WHAT CAN FOREST MANAGERS LEARN FROM RESEARCH ON FOSSIL INSECTS? LINKING FOREST ECOLOGICAL HISTORY, BIODIVERSITY AND MANAGEMENT

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Abstract—This paper outlines the usefulness of using fossil insects, particularly Coleoptera (beetles), preserved in waterlogged palaeoenvironmental and archaeological deposits in understanding the changing nature of forest ecosystems and their associated insect population dynamics over the last 10,000 years. Research in Europe has highlighted the complex nature of early forest ecosystems, in particular the role of dead wood and grazing animals. This research suggests that the north European primary forest has similarities to pasture woodlands, rather than the forest manager's perception of closed canopy systems. Human activity has had a major impact on forest ecosystems, resulting in an expansion of plants and animals associated with cleared landscapes and pasture and also the local extirpation of a sizeable proportion of taxa from the forests of northern Europe. The decline in these species has been seen as resulting from habitat loss due to human impact on the forest, which intensified from about 2500 years ago onwards, coupled with subtle climate change effects. These extirpations will be discussed, with particular reference to the management of forest ecosystems for the benefit of their invertebrates (particularly those associated with dead wood), and emphasising how the record from archaeological and palaeoecological sites has significant relevance to modern woodland management and conservation. Moreover, the role of disturbances in maintaining the structure and biodiversity of the "wildwood" will be emphasied.

INTRODUCTION

Insects, recovered as fossils, potentially provide one of the most effective means of reconstructing both past environments and the details of changing climate, being very sensitive to environmental change and occupying almost every possible habitat on land and in freshwater (Elias 1994). As a group, their remains may be the most frequent identifiable fossils in terrestrial, waterlogged sediments and are similarly common in anaerobic archaeological sediments (fig. 1). Most fossil insect research has focused on Coleoptera, but increasingly, other insect groups are studied, in particular the Diptera (e.g., Brooks and Birks 2000, Panagiotakopulu 2004). Much of the following account concentrates on the former rather than the latter, as these form the basis of our understanding of the palaeoentomology of woodlands, the subject of this paper.

In particular, many investigations provide an insight into what the primeval forest may have looked like and how landscape clearance affected the insect biota, allowing the expansion of species associated with cleared landscapes. Results of these investigations highlight the enormous changes effected upon the fauna of the British Isles, particularly since the onset of agriculture, but also provide an insight into their rapid colonisation and expansion as ice sheets retreated. Inevitably, much of the following account concentrates on results from the British Isles, as this is where the majority of this work has been carried out, although reference will be made to work elsewhere where possible. Management implications are particularly concerned with the European forest habitat, whether ancient or recently planted, although where possible implications for areas elsewhere are also made. This paper includes a background section which introduces the reader to the subject of fossil beetles, an area of research which may be unfamiliar to readers of this volume.

Coleoptera nomenclature follows Lucht (1987). Information on insect biology has been obtained from the entomological database BUGS (Buckland and others 1997). Where necessary, reference is made to the current threatened status of beetles. Many species discussed in this paper are included in

Figure 1—Coleoptera fossils from palaeochannel deposits dating to the mid-Holocene from Thorne Moors, Humberhead Levels.

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the Nature Conservancy Council's *British Red Data Books: 2, Insects* (Shirt 1987). This is a comprehensive statement on the status of most threatened insects in Great Britain. The book contains three major categories based upon degrees of threat, RDB ("Red Data Book") 1, 2 and 3 (respectively endangered vulnerable and rare). A further classification of Notable species (A and B) (Hyman 1992, 1994) is also used. Notable A species are those which do not fall within RDB categories but which are none-the-less uncommon and are thought to occur in 30 or fewer 10 km squares of the National Grid, whilst Notable B taxa are those which are thought to occur in between 31 and 100 10 km squares of the National Grid. One point worth remembering is that species that are rare today may not have been so in the past, and perhaps *vice versa* (Buckland and Dinnin 1993). Dates are expressed as BC/AD for dendrochronological (= tree rings) dates (followed by the appropriate bibliographic citation) and cal BC/AD for radiocarbon dates (range calculated to 95 percent level confidence and calibrated using INTCAL 1986 calibration curve, Pearson and others 1986). Figure 2 shows the location of sites discussed in the text.

