to infer land-use methods from the structure of the disturbance and the pollen types recorded within it (Zvelebil 1994). It is also possible that such palynological evidence could be used to predict the presence of humans in areas where archaeological evidence is as yet lacking (Whittington and Edwards 1994; Edwards 2004). Distinguishing natural disturbances from anthropogenic ones is difficult, however, and there are various natural events such as storms, floods, landslides and lightning strikes that can cause vegetation disturbance. One drawback is that many pollen types can not be identified to species level and so, if pollen grains can be identified only to genus or family level, the ecology of these records is equivocal. Grass (Poaceae) grains are a good example, as there are many grass species but identification is only secure to family level, so pollen may be generated by wetland or dry land grasses and interpretation remains imprecise. Taxa that can be identified to species level include *Plantago lanceolata* (ribwort plantain: Plate 1a) and other weed types that benefit from anthropogenic disturbance but it is the presence of pollen grains of cultigens that provides clear evidence of the arrival of farmers. Cereal pollen would be ideal for this, but unfortunately there are major problems with distinguishing cereal pollen from some wild grass pollen morphologically.

Fortunately, the Mesolithic-Neolithic transition occurred in the centuries before and including the major decline in *Ulmus* (elm; Plate 1b) pollen frequencies that forms a key biostratigraphic marker in north-west European pollen diagrams and which in the British Isles is dated to broadly 5000 radiocarbon years ago (c. 3850 cal. BC), although there is variation of a few centuries on either side of this average age (Parker et al. 2002). In Britain elm decline radiocarbon dates are generally earlier in lowland areas and later in uplands, and the difference can be as much as half a millennium, even over short distances. For example in the pollen diagrams from north-east Yorkshire used as illustrations in this paper (Fig.1) the lowland site of Newby Wiske has an elm decline date of 5241±32 BP (4227-3970 cal. BP) while only 25 km away on the North York

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Moors upland at Bonfield Gill the elm decline date is 4644±43 BP (3623-3350 cal. BP), a difference of at least c. 350 calendar years, and probably more. The elm decline date from the other North York Moors upland site used in this paper, North Gill, is 4730±80 BP (3653-3359 cal. BP), whereas in the Durham lowlands immediately to the north of the North York Moors, very early elm decline dates have been recorded (Bartley et al. 1976) including one of 5468±80 B.P. (4461-4055 cal. BP) at Neasham Fen, confirming the major lowland/upland time dichotomy for this key event in this area. The same dichotomy has been recorded in several regions of Britain (Parker et al. 2002). While finding the elm decline on pollen diagrams, therefore, does mean that an early Neolithic event has been established, and the sediment leading up to that elm decline will cover the period of the transition, it appears that in many areas, even over quite small distances, there was significant delay between the first and last occurrence of this key biostratigraphic benchmark event. This means that in parts of an area such as North Yorkshire, either the Neolithic was established in the upland well before the local elm decline, or Mesolithic people continued to occupy upland areas while Neolithic people had been long established in neighbouring lowlands. There are very late radiocarbon dates on some Mesolithic flint sites in North Yorkshire (Spikins 2002; Chatterton 2007) which support this possibility. These dating overlaps could therefore imply a few centuries of cultural co-existence between the Mesolithic and the Neolithic (Innes and Blackford 2009; Griffiths 2014a, b) who could have occupied different parts of the landscape. This cultural uncertainty and the spatial proximity of well-dated high-resolution pollen records make North Yorkshire an ideal area for research into the transition, hence our choice of pollen sites in this area as examples in this paper. Nevertheless, similar very late Mesolithic radiocarbon dates from Scotland (Ward 2010) and Wales (David 2007), and similar variability in elm decline dates, suggest that a period of cultural overlap could have been the case throughout Britain. Rigid cultural labels are perhaps unhelpful during this lengthy and complex period of culture change, with contemporaneous human groups at different stages of cultural or economic transition, and even employing transitional or hybrid forms of land use. Detailed reconstruction of vegetation history through high-resolution palynology may be the best way to access data that can elucidate these complex and perhaps often subtle changes.

The cereal-type pollen problem

Pollen grains described as of 'cereal-type' (or Cerealia, Plate 1c) have often been recorded in British and other north-west European pollen diagrams. These finds fit the morphological criteria for cereal pollen (Andersen 1979; Joly et al. 2007), primarily barley (*Hordeum*) or wheat (*Triticum*), but there are wild grass taxa that also fit these criteria, notably *Glyceria* and *Elymus*, so that the cereal attribution is insecure. Cereal-type pollen occur in the established Neolithic (post c. 5000 ^{14}C BP), but crucially even earlier, in sediments shown to be pre-Neolithic, either through radiocarbon dating, or by pre-dating the marker horizon of the *Ulmus* decline, which is approximately synchronous with the earliest Neolithic archaeology in the British Isles (Edwards and Hirons 1984; Edwards 1989b; Williams 1985; Innes et al. 2003a, b). Some cereal-type grains occur immediately before the elm decline and have been viewed as part of that event (e.g. O'Connell and Molloy 2001), or at least as a parallel process- the 'wave of advance' of Neolithic farmers recorded as woodland openings were created. Others, however, are recorded centuries before the elm decline, and by inference before the 'full' Neolithic, and so would appear to be of late Mesolithic age, as at North Gill (Figs. 1 and 2) on the North York Moors (Simmons and Innes 1996c). If only those records that occur in the millennium before the Elm Decline are considered, it would still mean the very early arrival of pioneer Neolithic settlers bringing cultigens with them, or the adoption of cereal cultivation by the later Mesolithic groups. This is a significant change from our perceived version of their forager economy possibly brought about via trade or exchange networks (Göransson 1988; Welinder 1998), as an addition to their forager resource base, or as a symbolic artefact, as the low numbers of pollen grains found suggest small quantities were grown. Both of these explanations are very controversial (Behre 2007; Tinner et al. 2007) and the 'early cereal' scenario has led to heated debate. It is accepted that hunter-gatherers did cultivate cereals in other parts of the world, for example China (Fuller et al. 2007; Innes et al. 2009) but these seem to have been wild cereal varieties that were locally available, as a phase on the way to domestication (Weiss et al. 2006). The absence of indigenous wild cereals in Britain, unless *Glyceria* could have been used in that way (Kubiak-Martens 1999), means that cereals had to be introduced by immigration or trade from a culturally Neolithic source. These identifications are based on morphological distinctions (Tweddle et al. 2005; Albert and Innes 2015), and the same forms are currently identified securely as cereals in the late Neolithic or Bronze Age. However, these are just as insecure identifications as in the Late Mesolithic, although more acceptable to current archaeological paradigms. The earliest cereal cultivation

