

# UNIVERSITY OF BIRMINGHAM

University of Birmingham  
Research at Birmingham

## Can we characterise 'openness' in the Holocene palaeoenvironmental record? Modern analogue studies of insect faunas and pollen spectra from Dunham Massey deer park and Epping Foresty England

Smith, David; Whitehouse, N; Bunting, MJ; Chapman, Henry

DOI:

[10.1177/0959683609350392](https://doi.org/10.1177/0959683609350392)

### Document Version

Publisher's PDF, also known as Version of record

### Citation for published version (Harvard):

Smith, D, Whitehouse, N, Bunting, MJ & Chapman, H 2010, 'Can we characterise 'openness' in the Holocene palaeoenvironmental record? Modern analogue studies of insect faunas and pollen spectra from Dunham Massey deer park and Epping Foresty England', *The Holocene*, vol. 20, no. 2, pp. 215-229.  
<https://doi.org/10.1177/0959683609350392>

[Link to publication on Research at Birmingham portal](#)

### General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

### Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact [UBIRA@lists.bham.ac.uk](mailto:UBIRA@lists.bham.ac.uk) providing details and we will remove access to the work immediately and investigate.

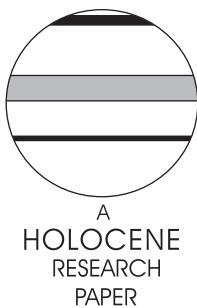
Download date: 24. Apr. 2024

# Can we characterise ‘openness’ in the Holocene palaeoenvironmental record? Modern analogue studies of insect faunas and pollen spectra from Dunham Massey deer park and Epping Forest, England

David Smith,<sup>1\*</sup> Nicki Whitehouse,<sup>2</sup> M. Jane Bunting<sup>3</sup>  
and Henry Chapman<sup>1</sup>

(<sup>1</sup>Institute of Archaeology and Antiquity, The University of Birmingham, Edgbaston, Birmingham B15 2TT, UK; <sup>2</sup>Palaeoecology Centre, School of Geography, Archaeology and Palaeoecology, Queen’s University Belfast, Belfast BT7 1NN, Northern Ireland, UK; <sup>3</sup>Department of Geography, University of Hull, Cottingham Road, Hull HU6 7RX, UK)

Received 15 May 2009; revised manuscript accepted 6 August 2009



**Abstract:** This paper examines the degree to which tree-associated Coleoptera (beetles) and pollen could be used to predict the degree of ‘openness’ in woodland. The results from two modern insect and pollen analogue studies from ponds at Dunham Massey, Cheshire and Epping Forest, Greater London are presented. We explore the reliability of modern pollen rain and sub-fossil beetle assemblages to represent varying degrees of canopy cover for up to 1000 m from a sampling site. Modern woodland canopy structure around the study sites has been assessed using GIS-based mapping at increasing radial distances as an independent check on the modern insect and pollen data sets. These preliminary results suggest that it is possible to use tree-associated Coleoptera to assess the degree of local vegetation openness. In addition, it appears that insect remains may indicate the relative intensity of land use by grazing animals. Our results also suggest most insects are collected from within a 100–200 m radius of the sampling site. The pollen results suggest that local vegetation and density of woodland in the immediate area of the sampling site can have a strong role in determining the pollen signal.

**Key words:** Woodland structure, Vera hypothesis, formation processes, insect death assemblages, modern analogues, actualistic study, Epping Forest, Dunham Massey.

## Introduction

Recently, there has been debate concerning the degree of ‘openness’ of wildwood during the early and middle Holocene (c. 9500–4000 cal BC) and the role that large Herbivores such as aurochs (*Bos primigenius primigenius* (Boj.)), wisent (*Bison bonasus* (L.)), horse (probably *Equus ferus ferus* Bod.) and elk (*Alces alces* Gray) may have played in forming and maintaining woodland clearings (Vera, 2000; Svenning, 2002; Bradshaw *et al.*, 2003; Bradshaw and Hannon, 2004; Whitehouse and Smith, 2004, in press; Birks, 2005; Mitchell, 2005; Moore, 2005; Fyfe, 2007; Bell, 2008). Clearance in Holocene woodland may have resulted from direct human action

such as controlled burning (Innes and Simmonds, 1988; Simmonds, 1996; Bell, 2008), farming (Iversen, 1941) or the construction of archaeological sites and ritual landscapes (Cummings and Whittle, 1993; Pollard, 1999, 2004; Thomas, 1999). The impact of introduced domesticated cattle, sheep and pigs on woodland structure from the Neolithic (c. 4000 cal BC) onwards also has been subject to debate (Buckland and Edwards, 1984; Bradshaw and Hannon, 1992; Bradshaw and Mitchell, 1999; Dinnin and Sadler, 1999; Robinson, 2000; Whitehouse and Smith, in press).

The degree to which proxy palaeoenvironmental data can be used to reliably indicate the presence of woodland clearings is therefore critical. This paper presents results from two modern analogues (Dunham Massey, Cheshire and Epping Forest, Greater London, UK – Figure 1), which were studied in order to examine

\*Author for correspondence (e-mail: d.n.smith@bham.ac.uk)



**Figure 1** Site locations

this issue in detail, part of a wider study that includes several sites, including Windsor Great Park (Surrey) and Hatfield Forest (Essex). The results of these latter sites will be published separately.

## Limitations to establishing past woodland structure

Traditionally, pollen analysis has been one of the main tools utilised to reconstruct Holocene woodlands (Huntley and Birks, 1983). Where palynological reconstruction has been less sure-footed, is the characterisation of how open or closed past woodland structure may have been. It is widely acknowledged there is generally a poor understanding of the relationship between arboreal pollen (AP) and non-arboreal pollen (NAP), in terms of production, representation, filtering effects and interpretation (Groenman-van Waateringe, 1986; Sugita *et al.*, 1999; Vera, 2000; Bunting *et al.*, 2004; Hicks, 2006; Sugita, 2007a,b; Hellman *et al.*, 2009).

Insect remains also have been used to reconstruct the nature and structure of Holocene woodlands (Dinnin and Sadler, 1999; Robinson, 2000; Whitehouse and Smith 2004, *in press*). Often this takes the form of a ratio of the relative proportions of beetles associated with dead wood and/or tree-dependant taxa against those directly associated with dung and 'open areas'. Typically a proportion of between 15 and 20% for tree/wood beetle taxa is considered indicative of closed old woodland and <5% is indicative of largely open landscapes (Robinson 1991, 2000). For the species of insect that indicate pasture/dung, a ratio of >10% is believed to indicate a largely pastoral landscape (Robinson 1991, 2000). The main

difficulty is that there is no clear understanding as to what these values actually mean, in quantitative landscape terms.

## Woodland structure and analogue studies

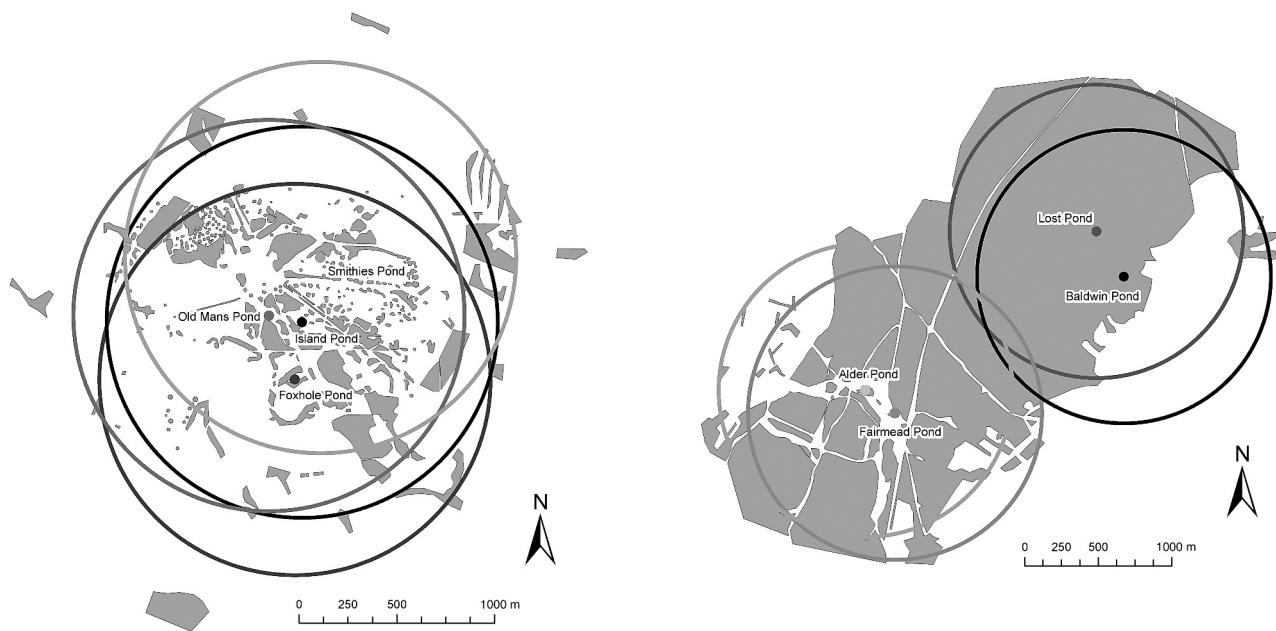
Analogue research to improve the interpretation of the pollen signal for openness in the landscape has been attempted in the past (Groenman-van Waateringe, 1986; Gaillard *et al.*, 1992, 1994; Broström *et al.*, 1998) and has recently been the focus of activities of the PolLandCal network (see [www.ecrc.ucl.ac.uk/pollandcal/](http://www.ecrc.ucl.ac.uk/pollandcal/)), which uses modern pollen data to establish a 'Landscape Reconstruction Algorithm' to overcome some of the problems concerning representation and distance weighting inherent in the deposition of pollen into small water bodies (Sugita *et al.*, 1999; Sugita 2007a,b; Hellman *et al.*, 2009). Such modern analogue studies show that it is possible to extract measures of landscape openness from pollen data, but that this is not a simple or straightforward exercise (McLauchlan *et al.*, 2007; Soepboer and Lotter, 2009).

Only a limited number of modern analogue studies have investigated how insect faunas reflect forest structure (Kenward, 1978, 2006). Kenward (2006) concluded that trees had to be located very close to the site of deposition to be 'visible' in insect faunas and that Robinson's (1991, 2000) proposed figures (discussed above) for closed canopy woodland were reasonable. However, Kenward (2006) was not able to define what differing proportions of species associated with trees might mean for indicating how open ancient woodlands may have been. There has also been no attempt to examine how insect and pollen analyses individually may represent the same modern landscape or how these proxy-indicators could be used together as an indicator package (Kenward and Hall, 1997) for different types of woodland and canopy cover in the past.

In this study, we have sampled sediments from a series of small woodland ponds, in order to produce modern insect 'death assemblages' (Kenward, 1975; Smith, 1996, 1998, 2000; Smith *et al.*, 1999, 2005) that could be suitable analogues for closed or open parkland woodland systems in the Holocene record. Small pond basins were chosen since their taphonomy and possible catchment is relatively simple. It was also felt that these ponds would collect insects from catchments that were comparable in scale to many archaeological and palaeoenvironmental sampling sites.