ORIGINS AND PRINCIPLES OF PALAEOENTOMOLOGY

The origins of modern palaeoentomology date back to the 1930s and 1940s when Carl Lindroth and fellow Scandinavian entomologists established the foundations of the modern discipline, but it was really when, in the mid 1950s, research activity moved to Britain and particularly to the geology department at Birmingham University (Morgan and Morgan 1987), with the work of Prof. Russell Coope, that the discipline gained wider attention. Coope began studying Quaternary insect fossils from Upon Warren, an interstadial deposit in the British Midlands dated to *c.* 40,000 radiocarbon years ago (Coope and others 1961). By making patient comparisons with modern specimens, he matched most of the material to modern species. Coope (1970, 1978, 1995, 2004) suggested that insects had remained evolutionarily stable in their morphology and their environmental requirements throughout the whole of the Quaternary period, responding to climate change by undergoing distributional shifts. The effect of such movement would keep the gene pool constantly mixed, preventing genetic isolation of populations and mutations which would result in speciation and ensuring that stasis is the norm for many Quaternary insects. Thus far, evidence for evolutionary change is extremely rare from Quaternary insect assemblages (e.g., Böcher 1986, 1997; Matthews 1970) and it seems that the overall composition of the assemblages of insect species which occur today, at least in the temperate zones, were established during late Tertiary times (Elias 1994). However, as Ashworth (2004) points out, stasis is not always corroborated by genetic evidence (e.g., Reiss and others 1999). This may possibly be true only for the northern temperate fauna, while the highly diverse tropics may be the place to look for evidence for divergence, where climatic oscillations may not have been so extreme. Moreover, this perspective may not hold true for narrow-range endemic taxa (see discussions by Ribera and Vogler 2004).

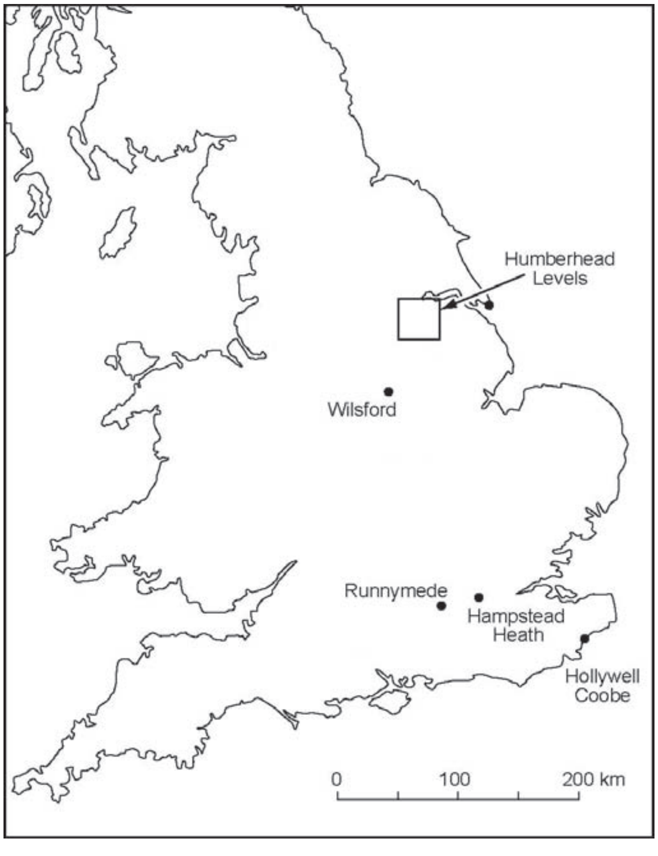

Figure 2—Location map of United Kingdom sites discussed in text.