was likely to occur at a small spatial scale within the forest (Göransson 1986; Edwards 1993) in small plots, perhaps even in restricted drier locations in wetlands (Cappers and Raemaekers 2008; Out and Verhoeven 2014). Unfortunately, cereal pollen production is low and it is poorly transported from its source, so for any pollen core to include a mid-Holocene record of cereal pollen it would have to be taken from close to the source. This would at least in part be because of good fortune in core location, although proximity to known archaeological finds can be used to refine the search (Innes et al 2003b; Albert and Innes 2015). In mid-Holocene forested environments the absence of cereal pollen is not proof of the absence of cereal cultivation, just as the presence of cereal-type pollen does not necessarily represent definitive evidence for such cultivation. More precise analyses, including scanning of slides after the pollen sum has been completed, are required to optimise the chances of detecting cereal-type pollen grains in palaeoecological studies (Edwards and McIntosh 1988; Edwards et al. 2005).

Fine resolution pollen analysis (FRPA)

In the search for more precise palaeoenvironmental data regarding the Mesolithic-Neolithic transition, advances in methodology have included high resolution pollen analysis (Moore 1989; Simmons et al. 1989). Fine-interval, and ideally contiguous, sampling of sediment allows a sharply focused temporal view of vegetation change (Turner and Peglar 1988). Sampling at one or two millimeter intervals can yield evidence that covers only a few years of vegetation history (Green 1983), or perhaps even annual records (Peglar 1993), whereas intervals of several centimeters provide only broader, multi-decadal patterns of vegetation change, inadequate for tracing human activity that might be short-lived. Fine resolution palynology has been applied to periods in the Mesolithic, including the latest Mesolithic, and in phases leading up to and covering the elm decline (Innes et al. 2013). During the Late Mesolithic, sites on the North York Moors have received close FRPA attention (Simmons et al. 1989; Innes and Simmons 2000; Innes et al. 2013). It allowed the recognition (Simmons and Innes 1996a, b) that at North Gill on Glaisdale Moor (Fig.1) Mesolithic age fire-disturbance phases actually comprised a succession of small-scale burning events around the same site, a much more complex structure and disturbance history than hitherto realized (Fig.3). *Alnus* and *Quercus* were the trees affected, with *Melampyrum*, ruderal weeds, *Corylus* and *Betula* the main beneficiaries of the fire-disturbance. Similar multi-fire events were also recognized at other Late Mesolithic age sites in

the area (Innes et al. 2013). The authors suggested that such small-scale repetitive burning around the same spring-head location was more likely to be produced by controlled, anthropogenic burning than by random natural lightning strikes.

FRPA has also been applied to studies of the elm decline and the period leading up to it (Sims 1978; Garbett 1981; Sturludottir and Turner 1985; Scaife 1988; Peglar 1993; Graumlich 1993) and has done much to elucidate the structure of that event, as the higher resolution data recovered has provided ecological insights previously denied to palynological investigators of this key pollen-stratigraphic horizon. Moore (1980) was able to distinguish successive phases within the elm decline, some of which included cereal cultivation, which implied changes in the type and location of human activity that had not been visible at coarser resolution. Garbett (1981) attempted to estimate the prevalence of dead elms during the decline by assessing the abundance of *Hedera* (ivy), a pollen proxy for dead or diseased trees. While this had limited success, ivy has since been detected by fine-resolution work as showing increased frequency during the elm decline (Innes et al. 2013). The other studies quoted above are alike in confirming the basic sequence of events at the elm decline as clearance, farming and regeneration, but in each case the very fine resolution sampling showed that the actual series of events was much more complex, with sub-phases of partial regeneration and different types of inferred land use in sub-phases of activity, a pattern confirmed by recent use of the technique (Innes et al. 2013). The increased detail over much shorter time intervals gained through the use of FRPA has greatly refined our understanding of the vegetation changes and events at the elm decline, and as such the changing landscapes of the early Neolithic.