## Study sites

The Old Park at Dunham Massey, Cheshire, England (Figure 2), is an ancient deer park dating back to at least AD 1362. The present-day landscape was mainly developed in the late 17th century by the Second Earl of Warrington, and the estate is now owned by the National Trust. It covers 101 hectares and is grazed by a substantial herd of fallow deer (*Dama dama* (L.)) (around 250 individuals). The open 'parkland landscape' (defined for this study as a landscape with large isolated trees set into grassland and with a canopy cover of between 20 and 50%) is mainly dominated by mature beech (*Fagus sylvatica* L.), oak (*Quercus* spp.) and ash (*Fraxinus excelsior* L.) trees, with smaller numbers of lime (*Tilia* spp.). These trees occur as isolated individuals or in small groups. The extent of tree cover can be seen in Figure 2. Four ponds from the site were sampled: Fox Hole, Island, Old Mans and Smithies Ponds. Table 1 shows the general dimensions, water pH and vegetation characteristics of each pond, as recorded in the field in summer 2006. No previous palaeoenvironmental work has been undertaken on this site as far as we have been able to ascertain, apart from an unpublished



**Figure 2** Digitised woodland landscapes for Dunham Massey (left) and Epping Forest (right), plotted in 2m<sup>2</sup> rasters in GIS

investigation by Russell G. Coope, of a Lateglacial and early Holocene beetle fauna (Coope pers. comm., 2008).

Epping Forest (Figure 2), Greater London, England, covers 2430 hectares and consists of large areas of dense canopy woodland (defined for this study as an area of dense enclosed woodland with canopy cover near to 100%) interspersed with open grassland 'plains', and small areas of heathland (Baker *et al.*, 1978). At least 70% of the trees are beech (*Fagus sylvatica* L.), oak (*Quercus* spp.) and hornbeam (*Carpinus betulus* L.), many of which occur as old pollards. Silver birch (*Betula pendula* L.) is also present, although in small numbers. The area is grazed by a wild herd of muntjac (*Muntiacus reevesi* (Ogilvy)) and fallow deer of ~500 individuals and part of the area also is grazed seasonally by a small herd of English longhorn cattle (*Bos primigenius taurus* L.) consisting of around 50–100 individuals, mainly restricted to grazing in the plains. Epping Forest is a remnant of the Royal Forest of Essex, established just after the Norman Conquest (AD 1066) and managed as wood pasture by the lords of the manors on behalf of the Crown until ownership was transferred to the Corporation of the City of London in 1878. Four ponds were sampled at Epping: Alder, Baldwins, Fairmead and Lost. Table 2 shows the general dimensions and vegetational characteristics of each pond, as recorded in the field in summer 2006. Previous palynological work from a shallow valley bog near the Iron Age camp at Ambresbury Banks indicated that Epping Forest was dominated by lime (*Tilia* spp. – most likely small-leaved lime *Tilia cordata* L.) woodland between the Neolithic and Roman periods and that today's dominance of beech (*Fagus sylvatica* L.) is a relatively recent phenomenon (Baker *et al.*, 1978; Grant and Dark, 2006).

## Sampling and methods

The ponds studied were sampled using a Ponar-type grab sampler (Mudroch and MacKnight, 1994: 31) from a boat. This approximately sampled the top 10 cm of sediment in the ponds. In addition to causing little disturbance at the surface of the sediment, ponar samplers have been shown to produce consistent samples of both invertebrate faunas and sediment types (Lewis *et al.*, 1982). Many of the ponds studied have recently been dredged (in the last 5–15 years or so) or appear to have very rapid sediment accumulation. This suggests that the insect sub-fossils and other palaeoenvironmental remains sampled have probably only been accumulating for over the last 1–2 decades at a maximum. All of the sampling sites chosen were believed to not have undergone any substantial landscape change during this period, except for the occasional thinning of trees (e.g. Smithies Pond, Dunham Massey).

Normally at least five samples were collected from each pond (four towards the sides and one in the middle). A sample usually consisted of ~10 L of sediment. A sub-sample of 10 ml was taken from each bulk sample for pollen analysis. All flots have been retained pending plant macrofossil analysis.

Samples examined for beetle analysis (22 from Dunham Massey and 19 from Epping Forest) were processed using the standard method of paraffin flotation for archaeoentomological samples, as outlined by Kenward *et al.* (1980). The insect remains recovered were identified by direct comparison with the Gorham and Girling collections of British Coleoptera housed at the University of Birmingham. Where applicable, ecological codes, based on those of Robinson (1981, 1983), have been assigned to individual taxa.

**Table 1** Description of the sampling locations at Dunham Massey

Pond	Physical Characteristics	Surrounding tree vegetation	Surrounding ground vegetation	Pond vegetation
Fox Hole	Sunken pond (? ex sand quarry) surrounded by trees on rim. Limited overhang of trees. Grazing pressure in vicinity probably intense judging by deer droppings. Dimensions: Roughly elliptical in shape, 51 X 29 m Depth: 1.5–2 metres pH: 7.48	Surrounded by a screen of oak ( <i>Quercus</i> spp.), beech ( <i>Fagus sylvatica</i> L.), holly ( <i>Ilex aquifolium</i> L.) and birch ( <i>Betula</i> spp.). Canopy height of c. 40 m.	bracken ( <i>Pteridium aquilinum</i> (L.) Kuhn); soft-rush ( <i>Juncus effusus</i> L.); skullcap ( <i>Scutellaria galericulata</i> L.); marsh bedstraw ( <i>Galium palustre</i> L.); Gypsywort ( <i>Lycopus europaeus</i> L.); tormentil ( <i>Potentilla erecta</i> (L.) Raeusch.)	On Pond: common duckweed ( <i>Lemna minor</i> L.). Pond edge: soft-rush ( <i>Juncus effusus</i> L.); watermint ( <i>Mentha aquatica</i> L.).
Island Pond	Kidney-shaped pond with a small island on one side, in the middle of deer park. 95% covered in water lily. Dimensions: 130m X 65 m Depth: 1.00–1.5 metres pH: 8.00	oak ( <i>Quercus</i> spp.), sweet chestnut ( <i>Castanea sativa</i> Mill.), sycamore ( <i>Acer pseudoplatanus</i> L.), rowan ( <i>Sorbus acuparia</i> L.). Canopy height of c. 40m. Canopy height of c. 40 m.	common nettle ( <i>Urtica dioica</i> L.), creeping buttercup ( <i>Ranunculus repens</i> L.); greater plantain ( <i>Plantago major</i> L.); hedge bindweed ( <i>Calystegia sepium</i> (L.) R. Br.); white clover ( <i>Trifolium repens</i> L.); tormentil ( <i>Potentilla erecta</i> (L.) Raeusch.); soft-rush ( <i>Juncus effusus</i> L.); bracken ( <i>Pteridium aquilinum</i> (L.) Kuhn); sharp-flowered rush ( <i>Juncus acutiflorus</i> Ehrh. ex Hoffm.); grass spp. (Poaceae); marsh bedstraw ( <i>Galium palustre</i> L.).	On Pond: rigid hornwort ( <i>Ceratophyllum demersum</i> L.); yellow waterlily ( <i>Nuphar lutea</i> L.). Pond edge: Sweet flag ( <i>Acorus calamus</i> L.); watermint ( <i>Mentha aquatica</i> L.); skullcap ( <i>Scutellaria galericulata</i> L.); field horse tail ( <i>Equisetum arvense</i> L.); Water pepper ( <i>Persicaria hydropiper</i> (L.) Spach.); Water Forget-me-not ( <i>Myosotis scorpioides</i> L.)
Old Mans Pond	Almost square, very shallow pond, with lots of pond edge vegetation. Small, round island in the middle. Dimensions: 70 m X 32 m. Depth: 50 cm-1m, in some places < 50cm. pH: 7.8	Oak (30%) ( <i>Quercus</i> spp.); lime ( <i>Tilia</i> spp.); beech ( <i>Fagus sylvatica</i> L.); sweet chestnut ( <i>Castanea sativa</i> Mill.). Canopy height of c. 40 m.	common bird's-foot-trefoil ( <i>Lotus corniculatus</i> L.); tormentil ( <i>Potentilla erecta</i> (L.) Raeusch.); skullcap ( <i>Scutellaria galericulata</i> L.); marsh horsetail ( <i>Equisetum palustre</i> L.); field horsetail ( <i>Equisetum arvense</i> L.); bracken ( <i>Pteridium aquilinum</i> (L.) Kuhn); common nettle ( <i>Urtica dioica</i> L.).	On Pond: Spiked water-milfoil ( <i>Myriophyllum spicatum</i> L.); Pond Edge: Bullrush ( <i>Typha latifolia</i> L.); Sweet flag ( <i>Acorus calamus</i> L.); Watermint ( <i>Mentha aquatica</i> L.); Watercress ( <i>Rorippa nasturtium-aquaticum</i> (L.) Hayek); Water pepper ( <i>Persicaria hydropiper</i> (L.) Spach.); marsh pennywort ( <i>Hydrocotyle vulgaris</i> L.); yellow iris ( <i>Iris pseudocorus</i> L.). Island: great willowherb ( <i>Epilobium hirsutum</i> L.); bramble/blackberry ( <i>Rubus</i> section Rubus.); bittersweet ( <i>Solanum dulcamara</i> L.).
Smithies Pond	Artificial pond, open with grass at one end, at other end overhanging trees (aok). Partially dominated by water-lily. Area fenced off to keep deer out. Oblong-shape pond. Dimensions: 108 X 65 m Depth: Shallow: 1 m. pH 7.72.	Scots pine ( <i>Pinus sylvestris</i> L.); rowan ( <i>Sorbus acuparia</i> L.); beech ( <i>Fagus sylvatica</i> L.); lime ( <i>Tilia</i> spp.); oak ( <i>Quercus</i> spp.). Canopy height of c. 40 m.	tormentil ( <i>Potentilla erecta</i> (L.) Raeusch.); common nettle ( <i>Urtica dioica</i> L.); soft-rush (50%) ( <i>Juncus effusus</i> L.); Grass (Poaceae); meadow buttercup ( <i>Ranunculus acris</i> L.); mare's-tail ( <i>Hippuris vulgaris</i> L.); black medick ( <i>Medicago lupulina</i> L.); white clover ( <i>Trifolium repens</i> L.); eyebright ( <i>Euphrasia</i> spp.); sharp-flowered rush ( <i>Juncus acutiflorus</i> Ehrh. ex Hoffm.).	On Pond: Yellow water lily ( <i>Nuphar lutea</i> L.); Water chick weed ( <i>Myosoton aquaticum</i> (L.) Moench) Pond Edge: skullcap ( <i>Scutellaria galericulata</i> L.); soft-rush ( <i>Juncus effusus</i> L.); bittersweet ( <i>Solanum dulcamara</i> L.)

