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How fragmented was the British Holocene wildwood? Perspectives on the “Vera” grazing debate from the fossil beetle record

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ABSTRACT

The reconstruction and structure of the European Holocene “wildwood” has been the focus of considerable academic debate. The ability of palaeoecological data and particularly pollen analysis to accurately reflect the density of wildwood canopy has also been widely discussed. Fossil insects, as a proxy for vegetation and landscape structure, provide a potential approach to address this argument. Here, we present a review and re-analysis of 36 early and mid-Holocene (9500–2000 cal BC) sub-fossil beetle assemblages from Britain, examining percentage values of tree, open ground and dung beetles as well as tree host data to gain an insight into vegetation structure, the role of grazing animals in driving such structure and establish independently the importance of different types of trees and associated shading in the early Holocene “wildwood”.

Open indicator beetle species are persistently present over the entire review period, although they fluctuate in importance. During the early Holocene (9500–6000 cal BC), these indicators are initially high, at levels which are not dissimilar to modern data from pasture woodland. However, during the latter stages of this and the next period, 6000–4000 cal BC, open ground and pasture indicators decline and are generally low compared with previously. Alongside this pattern, we see woodland indicators generally increase in importance, although there are significant local fluctuations. Levels of dung beetles are mostly low over these periods, with some exceptions to this pattern, especially towards the end of the Mesolithic and in floodplain areas. Host data associated with the fossil beetles indicate that trees associated with lighter canopy conditions such as oak, pine, hazel and birch are indeed important components of the tree canopy during the earlier Holocene (c. 9500–6000 cal BC), in accordance with much of the current pollen literature. Beetles associated with more shade-tolerant trees (such as lime and elm) become more frequent in the middle Holocene (6000–4000 cal BC) suggesting that at this stage the woodland canopy was less open than previously, although open ground and pasture areas appear to have persisted in some locations. The onset of agriculture (4000–2000 cal BC) coincides with significant fluctuations in woodland composition and taxa. This is presumably as a result of human impact, although here there are significant regional variations. There are also increases in the amounts of open ground represented and especially in the levels of dung beetles present in faunas, suggesting there is a direct relationship between the activities of grazing animals and the development of more open areas.

One of the most striking aspects of this review is the variable nature of the landscape suggested by the palaeoecological data, particularly but not exclusively with the onset of agriculture: some earlier sites indicate high variability between levels of tree-associated species on the one hand and the open ground beetle fauna on the other, indicating that in some locations, open areas were of local significance and can be regarded as important features of the Holocene landscape. The role of grazing animals in creating these areas of openness was apparently minimal until the onset of the Neolithic.

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1. Introduction

Insect faunas, usually the remains of Coleoptera (beetles), have been seen as valuable indicators to examine the ‘Vera hypothesis’ (c.f. Vera, 2000), its associated implications for palaeoenvironmental studies and the reconstruction of the structure of the ‘wildwood’ (c. 9500–2000 cal BC) in Northern Europe (Svenning, 2002;

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Bradshaw et al., 2003; Bradshaw and Hannon, 2004; Whitehouse and Smith, 2004; Birks, 2005; Mitchell, 2005; Rackham, 2006). The implications of this debate for modern conservation strategies and our understanding of present and past woodland ecology have also been widely explored (Vera, 2000; Kirby, 2003, 2004; Mitchell, 2005; Hodder et al., 2005; Soepboer and Lotter, 2009). An accurate reconstruction of the nature of 'primeval woodland' is seen as a starting point of present forest policy (Sutherland, 2002; Kirby, 2004). From palaeoecological perspectives, this debate has questioned our ability to reconstruct landscape structure, forest density and indicates that, as palaeoecologists, we could consider a more diverse range of Holocene landscape models.

The debate concerns two opposing viewpoints of past, present and future forest plant ecology. The 'traditional' view of the primeval forest is viewed as being driven by succession, resulting in closed canopy forest (forest 'climax'), where regeneration takes place in gaps and where openings in the forest canopy are the result of the death of individual trees and account for only a small proportion of the landscape of what was dense forest canopy (Iversen, 1960; Godwin, 1975; Peterken, 1996). In this 'traditional' view, the early forests of Northern Europe consisted of predominantly closed, dense canopy, or 'high forest' (Berglund et al., 1996). Other researchers have pointed out that succession was far more stochastic and a less simple process than implied within this traditional view, that woodland was never uniform, or indeed "stable" (i.e. fixed in structure), because of the effects of a range of disturbance factors (Bradshaw et al., 2003).

Set against this model, is a perspective that ancient forests were more akin to 'wood-pasture', with a relatively open mosaic landscape consisting of varying tree densities, structured and driven by grazing animals. The main proponent of this view has been Frans Vera (2000). The idea that the 'wildwood' was more akin to 'wood-pasture' has been made by several ecologists, well before Vera, notably Harding and Rose (1986), Rose (1993) and more recently, entomologists (Alexander, 2005). Some palaeoecologists have also argued that grazing animals may have been important in maintaining open areas of the forest (Buckland and Edwards, 1984; Bradshaw and Hannon, 1992; Bradshaw and Mitchell, 1999; Robinson, 2000a; Bradshaw et al., 2003), although none have suggested that grazing animals were integral to the structuring of the primeval forest, nor have argued that these environments were substantially more open than had previously been suggested. The detail of Vera's arguments have been summarised elsewhere (e.g. Mitchell, 2005) and we do not repeat these here, except to draw attention to the fact that Vera (2000) questions the ability of palaeoenvironmental data to accurately reconstruct all landscape types which might have existed in the past. This follows discussions about the possibly poor relationship between pollen production, transport and deposition in sediment and the vegetation which initially produced it. One particular criticism concerns the ability of pollen analysis to "see" open indicators such as grasses. Many are low pollen producers, but can be filtered out where tree pollen may 'swamp' floras (see Sugita et al., 1999; Bunting et al., 2004; Hicks, 2006). The PollandCal network has been enormously influential in advancing understanding of pollen-vegetation relationships (Gaillard et al., 2008), showing that, for instance, non-arboreal pollen (NAP) percentages have a non-linear relationship to vegetation and are not always a reliable measure of landscape openness (Sugita et al., 1999; Sugita, 2007a,b; Hellman et al., 2009). Recently, there have been considerable advances to enable pollen to provide quantitative reconstructions of vegetation via a series of theoretical models (Sugita, 2007a,b); simulations show that it may be hard to identify landscape openness from regional vegetational reconstructions, but that openness may be better picked up at a local scale (Fyfe, 2007; Soepboer and Lotter, 2009).

Vera (2000) makes the point that most pollen records for the early post-glacial period in northern Europe contain relatively large

proportions of oak (*Quercus*) and hazel (*Corylus*). These arboreal species are relatively shade-intolerant and tend to favour canopy openings whilst hazel will not flower under closed canopy conditions, leading him to argue that high quantities of hazel pollen indicate an un-shaded park-like landscape (when regenerating, however, established hazel is shade-tolerant, this can be seen in shaded coppiced areas, e.g. Hatfield Forest, Essex, England). Vera (2000) suggests the abundance of these pollen taxa could indicate an increased role for shade-intolerant trees and a reduced role for shade-throwing taxa such as beech (*Fagus*), lime (*Tilia*) and elm (*Ulmus*) in the "natural" Holocene forest.

In favour of the 'Vera hypothesis' are some workers in modern conservation policy (e.g. Alexander, 2002, 2005; Green, 2002; Eriksson et al., 2002). They suggest that the wood-pasture model explains an apparent ecological contradiction. Amongst the insects, lichens and fungi, many of the classic indicators for 'old growth forest' need large, open aspect trees growing in sunny conditions rather than the enclosed gloom of the full canopy 'high forest'. Vera's hypothesis solves this contradiction by giving the space and open conditions that these species need and explains their continued importance as 'indicator species' today (cf. Appelqvist et al., 2001).

Many plant ecologists, palaeoecologists and palaeo-botanists favour the 'climax/high forest' hypothesis, whilst recognising a number of current limitations and caveats to our understanding of palaeoenvironmental data. Svenning (2002) considered proportions of NAP from north-western European oceanic interglacial sites and compared them against estimates of vegetation openness inferred from beetle, mollusca and plant macrofossil remains and found them to be roughly in agreement. He concluded that low proportions of NAP could indeed be used reliably as an indicator of forest coverage and that the existing palynological reconstructions of closed 'high forest' were essentially correct. Bradshaw et al. (2003) have argued that since oak and hazel continue to thrive on the un-grazed island of Zealand there is no reason for seeing herbivores as the main drivers for the occurrence of these species. The effects of forest fires and storm events would equally have provided enough opportunity for oak and hazel to establish. They do, however, acknowledge that palynology may have underplayed the extent of open-ness of the primeval forest, a point emphasised by Soepboer and Lotter (2009) in recent modern pollen modelling experiments. Mitchell (2005) points out that Ireland in the early and mid Holocene appears to have lacked the large herbivores that are central to Vera's arguments but that there are no perceivable differences in the pollen spectra between Ireland and the rest of Europe. Mitchell's work has been seen as the 'smoking gun' that killed the 'Vera hypothesis' (see Birks, 2005; Moore, 2005). Others (e.g. Alexander, 2005; Bell and Walker, 2005; Rackham, 2006), including Mitchell himself (2005), point out that:

- Vera's unexplained 'oak – hazel problem' remains; how do these taxa regenerate under "closed canopy" conditions? Have their requirements for light changed over time, or has there been an under-estimation of the complexity of forest structure in the Holocene? Has the role of human activities, including coppicing, been properly considered in this debate?
- Is the current understanding of the taphonomy of pollen (or pollen "signatures") sufficiently well established to be able to accurately differentiate forest structure within these early and mid Holocene landscapes? Recent research (cf. Sugita et al., 1999; Sugita, 2007a,b) indicates that non-arboreal pollen percentages are not a reliable measure of landscape openness, as used by Mitchell (2005).
- Modern ecology suggests that the "wildwood" must have had a more open canopy structure for many forest species such as invertebrates to have survived.