Use of multiple pollen diagrams

As pollen assemblages are derived from a variety of vegetation source areas, palynological data record spatial variations in vegetation history (Edwards 1983). Turner et al. (1989) showed that although the general record will be the same, differences in detail occur in duplicate, closely-spaced pollen profiles taken within 1m of one another. In the wooded environments of the Late Mesolithic and early Neolithic, much of the pollen is likely to be derived from local sources (Jacobson and Bradshaw 1981), so that any human activity detected in the pollen record probably took place within 10-100m of the sampling site in well-forested locations. The use of a

multi-core pollen sampling approach therefore produces a 'three-dimensional' data set that will give information regarding the likely location and scale of events in the pollen record, and variations in their impact across the study site. A classic example of the value of multi-core investigations is that of Smith and Cloutman (1988) who prepared pollen records from thirteen cores around an upland bog where Mesolithic sites occurred. Localised evidence of Mesolithic fire-manipulation of the vegetation was found in all cores, with charcoal associated with peat initiation. The use of so many cores across the 500 m extent of the bog allowed a spatial reconstruction of vegetation change and recovered important evidence regarding the location and intensity of burning that would have been missed if only a single core had been studied. Turner et al. (1993) presented pollen diagrams from eleven coring sites only a few tens of metres apart along a stream valley at North Gill in the North York Moors, and so were able to explore in detail the spatial vegetation history through the Late Mesolithic and the elm decline at a site with clear and repeated disturbance evidence. Variations in the frequencies of indicator pollen taxa and in the abundance of microscopic charcoal (Plate 1d) allowed the location and scale of individual fire disturbance events to be inferred, as the same event was much more clearly defined in some cores than in others (Simmons and Innes 1996a; Innes and Simmons 2000). Other multi-profile studies aimed at elucidating Mesolithic environments and possible impacts have been carried out elsewhere in the country with notable success (Edwards 1990; Whittington et al. 1991; Edwards and Whittington 2000; Sugden and Edwards 2000; Edwards and Sugden 2003), with special reference to spatial analysis of microscopic charcoal records. One of the best examples of the method's potential for discerning spatial patterns in vegetation change is at Loch a'Bhogaidh on Islay, western Scotland, where several pollen diagrams within the area of an in-filled lake have shown that vegetation patterns in the early to mid-Holocene were locally very variable indeed (Sugden and Edwards 2000; Edwards and Sugden 2003). With good dating control, the records for individual taxa were shown to be markedly different in different areas around the lake basin. For example, the early Holocene rise in *Corylus* pollen frequencies did not correspond to increases in charcoal abundance, as might be predicted from models of Mesolithic activity, and while disturbance episodes of Mesolithic age could be seen in some cores, in others the behaviour of hazel could be correlated more with periods of cooler or warmer climate. It is this kind of high-precision, spatial palynological data that shows the localized nature of much vegetation change and allows the testing of palaeoecological and land-use hypotheses.

On a landscape scale, Fyfe and Woodbridge (2012) compared Late Mesolithic and early Neolithic pollen data from several pollen profiles on Dartmoor, which allowed a landscape scale assessment of human impact and vegetation change to be made, while Innes and Simmons (1988) did a similar study for the North York Moors. Davies and Tipping (2004) have used fine-spatial resolution pollen records to examine small-scale vegetation changes caused by human activity, while Tipping et al. (2009) used multi-profile pollen analyses to investigate human activity around an early Neolithic archaeological monument in north-east Scotland. Such conspectus views of Mesolithic and early Neolithic vegetation that synthesize data from many pollen diagrams are relatively common, but are valuable in providing three-dimensional models of broad vegetation patterns at sub-regional to landscape scales (e.g. Spikins 2000; Caseldine and Fyfe 2006; Fyfe 2007; Fyfe et al 2013).

Driving the Transition: the non-human factor

The Mesolithic-Neolithic transition in Britain was clearly a period during which one culture and economic way of life was eventually replaced by another, although the process of change would have been complex and may have been achieved via a variety of trajectories (Whittle and Cummings 2007; Griffiths 2014a). However, there may have been non-cultural factors that prompted or encouraged that change (Tipping 2004; Tipping and Tisdall 2004; Schulting 2010; Batchelor et al. 2014). Climate change has often been proposed as a driving factor in the switch from foraging to food production in the period before and around the elm decline (Bonsall et al. 2002; Tipping 2010) and such climatic shifts should be visible in the palynological record (Tipping 1995; Davis et al. 2003; Verrill and Tipping 2010) as well as in other sensitive proxies like plant macrofossils, particularly those preserved in raised bogs. In such bogs pollen and non-pollen palynomorphs (see below), including testate amoebae (Langdon et al. 2003) and algae that are highly sensitive to temperature, moisture and acidity levels, can provide high resolution data on climate change, indicating particularly periods of wetter and/or cooler climate that could have influenced human land use. Pioneer subsistence farmers might well have been particularly vulnerable to episodes of adverse climate (Tipping and Tisdall 2004). It is possible that such climate stress may have influenced the timing and nature of the adoption of food production techniques in Britain, and Tipping (2010) noted that a period of rapid and significant climate

change coincided with the period of the transition. Bonsall et al. (2002) explored the possibility that a change to a drier climate around 4000 BC might have encouraged the spread of cereal growing and other food production into the previously less congenial British Isles. It is also possible, however, that climatic deterioration made the forager resource base less reliable and encouraged a diversification of sources that included acceptance of agricultural foods (Tipping 2010). Detailed pollen records from the early transition show a decline in forest trees like oak and elm, and replacement by trees more tolerant of cool or wet conditions, including hazel and birch. At the same time, a spread of peat and wetland environments has been noted (Moore 1975). These structural changes however, are difficult to distinguish from the effects of human impacts, as birch is a pioneer of openings, hazel is favoured by fire, and peat can form in response to deforestation. It has long been suggested that the elm decline itself resulted primarily from climatic deterioration, and palynology of the pre-elm decline millennium does suggest in many places that climatic change had a significant influence on vegetation communities, and therefore human resources, at this time and during the transition (Tipping 1995; Cayless and Tipping 2002; Tipping 2010; Stolze et al. 2012). Palynological data, allied to other proxies, makes it seem likely that a drying of climate before and at the elm decline (Stolze et al. 2013) may have encouraged the introduction of agriculture, whereas wetter and colder conditions some centuries after the elm decline may have put climatic stress upon Neolithic communities, resulting in the major reduction in palynological evidence for agriculture in the mid-Neolithic, visible on pollen diagrams from across Britain and Ireland (O'Connell and Molloy 2001; Tipping and Tisdall 2004; Verrill and Tipping 2010; Whitehouse et al. 2014). It is tempting to speculate that the early cereal pollen records before and at the elm decline might reflect pioneer attempts at arable cultivation during a period of favourable dry climate, before post elm decline wetter and colder conditions caused the abandonment of cultivation in favour of pastoral agriculture, or even the withdrawal of farmers from much of the landscape altogether. While climate changes did not necessarily drive the changing economy of the transition, they may have created possibilities, and restricted others.