**Table 2** Description of the sampling locations at Epping

Pond	Physical Characteristics	Surrounding tree vegetation	Surrounding ground vegetation	Pond vegetation
Alder Pond	Small shaded pond covered in pondweed, close to actively grazed former common-land (long horn cattle). Dimensions: 14 X 11 metres Depth: 50–70 cm pH: 7.4	Dominated by over-hanging alder ( <i>Alnus</i> spp.) on three sides, within immediate 2–3 metres. One side open to unimproved pasture, 10% scrub cover in surrounding area (bramble, hawthorn), 10% tree cover in 500 m radius of site. Canopy height c. of 20 metres.	Grass (POACEAE); stinging nettle ( <i>Urtica dioica</i> L.); buttercup ( <i>Ranunculus</i> spp.)	On pond: duckweed ( <i>Lemna minor</i> L.), coverage almost 100%. Pond Edge: marsh thistle ( <i>Cirsium palustre</i> L. Scop.); soft-rush ( <i>Juncus effusus</i> L.); hemp agrimony ( <i>Eupatorium cannabinum</i> L.); curled leaved dock ( <i>Rumex crispus</i> L.); water pepper ( <i>Pericaria hydropiper</i> (L.) Spach.) On pond: white water-lily ( <i>Nymphaea alba</i> (L.) Sm), coverage 25%.
Fairmead Pond	Elliptical pond in the middle of grazing plain (long horn cattle), coppiced woodland to one side. Dimensions: 57 X 21 metres Depth: 1.5–2.00 metres pH: 7.9	Surrounded by coppiced willow ( <i>Salix</i> spp.), hornbeam ( <i>Carpinus</i> spp.), alder ( <i>Alnus</i> spp.) and poplar ( <i>Populus</i> spp.) on approximately half of one side, with nearby mixed coppice, set in a mostly open landscape (20% trees), with 30% scrub cover of bramble ( <i>Rubus fruticosus</i> L. agg.), birch ( <i>Betula</i> spp.), dog rose ( <i>Rosa canina</i> L.) Canopy height of c. 20 metres	creeping thistle ( <i>Cirsium arvense</i> (L.) Scop.); buttercup ( <i>Ranunculus</i> spp.); common ragwort ( <i>Senecio jacobaea</i> L.); bracken ( <i>Pteridium aquilinum</i> (L.) Kuhn); sheep sorrel ( <i>Rumex acetosella</i> L.); marsh thistle ( <i>Cirsium palustre</i> L. Scop.); common nettle ( <i>Urtica dioica</i> L.)	Pond edge: bramble/blackberry ( <i>Rubus</i> section Rubus); soft-rush ( <i>Juncus effusus</i> L.); bulrush ( <i>Typha latifolia</i> L.); gipsywort ( <i>Lycopus europaeus</i> L.); water mint ( <i>Mentha aquatica</i> L.); great willowherb ( <i>Epilobium hirsutum</i> L.); skullcap ( <i>Scutellaria galericulata</i> L.); skunkcabbage ( <i>Saururus chinensis</i> L.); bittersweet ( <i>Solanum dulcamara</i> L.); common water-plantain ( <i>Alisma plantago-aquatica</i> L.). On pond: bog pondweed ( <i>Potamogeton polygonifolius</i> Pourret).
Lost (or Blackweir) Pond	Woodland pond, deep in Epping Forest, surrounded by dense, mature, woodland, much of it pollarded. Significant amounts of deadwood in pond. Dimensions: Roughly circular, 54 X 46 m Depth: 1.00–1.5 metres. pH: 8.1	Entirely surrounded by woodland, mostly beech ( <i>Fagus sylvatica</i> L.) and oak ( <i>Quercus</i> spp.) pollards, with birch ( <i>Betula</i> spp.), holly ( <i>Ilex</i> spp.), willow ( <i>Salix</i> spp.), hornbeam ( <i>Carpinus</i> spp.). 100% tree cover in surrounding area, 5% scrub and 1% ground cover in surrounding area. Pond plants c. 15%.	bramble ( <i>Rubus</i> section Rubus); grasses (POACEAE).	Pond edge: yellow iris ( <i>Iris pseudacorus</i> L.); rosebay willowherb ( <i>Chamerion angustifolium</i> (L.) Holub); soft-rush ( <i>Juncus effusus</i> L.); gipsywort ( <i>Lycopus europaeus</i> L.)
Baldwins Pond	Elongated-shaped fishing pond made in c. 1875, possibly as a flood precaution. Dredged in 2000. Originally larger, but has started to silt up at eastern end. Surrounded by mature dense woodland, but open to south side. There is a small patch of meadowland 5 metres from the pond, to the east. The pond is stocked with fish (carp, roach, perch). Dimensions: 68 X 24 m at max extent Depth: 2.5 metres pH: 7.3.	Canopy height of c. 40–50 metres. Surrounded by dense mature beech ( <i>Fagus</i> spp.), oak ( <i>Quercus</i> spp.), hornbeam ( <i>Carpinus</i> spp.), Hoppy ( <i>Ilex</i> spp.) and hawthorn ( <i>Crataegus</i> spp.), much of it pollarded. c. 80% coverage, with canopy height of c. 50 metres +. Ground cover plants c. 10%, pond plants 10%.	Grasses (POACEAE); greater plantain ( <i>Plantago major</i> L.); water mint ( <i>Mentha aquatica</i> L.); bramble ( <i>Rubus</i> section Rubus); common nettle ( <i>Urtica dioica</i> L.); bracken ( <i>Pteridium aquilinum</i> (L.) Kuhn); white clover ( <i>Trifolium repens</i> L.); curled leaved dock ( <i>Rumex crispus</i> L.); hairy bird's-foot-trefoil ( <i>Lotus subtiliflorus</i> Leg.); wild angelica ( <i>Angelica sylvestris</i> L.); reed sweet-grass ( <i>Glyceria maxima</i> (Hartm.) Holmb.)	On Pond: bulrush ( <i>Typha latifolia</i> L.); broad-leaved pondweed ( <i>Potamogeton natans</i> L.). Pond Edge: water mint ( <i>Mentha aquatica</i> L.); Gipsywort ( <i>Lycopus europaeus</i> L.); yellow iris ( <i>Iris pseudacorus</i> L.); pendulous sedge ( <i>Carex pendula</i> Hudson); bulrush ( <i>Typha latifolia</i> L.); common water-plantain ( <i>Alisma plantago-aquatica</i> L.).

The ecological coding of the individual species is shown in the second column of Data File 1 (available online). The percentages of each ecological group discussed here (df = dung, p = open areas, dw = dead wood and lf = tree foliage feeders) are calculated as a proportion of all terrestrial MNI (minimum numbers of individuals) recovered (aquatics are removed as standard from this statistic). The results from the samples collected from each of the ponds have been averaged to give single values for each pond.

Samples for pollen analysis were processed using standard methods (Berglund and Ralska-Jasiewicsowa, 1986) including hydrofluoric acid treatment where sediments were clay-rich, acetolysis, staining with aqueous safranin and mounting in silicon oil. A minimum count of 400 terrestrial pollen types was made from each sample. Pollen taxonomy follows Bennett *et al.* (1994) and Bennett (1995–2007). In this paper, preliminary results are presented, based on a mean of three samples from Smithies, Dunham Massey (2, 5 and 6) and Old Mans, Dunham Massey (3, 5 and 6) and only one sample from each of the other ponds.

General nomenclature for plants observed during fieldwork follows Stace (1997).

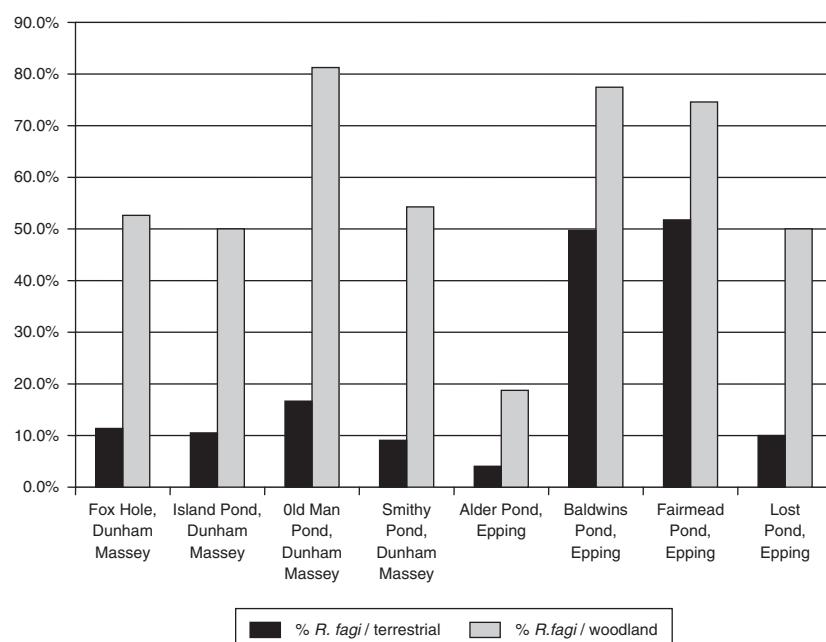
The percentage canopy coverage was calculated using ESRI ArcGIS 9.1 Geographical Information System (GIS) software. Areas of woodland, excluding isolated trees, were digitised directly from the high definition aerial photographs as binary polygons, which then were converted to a 2 m resolution continuous ‘raster’ recording the presence or absence of canopy cover (Burrough, 1986; Conolly and Lake, 2006). For each of the sampling sites, buffers were generated at 3 intervals of 100, 200 and 1000 m radius from the sampling site. These buffers were then used to clip the canopy raster so that canopy coverage within the three specific zones could be quantified as a percentage. Figure 2 illustrates the area of woodland digitised at each site and indicates the 1000 m radius circle for each of the ponds.

## Results

The full beetle lists for the samples from Dunham Massey and Epping are included in Data File 1 (available online). The taxonomy follows

Lucht (1987). In total, 1373 individuals (MNI) representing 209 taxa of Coleoptera, were recovered. Between 20 and 30% of the faunas recovered consist of a range of dytiscid, hydrophilid and hydroniid diving and water beetles (ecological grouping a = aquatics), typical of standing and slow-flowing waters. Grassland and open species (ecological group p) are represented by phytophage taxa such as the *Sitona*, *Phytobius* and *Ceutorynchus* weevils, accounting for 5–15% of the fauna. Species associated with animal dung (ecological group df), mainly *Aphodius contaminatus* and *A. sphacelatus*, account for ~4–15% of the terrestrial fauna at Dunham Massey and <5% at Epping Forest. Woodland taxa (ecological group dw + lf) usually account for 12–23% of the terrestrial fauna in the death assemblage from most of the ponds, with the exception of two ponds at Epping (Baldwins and Lost), which are set in dense canopy woodland where this figure rises to ~60–70%. Typically, this woodland fauna mainly consists of species associated with foliage (ecological group lf) which can account for between 10 and 50% of the terrestrial fauna recovered. Often this consists of one very abundant species, the beech leaf miner, *Rhynchaenus fagi*. *R. fagi* mines distinctive brown passages in young beech leaves in spring and summer. The dominance of this single species is clearly indicated when the relative proportion of this species as part of both the terrestrial fauna in general and as part of the tree/wood ecological grouping is calculated (Figure 3). This species will be considered further in the discussion below. Other insect species encountered here are associated with deadwood (ecological group dw). Typically, this group is represented by small numbers of the anobiids (furniture beetles) such as *Anobium punctatum* and *Ptilinus pectinicornis*. Several species of bark and pinhole scolytids, such as *Dryocoetes villosus* and *Xyleborus saxeseni*, occur in low numbers in many samples. Similarly, the introduced New Zealand weevil *Euophryum confine* is a common component of the faunas recovered. This grouping usually accounts for between 4 and 12% of the terrestrial fauna recovered.