Both viewpoints agree that other proxy indicators, such as insects and mollusca, may usefully be used to explore many of the issues highlighted by this debate.

Here, we set out to address the character of the fossil beetle record, and its potential use in understanding the nature and structure of the Holocene landscape. We present a review and new analysis of the published corpus of early- and mid-Holocene sub-fossil beetle faunas from Britain, the region from where the majority of fossil beetle data relating to this period come from. In particular, we focus on:

- Issues concerning the character of the palaeontological data set and the interpretation of fossil beetle data;
- How insects can be used to examine clearance in the landscape, forest structure and the role of grazing animals and how these change over the early-mid-Holocene;
- The changing frequency of tree taxa inferred from the beetle record and how this compliments and/or contrasts with palaeontological evidence for this period, in particular to confirm whether these data agree that lighter-demanding trees such as *Quercus* (oak) and *Corylus* (hazel) were indeed important aspects of the tree canopy in early- and mid-Holocene forest, as highlighted by Vera (2000).

2. Beetles as landscape and forest structure indicators

Beetles are useful proxies to look at landscape and forest structure for a number of reasons. Where preservation levels are good (most waterlogged and organic-rich sediments, clays, silts and peats) it is possible to identify sub-fossils to species level in about c. 70% of cases, at least in Northern Europe. Willis and Birks (2006) have highlighted the high value of good taxonomic resolution in the fossil record as this enhances their biological value. Thus, the fossil beetle record offers the taxonomic resolution required to address questions concerned with past biodiversity, ecosystems and biological conservation. The ability to identify taxa to species level means it is possible to reconstruct the environment in some detail, since the ecological requirements of many beetles (at least for Europe) are relatively well-known. Insect communities and assemblages are shaped by the compositional and structural mosaic of the landscape. Thus, many beetle species are tied to specific woodland ecological niches and habitats such as the foliage and living tissues of specific species of tree, dead wood, and associated woodland fungi. Light and aspect are also important for some taxa, especially those associated with the woodland edge and meadow. Pasture and open areas also attract their own suite of species, including taxa characteristic of meadowland and its associated herbs, along with the scarabeoid dung beetles, many of which are tied to animal dung.

Issues surrounding Holocene forest clearance have previously been explored using percentage values of fossil dung beetles versus the abundance of wood and tree-dependant beetles. Often this has been used as a way to understand the effect of grazing domestic mammals on the early agricultural landscape of the British Neolithic (Robinson, 2000a). There have also been attempts to obtain arable/pastoral ratios from insects (Robinson, 1983), as a way to infer the proportion of a landscape surrounding a site which is cultivated versus grassland. Woodland structure has also been explored. Dinnin and Sadler (1999) examined the changing ratios of woodland species versus open taxa through the Holocene in an early attempt to examine landscape structure. Svenning (2002) used the presence of dung beetles and other insects that indicate open ground from interglacial sites to corroborate his conclusions that there is indeed a direct relationship between arboreal and non-arboreal pollen (see

particularly his Fig. 1, p. 135), in his examination of the Vera hypothesis. However, there are a number of problems with his treatment of the fossil beetle data (Whitehouse and Smith, 2004 and comments therein), not least because it is unclear how the fossil beetle data showing dung and open ground indicators are obtained or quantified. Whitehouse and Smith (2004), in a short review of early Holocene insect faunas draw attention to the persistent levels of pasture/dung and open ground taxa species in several early Holocene insect assemblages. Alexander (2005), drawing upon fossil beetle work (cf. Dinnin and Sadler, 1999; Whitehouse and Smith, 2004) and using modern ecological data related to species' responses to light and shade, highlights that the many old growth-associated beetle species characteristic of the early Holocene fossil insect record, commonly used to indicate closed forest conditions, in fact need open, sunny conditions in open canopy forest. He suggests that low proportions of these taxa should be taken as indicators for closed canopy forest and that when found in higher proportions, such as commonly found in the fossil beetle record, as evidence of pasture woodland. Most recently, Hodder et al. (2005) have reviewed the ecological and palaeoecological evidence for the Vera hypothesis. Here, Buckland (2005a) provides a detailed review of the fossil beetle Holocene record, which we contrast with our findings below. We draw upon similar sites, although our approach and analysis of the data are very different and we have re-considered the chronology of sites in some detail.

These investigations indicate that fossil insects can play a very useful role in the continuing debate about natural forest structure and in furthering our understanding of the Holocene natural landscape. There are, however, several interpretational issues which should be drawn attention to and explored before we move onto present the results of our analyses.

3. Interpretational issues

One of the most common ways in which palaeontologists have examined landscape structure in the Holocene involves the use of habitat categories: species within an assemblage are categorised according to which habitat they belong to. The main proponent of this approach has been Robinson (1981, 1983), with subsequent additions and modifications, dependant upon the environment being studied (e.g. Carrot and Kenward, 2001; Whitehouse, 2004). Abundances within categories are then either shown as raw counts (i.e. MNI's, minimum numbers of individuals) or MNI percentage values of the terrestrial component, since the aquatic component will always over-dominate a waterlogged assemblage. Sometimes it is desirable to include this aquatic component within the sum, especially where wetland development is being studied (e.g. Whitehouse, 2004). The use of habitat categories is an interpretative tool and suffers from certain limitations, particularly in the subjective nature of selection, assignment and interpretation of categories. It is important to note that the categories used reflect abundances within assemblages and are not intended to indicate *direct proportions of associated habitat* (Kenward, 1975, 1978; Whitehouse, 2004). Nevertheless, there is a relationship between species, abundances and extents of habitats, even if this relationship is non-linear and fuzzy. Thus, Robinson (1991) has suggested that values of between 18 and 20% for tree/wood beetle taxa are indicative of closed old forest and <2% are indicative of largely open landscapes. Figures of 1% pasture/dung are suggested for closed old forest, whilst >10% pasture/dung values are seen as largely pastoral. These figures are based upon modern collecting in these environments (Robinson, *pers. comm.* 2007), but are subject to quite a lot of uncertainty and debate (e.g. Dinnin and Sadler, 1999; Whitehouse and Smith, 2004). A recent review of the visibility of past trees and forest by Kenward (2006)

suggests that for heavily forested environments these figures seem reasonable. In addition, the spatial resolution of much of the fossil beetle data is subject to quite a lot of uncertainty, in terms of our understanding of the catchment represented within an archaeological or palaeoecological deposit. Recent work by us suggests that catchments are probably in the region of 100 metres from the deposit, but that this will vary according to site and surrounding vegetation (Smith et al., 2010).

One clear problem is the uncertainty in knowing what a 10% presence of an indicator group in an insect death assemblage really represents in terms of percentage ground cover in 'the real world' (Kenward, 1975, 1978). Kenward (2006), looking at modern insect death assemblages from a range of tree-dominated environments has indicated that there is not a straightforward relationship between the proportions of tree indicators present and the density of canopy. Thus, it is likely that the relationship between insect death assemblages and 'open-ness' in forest is no less 'noisy' than the relationship between arboreal and non-arboreal pollen production. In passing, it is worth noting that Davies (2003) has found similar problems with using mollusca to address open-ness and tree cover.

We have some grounds for optimism, however. New research (Smith et al., 2010) provides some insights into the relationship between beetles and forest canopy. Following modern sampling of sub-recent material (<10 years old) from a series of woodland ponds at Dunham Massey, England, within grazed deer park and pasture woodland, percentage of canopy cover is moderately well correlated to the percentage of woodland fossil beetle taxa. Additionally, the results indicate that it is possible to have quite high values of tree taxa (12.9–21.1%) in relatively open, pasture woodland, and that such values do not necessarily imply dense canopy woodland (*contra* Robinson, 1991), although this can be dependant, for instance, upon the closeness of overhanging trees to sampled deposits and the amount of dead wood within the vicinity. Open and pasture indicators are much more variable across the ponds examined, accounting for 17.7–32.9% of the terrestrial fauna. Initial analysis suggests that this variability seems to be determined by the size of the population of dung beetles (a function of grazing animals) rather than that of the open indicators. This is a point noted by Robinson (2000a – see Fig. 3.1) in his examination of Neolithic beetle assemblages. It may be that it is the population level and intensity of grazing animals which is of more importance here than the degree of open-ness. It, therefore, seems fair to suggest that, on the basis of this modern analogue work, that pasture woodland could be distinguished in the fossil record by relatively high levels of both woodland taxa as well as open/pasture/dung beetle taxa – as one might perhaps anticipate.

4. Methods: data analysis, selection of sites and chronological issues

The results of a review and re-analysis of 36 early- and mid-Holocene published British fossil beetle faunas from a range of archaeological and palaeoecological sites and samples (assemblages) are presented here. Table 1 (see supplementary information) shows details of the assemblages selected, with the location of sites illustrated in Fig. 1. All published data sets are archived on the BugsCEP database (Buckland and Buckland, 2006); the raw count species data used here are available to download via www.bugscep.com. Only the data sets from Rossington, South Yorkshire and Atlas Warf, Isle of Dogs are awaiting publication (Whitehouse, 1998; Smith, in press).