Starting the Transition: Late Mesolithic palaeoecology

To understand the Mesolithic-Neolithic Transition, it is necessary to know the environmental circumstances existing at its beginning, to provide a benchmark against which the changes that

occurred during the transition may be measured, and perhaps to inform our evaluation of their scale and character. Mesolithic forager populations had occupied the British landscape for millennia and their land-use methods and economic strategies need to be assessed to provide an ecological context for the later transformations that Neolithization brought. Until the 1960s the accepted paradigm was that Late Mesolithic people had a passive relationship with the landscape, having little effect on vegetation patterns and communities. Their environmental impact was thought to have been ephemeral, and restricted to limited woodland disturbance around their hunting camps and settlements, when trees might have been cut for fuel and shelter, or perhaps when domestic fires accidentally got out of hand (Bennett et al. 1990). Palynological study was instrumental in changing that view, providing evidence that some places in Britain had seen disturbance in woodland areas before the Neolithic. Woodland can be seen in the pollen evidence to have been both diverse and secondary (it had already shown signs of regrowth) in nature (Simmons 1969; Mitchell 2005) and had been subject to long-term disturbance on a landscape scale. Macroscopic and microscopic charcoal evidence from organic sediments located away from archaeological sites (off-site records) showed that the presence of fire in the forest was associated with this disturbance, not just around human occupation sites, but throughout much of the wider woodland, with the inference being that the fires caused the disturbance. While natural fires after lightning strikes must have occurred (Brown 1997), particularly in periods of drier climate that occurred in the mid-Holocene (Tipping 1996; Sandweiss et al. 1999; Grant et al. 2014), workers drew upon the ethnographic records of near–recent hunter-gatherers (Lewis 1982; Gammage 2011) to suggest that Late Mesolithic people may have been using fire as a means of opening up the woodland, creating a mosaic of more productive local habitats (Fyfe 2007), where previously there would have been a homogeneous biome of mature, closed mixed-oak forest typical of mid-postglacial climax vegetation.

Pollen studies at individual sites began to show woodland recession events, with or without microscopic charcoal, recording significant reductions in woodland cover followed by a regeneration complex of plants that included shrubby and herbaceous species favoured by fire and taxa benefiting from disturbed ground, including many that would have been of benefit to hunter-gatherers (Fig.3). The increased opportunities for grazing and browsing for game animals in these regenerating clearings, as well as increased vegetable foods for direct human

consumption (Zvelebil 1994), of which hazelnuts are the most obvious example (Regnell 2012) although not the only one (Mason 2000), suggested that in many cases the fires causing woodland openings might well have been deliberately started by Mesolithic hunters, although of course this can never be proven. Even where Mesolithic flints are found directly associated with charcoal layers, a human ignition source for the fire must remain circumstantial. As the decades of research passed, however, the number of woodland disturbance events recognized in a Late Mesolithic context by palaeoecologists became so great that it became clear that any hunter-gatherer impacts on the vegetation through burning of woodland must have been of landscape-scale significance, and that the British woodland on the verge of the transition had been modified by long-term disturbance into a more open, sub-climax mosaic state of considerable economic resource potential. Hazel and alder in particular benefitted, along with understory taxa including *Pteridium* (bracken), grasses, *Melampyrum* (cow-wheat) and the docks and sorrels. The pyrophyte *Melampyrum* (Plate 1e) in particular is considered to be a good indicator of burning within woodland. It should be noted, however, that charcoal is recorded in basal blanket peat horizons of Late Mesolithic and Meso-Neolithic transition age at many sites in the British uplands (Simmons and Innes 1987; McCarroll et al. 2015) and fire disturbance, especially if repeated at a site, may have initiated peat formation by altering the hydrology and encouraging local surface water surpluses. North Gill (Simmons 1969) and May Moss (Atherden 1979) on the North York Moors, Mire Holes in the North Pennines (Squires 1978) and the Aukhorn peat mounds in northern Scotland (Robinson 1987) are good examples. Although generally the spread of peat in the mid-Holocene was linked to climatic factors (Tipping 2008), locally the development of bog or heath could also become part of this post-disturbance vegetation mosaic as a consequence of fire (Simmons and Innes 1985; Simmons 1996) and palynology shows the expansion of marsh and wetland taxa during such charcoal-rich basal peat horizons. Throughout the British Isles, and presumably in other areas of north-west Europe also, considerable restructuring of the woodland by Mesolithic activity may well have taken place (Warren et al. 2014; Bishop et al. 2015). These patterns of disturbance and change suggest that some form of resource control and landscape management already existed towards the end of the Late Mesolithic (Jacobi et al. 1976), with repeated fire-disturbance of woodland proposed as deliberate and systematic human manipulation of the vegetation, intended to improve the supply of plant and wild game resources (Mellars 1976; Simmons et al. 1983; Caseldine and Hatton

1993; Simmons 1996; Ryan and Blackford 2009, 2010; Innes et al. 2010). In its most developed form this could have resembled a type of basic animal husbandry. These impacts occurred throughout the later Mesolithic, although they do seem to increase in number in the millennium before the elm decline (Simmons and Innes 1985, 1987). In this area of research, palynology has led the redefinition of the Mesolithic, and of the relationship between hunter-gatherer-foragers, the landscapes they occupied and the wildlife they depended on.