The various proportions of the terrestrial insect ecological groupings for both sites have been calculated and plotted in Figures 4–6. Figure 4 presents the relative proportions of woodland insect indicators, expressed as a percentage of the terrestrial fauna. The relative proportions of indicators of dead wood (dw) and tree leaf



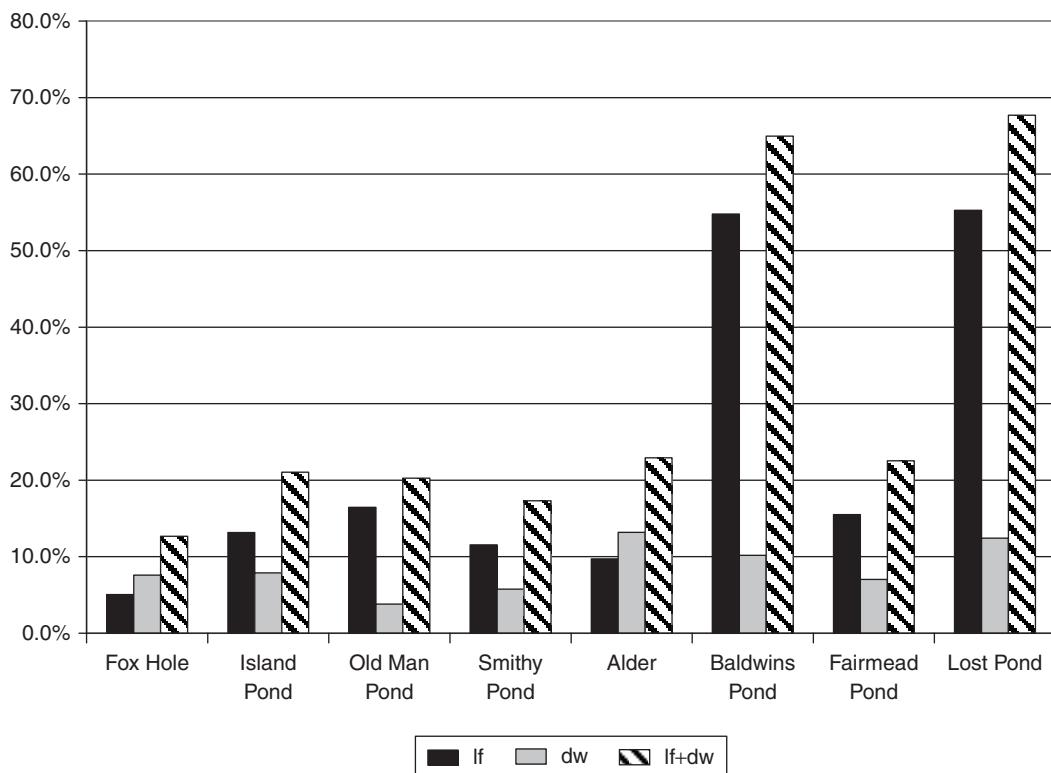
**Figure 3** The relative proportion of *Rhynchaenus fagi* as part of the total terrestrial fauna and the overall tree/wood (ecological groups dw and lf) fauna, respectively, for ponds at Dunham Massey and Epping Forest

associated insects (If), along with the combined sum of these two groups, are plotted in Figure 4. Figure 5 presents the same data as Figure 4 but with *R. fagi* removed from the calculations. The reason for the removal of this species is explained further below.

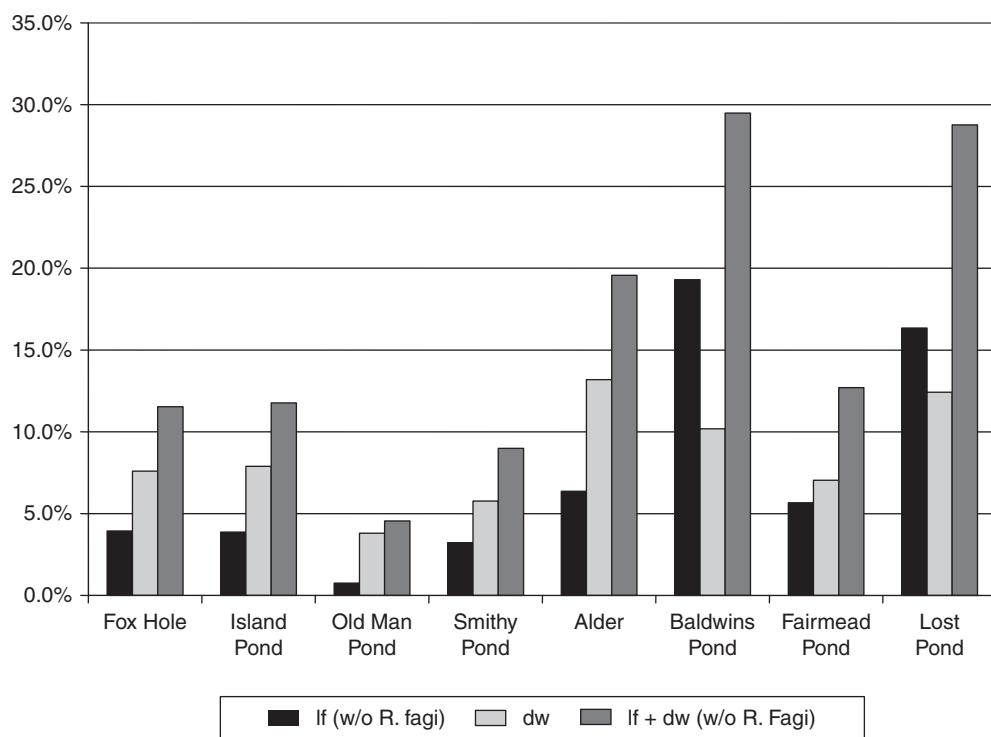
Figure 6 presents the relative proportions of beetle taxa associated with open landscapes, grass and meadowlands. Again, these data are

presented as both a combined sum and with the taxa associated with herbivore dung (df) and grasslands (p) clearly separated out.

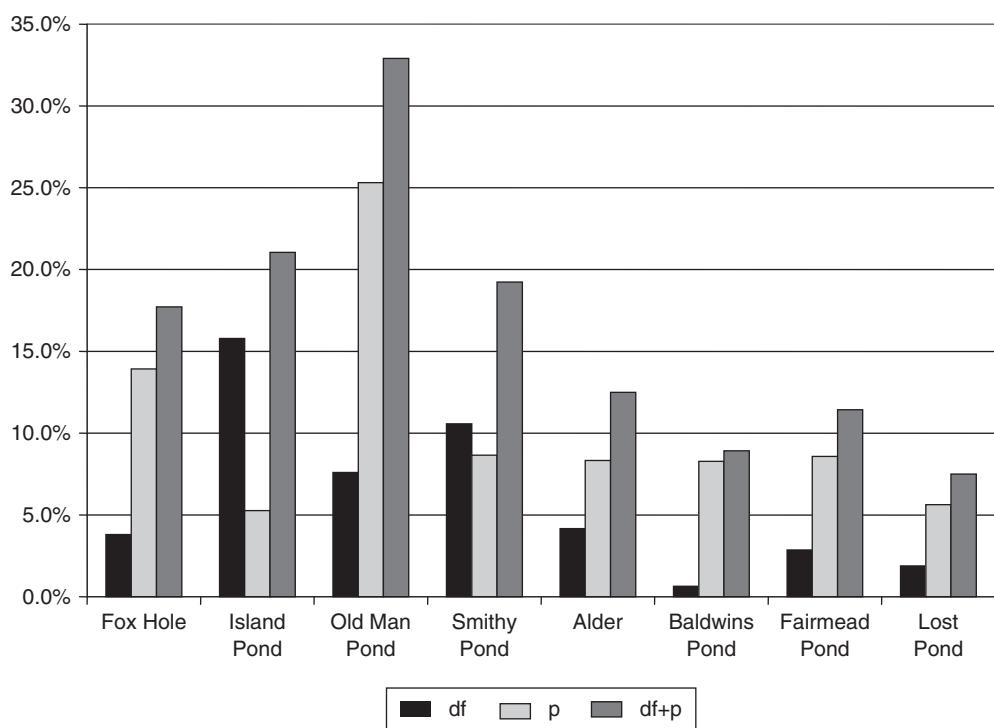
The pollen assemblages are grouped into four vegetation indicator classes for the purposes of this study (Figure 7). Pollen grains from plants, which are believed to have a strong affinity with human activity (Behr, 1981), are grouped separately from grasses



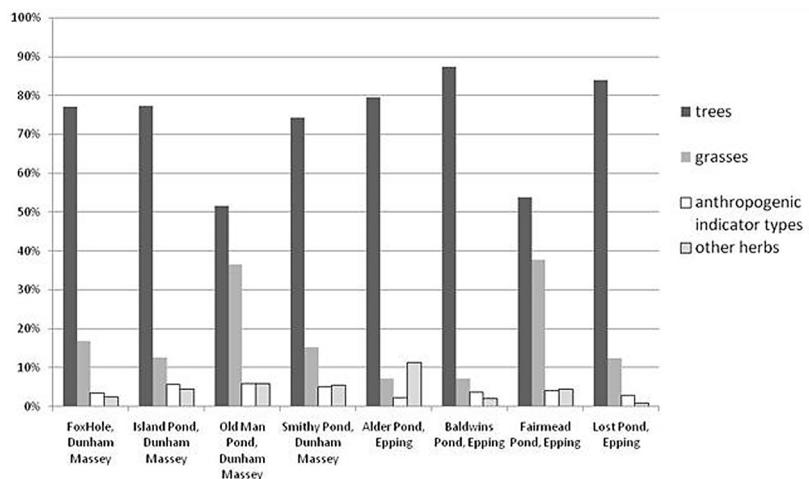
**Figure 4** The relative proportion of insect indicators for woodland shown individually for deadwood (dw) and tree leaf (If) ecological groups and with both groups combined (including *Rhyphaenus fagi* in all cases)



**Figure 5** The relative proportion of insect indicators for woodland shown individually for deadwood (dw) and tree leaf (If) ecological groups and with both groups combined (excluding *Rhyphaenus fagi* in all cases)



**Figure 6** The relative proportion of insect indicators for animal dung (df) and indicators for open ground (p) shown individually and combined from ponds at Dunham Massey and Epping Forest



**Figure 7** Relative proportion of total land pollen (TLP) assemblages from the study sites

and other herbs and listed in the caption to Figure 7. The tree and shrub assemblage from Dunham Massey is dominated by oak (*Quercus* spp.) pollen, with alder (*Alnus glutinosa*), beech (*Fagus sylvatica*) and birch (*Betula* spp.) also common. Other tree and shrub taxa recovered include ash (*Fraxinus excelsior*), maple or sycamore (*Acer campestre* L.-type), elm (*Ulmus* spp.), lime (*Tilia* spp.) and pine (*Pinus* spp.). Approximately 30% of the grass pollen grains measure <26 µm in the longest dimension, suggesting that these originate from common reed (*Phragmites australis*). In samples from Epping Forest, the composition of the tree and shrub sum is more varied, with oak, beech, birch and hornbeam (*Carpinus betulus*) dominating in varying proportions. Alder pollen accounts for 40% of total land pollen (TLP) at Alder Pond, but only occurs in low numbers at the other ponds. This is not altogether surprising since a 5-m wide ring of alder trees overhangs Alder Pond.