We have analysed the data to obtain:

- (1) The relative proportions of beetles based on MNI associated with wood/trees (including dead wood), open ground/pasture and dung beetles. These are expressed as a percentage of the

terrestrial insect fauna (i.e. excluding all aquatics). This provides an insight into the different habitats represented by the beetles, including vegetation 'structure' and clearance at each site/period. Habitat categories used follow Robinson (1981, 1983).

- (2) The number of obligate phytophage beetle species for tree taxa at each site, where it has been possible to assign host data. What we wanted to examine here was whether, effectively, the beetles reflect, in broad terms, that shade intolerant tree species are important elements of the "wildwood" as argued by Vera (2000) or, whether they reflect in essence other palaeo-environmental records such as pollen. For many beetle species, of course, it was not possible to assign host data (behaviour is dictated more by the presence of specific fungi or moulds rather than a specific tree e.g. Alexander, 2002; where there was no specificity, these data were excluded from the analysis), but for some leaf beetles (Chrysomelidae), weevils (Curculionidae) and wood-borers (Scolytidae), there is some host specificity. It was sometimes difficult to assign specific hosts to some species; for instance, beetles associated with oak and beech are commonly associated with both trees. In some cases researchers have assigned hosts for beetle species based on the tree plant macrofossils present on site, we have accepted these interpretations. The fact that the pollen of beech does not appear clearly in many sites until 1400–1100 cal BC (3000 BP) (Birks, 1989) suggests we can be reasonably sure that the majority of the oak/beech beetle-associate category in fact represents the presence of oak, although it should be noted that there are earlier pollen records (e.g. Godwin, 1975; Greig, 1996). Moreover, recent research in the New Forest indicates that beech was present in southern Britain by 4000 cal BC, albeit as a minor woodland component (Grant and Edwards, 2008) – significant expansions in its range appear to have happened in tandem with disturbance activities (e.g. human clearance, forest fires), along with climate changes (Giesecke et al., 2007). Likewise, it should be noted that trees support different numbers of beetle taxa. Fig. 2 shows the number of Coleoptera that are associated with the common trees of the British Isles. Some trees support greater numbers of insects: oak supports over 90 species of beetles, whilst hazel, lime and alder considerably fewer. These differences are important when interpreting the results of the analysis and should be seen as functioning in a similar way in palaeoentomology as differences in pollen production function in palynology.

Both exercises represent substantial new analyses of the data sets. Many sites included hundreds of taxa and numbers of individuals. In the first exercise, to calculate proportions of different habitats, raw MNI counts from assemblages were manually categorised into the assigned terrestrial categories. These groups were based upon published ecological literature and categories recorded in BUGSCEP database. Once raw counts were created, they were converted into percentage values of the terrestrial MNI component for each assemblage. Where more than one sample contributed to an assemblage, as in the majority of cases (see Table 1, supplementary information), all MNI data were collated together and treated as a single sample and then converted into a percentage value for that particular assemblage. Each percentage value created for the different habitats were thus effectively treated as if emanating from a single sample, even when multiple samples were represented, because of the chronological and sample resolution issues we discuss below. The percentage values can be found in the supporting Appendix information; the faunal groups represented by other ecological categories (not shown) include taxa associated with wetlands and marshes, peatland habitats, carrion, rotting vegetation, mouldy habitats, eurytopic species and unclassified taxa.

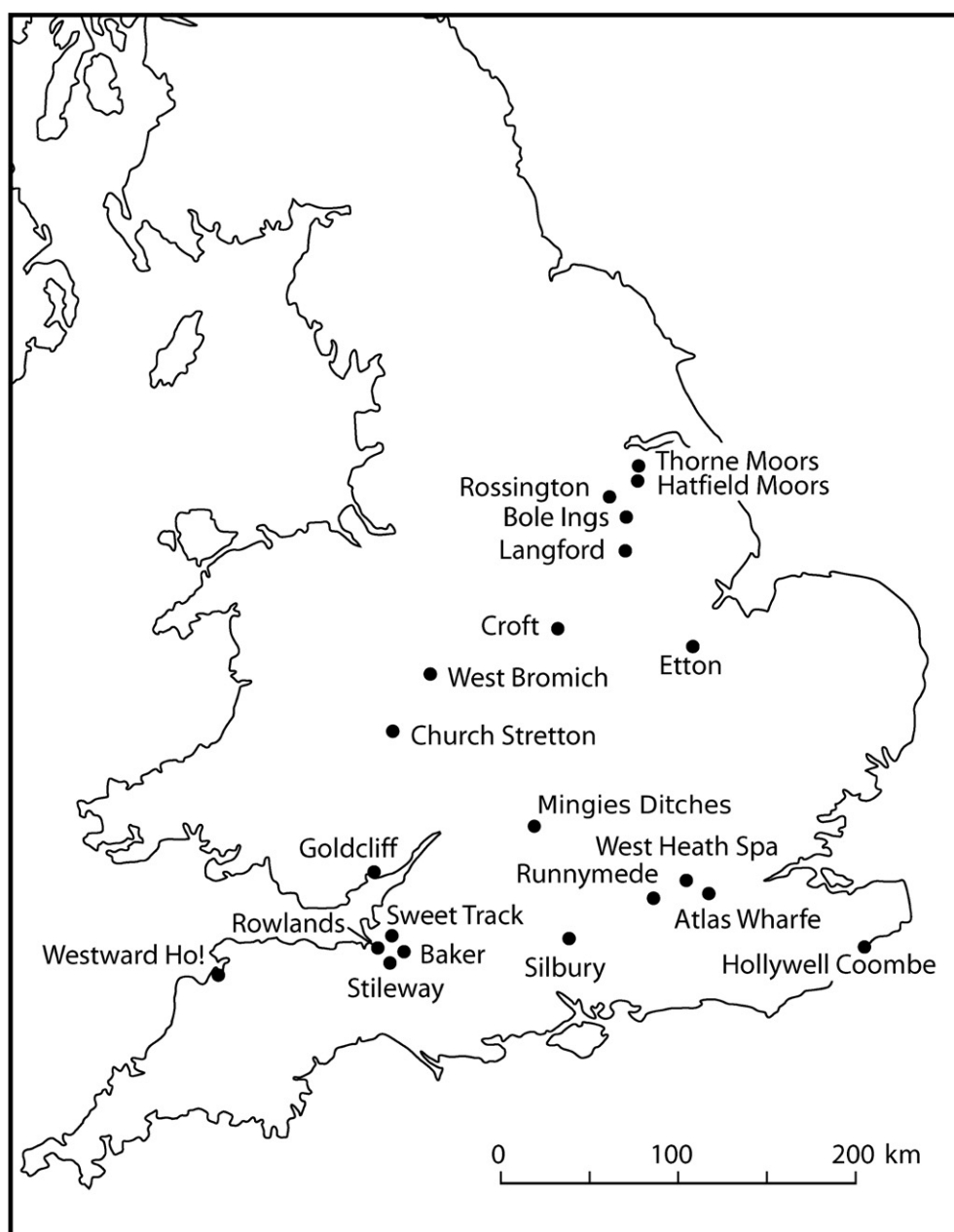


Fig. 1. Location map of study sites.

Sample sizes are frequently not recorded, where they are, they are highly variable (see Table 1, supplementary information); the same is often true of sample resolution. Poor chronological control exacerbates this situation. Converting MNI data into percentages, as undertaken in the first analysis helps to address aspects of this problem, however, in the second exercise, this wasn't possible, since the data are based on simple counts of obligate tree-associated species, rather than on MNI data. Given the overall fluctuations in such obligate taxa in the natural world (Fig. 2) and the low values represented, converting such figures into percentages could potentially be misleading and we have thus retained the values as counts. Since sample sizes have varied across sites (see Table 1, supplementary information), this may have caused low counts of some taxa, suggesting that the absence of a particular tree associate should not be taken to represent evidence of its absence. We have taken care to include only sites with what are considered to have

adequate, representative sample sizes and species lists into the analyses. Because of these difficulties, it's important to appreciate that it's the trend of the overall data set with which we are concerned, rather than fluctuations within individual datasets.