The role of Non-Pollen Palynomorphs (NPPs)

Reliance only on pollen and charcoal for palaeoenvironmental information is to neglect a rich source of additional data provided by the wide variety of non-pollen microfossils (NPPs) present on microscope slides prepared for pollen analysis, many of which have important value as ecological indicators (van Geel 1986, 2001; van Geel and Aptroot 2006). In particular fungal spores are an important class of NPP that can yield diagnostic information regarding palaeoenvironmental conditions and are usually common in pollen preparations. Until recently, their potential value has been neglected and their analysis remains under-represented as a research tool. Their use can provide detailed information with which to reconstruct wetland hydrology and bog development, as fungal, algal and other taxa reflect very closely local environmental change within wetland systems. Semi-natural depositional environments associated with archaeological sites, such as ditches, pits and moats, have also been studied (van Geel et al. 2003). In the context of the Mesolithic-Neolithic transition, however, it is fungal spores that provide information on woodland condition, disturbance processes such as burning or erosion, and the presence of animal and human populations that are most useful, as they are often diagnostic indicators of such potent ecological factors (Lageard and Ryan 2013). Woodland disturbance and opening may initiate soil erosion and the presence in wetland sediments of spores from soil-inhabiting fungi may be a signature of vegetation destabilisation and erosion, either by human or natural processes. Abundant *Glomus* spores have been interpreted in this way (van Geel 1986; Ejarque et al. 2010) and often occur within phases of disturbance during the transition, although while this interpretation certainly holds good for lake sediments it is less secure in peat deposits where the spores may be intrusive, introduced by root penetration from plants growing on the peat surface (Kołaczek et al 2013). Fire is a major force on vegetation and in woodlands and other plant communities fungal growth is often stimulated

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by fire. Some fungal taxa are favoured by burning, either directly or by the provision of very dry mire surfaces, for example spores of some *Neurospora* will not germinate without the high temperatures caused by fire, even if all other environmental variables are favourable. Charcoal layers in peat deposits are sometimes found (Innes et al. 2004) to be associated with high *Neurospora* frequencies as at North Gill (Fig.4), which can therefore be used as a proxy for highly localised surface burning. *Gelasinospora* responds in the same way, and it is likely that the reduction of competitor fungi by burning allows the proliferation of the more resistant *Gelasinospora* immediately after the fire. Some species of *Coniochaeta* are also pyrenomycetes. In combination with microscopic charcoal frequencies, NPP taxa can help to reconstruct local fire history on and around mid-Holocene wetland sediments.

There is a wide range of coprophilous fungi that exploit dung and the presence of their spores in sediment profiles may be interpreted as indicating increased deposition of animal dung (Baker et al. 2013), and by extension the increased concentration or population of large herbivores, wild or domestic. Some types, such as *Sporormiella* (Plate 1f), are obligate dung fungi. Although some caution is required in wetland sediments (Wood and Wilmshurst 2012), high percentages of this fungal spore type, and others including *Cercophora* and *Podospora*, have been used as an indicator of high herbivore numbers and increased grazing in various ecological contexts (Davis and Schafer 2006). In central Europe (Speranza et al. 2000) and Britain (Innes and Blackford 2003) *Sporormiella* peaks have occurred at pollen levels that were viewed as indicating phases of mid-Holocene human activity involving woodland disturbance and increased deer or cattle grazing, providing strong supporting evidence for that interpretation, as at North Gill (Fig.4). As the rationale of the Late Mesolithic land-use model rests upon the attraction of high game populations to burned clearings within woodland, Innes and Blackford (2003) used *Sporormiella* frequencies to test whether an increased large ungulate presence could be supported after a phase of fire disturbance in northern England. The main phase of burning contains peaks of *Neurospora* and *Gelasinospora* that match the microcharcoal evidence for fire. A major increase in *Sporormiella* occurred during vegetation regeneration after the burning, suggesting a significant increase in visits to the site by animals, presumably deer and other game, after the fire disturbance. Whether hunters had initiated the fire or not, the fungal evidence at this site supports the ecological model that underpins theories of Late

Mesolithic activity. Individual fungal spore types need not always be present, however, and Blackford et al. (2006) did not find *Sporormiella* in clear, charcoal-rich phases of Mesolithic age disturbance at a site on Dartmoor, although other fungal indicators of disturbance were present. Local factors of site scale and sample location might be very important, as fungal spores have a strongly local distribution.