Table 3 presents a comparison between the proportion of canopy cover indicated by the GIS model and the relative proportion of the indicators for woodland obtained from both the insect and pollen assemblages for the eight ponds studied. The GIS analysis indicates that within 100 m of the ponds at Dunham Massey, values for tree cover varied widely (23.2% at Fox Hole, 36.2% at Island, 49.5% at Old Mans and 23.7% at Smithies) but at 1000 m the degree of variation in canopy cover between the four ponds has declined greatly (15.4% at Fox Hole, 16.6% at Island, 16.2% at Old Mans and 17.2% at Smithies – see Data File 1 (available online)). At Epping, two of the ponds studied (Alder and Fairmead) are set into open parkland environment similar to that seen at Dunham Massey, consisting of grazing land with isolated and mature trees and have similar GIS estimation of canopy cover within 100 m (31.7% at Alder and 35.2% at Fairmead). In contrast,

**Table 3** Direct comparison between the various methods to reconstruct the relative proportion of tree cover at Dunham Massey and Epping Forest

		Dunham Massey				Epping Forest			
		Fox Hole	Island	old Man	Smithies	Alder	Baldwin	Fairmead	Lost
GIS (Calculation for radius)	100 m	23.2%	36.2%	49.5%	23.7%	31.7%	100%	35.1%	100%
	200 m	26.1%	39.9%	37.1%	31.5%	54.1%	93.9%	45.3%	100%
	1000 m	15.4%	16.6%	16.2%	17.2%	67.8%	59%	69.9%	77.2%
Insect analysis	Dung and open ground	17.7%	21.1%	32.9%	19.2%	12.5%	8.9%	11.4%	7.5%
	Deadwood and tree leaf <sup>a</sup> (including <i>R. fagi</i> )	12.6%	21.0%	20.2%	16.8%	22.2%	64.9%	22.8%	67.5%
	Deadwood and tree leaf (excluding <i>R. fagi</i> )	11.5%	11.8%	4.5%	9.0%	19.6%	29.5%	12.7%	28.8%
Pollen analysis	Canopy indicators	77.2%	77.3%	51.7%	74.2%	79.5%	87.3%	53.8%	84.0%

<sup>a</sup>dw = dead wood and lf = tree leaf litter are the codings used in Tables 1–2, and Figures 3–6.

Baldwins and Lost at Epping, are set into very dense canopy woodland with very little under-storey vegetation or open areas. Both Baldwins and Lost have GIS estimates of canopy cover of 100% at 100 m. At 1000 m, this estimate has dropped to 59% (Baldwins) and 77.2% (Lost), respectively.

## Discussion

The results discussed above raise a number of issues that need further consideration:

### Can the insect taxa recovered provide a suitable analogue for woodlands of the past?

From the outset, it was clear that the modern woodland environments we are studying could not be considered to be exact equivalents for the ancient woodlands of the early Holocene. Such forests included small-leaved lime (*Tilia cordata* L.) and certainly had a different species composition. It is likely that beech (*Fagus sylvatica* L.) was not as dominant in the Holocene woodland as it was at both of the modern analogue sites (Grant and Edwards, 2008). Large wild herbivores such as aurochs, wisent and elk are no longer present in the British Isles and their possible role, along with that of humans, in structuring past woodland cannot be replicated.

Moreover, there are some obvious differences between our modern analogue insect faunas and those normally recovered from Holocene deposits. Firstly, a number of species recovered at Dunham Massey and Epping are not indigenous to Britain, but are now frequently recovered in modern assemblages. This includes the Australasian species *Lathridius bifaciatus*, present in Britain only since 1949 (Hammond, 1974). *Lathridius nodifer* may also be a relatively recent introduction; Hammond (1974) suggests the first record for its presence in Britain is 1839. The same seems to be true of the cossinine weevil *Euophryum confine*, which appears to have been introduced in 1937 (Morgan, 1978) and now seems to have become one of our most widely distributed and common deadwood insects (Hammond, 1974; Kenward and Tipper, 2008). Whether these species have moved into unoccupied niches in the environment or have out-competed indigenous species is not clear.

Secondly, many early Holocene deposits associated with wood peat contain taxa which are today endangered, considered to be rare '*Urwaldrelik*' or, in the case of over 40 species, considered to be extirpated from the British Isles at present (Buckland, 1979, 2005; Buckland and Dinnin, 1992; Whitehouse, 1997, 2006; Smith and Whitehouse, 2005). The lists of taxa from modern Dunham Massey and Epping, conversely, only contain 11 taxa

(5%), which are uncommon (ranked as Notable B in the British Red Data Book (Hymen and Parsons, 1992)). This probably results from deadwood habitats being a more common part of the structure of earlier Holocene woodlands than they are today (Buckland and Dinnin, 1989; Whitehouse, 1997, 2006; Smith and Whitehouse, 2005).

A more specific problem for this study is that these modern woodland faunas are dominated by the beech leaf miner *Rhynchaenus fagi* (proportion of *R. fagi* in terrestrial fauna: 11.4% at Fox Hole, 10.5% at Island, 16.7% at Old Mans, 9.1% at Smithies, 4.1% at Alder, 49.7% at Baldwins, 51.8% at Fairmead and 10% at Lost). Moreover, *R. fagi* accounts for >50% of the indicators for tree/woods (lf & dw) recovered in many instances (52.6% at Fox Hole, 50% at Island, 81.3% at Old Mans, 54.3% at Smithies, 18.8% at Alder, 77.5% at Baldwins, 74.6% at Fairmead and 50% at Lost; also see Figure 3). Leaf feeders, such as *R. fagi* are comparatively rarer than deadwood species in the palaeoentomological record (Smith and Whitehouse, 2005). The exceptional abundance of the leaf feeder *R. fagi* in most of these modern sites must primarily result from beech being common at these sites. Many of the beech trees at both sites are large mature pollards carrying an abnormally dense head of foliage compared to un-pollarded, wild beeches. Many such old pollards have also now reached an age where limbs are being thinned out by natural die-off as the trees return to a more normal canopy structure; it may be that the foliage of such limbs is more susceptible to attack by pests (Michael Grant, pers. comm.). Also, the shallow rooting system of beech appears to make it more susceptible to the effects of drought over a recent series of dry summers in the first half of this decade (Grant and Edwards, 2008). This, along with possible rising pollution levels over the last decade, has resulted in notable beech decline in England, with beech becoming more susceptible to pathogens and other pest problems (Woodcock *et al.* 1995; Peterken and Mountford, 1996; Powers *et al.*, 2004; Grant and Edwards, 2008; UK Forestry Commission, website accessed March 2008). As beech trees become progressively more stressed, they appear to support a very large population of *Rhynchaenus fagi*. The dominance of this species in these faunas is probably not typical for these sites over a longer period of time. One way to more fully explore the effects of the super-abundance of this species is to treat it as an outlier and remove it from the calculations. There is some history for adopting such an approach for super-abundant species (>10%) in the archaeoentomological record, since it enables other patterns in the data to be explored more fully (Kenward, 1978).

In conclusion, we cannot attempt to use these analogues as direct 'mirrors' for the past. We are simply exploring the reliability of proxy environmental data to reconstruct the nature of

canopy cover and the intensity of grazing in broadleaf European woodland environments. If we can demonstrate this with modern data, it seems reasonable to presume the same approach applies in the past. It is the principle, rather than the precise detail, that we are investigating, and therefore the fact that the species list has changed since the earlier Holocene does not matter, since the functional groups of taxa (e.g. deadwood versus dung beetles) are our main concern.

### **How well is the 'actual' landscape surrounding the ponds reflected by the proxies: can we separate 'parkland landscapes' from closed canopy woodland?**

The results from this initial study suggest that palaeoentomological insect faunas can be used to directly examine the nature of past canopy cover and assess openness. The various proportions of woodland insects recovered suggest that it is possible to distinguish between faunas recovered from the ponds in parkland landscapes and those in 'dense canopy' woodland. At Dunham Massey, insect indicators for trees/woods accounted for 12.6% of the terrestrial fauna at Fox Hole, 21% at Island, 20.2% at Old Mans and 16.8% at Smithies (Figure 3). At Epping, the two ponds set into the relatively open plains produced similar proportions of these tree/woodland taxa (22.2% at Fairmead and 22.8% at Alder). However, the two 'enclosed canopy' ponds (Baldwins and Lost) produced strikingly higher proportions of woodland insects (64.9% at Baldwins and 67.5% at Lost). If this dramatic difference can be replicated across a wider range of modern studies, it should also be expected to occur in the palaeoecological record.

However, the dominance of *Rhynchaenus fagi* in the woodland insects recovered might be seen to be causing this difference in the values for woodland insects between the parkland and closed canopy woodlands. Figure 5 presents the relative proportions for open landscape and woodland insect indicators for both Dunham Massey and Epping Forest, without *Rhynchaenus fagi*. The ponds from the parkland landscapes now produce even lower values of woodland indicators (11.5% at Fox Hole, 11.8% at Island, 4.5% at Old Mans, 9.0% at Smithies, 12.7% at Fairmead and 22.2% at Alder). These lower figures make sense given the relatively low values from the GIS canopy estimates at 100 m for these ponds (Fox Hole 23.2%, Island 36%, Old Mans 49%, Smithies 23.7%, Alder 31.7% and Fairmead 35.1%). Conversely, Alder Pond at Epping, despite having a relatively low GIS estimate of tree cover at 100 m (31.7%), still maintains a relatively high proportion of woodland insects (19.6%). It is probable that the overhanging alder and willow trees at Alder Pond have contributed their own specific insect fauna into the pond, which has raised the occurrence of this specific ecological group. Both of the enclosed canopy ponds at Epping still produce high proportions of insects associated with trees (24.3% at Baldwins and 41.8% at Lost). This suggests that even after *R. fagi* has been removed from the calculations there is still a quantitative difference in the amount of tree and woodland taxa represented in the insect faunas between parkland and closed canopy landscapes.

This study therefore suggests that for insect taxa the 'rough rule of thumb' established by Robinson (1981, 1982) and Kenward (2006) does, broadly, hold true. Insect faunas, where woodland species account for >20–25% of the terrestrial taxa, probably indicate closed canopy woodland and values <5% probably indicate a largely cleared landscape. The analysis presented here suggests that values between 5 and 15% may indicate parkland or pasture woodland landscapes. However, further study of a range of modern woodland settings of varying structure and density is necessary to be fully confident of this provisional statistic.

A similar pattern can be seen in pollen data when the floras from parkland landscapes and the closed canopy are compared. The

pollen assemblages from the four Dunham Massey ponds are dominated by tree pollen (Fox Hole 77.2%, Island 77.3%, Old Mans 51.7% and Smithies 74.2%) (Figure 7 and Data File 1 (available online)). This is lower than the 90–95% AP commonly associated with the 'high woodland phase' in the early and mid-Holocene and reflects the 'pasture-park woodland' landscape at these sites. For the two enclosed canopy sites of Lost and Baldwins ponds at Epping, total tree (arboreal) pollen values of 84.0 and 87.0% are recorded respectively, a slightly higher value than those obtained at the parkland landscape sampling sites. Rules of thumb are not widely available in the palynological literature, although Birks (1988) suggests that >50% tree pollen indicates local woodland presence in an upland area, and Groenman-van Waateringe (1986) argued that 25–55% AP reflect open forest or the forest edge, and values over 70% suggest closed forest which only can support limited grazing. One explanation for the apparent difference between the results presented here and those of Groenman-van Waateringe (1986) may be the fact that the pollen in this analogue study is from pond sediments whereas Groenman-van Waateringe analysed subsurface soil samples. Even a small pond will have a substantially larger relevant source area of pollen than a soil sample (Sugita, 1994). In addition, the threshold will vary with the types of trees present, since pollen production varies by up to an order of magnitude between tree species (Broström *et al.*, 2009). The same is also true for any attempt to use the modern analogue data presented here as a direct comparison to the palaeoenvironmental record. For example, oak is a very common and often dominant tree at both Dunham Massey and Epping Forest, but is clearly less common in early Holocene (e.g. Mesolithic/Neolithic) 'high forest', which probably had higher proportions of lime (*Tilia* spp.) and elm (*Ulmus* spp.). Sugita *et al.* (1999) estimate that oak produces ~7.5× as much pollen per unit area as grass, compared to 1.3× for lime and 0.8× for elm. Therefore, the arboreal to grass pollen ratio will be higher in the modern oak dominated landscape than if lime or elm were the main trees present, without any changes in the distribution or extent of woodland canopy.