Insect groups identified are generally the beetles (Coleoptera), because the robust exoskeleton survives well in waterlogged deposits, leaving many of their diagnostic features still evident. Identification is still very much of a specialist activity because of the range of species present in the fossil record. Other insect orders are available for analysis, such as the Chironomidae (Diptera)—this group has recently received considerable research attention (e.g., Brooks and Birks 2000; Brooks and others 1997a, 1997b; Walker and others 1991). Work on other dipterous (fly) remains is being pioneered through the work of Pete Skidmore (1995) and more recently Eva Panagiotapopolou (2004). Trichoptera (caddis) have also received some attention (e.g., Wilkinson 1984) and have recently been recognised as important environmental and climate change indicators (Greenwood and others 2003). Increasingly, there is the use of several insect groups to refine reconstruction of past environments, particularly where high quality data are required concerning periods of rapid environmental change. A good example of this approach is provided by the Kråkenes Project, which has investigated the ecosystem of this lake in western Norway during the late-glacial and early-Holocene (Birks and others 2000).

Reconstruction of past environments operates upon on the major assumption that the ecological requirements of insects have not dramatically changed. The fact that groups of species have consistently been found together suggests that the ecological requirements of most species have not altered (Kenward 1975). However, there are considerable difficulties in establishing the ecological requirements of single species and their significance in fossil faunal assemblages. Even when the biology of species is known in some detail, this may not cover all the suitable habitats, especially in situations when microhabitats may provide suitable locations while the *overall* situation may provide a rather different ecological environment (Kenward 1978). It is therefore recommended that a large number of taxa and individuals are utilised, which when examined together provide a picture of past environments and conditions, an approach known as the "mosaic" approach (Kenward 1976). The setting up of a habitat and fossil database (BUGS: http://www.umu.se/envarchlab/bugs.html) formerly at the University of Sheffield, now at the University of Bournemouth, England, has greatly facilitated the use of this approach (*cf.* Buckland and others 1997).

Sampling of material suitable for fossil beetles entails the removal of material from an exposed sediment section or bulk sampling from an archaeological or palaeoecological context (e.g., cesspit; fossil tree rot hole). Occasionally, a coring device may be used to extract material from lakes, bogs, hollows and where no section is accessible. Samples are usually removed in 5-10 cm thick contiguous "slices", usually of at least 5 litres, or entire contexts. The extraction of fossil Coleoptera follows a technique devised by Coope and Osborne (1968), using paraffin (kerosene) to concentrate remains. The identification of insect fossil material is carried out through the use of entomological keys and through direct comparison with a range of modern comparative material (Buckland and Coope 1991). Much of the sampling for fossil insects has been through the use of palaeoentomology in archaeological investigations, dating both from the prehistoric and historic periods (e.g., Buckland and others 1996; Girling 1976; Kenward and Hall 1995; Robinson 1991, 2000). There have also been studies which have examined "natural" deposits—those not directly associated with archaeological features—but which carry a record of the wider environment, as well as human impact on the landscape. Anaerobic conditions ensure excellent preservation of fossils and the often rapid built-up of deposits provides good temporal resolution. Floodplain deposits, for instance, are immensely valuable, as they provide records of fluvial histories, floodplain evolution and change, vegetation composition and structure as well as the nature and scale of human impact (e.g., Andrieu-Ponel and others 2000; Dinnin 1997; Osborne 1988, 1995; Smith and Howard 2004). Bogs and fens are also rich sources of fossil insect assemblages, although fen peats tend to be richer in insect remains than acid peats (e.g., Buckland 1979; Elias 1994; Klinger and others 1990; Ponel and others 2001; Roper 1996; Whitehouse 1997b, 2004). Wood peats are especially useful in the study of the forest faunas, as elaborated in further detail below.

Perhaps one of the greatest contributions of Quaternary entomology has been its role in helping our understanding of rapid climate change—particularly associated with the termination of the last ice age and of the nature of climate during previous interglacials. Through work on many sites, palaeoentomologists have been able to reconstruct quantified temperatures covering the last 45,000 years, showing the rate and rapidity of climate change during the late-glacial across northern Europe (*c.* 14,000 -10,000 radiocarbon years ago) (Atkinson and others 1987; Coope 1977, 1994; Coope and Brophy 1972; Coope and Lemdahl 1995; Coope and others 1998; Vandenberghe and others 1998; Walker and others 1993). Elias (1996, 1997) and Elias and others (1996) has produced similar data for the American continent, whilst Marra and others (2004) have produced promising new results for the southern hemisphere.