NPP data can also be used to shed light on the Neolithic stages of the transition, as any human activity at the time of the mid-Holocene Elm Decline (Parker et al. 2002) has been presumed to be caused by Neolithic agriculturalists, perhaps in conjunction with an elm pathogen (Peglar and Birks 1993). It is unfortunate that a disease origin for the decline (Waller 2013) cannot be directly tested with fungal spore data, as the spores of the pathogen of Dutch Elm Disease, the ascomycete fungus *Ophiostoma* (previously *Ceratocystis*) *ulmi*, have never been recovered from fossil deposits. The spores are very small, transparent and fragile, do not preserve easily and are also very unlikely to survive conventional pollen preparation procedures. It means that there is no clear evidence to link this major fall in elm pollen abundance to pathogen attacks. Spores of wood rot fungi such as *Coniochaeta* and *Kretzschmaria*, however, are common in elm decline levels (Waller and Grant 2012; Waller 2013) and show that it was a time of stressed, wounded or dead trees. *Kretzschmaria deusta* (Plate 1g) in particular has been recorded, as at Bonfield Gill Head on the North York Moors (Figs.1 and 5) in substantial frequencies at the start of the elm decline (Innes et al. 2010, 2013) and, as a parasite of deciduous trees, has been proposed as an indicator of Neolithic woodland management techniques such as girdling (Innes et al. 2006) which wounds and gradually kills trees. *K. deusta* frequencies are particularly high during the elm decline phase at Newby Wiske (Fig.6), perhaps reflecting the scale of the event at this site on good, limestone lowland soils. Pasturing of animals within the forest may have been an important element of Neolithic land use, with such management of tree populations as an integral part (see below). Fungal spores may also be used to investigate Neolithic animal husbandry practices in other ways. Although collection of hay or leaf fodder (Heybroek 1963) for the winter feeding of stalled animals is no longer thought to be the main cause of the elm decline, there is substantial evidence for its use during the Neolithic (Rasmussen 1990). Analysis of preserved herbivore dung from archaeological sites has provided insights into this aspect of the early pastoralist economy. Fungal spore analyses of cattle dung from 5000 year old

Neolithic sites in Switzerland support plant macrofossil evidence from the dung that the animals were stalled over the winter and fed mainly on leaf and twig fodder (Rasmussen 1990; Innes 2005). Almost excusively, fungi associated with woodland biotopes were found in the preserved cattle dung. Dung fungi were virtually absent, suggesting that the dung became preserved in the waterlogged sediments before it had time to decompose. In contrast, fungal spores associated with plant material, presumably bedding, were abundant in these studies.

Early Neolithic land-use: forest farmers?

The nature of the earliest farming in forested north-west Europe probably varied through time as the Neolithic spread northwards and westwards, and by location, including latitudinal and altitudinal factors. In some cases a 'slash and burn' patch agriculture has been inferred, analogous to the system used by recent forest farmers, but in other locations, more permanent and field-scale clearances have been identified. Subsistence farming within a forest environment is difficult to detect using palynology. Inferences can be made based upon subtle changes in the pollen and spore data (Molloy and O'Connell 1987; Peglar and Birks 1993; Parker et al. 2002; Innes et al. 2013; Batchelor et al. 2014), especially in the herbaceous taxa that benefit from either pastoral farming, arable food production or both. Detecting the timing and duration of disturbance events in many locations has been tied into palynological studies around the elm decline, and at many sites more than one elm decline can be recognized. In places the classic large-scale fall in *Ulmus* frequencies is presaged by a preliminary decline in elm values, usually accompanied by pollen indicators of small-scale disturbance and probable human activity, particularly *Plantago lanceolata*, *Rumex*, *Taraxacum*-type and *Artemisia*. Elsewhere the initial elm decline, after a partial recovery, is followed by further declines of elm of varying intensity (Hirons and Edwards 1986; Smith and Cloutman 1988; Whittington et al. 1991). In most examples of woodland disturbance in the period leading up to the elm decline, the fall in total tree pollen frequency and rise in non-arboreal pollen is not of a great enough scale to suggest major tree removal, as would occur during a 'shifting cultivation' type of farming, where clearings of significant size are made for the growing of crops by slash-and-burn methods (Rowley-Conwy 1981). Such shifting cultivation clearances do not last long, perhaps only a few decades, before the farmers have to move to a new location, and the duration of most of the agricultural phases at and after the elm decline in Britain and Ireland suggest a much more

prolonged but lower intensity episode of activity. A good example of such a prolonged 'landnam' phase of predominantly pastoral farming comes from western Ireland (Ghilardi and O'Connell 2013) where the farming phase lasted for several centuries. This is not untypical of the duration of 'landnam' in many parts of the British Isles. Grazing of domestic animals within the disturbed woodland would encourage the long-term transformation of woodland to grassland, and would be apparent on pollen diagrams as a disturbance lasting some centuries (Rowley-Conwy 1982; Groenman-van Waateringe 1983; Robinson 2014). Some elm decline phases on better soils in lowland Britain do seem to be higher-intensity events, with more complete clearance and cereal cultivation in a long phase of agriculture, as on limestone soils at Newby Wiske (Figs.1 and 6) in North Yorkshire (Bridgland et al. 2011) or in south-east Durham (Bartley et al. 1976). In the latter case the date of the elm decline and forest disturbance is 'early' (up to 300 hundred years before the more common regional mean) and probably reflects the attractiveness of these soils to early agriculturalists. Some lasting and significant local impacts on the woodland are recorded at such sites, with high levels of disturbance followed by limited woodland regeneration. At Newby Wiske the cereal curve increases in the period following the initial elm decline event, and grassland and open ground indicators including Poaceae, *Plantago lanceolata*, ruderal weeds and *Pteridium* all maintain high frequencies (Fig.6), suggesting long-term human settlement and farming. Most of the earlier Neolithic examples, however, particularly those before the elm decline, are more ephemeral, as though no great inroads were made into the forest, and farming took place within a partially-opened woodland environment. In combination, however, many small episodes of woodland grazing over the long term in a protracted 'landnam' phase would cause opening and eventual removal of woodland.