The dates of the assemblages used are presented in Table 1 (supplementary information). For both analyses, groups of samples from individual sites have been divided into discrete time periods, where the chronology allowed such distinctions. The division into these periods was far from straightforward and subject to a certain level of subjectivity, since the number of available ^{14}C dates at many sites was very limited. In many cases it was very hard to ascertain the full period of time represented by each assemblage, especially as many sites have routinely obtained ^{14}C dates for the basal but not top part of sequences (e.g. successions above trackways). We have therefore identified clearly the number of samples used in each assemblage allocated to a time period, so that readers have some

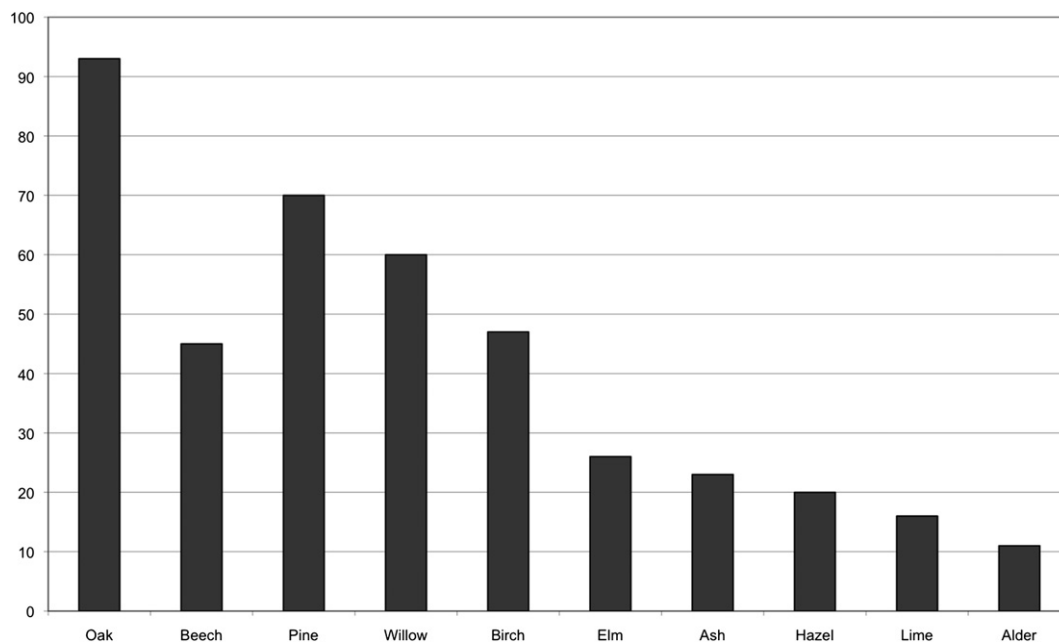


Fig. 2. Numbers of species of Coleoptera associated with each of the common trees in the British Isles (data after Bullock, 1992).

indication of the resolution of the assemblages used (Table 1, column 3, supplementary information), or at least an indication of the sediment represented, but these constraints mean that some assemblages will inevitably represent longer periods of time than others. The information in Table 1 draws attention where larger groups of samples have had to be lumped together and attempts, where possible, to identify the periods of time which may be represented within each assemblage, although in many cases this was simply impossible because of poor dating strategies. The assemblages are arranged, as far as possible, and within the constraints described above, in broad chronological order. There is no attempt to assign any scale to this orderings, other than older to younger, left to right.

We have confined our review to sites that date to the first half of the Holocene (from c. 9500 cal BC to c. 2000 cal BC). After this point in time, most pollen records indicate that farming became large scale and landscapes were cleared of much “wildwood”. We have judged that this time period best reflects a largely “natural” landscape, although it could be argued that faunas from between 4000–2000 cal BC (at least in some cases) fail to represent the true untouched forest of Vera’s vision. However, they provide important base-line information against which earlier faunas may be compared with and allow us to examine the changing nature of the British Holocene landscape over this crucial time period. Moreover, there are very few sites that date to the first few millennia of the Holocene: only five of the sites/groups of samples investigated belong to the period between c. 9500–6000 cal BC, seven to the period 6000–4000 cal BC, with 24 sites/samples dating to between 4000–2000 cal BC.

We have used all published sites for the time period available within the BUGSCEP database in the analyses, apart from two sites where it was impossible to assign a time period for the material (occupation layers at Eilean Domhnuill, on North Uist [Warsop, 2000]) or where the context was at odds with the analysis (Church Moss [Hughes et al., 2000], a mire sequence with few terrestrial components). To allow comparison between the different time periods, we have presented the data in three time slices: c. 9500–6000 cal BC; 6000–4000 cal BC; 4000–2000 cal BC, representing the (1) early-mid Mesolithic, (2) late Mesolithic and transition to

the Neolithic and (3) the Neolithic, displayed and arranged in chronological order as far as this has been possible.

There are several archaeological implications that are relevant in considering these data. Archaeological and palaeoenvironmental work have suggested possible direct human manipulation of forest structure (e.g. through fire), even in the Mesolithic period (c. 9500–4500 cal BC) (Mellars, 1976; Simmonds, 1996). Traditionally, the Neolithic has been seen as a time of increasing agricultural dominance and woodland clearance. However, there has recently been active debate in archaeological circles concerning the whole nature of the Neolithic in the British Isles and the degree of clearance of the wooded landscape during this period (e.g. Moffett et al., 1989; Thomas, 1999, 2003; Jones, 2000; Robinson, 2000b; Schulting and Richards, 2002; Richards et al., 2003; Rowley-Conwy, 2004; but see Cooney, 2000 for Ireland). Much of the archaeological and palaeoenvironmental evidence suggests that, aside from the large ritual landscapes of Wessex, the south of England and large monuments complexes in Scotland which may have been subjected to early and sustained clearance (e.g. Noble, 2006), the scale of Neolithic clearance, probably for agriculture, was apparently relatively minimal with no large scale clearance until c. 2200 cal BC. Relative arboreal pollen values essentially continue at the same levels in most areas of the British Isles suggesting a continuation in closed forest conditions (Richmond, 1999; Thomas, 1999; Bell and Walker, 2005) and very limited evidence for large scale agricultural adoption (Tipping, 1994). The scale of Neolithic agriculture has also been the subject of significant debate, with increasing evidence for small scale, intensive, garden plot cultivation appearing more likely (Bogaard, 2004; Jones and Rowley-Conwy, 2007). Recent palynological analyses indicate such intensive but local scale land use cannot usually be discerned in region-scale pollen analyses, even when located within a few kilometres to archaeological sites, and require targeted sampling directly associated with Neolithic archaeological structures (Tipping et al., 2009). So, although all Holocene palaeoenvironmental results should be seen against a backdrop of increasing human impact, this could have been highly variable across the landscape, at relatively small but intensive scale throughout the period, and difficult to identify using palynological data alone.

Many sites and samples examined have formed under different depositional environments. For instance, assemblages from Thorne and Hatfield Moors, which represent data from seven different sampling locations from across both raised mires, probably derive from the local environment having been sampled in wood peats, they also show enhanced values for wood species because of their sedimentary context. Contrasting with this are a range of sites, such as Croft and Langford on the river Trent where deposits were formed during flooding and can be expected to contain insect faunas from a much larger ‘catchment’. Equally, the dominance of some insect taxa over others will be dictated by the availability of their tree hosts at individual sites, themselves affected by edaphic and biological factors, which may have differed in space and time. Fig. 1 illustrates one clear problem; all sites are from lowland situations and largely from locations from Yorkshire, the Midlands and southern England; the data are therefore largely biased towards these landscapes.

The vicinity of the samples to archaeological sites is another potential issue, as it is inevitable that material from near to or from an archaeological site may show enhanced “open” and “dung” values. In terms of the split between archaeological and palaeoecological sites used, nine assemblages (i.e. groups of samples/sites) are directly or indirectly associated with known archaeological features or sites (see supplementary information Table 1 for details; such sites are clearly identified in Figs. 3 and 4). Temporally, these are distributed within the time slices 6000–4000 cal BC (two out of seven samples/sites used) and the period 4000–2000 cal BC (8 sites out of 23 sites/samples). All samples from 9500–6000 cal BC come from palaeoecological deposits, and therefore are considered to be largely “natural” in origin.

If we look at this issue more closely, however, many of these assemblages seem not to be directly (or very indirectly) associated

with archaeological activity. Thus, the assemblages from West Heath Spa come from adjacent to the archaeological site and relate poorly to the archaeology with many samples pre-dating the occupation layers. Similar issues are pertinent to the faunas from Mingies Ditch and Westwood Ho! The wood peats associated with many of the trackways sites (e.g. Sweet Track, Rowlands) post-date the use of the trackways. With the exception of sites such as Etton and Silbury Hill and possibly Runnymede, many samples which are apparently associated with archaeological sites are probably essentially palaeoenvironmental. We therefore believe that human effects registered within the faunas are likely to be relatively minimal. We draw attention to this where we feel this aspect is important and affects the interpretation of the records presented.

5. Results and interpretation

Count and percentage data used to generate Figs. 3 and 4 can be found in the supplementary data (Appendix), raw counts for each site used can be downloaded via www.bugscep.com (see Site Manager).

(1) *Vegetation structure: trees, open environments and browsing animals*

Fig. 3 shows the proportions of (1) wood and tree (2) open ground/pasture and (3) dung beetle fauna over the review period, arranged in chronological order, left to right.