### **Can we see the subtle differences in canopy cover between the ponds in the 'parkland' landscapes reflected in the proxies?**

The data presented in Data File 1 (available online) also suggest that it may be possible to distinguish differing areas of canopy cover, even within single landscapes such as parkland. Examined pond by pond, the estimated canopy cover and the proportions of woodland insect species seem to correlate. This is not what we would have predicted when we started this study. At this local level, where essentially similar landscapes were being dealt with, factors such as the degree of canopy cover, the extent to which trees overhang the ponds and the amount of deadwood in the local landscape would have been expected to have more influence over the nature of the woodland fauna recovered than relative canopy cover alone. This may, of course, only be coincidence, given that we are dealing with only eight sampling sites and the faunas recovered are small. Nevertheless, this is encouraging and suggests that woodland insect faunas may be more sensitive indicators for examining canopy structure than previously thought. It will be interesting to see if the larger faunas recovered from Windsor Great Park and Hatfield Forest, our other study sites which form this modern analogue work, also reflect such a close degree of correspondence between canopy cover and the relative proportions of insect species associated with trees.

There is less variation in percentage tree pollen in response to variations in canopy cover. Pollen spectra are best understood as a distance-weighted vegetation signal (Prentice, 1985), whereas the canopy data provided here are a simple sum with no distance weighting within the radius selected. For example, at Alder Pond,

tree cover within 100 m is relatively low (31.7%) but tree pollen accounts for 79.5% of the terrestrial pollen. More than 50% of the tree pollen is from alder, and alder has fairly high relative pollen productivity ( $\times 4.2$  relative to grass; Sugita *et al.*, 1999). Since a few alder trees immediately overhang the surface of the pond, this local input has a greater influence on the pollen signal than the relatively open land elsewhere within the 100 m circle.

### **Is ‘openness’ reflected by the insect species associated with grassland and pasture?**

Unfortunately, it seems that insects associated with pasture (ecological group p) and animal dung (ecological group df) do not reflect the degree of openness in the landscape in a direct way. With the exception of Old Mans Pond at Dunham Massey (25.3%), most of the values for grassland and pasture insects (ecological group p) are fairly similar and comparatively low (13.9% at Fox Hole, 5.3% at Island and 8.7% at Smithies in Dunham Massey and 8.3% at Alder, 8.3% at Baldwins, 8.5% at Fairmead and 5.6% at Lost in Epping). This is despite very clear differences between these sites in terms of the 100 m canopy cover calculated by the GIS survey (See Data File 1 (available online) for the comparable GIS values). Old Mans Pond is also one of the two sites in this survey that shows raised proportions of grass pollen (Figure 7). The second site where grass pollen also has raised values is Fairmead Pond at Epping, but here there is no accompanying rise in the values of insect indicators for grassland and pasture. We suspect that many of the insect species that form this ecological group (e.g. the genera *Sitona*, *Hypera*, *Gymnetron*, *Rhinocus* and *Ceutorhynchus*) are very local in their distribution, since they are dependant on specific host plants. Probably extremely local differences in the vegetation, such as clover or dock being more common in the grass sward at one location than another, are the explanation for these differences in the insect fauna.

In terms of the species associated with dung at Dunham Massey, there appears to be no clear correlation with the GIS estimates of tree cover at 100 m (Data File 1 (available online)). This probably relates to the way the deer herd uses the landscape at Dunham Massey or reflects the contribution of surface and stream run off into the ponds. The two ponds with the highest values (Smithies and Island) both have streams and culverts associated with them and in the case of Smithies Pond very little surrounding waterside vegetation. Moreover, Fox Hole is bordered by a wide strip of soft and boggy ground, which may prevent access to the pond for the deer. It therefore appears that the proportions of species associated with dung in the terrestrial faunas are a very poor indicator for openness. This probably results from the action of a number of very local effects and taphonomic problems (Kenward, 1975).

However, when the proportions of dung beetles at Dunham Massey and Epping are compared, an interesting effect is seen. The proportions of species associated only with animal dung (ecological group df) are relatively higher at three of the Dunham Massey ponds (15.8% at Island, 7.6% at Old Mans and 10.6% at Smithies) than at Epping (4.2% at Alder, 0.6% at Baldwins, 2.8% at Fairmead and 1.9% at Lost). This pronounced difference between the two sites appears to relate to actual differences between the size and density of the deer/cattle herd at these two sites. At Dunham Massey, there is a large maintained herd of around 250 fallow deer in the 101 hectare park (c. 2.5 animals per hectare). At Epping, there is a much smaller and less dense, wild herd of ~500 fallow and muntjac deer spread over ~2400 hectares (c. 0.5 animals per hectare) and a cattle herd also is maintained at the location of Fairmead and Alder ponds and other glades in the area. Fox Hole at Dunham Massey is an exception to this pattern with an animal dung group value of 3.8%. However, as suggested above, deer may have limited access to this pond. The results out-

lined here may suggest that insect remains from small bodies of water have a potential to reflect the intensity of grazing pressure in an area. It is suggested that values for dung beetles of >10% in a terrestrial fauna probably indicate the presence of dense or large herds of grazing animals, whilst levels of <5% may reflect grazing by natural populations of animals or ‘naturalistic’ grazing by domestic animals. We will need to undertake further analyses at our other study sites to establish whether these trends are reliable.

### **What distance around the ponds (catchment area) is represented by the insects and pollen?**

Though substantial research has been undertaken on how pollen signals can represent different source areas and the relative size of catchments these may represent (Sugita, 1994; Bunting *et al.*, 2004) similar work for insect remains is relatively scarce (Kenward, 2006). However, there has been a widely discussed assumption that many insect fragments in most small bodies of water such as ponds, mires and palaeochannels are local (i.e. <100 m) and they do not come from as wide a ‘catchment’ as pollen (i.e. >1000 m). The analogue data presented here allows us to address this issue for the first time in a quantitative way.

As discussed above, it is seems that the extent of local (i.e. <100 m) canopy can directly affect the proportions of woodland insects (ecological group dw + lf) recovered from the pond samples. Conversely, indicators for openness (ecological groups df + p) do not appear to closely shadow canopy cover and/or the extent of open ground at all. It could therefore be suggested that the insect faunas from small bodies of water can be disproportionately influenced by the immediate presence of relatively small patches of trees, deadwood or indeed species-rich grassland. This is not a surprising result since it has been long understood that certain taxa in archaeoentomological faunas will occur in abundance, even when the actual material, or landscape, present may only be a minor component of the archaeological record (Kenward, 1975, 1978).

It also seems that the sediment in these small ponds are not collecting insect taxa from a considerable distance (i.e. >1000 m). This can be shown by examining how the two parkland landscapes at Dunham Massey and Epping differ in terms of the nature of tree cover at wider distances and how the insect faunas appear to respond to this change. The GIS values for the four ponds at Dunham Massey suggest a landscape in which canopy cover progressively decreases with distance (an average tree cover of 33.2% at 100 m and 21.1% at 1000 m). This is in contrast to the situation at Fairmead and Alder ponds in the plains at Epping. Here the GIS estimate of tree cover increases with distance (an average of 33.4% at 100 m and 86.8% at 1000 m). However, this distinction between these two landscapes is not reflected in the relative proportions of insect tree species in the terrestrial faunas at these sites. Both locations produce essentially similar, and relatively low, proportions of these species (an average of 17.6% in the four ponds at Dunham Massey and 13.5% at Fairmead and Alder at Epping). It would seem, therefore, that most of the woodland insects present are collected from an area which is <1000 m radius from the sampling location. It may be possible to apply a ‘distance weighting’ on this analogue data to see if this distance can be estimated more precisely.

The pollen signal, on the other hand, includes a background signal (reflecting the difference in landscape openness at Dunham Massey and at Epping) and a local signal (which reflects details of tree cover close to the basin, as at Alder Pond). Comparison of pollen data with non-distance-weighted vegetation is expected to show weak correlation with regional variations (Sugita *et al.*, 1999; Figure 8), so the lack of fit between the GIS measurement of actual tree cover and reconstruction of tree and shrub cover from modern sub-fossil pollen data is not surprising. It will also be interesting to see the extent to which the nature of the lands-

cape around the various ponds might be reflected in the plant macrofossils from these ponds, and how local this signature may be. Research by Zhao *et al.* (2006), for instance, indicates that like insect remains, plant-macrofossils are not evenly distributed across small, shallow lakes but tend to remain within 20–30 m of the location where the plants originally grew.

## Conclusions and future analysis

The survey of the insect faunas from a range of ponds set in woodland of varying densities and grazing pressure has, in the way of many analogue studies, produced as many questions as answers.

It seems that local factors are important in shaping the contents of palaeoentomological insect faunas and determining how they are deposited. Factors, such as the nature of canopy structure, the degree that trees overhang deposits, the nearness and patchiness of areas of species rich grassland and if there is an active water flow through the ponds, can clearly influence composition of insect faunas.

The woodland insect faunas from these modern studies are dominated by insect species associated with living tree leaf rather than dead wood species. This is true even for Dunham Massey, which is recognised for its rich deadwood insect assemblage and where considerable care has been taken to preserve deadwood as part of the parkland landscape. This dominance of leaf feeding insects is not seen in the woodland insect faunas of the early and middle Holocene, where large faunas associated with deadwood and decaying timber are routinely recovered but the presence of leaf feeding taxa is comparatively rare. This is an issue that needs more detailed analysis and discussion, but suggests that the deadwood habitat of dead trees, dropped branches, decaying stumps or the rotting heartwood and dead ‘snags’ of mature and still living trees (Alexander, 2008), must have been a very important, if not dominant, component of past forests.

This study also suggests that the proportion of terrestrial insects associated with trees does have the potential to generally indicate the degrees of ‘openness’ and the presence of ‘dense forest’ in the past. It is noticeable that in the palaeoentomological record there is a change in the nature of insect faunas between the ‘forested’ Neolithic and Early Bronze Age (c. 4000–1000 cal BC) and the ‘cleared’ and farmed landscapes of the Iron Age (c. 1000–0 cal BC). A number of studies and surveys suggest that 15–25% of terrestrial insect faunas consist of woodland species in the earlier period and <10% in the latter (Dinnin and Sadler, 1999; Robinson, 2000; Whitehouse and Smith, 2005; Whitehouse and Smith, in press). The results presented here provide some insight into the structure of such woodlands on the basis of the modern analogue work presented, although we do not feel we can comment on the full significance of these findings until results from our additional survey work from Hatfield Forest and Windsor Great Park have been presented. We hope these results will allow us to revisit issues concerning the ‘openness’ in past woodlands (cf. Whitehouse and Smith, in press) with further supporting data.