The earliest Neolithic in the region is regarded in most models as being a forest farming culture (Edwards 1993), with food production within woodland, mainly cattle grazing but perhaps also small cultivation plots. Of the various models proposed for early Neolithic land use in north-west Europe (Edwards 1993), this model (Rowley-Conwy 1982; Bogucki 1988) seems most appropriate for the period before and at the elm decline in Britain. As the consensus of palynological data suggests an alteration of woodland structure rather than its removal, it is likely that woodland management was the aim of these early Neolithic agriculturalists, probably primarily for grazing and browsing resources for domestic animals in a mainly pastoral land-use

strategy. Coppicing and pollarding are the most likely management tools, and examples of coppiced wood have been found in early Neolithic contexts (e.g. Coles and Orme 1977). The restructuring of the woodland caused by coppicing, either by Mesolithic hunter-gatherers (Bishop et al. 2015) or by early Neolithic farmers (Göransson 1982), may be discernable in pollen data (Waller et al. 2012) as it causes diagnostic fluctuations in pollen frequencies during the coppice rotation period, favouring pollen production by coppiced under-storey types like *Corylus* (hazel: Plate 1h), even under short coppicing cycles, and greatly reduces the representation of other coppiced trees like *Tilia* (lime). For reasons of taphonomy and production, however, pollen assemblages from coppiced woodland are highly variable, and at present no unambiguous signals of coppice management can be defined and applied to the fossil record, although this is a promising area of study (Bunting et al. 2016). Göransson (1982, 1986) has suggested an hypothesis where ring-barking of trees may have been the preferred method for opening the woodland, although shredding and leaf-collecting may also have played a role (Moe and Rackham 1992).

Within both forest farming models, while animal husbandry, wood pasture and the provision of forest products may have been the main aims, the creation of a small cultivation plot within the opened area may well have been part of the strategy, as has been inferred from cereal-type pollen grains. Simmons and Innes (1996c) recorded a brief phase of cereal-cultivation at the end of a phase of forest opening before the elm decline at North Gill in North Yorkshire (Fig.2). While the high microcharcoal phase contained typical Mesolithic-age disturbance indicators like *Melampyrum*, *Salix* and *Corylus*-type, the succeeding cereal-phase contained a different suite of open-ground indicators, primarily *Plantago lanceolata* and *Calluna*, suggesting a different form of land use. Innes et al. (2013) in their fine-resolution study of the elm decline at the nearby site of Bonfield Gill Head, also noted that a short-lived phase of cereal growing occurred in the final phases of the event, as tree regeneration was under way (Fig.5). Many elm decline events in most parts of Britain contain cereal-type pollen as well as other indicators of woodland opening and disturbance, but usually these are in very small numbers and suggest that cultivation was not the primary aim of the earliest Neolithic woodland disturbances, with arable plots perhaps added as a late phase when the initial woodland manipulation phase was completed.

Palynology has the potential to provide diagnostic information regarding early Neolithic land use, but fine-resolution sampling, ideally sub-decadal, is necessary to recognise structure within the disturbance events such as multiple phases and partial regeneration, and trace short-term changes in the vegetation, and so test models of forest farming. As noted above, the recognition of spores of the wood-rot fungus *Kretzschmaria deusta* has been used to suggest support for Göransson's theory of tree girdling as the first stage in opening the woodland. Wood rot fungi could also increase due to natural changes such as an initial attack of a pathogenic fungus, and on its own is not evidence of anthropogenic activity. However, although more research is needed at more sites, Innes et al. (2006; 2010; 2013) have noted peaks of this fungal spore just before and at the start of the elm decline at several sites, perhaps indicating the gradual tree death that girdling brings. Fine-resolution work at Bonfield Gill Head (Innes et al. 2013), noted this initial *K. deusta* phase, but also showed subsequent periods of disturbance of different types that together made up the full elm decline episode, separated by phases of limited tree regeneration with reduced or no disturbance activity. The elm decline here, and presumably at other sites also, was a multi-phase composite event with different elements of land-use activity utilised in different phases. Elevated frequencies of dung fungus spores in the second phase suggested that was when the most intensive wood pasture with most animals occurred. Limited cereal growing occurred in the last activity phase, before final abandonment. The high resolution palynological data at Bonfield Gill Head indicate that the elm decline was a complex palaeoecological process, reflecting sophisticated land-use techniques in the early Neolithic. This agrees with other fine-resolution data for the event (Scaife 1988; Peglar 1993) which suggest a complex succession of within-woodland land-use techniques that modified but did not replace the woodland, although it will have increased the ratio of open ground to tree cover, perhaps at the landscape scale (Caseldine and Fyfe 2006; Woodbridge et al. 2014).

The transition completed

It is somewhat arbitrary to define an end to the Mesolithic-Neolithic transition in Britain. As the palynological feature of the elm decline, with its attendant evidence in many places of agricultural activity, has its earlier dates broadly at the same time as the appearance of archaeological evidence for Neolithic cultures (Woodman 2000), it is reasonable to infer that the fall in elm pollen heralds the Neolithic cultural period, even if direct causality can still be

questioned. There are reasons to describe the transition during the several centuries that encompass the date-range of the elm decline as incomplete, however. Firstly, the palynological evidence for ecological changes at the elm decline, as described above, suggest that the cultural Neolithic of the elm decline may have been ephemeral, with a small population and with low-scale and low-intensity agriculture. Although different in character to the preceding Late Mesolithic, it may therefore not have had a considerable impact on the forested landscape (Edwards 1993). Secondly, as discussed above, there are late Mesolithic flint sites, particularly in upland northern England, which have radiocarbon dates that place them at and even after the mid-range ages for the elm decline, at around 5000 ^{14}C BP, although before the date of the elm decline in their local area (Spikins 2002; Chatterton 2007). If some cultural overlap occurred at this time, with Mesolithic groups persisting in marginal areas while Neolithic people farmed better agricultural areas (Innes and Blackford 2009; Griffiths 2014a), it would be premature to equate the elm decline with the end of the transition in any particular area. The transition therefore can be seen as complete when Mesolithic groups had been entirely supplanted and more fully developed Neolithic farming societies expanded to occupy the majority of the landscape, and create significant and lasting forest clearance. Certainly, by the time that clearances of the 'landnam' type occur after the elm decline, such as seen in high resolution at Lough Sheeauns in western Ireland (O'Connell and Molloy 2001), the transition can be considered to be long over and a fully Neolithic, mainly pastoral, economy established.