Early in the Holocene, the tree fauna accounts for between <5% (e.g. basal samples from Hollywell, dated to 9700–8800 cal BC) through to >16% of the terrestrial fauna (e.g. Lea Marsdon B, dated to >9396–8306 cal BC). By c. 8200–7000 cal BC, the tree fauna has increased substantially (>25%). Over the same period open taxa

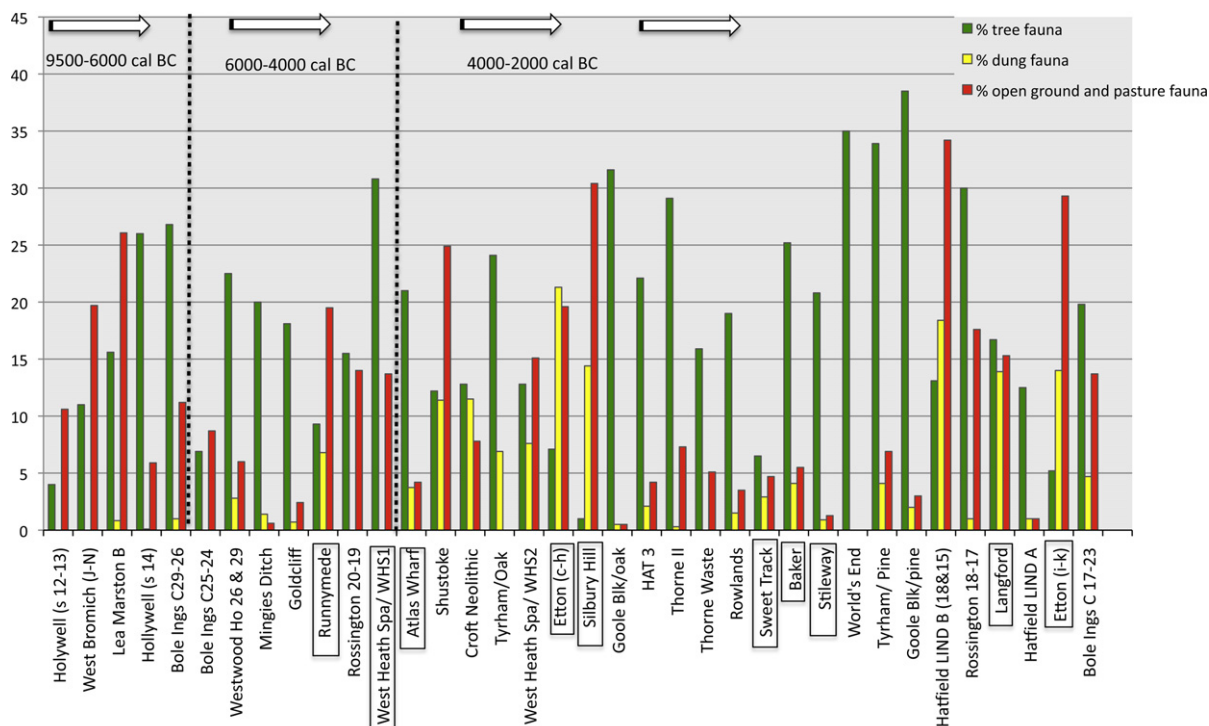


Fig. 3. Proportions of tree fauna, open ground/pasture and dung beetle fauna over the study period, expressed as a percentage of the terrestrial fauna, arranged in rough chronological order (as far as possible within the constraint of the chronologies), left to right and grouped into chronological periods as follows: 9500–6000 cal BC (N = 5 sites/samples), 6000–4000 cal BC (N = 7 sites/samples) and 4000–2000 cal BC (N = 24 sites/samples). Details of individual sites and associated chronologies/contexts may be found in Table 1. Boxes around site names denote archaeological sites, other sites are deemed palaeoecological (i.e. not demonstrably connected to archaeological material).

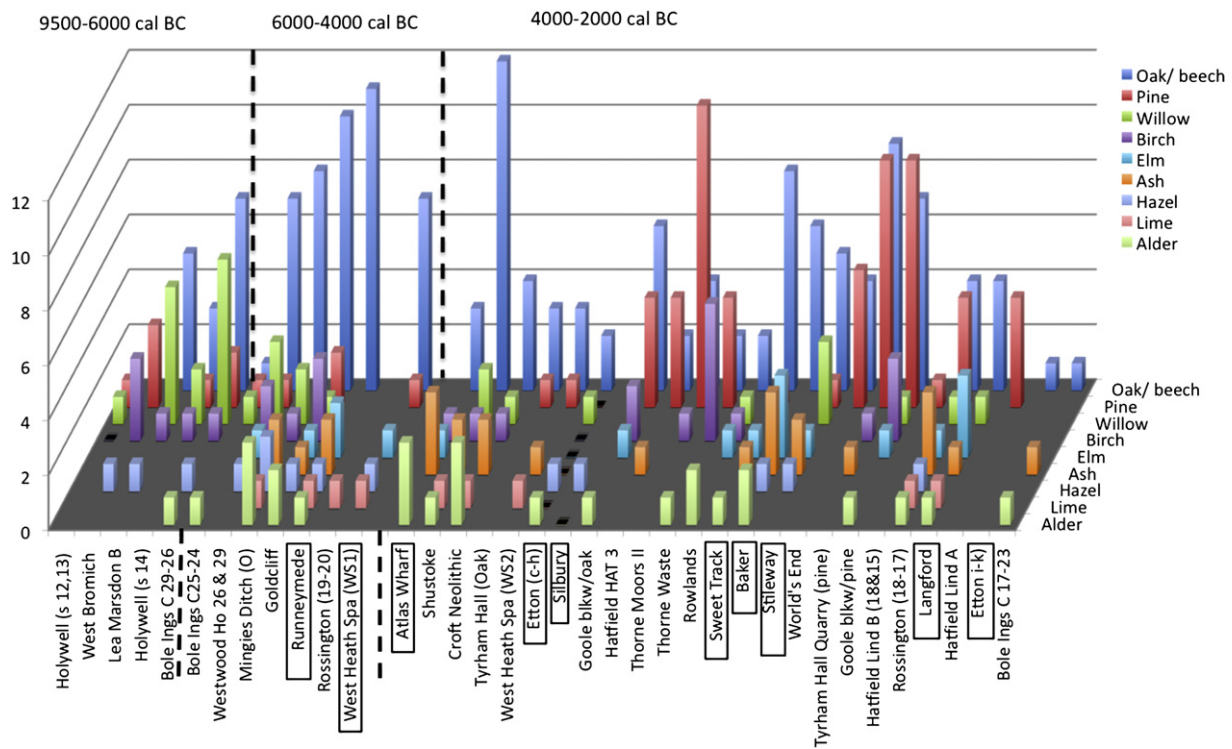


Fig. 4. Numbers of obligate tree species associates for the study period, by study site and arranged in chronological order left to right: 9500–6000 cal BC ($N = 5$ sites/samples), 6000–4000 cal BC ($N = 7$ sites/samples) and 4000–2000 cal BC ($N = 23$ sites/samples). Preferences are taken mainly from Bullock (1992) and Koch (1989, 1992). Boxes around site names denote archaeological sites, other sites are deemed palaeoecological (i.e. not demonstrably connected to archaeological material).

account for between c. 7% (Hollywell Coombe, <8200–7450 cal BC) and 27% of the terrestrial fauna (Lea Marston B), but as the tree fauna increases, some open communities remain important (e.g. with up to 12% at Bole Ings). Values of dung beetles remain extremely low at this stage, representing barely more than 1% of the fauna and are present at just a couple of sites (Lea Marston B and Bole Ings), both situated in river valleys, where one might expect to see greater activity from wild grazing animals.

Between 6000 and 4000 cal BC, the proportions of tree taxa cover a similar range (7%–31%), although levels at some sites are surprisingly low, such as at Bole Ings (C25–24) and Runnymede, both floodplain locations. Open ground/pasture species on the whole occur in significantly lower numbers, just 1–7% of the fauna, although there are several sites where these taxa are more important (Runnymede, Rossington and West Heath Spa, WHS1), between 14% and 20% of the fauna. Runnymede and Rossington are both floodplain sites, whilst Runnymede and West Heath Spa are (to a greater and lesser extent, respectively) associated with archaeological material. Both these aspects could explain these higher values of open indicators. Proportions of dung beetles also increase during this period, ranging from 1%–7% at some sites and are noticeably higher than previously. Runnymede includes the highest value for this faunal category, which, in tandem with its high levels of open taxa and lower levels of tree taxa clearly suggests a relatively open environment, where browsing animals appear to have been important. Its floodplain location is clearly critical but also its vicinity to a Neolithic settlement may suggest earlier anthropogenic activity (i.e. late Mesolithic) than apparent from the archaeology alone.

From 4000–2000 cal BC, there is considerable variability amongst the study sites, but also a continuation of some trends which had begun to emerge towards the end of the previous period. Taking the first group of 7 assemblages together (Atlas Wharfe to

Silbury Hill, Fig. 3 – Group A), dating approximately between 3900–3500 cal BC, it is noticeable that tree taxa have lower values compared with previously, although most sites exhibit values of over 10% and some as much as 24% (Tyrham/Oak). The latter value is not altogether surprising since the assemblages studied came from wood peat deposits. Values for open indicators are generally higher compared with previously, ranging from as little as 4% (Atlas Wharfe) to >30% (Silbury Hill), with most sites displaying values of 7%–25%. This suggests that open habitats have increased substantially compared with previously and are often close to values seen by Robinson (1991) as representing largely pastoral landscapes, although the accompanying high tree values at some sites indicates forest areas are still important, perhaps dominant habitats at this time. The most noticeable aspect of these assemblages is the large initial increase in values of dung beetles, from just under 4% at Atlas Wharfe to over 21% at Etton (c-h), with several other sites showing high values, between 11–14% at Shustoke, Croft Neolithic and Silbury Hill. The activities of grazing animals are clearly important at this time. Where values of open ground and dung proportions are high, we see clear decreases in tree taxa, suggesting considerably open environments at sites such as Shustoke, Croft Neolithic, West Heath Spa (WHS2), Etton and Silbury Hill. The latter two sites are directly associated with archaeological material, but values at Shustoke, an alluvial sequence associated with the River Bourne, are almost as high, along with Croft Neolithic, another alluvial sequence. These higher values may reflect wider grazing of river floodplain areas by domesticated stock, whilst values at West Heath Spa (WHS2) although post-dating the known Mesolithic archaeology, may well reflect continued archaeological activities in the area, although forest areas are still apparently important. These more open sites have high values for dung beetles, suggesting relatively mixed landscapes, where the role of grazing animals appears important and either directly or indirectly associated with

archaeology or suspected wider clearance of the landscape, although still maintaining areas of forest. Only at the archaeological site at Atlas Wharfe do we see an apparent dominance of tree taxa, but this seems to be the exception rather than the rule. This may be explained by the timber structures found on site, causing an over-abundance of tree-associated taxa, but the low values of open indicators and dung beetles would also support the idea that the site was situated in a primarily closed, forested landscape.