It would seem that, potentially, dung beetles can be used to estimate the relative density and size of herds of grazing animals. However, there are several caveats that need to be clearly delineated. The set of modern analogues presented here is relatively limited, and this hypothesis needs to be tested against other sets of analogous data. At present, there are no analogue studies that examine the extent to which dung beetle numbers may reflect the relative population densities of large, wild ungulates and grazers such as aurochs, bison. Wild grazers will inevitably have been more widely distributed across the landscape, following grazing areas and herd behaviours, and their distribution may well have been influenced by predation risk (e.g. humans, wolves). Recent research indicates that various ungulate species select differently

for such predation risks, but that human predation is likely to have been an important factor in the density distribution of ungulates, more so than natural predators (Theuerkauf and Rouys, 2008). Moreover, it is clear from carbon isotope signatures that different wild ungulates exploited different types of habitats during the Holocene (Drucker *et al.*, 2008). Turning to domesticated grazing patterns, there is no information on how changes in the population density of domesticated cattle herds might also be reflected in the density of dung beetle populations. These are all issues that will require further analogue research. If it can be shown that proportions of dung beetles recovered from circumstances such as this can be used to indicate the relative size of grazing herds, this has profound implications for several archaeological issues and questions including the ‘Vera hypothesis’, as well as examining the use and extent of grazing in both the Neolithic and Bronze Age woodland and Iron Age and Romano-British field systems.

The AP component in all ponds is below the 90–95% tree pollen proportion generally interpreted as closed canopy ‘wildwood’. Further comparison of pollen signals within and between ponds with distance-weighted canopy cover is expected to show the strong role of local vegetation composition in determining the pollen signal.

Although the spatial distribution of different habitats around sites has been compared with modern pollen assemblages before, comparison with insect faunas is, as far as we know, a new approach. This paper shows that such a comparison allows a more sophisticated interpretation of faunal assemblages, and we intend to explore the relationship between faunal assemblage and vegetation distribution more explicitly once data from all four study sites is available, in order to postulate a ‘beetle source area’ analogous to the relevant source area of pollen (Sugita, 1994; Bunting *et al.*, 2004).

Finally, it would be advantageous to include waterlogged plant macrofossils into this data set, since this proxy environmental evidence is also typically applied to the palaeoenvironmental record from ancient woodlands. It is the hope of the authors to expand on these initial results to explore the reliability of modern analogue data for the palaeoenvironmental record, in order to attempt to develop an ‘indicator package’ (Kenward and Hall, 1997) for ancient forest structure and woodland clearing.

This study also has implications for the resolution of archaeoentomological and palynological data from Holocene deposits. In particular, the results presented here suggest that the key woodland indicators from palynological or palaeoentomological analyses represent an extremely limited window into past landscapes – possibly no more than a 100 m radius from ponds located within relatively wooded environments. This has major implications for the collection of environmental data from archaeological sites, suggesting multiple samples, incorporating off-site sampling (possibly in transects of some distance), are essential to reliably characterise past vegetation (Caseldine *et al.*, 2008).

## Acknowledgements

This research has been funded by NERC (NE/D007577/1, to Whitehouse and Smith), ‘Fossil insect remains as indicators of the primeval forest; a modern analogue approach’. We are grateful to Pam Grinter, Andy Howard and Kat Sharock Walsh (IAA, University of Birmingham), who all helped at various stages with the sampling from Dunham Massey and Epping Forest. Initial processing and sample division was undertaken at Birmingham by Kalla Nayyar, whilst paraffin flotation and float sorting was undertaken by Dr Sarah Coulter (née Davies) and Kerry Allen at Queen’s University, Belfast. The insect remains were sorted and laid out at Birmingham by Katie Ward. Preparation of pollen sam-

ples was undertaken by Dr Sarah Coulter and the floras were recorded by Jane Bunting. The Ponar grab sampler used in this study was kindly loaned to us by colleagues at the Department of Geography, Geology and Earth Sciences at the University of Birmingham. The rubber boat, christened 'unsinkable Molly' was kindly loaned by Prof Ian Foster (Department of Geography, Environment and Disaster Management, Coventry University). We would like to thank Dr Wendy Smith (Oxford Archaeology) for comments on an earlier draft of this paper and Prof Russell Coope for access to his unpublished data from previous palaeoenvironmental work on Dunham Massey.

David Smith is particularly grateful to Michael Grant (Wessex Archaeology) for a discussion about beech pollards, their decline and the role that canopy structure and present decline may play in terms of understanding the high numbers of *R. fagi* seen at these sites.

At Dunham Massey, invaluable help and support was given by Andrew Wylie (National Trust) and at Epping, Corporation of London, by both Jeremy Dagley and Imogen Wilde. We would also like to thank Keith Alexander (independent consultant entomologist) for suggesting suitable sites for study as part of this investigation. We are grateful to Michael Grant and Petra Dark for allowing us to cite from their unpublished report on the palaeoecology of Lodge Road, Epping Forest. We would like to thank the referees for their helpful comments.

## References

- Alexander, J.** 2008: Tree biology and Saproxylic Coleoptera: Issues of definitions and conservation language. *Revue d' Ecologie (Terre Vie)* 63, 1–5.
- Baker, C., Moxey, P.A. and Oxford, P.M.** 1978: Woodland continuity and change in Epping Forest. *Field Studies* 4, 645–69.
- Behre, K.E.** 1981: The interpretation of anthropogenic indicators from pollen diagrams. *Pollen et Spores* 23, 225–45.
- Bell, M.** 2008: *Prehistoric Coastal Communities: The Mesolithic in Western Britain* (Council for British Archaeology Research Report 149). York: Council for British Archaeology.
- Bennett, K.D.** 1995–2007: *Catalogue of British Pollen types*. Available online at [www.chrono.qub.ac.uk/pollen/pc-intro.html](http://www.chrono.qub.ac.uk/pollen/pc-intro.html)
- Bennett, K.D., Whittington, G. and Edwards, K.J.** 1994: Recent plant nomenclatural changes and pollen morphology in the British Isles. *Quaternary Newsletter* 74, 1–6.
- Birks, H.J.B.** 2005: Mind the gap: How open were European primeval forests? *Trends in Ecological Evolution* 20, 154–56.
- Bradshaw, R. and Hannon, G.** 1992: Climatic change, human influence and disturbance regime in the control of vegetation dynamics within Fiby Forest, Sweden. *Journal of Ecology* 80, 625–32.
- Bradshaw, R.H.W. and Hannon, G.E.** 2004: The Holocene structure of northwest European temperate forest induced from palaeoecological data. In Honnay, O., Verheyen, K., Bossuyt, B. and Hermy, M., editors, *Forest Biodiversity: Lessons from History for Conservation*. Wallingford: CABI Publishing, Wallingford, pp. 11–26.
- Bradshaw, R.H.W., Hannon, G.E. and Lister, A.M.** 2003: A long term perspective on ungulate-vegetation interactions. *Forest Ecology and Management* 181, 267–80.
- Bradshaw, R. and Mitchell, F.J.G.** 1999: The palaeoecological approach to reconstructing former grazing-vegetation interactions. *Forest Ecology and Management* 120, 3–12.
- Berglund, B.E. and Ralska-Jasiewicsowa, M.** 1986: Pollen analysis and pollen diagrams In Berglund, B.E., editor, *Handbook of Holocene Palaeoecology and Palaeohydrology*. Chichester: John Wiley, pp. 455–83.
- Birks, H.J.B.** 1988: Long-term ecological change in the British uplands. In Usher, M.B. and Thompson, D.B.A., editors, *Ecological Change in the Uplands*, Oxford: Blackwell Scientific Publications, pp. 37–53.
- Broström, A., Gaillard, M.-J., Ihse, M. and vad Odgaard, B.** 1998: Pollen–landscape relationships in modern analogues of ancient cultural landscapes in southern Sweden – a first step towards quantification of vegetation openness in the past. *Vegetation History and Archaeobotany* 7, 189–201.
- Buckland, P.C.** 1979: *Thorne Moors: A Palaeoecological Study of a Bronze Age Site: A Contribution to the History of the British Insect Fauna*. Department of Geography, University of Birmingham, Occasional Publication Number 8, Birmingham: University of Birmingham.
- 2005: Palaeoecological evidence for the Vera hypothesis. In Hodder, K.E., Bullock, J.M., Buckland, P.C. and Kirby, K.J., editors, *Large Herbivores in the Wildwood and Modern Naturalistic Grazing Systems*. (English Nature Research Report 648). Peterborough: English Nature, pp. 62–116.
- Buckland, P.C. and Dinnin, M.H.** 1993: Holocene woodlands, the fossil insect evidence. In Kirby K.J. and Drake C.M., editors, *Dead Wood Matters: The Ecology and Conservation of Saproxylic Invertebrates in Britain*. (English Nature Science 7). Peterborough: English Nature, pp. 6–20.
- Buckland, P.C. and Edwards, K.** 1984: The longevity of pastoral episodes of clearance activity in pollen diagrams: the role of post-occupation grazing. *Journal of Biogeography* 1, 243–49.
- Bunting, M.J., Gaillard, M.-J., Sugita, S., Middleton, R. and Broström, A.** 2004: Vegetation structure and pollen source area. *The Holocene*, 14, 651–60.
- Burrough, P.A.** 1986: *Principles of Geographical Information Systems for Land Resources Assessment*. Oxford: Oxford University Press.
- Caseldine, C., Fyfe, R. and Hjelle, K.** 2008: Pollen modelling, palaeoecology and archaeology: virtualisation and/or visualisation of the past? *Vegetation History and Archaeobotany* 17, 543–49.
- Conolly, J. and Lake, M.** 2006: *Geographical Information Systems in Archaeology*. Cambridge: Cambridge University Press.
- Cummings, V. and Whittle, A.** 2003: Tombs with a view: landscape, monuments and trees. *Antiquity* 77, 255–66.
- Dinnin, M.H. and Sadler, J.P.** 1999: 10 000 years of change: the Holocene entomofauna of the British Isles. *Quaternary Proceedings* 7, 545–62.
- Drucker, D.G., Bridault, A., Hobson, K.A., Szuma, E. and Bocherens, H.** 2008: Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. *Palaeogeography, Palaeoclimatology, Palaeoecology* 266, 69–82.
- Fyfe, R.** 2007: The importance of local-scale openness within regions dominated by closed woodland. *Journal of Quaternary Science* 22, 571–78.
- Gaillard, M.-J., Birks, H.J.B., Emanuelsson, U. and Berglund, B.E.** 1992: Modern pollen/land-use relationships as an aid in the reconstruction of past land-uses and cultural landscapes: an example from south Sweden. *Vegetation History and Archaeobotany* 1, 3–17.
- Gaillard, M.-J., Birks, H.J.B., Emanuelsson, U., Karlsson, S., Lagerås, P. and Olausson, D.** 1994: Application of modern pollen land-use relationships to the interpretation of pollen diagrams – reconstructions of land-use history in South Sweden, 3000–0 BP. *Review of Palaeobotany and Palynology* 82, 47–73.
- Grant, M.J. and Dark, P.** 2006: Re-evaluating the concept of woodland continuity and change in Epping Forest: new dating evidence from Lodge Road. Unpublished Report for the Corporation of London (cited with the authors' permission).
- Grant, M.J. and Edwards, M.E.** 2008: Conserving idealized landscapes: past history, public perception and future management in the New Forest (UK). *Vegetation History and Archaeobotany* 17, 551–62.
- Groenman-van Waateringe, W.** 1986: Grazing possibilities in the Neolithic of the Netherlands based on palynological data in Behre, K.-L., editor, *Anthropogenic Indicators in Pollen Diagrams*. Rotterdam: A.A. Balkema, pp. 187–202.
- Hammond, P.M.** 1974: Changes in the British Coleopterous fauna. In Hawksworth, D.L., editor, *The Changing Flora and Fauna of Britain* (Systematics Association Special Volume 6), London: Academic Press, pp. 323–69.
- Hellman, S., Gaillard, M.-J., Broström, A. and Sugita, S.** 2008: The REVEALS model, a new tool to estimate regional plant abundance from pollen data in large lakes: validation in southern Sweden. *Journal of Quaternary Science* 23, 21–42.