Conclusions

During the several centuries of the Mesolithic-Neolithic transition, major and irreversible changes must have taken place in human relations with the biophysical environment. The replacement of foraging by farming allowed increases in human populations that meant agriculture became an indispensible part of the human economy, although hunting and collecting would remain an element well into the future (Cummings and Harris 2011). It is tempting to see early Neolithic 'forest farming' cultivation and animal husbandry as an adaptation of the Late Mesolithic fire strategy for manipulating the vegetation, with cereals and cattle substituted for hazelnuts and deer. It is clear, however, that by the time the transition was complete, entirely different ecological niches were being established that were quite different to those of the old foraging lifestyle, and which modified the landscape in more permanent ways (Rowley-Conwy

and Layton 2011). Palynology, including quantified charcoal and non-pollen microfossils, can have a very important role to play, often in the absence of archaeological evidence, in detecting and deciphering vegetation change, disturbance and changes in landscape ecology across the Mesolithic-Neolithic transition in the British Isles. It needs to be remembered, however, that disturbance can occur due to a wide range of non-human factors (Tipping 2004) and that attribution of disturbance to human activity, even when human artefacts occur in association with disturbance, can not be proven, only inferred. Unless secure evidence of cultigens is present, a difficulty with palynology, the evidence for a human agency for disturbance must remain circumstantial, if persuasive. With that proviso, it remains to consider how palynology can contribute to the future study of the Mesolithic-Neolithic transition. Very fine spatial and temporal resolution analyses of pollen and other proxy data are likely to be the way forward (Ghilardi and O'Connell 2013; Innes et al. 2013), if combined with recent advances in high-precision dating and Bayesian age-depth modelling (Griffiths 2014a, b; Albert and Innes 2015). Such high-resolution, multi-profile, multi-proxy records are needed at individual sites to provide high precision data from which key insights may be made. Methodological advances are also required, including secure identification of key pollen indicators of agriculture, such as cereals and their separation from pollen of non-cultivated Poaceae. Knowledge of the ecological meaning of many NPP types needs to be greatly refined, as some may be associated with cultivated plants or types of land use. Such advances in methodology and precision, allied to integration with other developing research techniques, will ensure that palynology remains key to providing insights which will help us understand this critical period in British prehistory.

Acknowledgements

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Captions to figures

Fig. 1. Location of the three North Yorkshire sites used as examples in this paper in Figs. 2 to 6: North Gill and Bonfield Gill Head in the North York Moors, and Newby Wiske in the Vale of Mowbray.

Fig. 2. Fine resolution selected taxa pollen diagram from North Gill 1A (NZ726006), North York Moors (Simmons and Innes 1996c), showing cereal-type pollen at the end of a disturbance phase, several centuries before the local elm decline. Frequencies are shown as percentages of total tree pollen.

Fig. 3. Fine resolution selected taxa pollen diagram from North Gill 5B (NZ726007), North York Moors (Simmons and Innes, 1987), showing two burning and disturbance events in the upper profile several centuries before the local elm decline. Frequencies are shown as percentages of total tree pollen.

Fig. 4. Non-pollen palynomorph diagram from North Gill 5B (NZ726007), North York Moors (Innes and Blackford 2003), showing the abundance of *Sporormiella* spores during regeneration after an initial phase of burning and woodland disturbance at the base of the peat profile. Frequencies are shown as percentages of total NPPs.

Fig. 5. Fine resolution selected taxa pollen and non-pollen palynomorph diagram from Bonfield Gill Head (SE598598), North York Moors (Innes et al. 2013), showing the phases of vegetation change through the elm decline. Frequencies are shown as percentages of total tree pollen. *Alnus* is excluded from the tree pollen sum.

Fig. 6 Selected taxa pollen and non-pollen palynomorph diagram from Newby Wiske (SE369865), North Yorkshire (Bridgland et al. 2011), showing intensive agriculture at the elm decline, followed by continuing large-scale cereal cultivation in a long 'landnam' phase. Percentages of the wood-rot fungus *Kretzschmaria deusta* are high across the elm decline. Frequencies are shown as percentages of total tree pollen.

Plate 1 Photographs of indicator pollen, fungal spore taxa and microcharcoal. The prefix HdV refers to the type number in the NPP catalogue of the Hugo de Vries Laboratory, Amsterdam, The Netherlands. 1a: *Plantago lanceolata* (ribwort plantain: 28 x 28 µm) 1b: *Ulmus* (elm: 30 x 30 µm) 1c: Cereal-type (*Triticum*: 42 x 40 µm) 1d: Microcharcoal (80 x 50 µm) 1e: *Melampyrum* (cow-wheat: 20 x 18 µm) 1f: Fungal spore type HdV-113 (*Sporormiella*: 18 x 12 µm) 1g: Fungal spore type HdV-44 (*Kretzschmaria deusta*: 30 x 8 µm) 1h: *Corylus* (hazel: 25 x 25 µm)