The next suite of assemblages from this time period (Goole Blk/Oak to Goole Blk/pine, Fig. 3 – Group B), represented by 11 datasets, belongs approximately to the period 3500–2500 cal BC. This group of assemblages is in marked contrast to the previous Group (A), with much higher levels of tree taxa, this component representing between 15–35% at many sites, with up to 30–40% common in assemblages from Thorne and Hatfield Moors. On the whole, open indicators appear to have decreased compared with previously, representing 5–7% of the terrestrial fauna, in contrast to sites such as Silbury Hill and Etton. Dung beetles are also decreased compared with previously, representing levels of between 2–4% at many sites and displaying similar levels as those evident during the Mesolithic, 6000–4000 cal BC. These figures suggest the landscape represented at these sites was primarily forested, with limited open areas, where the role of grazing animals was not especially important. It is noticeable that this trend does not differ between archaeological nor palaeoecological sites. However, although the data may indeed support this general trend, if we look more closely at the assemblages the picture may not be so straight-forward. Many of the sites which show increases in woodland components and decreases in open indicators come from the wood peats of the raised mires of Thorne and Hatfield Moors, which seem to have been rather atypical sites and essentially appear to have acted as refugial areas at this time (Buckland, 1979; Whitehouse, 2006). The middle of a raised bog is not an environment where one might expect agricultural or pastoral activity! The same point is also relevant to the Somerset Levels trackway sites that would have been Alder carr or wet fen at this time. Several other sites are alluvial (e.g. Worlds End), where open-ness may be more typical of that environment.

If we turn to the final group of assemblages (Group C), represented by 6 datasets (Hatfield Lind B 18 & 15 to Bole Ings C17–23, Fig. 3) dated up to 2000 cal BC, we see an apparent return of trends seen earlier in the Neolithic (Group A sites). Values of tree taxa are still very high at some sites (e.g. Rossington, 30% and Bole Ings, 20%), but many sites show much greater similarities to those seen earlier in the Neolithic (e.g. Langford 16%, Etton 5%), although there is quite a lot of variation. Open indicators increase quite dramatically, with some very high levels shown (Hatfield, Etton, Rossington, Langford), accompanied by high levels of dung indicators at almost all sites (e.g. Hatfield, Etton, Langford). The relationships shown between open and dung indicators strongly suggest that there is a direct association between the increase in open areas and the activities of grazing animals.

In summary, therefore, over the Neolithic, the tree fauna does not become increasingly diminished, as one might expect with progressive clearance of the landscape, although there are significant local variations to this trend; in fact, as the period progresses there are increasing assemblages with higher proportions of tree phytophages. After an early peak of open taxa, these indicators decline followed by an increase once again towards the latter parts of the Neolithic. A similar story is evident from the distribution of dung beetles over this period. However, at some important Neolithic archaeological sites such as Middle Neolithic Silbury Hill (3550–2900 cal BC) and Etton (2940–2200 cal BC), it would seem an open landscape had developed and remained throughout the Neolithic period (Robinson, 1997, 1998). At Silbury, the fauna indicates a wholly open landscape, in which herb-rich chalk grassland elements are

strongly represented (Robinson, 1997). Robinson (1997) suggested this site appeared largely atypical of the Neolithic and has greater similarities to Bronze Age sites such as the Wilsford Shaft (Osborne, 1969). The analysis presented here suggests that although this statement is still largely true, when compared with other sites is part of an increasing trend evident at several other locations during this period and therefore not altogether anomalous.

Its worth pointing out that at some Neolithic sites relatively high values of open and dung beetle taxa are also matched by high values for tree-associated taxa (e.g. Bole Ings: 20% trees, 13% open taxa and 5% dung beetles; Atlas Wharf: 21% trees, 4% open taxa, 3% dung beetles; Rossington (18–17): 30% trees: 17% open taxa, 1% dung beetles; Langford: 17% tree, 15% open indicators, 14% dung beetles). The faunal assemblages have important mixed components of tree-associated, open-ground and dung beetles, suggesting important tree and pastoral landscapes.

(2) Reconstructing tree composition and density from insect faunas

Fig. 4 shows the numbers of obligate tree beetle species at each site/assemblage, arranged in chronological order, left to right, following the same order as Fig. 3. The relationship between these data and forest composition is not straight-forward. We have already drawn attention to the inherent variability of numbers of beetle species associated with specific tree taxa at the present day (Fig. 2). The data in Fig. 4 are no more than a slightly 'noisy' version of the same pattern. The overall abundance of species reflect the potential number of insects these trees may play host to rather than their percentage occurrence in the canopy of the forest. However, despite the fact that it is not possible to indicate the individual proportions of each of the forest trees represented by this data, it is clear that values have shifted and changed over time and this can provide useful information about the changing composition of the forest.

Between 9500 and 6000 cal BC, insect taxa associated with oak, pine, willow, birch and hazel appear to be important, with alder becoming more prevalent at a slightly later stage. These taxa which prefer less shaded conditions are typical of pollen diagrams of this period (cf. Greig, 1996) and are characteristic of the pioneer communities of the early Holocene. Ash-associated insects appear for the first time at Westwood Ho!, dated to 6000–5450 cal BC, which corresponds to the period identified by Birks (1989) for the expansion of this tree in England. Beetles associated with trees which prefer more shaded conditions appear to be under-represented during this period.

For the period 6000–4000 cal BC, a more diverse assemblage of tree-associated beetles becomes important. Taxa associated with oak are generally more frequent than previously, whilst pine habitats remain present, but less frequent. Willow-associated retain background levels, but do not play the role they seem to have enjoyed during the earlier part of the Holocene. Beetles associated with trees associated with more shaded conditions become important during the earlier part of this period (c. 6000 cal BC) and subsequently. Lime-associated appear for the first time in the record at Mingies Ditch, in deposits dated to 5630–5340 cal BC, and elm-associated at Westwood Ho! in deposits dated to 6000–5450 cal BC. The pollen record indicates the trees are present in Britain from at least 6400–6200 cal BC (7500 BP) (Birks, 1989), suggesting that the taxa associated with these trees are likely present before their occurrences noted here. Beetles associated with trees which prefer less shaded, more open conditions, especially hazel and birch, exhibit similar levels to previously, with some sites (e.g. Goldcliff) showing increased levels. The behaviour of hazel is quite interesting; most of the sites where its associates are recovered from are generally those which have higher levels of open and dung

beetle indicators. This is especially the case for the early Holocene, but is true for the latter parts of 6000–4000 BC, being present in assemblages from Runnymede and West Heath Spa (WS1) and, more latterly, Etton, and Silbury in the later Holocene. There are some exceptions to this pattern (e.g. Mingies Ditch, Goldcliff) which suggest that although there may have been a preference for more open locations, other edaphic factors (e.g. hydrological changes) must have also been important. It is curious that the 'Elm decline' is not immediately evident, although there does seem to be a very subtle decline in the frequency of its associates at about the time of this palaeoecological event. This may be because there are very few study sites which cover this period (exceptions are West Heath Spa and Rossington).

Between 4000 and 2000 cal BC, all sites show declining numbers of tree associates and an increasing variability in the range of tree-associated beetle taxa recovered. For example, oak/beech-associates mostly show a decline over the Neolithic period – with some exceptions – similarly, pine-associates, probably reflecting the 'pine decline' at c. 3000 cal BC which is well-documented within the palynological record (Birks, 1972; Bennett, 1984) and which led to the extirpation of some pine-associated beetles (Whitehouse, 1997b). Exceptions to this pattern are those assemblages from Thorne and Hatfield Moors where pine and oak remained important through to the historic period (Whitehouse, 2004), especially the former. These sites acted as unique island biogeographic areas and indicate the persistence of local pine populations long after its decline elsewhere, a point which has been noted for other regions (cf. Tipping et al., 2008).

Other species which decline in importance include hazel and lime, the former appearing rather sporadically through this period, especially in substantially cleared landscapes such as Silbury Hill and Etton, whilst the decline of the latter may be related to the 'lime decline' seen in several late Neolithic and later pollen diagrams (Turner, 1962; Greig, 1996). Many of the river valley sites (e.g. Shustoke, Rossington, Croft, Langford) included the lime wood-borer, *Ernoporus caucasicus* Lindem., suggesting that lime must have been a common or even dominant component in the lowland floodplain forests of the mid Holocene (Greig, 1982). Given lime's shade tolerances, this also suggests relatively dense forest situations in these areas.

The composition of the local tree assemblage type differs significantly between locations. These diverse wooded environments and their insect faunas have been discussed in some detail by Smith and Whitehouse (2005), who draw attention to the inherent range and variability of early Holocene forest composition (and hence natural structure) which is often not considered in the discussion of Vera's hypothesis. Indeed, the range was probably even more varied (see Bennett, 1989). Moreover, it is likely that spatial variation could have been considerable at a regional level, depending upon human impact, geology and edaphic factors.

6. Discussion

What does this exercise tell us about our understanding of the Holocene British landscape over this period and its degree of openness? What was the character of the "natural" landscape or "wildwood"?