- Hellman, S., Bunting, M.J. and Gaillard, M-J.** 2009: Relevant Source Area of Pollen in patchy cultural landscapes and signals of anthropogenic landscape disturbance in the pollen record: A simulation approach. *Review of Palaeobotany and Palynology* 153, 245–58.
- Hicks, S.** 2006: When no pollen does not mean no trees. *Vegetation History and Archaeobotany* 15, 253–61.
- Hyman, P. and Parsons, M.S.** 1992: *A Review of the Scarce and Threatened Coleoptera of Great Britain* (UK Nature Conservation 3). Peterborough: UK Joint Nature Conservation Committee.
- Huntley, B. and Birks, H.J.B.** 1983: *An Atlas of Past and Present Pollen Maps of Europe 0–13 000 years ago*. Cambridge: Cambridge University Press.
- Innes, J.B. and Simmons, I.G.** 1988: Disturbance and diversity: floristic changes associated with pre-elm decline woodland recession in North East Yorkshire. In Jones, M., editor, *Archaeology and the Flora of the British Isles* (Oxford University Committee for Archaeology Monograph Number 14). Oxford: Oxford University Committee for Archaeology, pp. 7–20.
- Iversen, J.** 1941: Land occupation in Denmark's Stone age. *Damarks Geologiske Undersøgelse, Raekke 2/66*, 7–69.
- 1960: Problems of the Early Post-Glacial forest development in Denmark. *Damarks Geologiske Undersøgelse* (IV Raekke) 4, 1–32.
- Kenward, H.K.** 1975: Pitfalls in the environmental interpretation of insect death assemblages. *Journal of Archaeological Science* 2, 85–94.
- 1978: *The Analysis of Archaeological Insect Assemblages: A New Approach*. (Archaeology of York, 19/1). London: Council for British Archaeology for York Archaeological Trust.
- 2006: The visibility of past trees and woodlands: Testing the value of insect remains. *Journal of Archaeological Science* 33, 1368–80.
- Kenward, H.K. and Hall, A.R.** 1997: Enhancing bio-archaeological interpretation using indicator groups: stable manure as a paradigm. *Journal of Archaeological Science* 24, 663–73.
- Kenward, H.K., Hall, A.R. and Jones, A.K.G.** 1980: A tested set of techniques for the extraction of plant and animal macrofossils from waterlogged archaeological deposits. *Science and Archaeology* 22, 3–15.
- Kenward, H. and Tipper, J.** 2008: Insect invaders of reconstructed Anglo-Saxon houses at West Stow, Suffolk, England. *Environmental Archaeology* 13, 51–58.
- Koch, K.** 1992: *Die Käfer Mitteleuropas* (Ökologie Band 3). Krefeld: Goecke and Evers.
- Lewis, P.A., Mason, W.T. Jr. and Weber, C.I.** 1982: Evaluation of three bottom grab samplers for collecting river benthos. *Ohio Journal of Science* 82, 107–13.
- Lucht, W.H.** 1987. *Die Käfer Mitteleuropas* (Katalog). Krefeld: Goecke and Evers.
- McLaughlan, K.K., Elmore, A.J., Oswald, W.W. and Sugita, S.** 2007: Detecting open vegetation in a forested landscape: pollen and remote sensing data from New England, USA. *Holocene* 17, 1233–43.
- Mitchell, F.J.G.** 2005: How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology* 93, 168–77.
- Morgan, M.J.** 1978: *Euophryum confine* Broun (Col., Curculionidae) in Wales. *Entomologist's Monthly Magazine* 113, 98.
- Moore, P.D.** 2005: Down to the woods yesterday. *Nature* 433, 588–89.
- Mudroch, A. and MacKnight, S.** 1994L *Handbook of Techniques for Aquatic Sediments Sampling* (2nd edition). Boca Raton, FL: CRC press.
- Peterken, G.F. and Mountford, E.P.** 1996: Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. *Forestry*, 69, 125–36
- Pollard, J.** 1999: 'These places have their moments': thoughts on settlement practices in the British Neolithic'. In Brück, J. and Goodman, M., editors, *Making Places in the Prehistoric World*. London: University College London Press, pp. 76–93.
- 2004: 'A 'movement of becoming': realms of existence in the early Neolithic of Southern Britain'. In Chadwick, A.M., editor, *Stories of the Landscape: Archaeologies of Inhabitation* (British Archaeological Reports International Series 1238). Oxford: Archaeopress, pp. 55–70.
- Power, S.A., Ashmore, M.R. and Ling, K.A.** 2004: Recent trends in beech tree health in southern Britain and the influence of soil type. *Water, Air and Soil Pollution* 185, 1293–98.
- Robinson, M.A.** 1981: The use of ecological groupings of Coleoptera for comparing sites. In Jones, M. and Dimbleby, G., editors, *The Environment of Man: The Iron Age to the Anglo-Saxon Period* (British Archaeological Reports, British Series 87). Oxford: British Archaeological Reports, pp. 251–86.
- 1983: 'Arable/pastoral ratios from insects?' In Jones, M., editor, *Integrating the Subsistence Economy*, (British Archaeological Reports, International Series 181). Oxford: British Archaeological Reports, pp. 19–47.
- 1991: The Neolithic and Late Bronze Age insect assemblages. In Needham, S., editor, *Excavation and salvage at Runnymede Bridge, 1978: the Late Bronze Age waterfront site*. British Museum Press, London, pp. 277–325.
- 2000: Coleopteran evidence for the elm decline, Neolithic activity in woodland, clearance and the use of the landscape. In Fairbairn, A.S., editor, *Plants in Neolithic Britain and Beyond* (Neolithic studies group seminar papers 5) Oxford: Oxbow Books, pp. 27–36.
- Simmonds, I.G.** 1996: *The Environmental Impact of Later Mesolithic Cultures*. Edinburgh: Edinburgh University Press.
- Smith, D.** 1996: Thatch, turves and floor deposits: A survey of Coleoptera in materials from abandoned Hebridean blackhouses and the implications for their visibility in the archaeological record. *Journal of Archaeological Science* 23, 161–74.
- 1998: Beyond the barn beetles: Difficulties in using some Coleoptera as indicators for stored fodder. *The Journal of Environmental Archaeology* 1, 63–70.
- Smith, D.N.** 2000: Detecting the nature of materials on farms using Coleoptera. In Huntley, J.P. and Stallibrass, S., editors, *Taphonomy and Interpretation* (AEA symposia no. 14). Oxford: Oxbow Books, pp. 71–84.
- Smith, D., Letts, J.P. and Cox, A.** 1999: Coleoptera from Late Medieval smoke blackened thatch (SBT): their archaeological implications. *Environmental Archaeology* 4, 9–18.
- Smith, D.N., Letts, J. and Jones, M.** 2005: The insects from non-cereal stalk smoked blackened thatch. *Environmental Archaeology* 10, 171–78.
- Smith, D.N., Roseff, R., Bevan, L., Brown, A.G., Butler, S., Hughes, G. and Monckton, A.** 2005: Archaeological and Environmental Investigations of a Late Glacial and Holocene sedimentary sequence on the River Soar, at Croft, Leicestershire. *The Holocene* 15, 353–77
- Smith, D.N. and Whitehouse, N.** 2005: Not seeing the trees for the woods: a palaeoentomological perspective on Holocene woodland composition. In Smith, D.N., Brickley, M.B. and Smith, W., editors, *Fertile Ground: Papers in Honour of Professor Susan Limbrey* (AEA Symposia No. 24). Oxford: Oxbow books, pp. 136–61.
- Soepboer, W. and Lotter, A.F.** 2009: Estimating past vegetation openness using pollen-vegetation relationships: a modelling approach. *Review of Palaeobotany and Palynology* 153, 102–107.
- Stace, C.** 1997. *New Flora of the British Isles* (2nd edition). Cambridge: Cambridge University Press.
- Sugita, S.** 1994: Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology*, 82, 881–897.
- 2007a: Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEAL regional vegetation composition. *Holocene* 17, 229–41.
- 2007b: Theory of quantitative reconstruction of vegetation II: all you need is LOVE. *Holocene* 17, 243–57.
- Sugita, S., Gaillard, J. and Broström, A.** 1999: Landscape openness and pollen records: a simulation approach. *Holocene* 9, 409–21.
- Sutherland, W.J.** 2002: Openness in management. *Nature* 418, 834–835.
- Svenning, J-C.** 2002: A review of natural vegetation openness in north-western Europe. *Biological Conservation* 104, 133–48.

- Theuerkauf, J. and Rouys, S.** 2008: Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. *Forest Ecology and Management* 256, 1325–32.
- Thomas, J.** 1999: *Understanding the Neolithic*. London: Routledge.
- Vera, F.W.M.** 2000: *Grazing ecology and Forest History*. Wallingford, Oxfordshire: CABI Publishing.
- Whitehouse, N.J.** 1997: Insect faunas associated with *Pinus sylvestris* L. from the mid-Holocene of the Humberhead Levels, Yorkshire, UK. *Quaternary Proceedings* 5, 293–303.
- 2006: The Holocene British and Irish ancient forest fossil beetle fauna: implications for forest history, biodiversity and faunal colonisation. *Quaternary Science Reviews* 25, 1755–89.
- Whitehouse, N.J. and Smith, D.N.** 2004: ‘Islands’ in Holocene forests: Implications for forest openness, landscape clearance and ‘culture steppe’ species. *Environmental Archaeology* 9, 203–212.
- in press. How fragmented was the British Holocene wildwood? Perspectives on the ‘Vera’ grazing debate from the fossil beetle record. *Quaternary Science Reviews*.
- Woodcock, H., Vollenweider, P., Dubs, R. and Hofer, R.** 1995. Crown alterations induced by decline: A study of relationships between growth rate and crown morphology in beech (*Fagus sylvatica* L.) Trees – *Structure and Function* 9, 279–88.
- UK Forestry Commission.** ‘Forest condition’, [www.forestry.gov.uk/forestry/infd-78cfe8](http://www.forestry.gov.uk/forestry/infd-78cfe8) (accessed March 2008)
- Zhao, Y., Sayer, C.D., Birks, H.H., Hughes, M. and Peglar, S.M.** 2006: Spatial representation of aquatic vegetation by macrofossils and pollen in a small and shallow lake. *Journal of Palaeolimnology* 35, 335–50.c