6.1. Period 9500–4000 cal BC (Mesolithic)

The high degree of variability seen in the levels of forest and open indicators over the period 9500–6000 cal BC reflects the dynamic nature of the landscape during this earlier stage of the Holocene. At several sites relatively open conditions are indicated, reflecting the behaviour of pioneer communities, with levels of trees and open

ground (e.g. Lea Marston B) not unlike to those from one of our modern analogue sites, the pasture woodland site of Dunham Massey (Smith et al., 2010), suggesting a possibly similar landscape structure. Towards the end of this period, woodland communities increase in importance, but open ground and pasture species persist at reduced levels, indicating that both woodland and open clearings were present but it's unclear what the balance between these different components may have been. Based on our analyses at Dunham Massey and Epping Forest, Essex (Smith et al., 2010), it seems unlikely these figures represent pasture woodland, nor do they seem to indicate dense, closed canopy woodland, but rather a wooded landscape with limited open areas, but not of the extent suggested by Vera (2000). Some pollen diagrams of this period show small levels of grasses at this time (e.g. Haddenham Mere, Cambridgeshire, herb pollen 5%, see Greig, 1996), with some diagrams from chalk grasslands showing sustained and relatively high levels (e.g. Willow Garth, in the Yorkshire Wolds; Bush and Flenley, 1987; Bush, 1988, 1989). At Willow Garth, Thomas (1989), subsequently argued that some of this 'grassland' pollen may have derived from marshland plants, but failed to appreciate the importance of fossil beetle evidence described by Bush (1988) in his evaluation (Whitehouse and Smith, 2004). Fossil beetles from the same levels as the grassland pollen included species typical of open grassland (*Phyllopertha horticola* (L.), *Cantharis rustica* Fall. and *Serica brunnea* L.), suggesting that this habitat is indeed represented here. Since this work was done, further sites indicate the continued existence of more open areas throughout the Holocene in chalk regions, including studies from the South Downs (Waller and Hamilton, 2000) and the Cranborne Chase area of Dorset (French, 2003), whilst Holocene tufa deposits in the Test Valley, Hampshire, showed extended periods of open conditions over the Mesolithic period (Davies and Griffiths, 2005). Equally, other areas of chalk clearly supported extensive areas of woodland (e.g. Holywell Combe – both from this study and pollen evidence) and it is clear this was the case for many areas of Britain (Greig, 1996). Buckland (2005a,b) makes the point that heathland habitats appear during the lateglacial and that some habitat continuity must have occurred for their associated invertebrates to have survived into the Neolithic when heathland seems to have undergone a major expansion. Many of the refuges may have existed in coastal (e.g. sea cliffs, sand dunes) and upland localities (steep slopes), but much more evidence, including from palynology, is needed in chalk and limestone areas where natural grazing may have maintained open ground required of these taxa. Pigott and Walters (1954) make similar points in discussions of the modern discontinuous distributions of certain open habitat plant species. The origins of chalk grassland have been the focus of some controversy over the years (e.g. Bush, 1988, 1989), but it is clear that these areas merit greater research attention. Thus, it seems that the fossil beetle data, alongside some pollen evidence, suggest that a greater patchiness of the landscape existed during this period than has perhaps been emphasised. Moreover, recent modelled pollen records suggest that closed forest cannot wholly explain the variation seen in the pollen records of this period, but that the extent of landscape openness suggested by Vera (2000) is too high (Soepboer and Lotter, 2009).

The later Mesolithic, 6000–4000 cal BC, is dominated by tree-indicating taxa, with open ground species occurring in significantly lower proportions suggesting a closing of the forest canopy. Even here, however, some sites (e.g. Rossington and to a less extent, Runnymede), indicate that the landscape still retained some significant open areas, suggesting a mosaic of tree-dominated areas, small clearances and open areas. Proportions of dung beetles also increase at some sites during this period, many such sites are alluvial sequences. River valley systems often appear to contain open areas of marsh and meadow which result from floodplain

disturbance such as lateral migration of river channels over time, indicating that at the local scale there may have been significant open-ness in the vegetation in these areas and may have been important areas for natural grazing.

Oak, pine, hazel, willow and birch were clearly important components of the mixed forest landscape during the earlier and mid Holocene (Fig. 4). Was oak indeed a dominant component of the wildwood (and not simply the product of pollen taphonomy) in the early Holocene? The fossil beetle record cannot indicate how dominant this component was in the woodland, however, during the earlier part of the Holocene, 9500–6000 cal BC, the landscape appears to have been dominated by trees which prefer more open conditions and there is a relative absence of shade-tolerant trees (e.g. elm). Open areas are important (Fig. 3), especially during the earlier part of this period, indicating that the right conditions were available for oak to thrive. From 6000 cal BC onwards, although oak remains significant, shade-tolerant taxa such as elm and lime become more prevalent and possibly more important given the relatively few insect associates which live on these trees compared with oak (Fig. 4). The forest canopy during this period must have been more closed (shaded) and denser compared with previously, though the continued presence of shade-intolerant trees and low levels of open ground and an increasing dung beetle fauna indicates that the landscape included some open habitats, especially in river valleys and close to archaeological sites. Oak continued to regenerate under these more closed canopy conditions and indeed appears to increase its habitats compared with previously; it is interesting to note many of the sites its beetles are found at are either associated with floodplains and/or with archaeological sites, where conditions seem to have been more open. The pollen record from many sites across the British Isles suggests that woodland was its maximum and densest during this period, c. 5000–3800 cal BC (c. 6000–5000 BP) (Greig, 1996).

6.2. Period 4000–2000 cal BC (Neolithic)

Between 4000 and 2000 cal BC, there is increasing landscape complexity, with a trend for opening of the landscape, but where tree and wood-decay communities remain significant at some sites. Values of tree, open taxa and dung beetles fluctuate significantly both in space and time, suggesting a shifting mosaic landscape, in which tree clearance, regeneration and the activities of grazing animals were important. Open areas became progressively more significant, but there are areas that remained important for their tree-associated fauna until relatively late (e.g. Thorne and Hatfield Moors). Despite substantial clearance indicated in some areas (e.g. the Avebury chalk lands region associated with Silbury Hill) which have in some respects anomalously high values for their open ground and pasture fauna, many areas remained substantially un-cleared of woodland. These areas are major monument complexes and potentially could be viewed as exceptional within the wider landscape. Bell and Walker (2005) make the point that natural environmental patchiness may have been important in the citing of concentrations of monuments in this landscape. This finding is very much in line with other palaeoenvironmental evidence which suggests that apart from the large ritual landscapes of Wessex, and other areas where large monumental complexes were important and which may have been subjected to sustained clearance (e.g. Noble, 2006, but see also Plunkett et al., 2008, for an exception of this in Neolithic Ireland), that large scale Neolithic clearance for agriculture was relatively small scale, at least until the later parts of the Neolithic and that cultivation may have been more akin to garden type agriculture at this time (Bogaard, 2005; Jones and Rowley-Conwy, 2007).

Aside from an early burst of Neolithic activity, accompanied by clearance and grazing of the landscape (Group A sites, 4000–3500

cal BC), the palaeontomological record suggests re-afforestation and/or limited clearance/grazing during the middle Neolithic (Group B sites, 3500–2500 cal BC), with clearance and grazing activities apparently becoming more prevalent during the later Neolithic (Group C sites, 2500–2000 cal BC), although there are marked temporal and spatial contrasts here. There are some biases within the Group B sites which we have already drawn attention to, but, broadly speaking, the patterns seem to compliment the prevailing patterns within the pollen data of the period, although there are considerable regional variances here (cf. Greig, 1996). Thus, many pollen diagrams show clear evidence for clearance and cultivation early in the Neolithic often associated with the elm decline, followed by a recovery of pollen values and woodland regeneration, until a main phase of woodland clearance from c. 2000 cal BC onwards (Smith, 1981; Day, 1991; Greig, 1996). It is clear that the wildwood wasn't extensively cleared in most regions until into the Bronze Age, c. 1300 cal BC (c. 3000 BP), i.e. after many of the sites presented (Greig, 1996); the data presented here would tend to support this, although there are some significant exceptions, as we have already highlighted above. It is also important to remember that whilst pollen will be recording the wider regional picture of environmental change, the fossil insect record will essentially be recording a much localised picture; it is inevitable that although at the broad scale patterns may compliment each other, at the local scale there will be substantial differences.

Researchers have argued that there was a relatively abrupt transition into agriculture at the start of the Neolithic, based upon isotopic evidence of human dietary change (e.g. Richards et al., 2003). This abrupt transition appears evident in the early Neolithic sites investigated here and amongst the levels of dung beetles indicative of the activities of grazing animals, but that after this phase, the picture is more complex, with some afforestation in the middle Neolithic. It is a pity we have relatively few sites covering this very early period, it would be especially useful to have more data from occupation sites in order to examine these patterns further. It is worth noting that this trend compliments quite nicely newly emerging archaeological data for this period, which are starting to emphasise an early Neolithic with intense activity coinciding with the period c. 3700–3500 cal BC (Bayliss et al., 2007; McSparron, 2008), followed by an apparently less intensive use of the landscape. In terms of the range of trees represented during this period (Fig. 4) some areas retain a range of taxa, whilst others are substantially cleared of former tree diversity. Between 4000–2000 cal BC, all sites show declining numbers of tree associates and an increasing variability in the range of tree-associated insect taxa recovered. This may reflect human impact on the landscape affecting tree taxa in diverse ways.

6.3. Archaeological versus Palaeoecological sites

A mixture of archaeological and palaeoecological sites were used in this review. One might have expected that archaeological sites would include rather more open indicator species compared with palaeoecological sites. However, there is no discernable relationship between the results and whether these came from an archaeological or palaeoecological sites, apart from the Neolithic sites discussed above. This is likely to, in part, reflect the fact that there is often no direct (or a very poor) relationship between the palaeontomological material sampled and the cultural deposits that actually form the archaeological site. Indeed, there are very few archaeological sites of this period which have been comprehensively sampled for their fossil beetle fauna, unlike later prehistoric and historic archaeological sites. We conclude that the patterns identified are therefore a real reflection of the wider Holocene landscape and, on the whole, not the product of being

associated with human activities. On the other hand, quite a number of sites with high levels of dung beetles and open indicator taxa are associated with floodplain deposits, suggesting these areas were important in maintaining an open mosaic landscape, encouraging either wild grazing animals and later on perhaps used deliberately as grazing areas for domesticates. The importance of these areas is similarly emphasised by Kreutz (2008) in a consideration of early Neolithic use of the landscape at European Linearbandkeramik archaeological sites.

6.4. The role of natural grazing in the structure of the Holocene “wildwood”

Although we have shown that the Holocene forest was, at times, patchy and a constantly evolving and changing ecosystem, the data presented do not suggest that open areas were driven by the activities of large herbivore grazing. Dung beetle frequencies (Fig. 3) do not become important until the Neolithic period, although there are hints of the rising importance of this habitat between 6000 and 4000 cal BC. This strongly suggests that the dung beetles' hosts, grazing animals, are not apparently important during these earlier phases and that their impact is only evident during the Neolithic. This impact is dramatic and coincides with the arrival and usage of domesticated herbivores. One could therefore conclude that the open areas evident within the records are not driven by the activities of grazing animals, that herbivore density does not control natural forest structure, effectively nullifying the crux of the Vera hypothesis. However, some caution is necessary. The figures inevitably draw attention to the dramatic increases in dung beetles seen in the Neolithic, a landscape which has clearly been modified by anthropogenic activities, but they may not necessarily be typical of “natural” grazing activities, where the effects of natural grazers might be expected to be at relatively low, dispersed, levels. It may therefore be hard to “see” grazing activities before the Neolithic as grazing may have been at very low levels and almost invisible palaeoecologically, in contrast to what appears to be happening during the Neolithic. This question also rather depends on the nature and intensity of grazing activities during the Neolithic itself; Robinson (2000a,b) has suggested that larger herds of domesticated animals (cattle and pig) were “forest grazing”, in an open and loosely controlled way, which could be perceived to mimic “naturalistic” grazing, but it is hard to be sure on this point. The Neolithic data are certainly more heavily biased towards archaeological sites and floodplain areas, where one might expect to see greater impact of grazing animals.

It will only be possible to be certain what “natural” grazing activities might look like in the palaeoecological record by undertaking modern actualistic studies, in which the activities of grazing animals mimic (as much as is possible) those of the “wildwood”. Such work is already underway (Smith et al., 2010). Results from our analogue studies at Dunham Massey, Epping Forest, Hatfield Forest (Essex) and Windsor Great Park (Berkshire) suggest that it possible to use the proportions of dung beetles in terrestrial insect faunas to establish the density of animal herds and the intensity of grazing, but further research and study sites are necessary to investigate this further.

Conversely, there has been a long running debate concerning the role of fire, whether natural or the result of human action, in creating clearings and structuring the landscape (Mellars, 1976; Bradshaw and Hannon, 1992; Simmonds, 1996; Whitehouse, 2000, 2006; Svenning, 2002; Buckland, 2005a; Fyfe, 2007; Kreutz, 2008), possibly as early as the Mesolithic. There is an extensive literature on Mesolithic hunter-gatherer burning of the forest, could human-induced burning been an important factor in preventing the development of closed woodland at this time (cf. Smith and

Cloutman, 1988)? Bell and Walker (2005) argue that it is striking that in Britain at least, evidence for burning in the Mesolithic is abundant and is present in many different situations, in contrast to many other European landscapes at this time, suggesting that it was linked to an insular cultural tradition. Other disturbance factors including the death of trees, insect attack, flooding and wind-throw are also considered important (e.g. Patterson and Backman, 1988; Schelhaas et al., 2003). Svenning (2002), Bradshaw et al. (2003), Whitehouse and Smith (2004), Mitchell (2005) and Buckland (2005a) all conclude that these factors may have been more important in structuring the landscape than grazing animals alone. Moreover, early Neolithic track ways in the Somerset Levels indicate the use of coppiced wood (Coles and Orme, 1988). Bell and Walker (2005) have suggested that this practice might partly explain the high hazel values at both Mesolithic and Neolithic sites. Coppicing affects pollen production, causing over-production (Rackham, 2006). Similar arguments could also be advanced for the collection of oak leaf for fodder known as ‘shredding’ (Halstead and Tierney, 1998; Smith, 1998). Both these suggestions could explain, at least in part, the high values of oak and hazel pollen which Vera (2000) draws attention to, although, coppicing is not restricted to just these species (Rackham, 2006).

There is, however, good accord in general terms between the picture presented by the fossil beetle record and that from palynology, especially with respect to the importance of various trees within the wider landscape. The apparent importance of more open-indicating taxa such as oak and hazel during the earlier Holocene is borne out by the fossil beetle record, suggesting that these trees played an important role in the wider landscape, rather than being the product of over-production of pollen due to coppicing or other forest management technique. There are also indications that the fossil beetle record picks up patterns of deforestation and re-afforestation evident within Neolithic pollen records. At a local level, there are indications that the landscape exhibited quite a lot of patchiness, above that which appears to be exhibited in the pollen record. This could be explained via two separate factors: the differing catchments of fossil beetle records (very localised) versus pollen records (more regional) as well as issues over the sensitivity of NAP percentages already discussed previously. Thus, the patchiness exhibited by the fossil beetle record may reflect quite small cleared areas in the wider landscape, which may be harder or impossible to establish from many regional pollen diagrams.

Comparing our findings with Buckland (2005a), our results are in accord with his conclusion that there are clear indications of open ground taxa being present in the “Atlantic forest”, although he suggests that such habitats probably formed a limited part of the overall landscape. Like us, he highlights the role of human impact in these systems probably well before the onset of agriculture and draws attention to the role of human impact in structuring forest systems. Where our findings differ is that our results show perhaps rather clearly the contribution of the open taxa and dung beetles to the faunal assemblages and different tree-associates in the early and mid-Holocene, and how variable these contributions seem to have been across the range of sites investigated. The levels of openness appear to have fluctuated in space and time and whilst the early Holocene appears to have supported a more open forest, this does not generally seem to have been the case in the middle Holocene, although even here there are some exceptions. The Neolithic is characterised by significant patchiness and the role of grazing animals in this landscape structuring is evident; the apparent differences evident in the fossil beetle record over this time period, with early clearance, followed by regeneration and then further clearance have not been identified previously in these records.

7. Conclusions

Mitchell (2005) concludes that open forest is only developed once human impact becomes important and that the pollen evidence does not support the concept of the open forest system before this stage, being essentially dense canopy ecosystems. Our results partly concur with this finding, but we believe that local, open areas may have been more important in the earlier part of the Holocene than have been appreciated and that open areas persisted in some areas for the whole of the review period. There is limited evidence to suggest such open areas were driven by the activities of herds of wild grazing animals and it is likely that other disturbance indicators were more important. Overall, there is considerable variation in the patterns seen and the largest challenge we encounter is a poor appreciation for the landscape catchment represented by the fossil beetles and how these data translate into landscape terms.

The insect record presented here shows that landscape structure varied considerably. Over the course of 9500–2000 cal BC there are high values for both trees and open areas, there is considerable variability between the different periods and some sites, suggesting landscape heterogeneity and local scale patchiness. The early Holocene is characterised by quite open woodland, which apparently shares some characteristics with pasture woodland. Later on, however, the canopy of the woodland clearly closes, with a corresponding decline in open indicators, although at some locations local patchiness is still indicated. Levels of dung beetles associated with grazing animals remain low. At c. 4000 cal BC we see what could have been a relatively dramatic clearance of the landscape in some limited locations, followed by apparent afforestation and more sustained clearance towards the end of the Neolithic period, c. 2500–2000 cal BC. Effectively, the British “wildwood” was a constantly evolving and changing ecosystem; we should perhaps be wary of trying to impose a largely static high forest model of its perceived “natural” state on a system which may have been constantly shifting and altering in response to autogenic and allogenic processes. The role of grazing animals appears on the evidence provided to have been relatively minimal, but must await further clarification; it is likely that other disturbance factors were equally if not more important.

There is a need to develop a much better understanding of the relationship between fossil beetle remains and vegetation structure, as well as pollen-fossil beetle relationships. We need to obtain better-stratified and dated insect faunas from the early Holocene, particularly all periods of the Mesolithic, which represents a key period for the ‘Vera debate’. In terms of funding, conservation and curatorial priorities we believe deposits of this date should be given precedence. There are a series of interpretational challenges which need to be overcome if we are to be confident about the degree of actual clearance represented in the fossil beetle record. A project currently being undertaken by the authors, of which the Dunham Massey results form part, is examining the representation of tree versus open beetle taxa from a series of small ponds in grazed and un-grazed forests and pasture woodlands, under varying tree structure. As part of this work, the analysis of pollen from the same sites is also being undertaken. This new research will allow us to re-evaluate the evidence presented here within a stronger paradigm.

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Appendix. Supplementary information

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.quascirev.2009.10.010.

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