Despite the success in examining late glacial climatic change, Holocene climatic change (the last 10,000 years) has been less easy to infer from the Coleopteran record, although evidence from ice and ocean cores indicates that periodic changes to climatic regimes have taken place (Bond and others 1997, 2001). From the mid-Holocene onwards, palaeoecological studies highlight the increasing scale and extent of environmental change, particularly in Europe. In America, similar scales of human impact are noticeable within a few centuries of the arrival of Europeans, with concurrent dramatic environmental impacts (e.g., Baker and others 1996, Schwert 1996). Data clearly indicate that not only is human impact of considerable importance, but that it may swamp and mask low magnitude climatic events. The scale of these human impacts, particularly upon the forest, was massive, as discussed below. These studies have also provided us with valuable insights into the nature of the primeval forest ecosystem, before major human impact. Figure 2 shows the location of sites discussed in the text.

THE ANCIENT FOREST FOSSIL BEETLE RECORD

The Nature and Structure of "Wildwood"

We know from the pollen record that during the early phases of the present interglacial, rapid climatic warming enabled tree species to re-colonise areas of tundra of northern Europe, at varying rates of expansion from their respective glacial refugia (*cf.* Bennett and others 1991, Willis 1996) and according to their edaphic requirements. These "wildwoods" (also known as *Urwald*) appear to have been structurally complex and rich ecosystems, characterised by significant numbers of large, long-lived trees. Dead, dying and moribund wood appears to have been a major component of this habitat (Smith and Whitehouse 2005), often referred to as coarse woody debris (CWD) (Franklin 1988). We know this because fossil insect assemblages from this period are characterised by large numbers of species associated with this component, including primary colonisers and large numbers of secondary saproxylics (xylophages) and predators which invade wood when very rotten and feed upon the primary colonisers of rotting wood (Smith and Whitehouse 2005, Whitehouse 1997b). This wood-decomposing system has exceptional species diversity (Biström and Väisänen 1988, Harding and Rose 1986). Coarse woody debris is often thought to compose between 15-25 percent of the total wood mass in 'virgin' temperate forest habitats (Peterken 1996). This may be as high as 50 percent in undisturbed forests (Elton 1966, Warren and Key 1991), a figure which would not be inconsistent with the fossil beetle record. As a result, CWD must have been a dominant aspect of the ecology and appearance of ancient woodlands (Smith and Whitehouse 2005).

These wildwoods supported a distinctive invertebrate population of *Urwaldtiere* (*cf.* Palm 1951; undisturbed relict taxa). It is difficult to know exactly when species arrived after the retreat of the ice sheets because of the paucity of sites covering the earlier part of the Holocene, although several studies provide insights into this period (*cf.* Coope 1998; Dinnin 1997; Osborne 1972, 1974, 1980). Deposits at Holywell Coombe in

Kent, southern England, include a valuable record covering the late glacial and first millennium of the Holocene (Coope 1998). Deposits spanning the first thousand years of the Holocene indicate a community of beetles associated with open ground and light woodland. By 8630-8280 cal BC (9230 ± 75 BP, Q-2710) a suite of specialist species had already arrived, including the Notable B *Melasis buprestoides* (L.), RDB 1 *Eucnemis capucina* Ehr., RDB 3 *Dirhagus pygmaeus* (F.) and Notable B *Anaglypus mysticus* (L.) all dependant upon rotting wood and dry heart-wood of deciduous trees, whilst the non-British *Rhyncolus elongatus* (Gyll.) is normally associated with dead and rotting wood of conifers, although in this context may have been living in deciduous wood. This latter species is not on the present list of British Coleoptera, but still lives in central Europe. As tree species expanded from Europe and habitats became more diverse, their associated fauna moved northwards over the next few thousand years, including a diverse range of specialist saproxylics that no longer live in Britain and Ireland (Buckland and Dinnin 1993; Dinnin and Sadler 1999; Whitehouse 1997a, in press). By about *c.* 6000 cal BC, increased diversification of saproxylic communities seems to have occurred (Dinnin and Sadler 1999). These increases were probably caused by the availability of the full range of forest habitats at different successional stages and the arrival of the highly specialised thermophilous *Urwaldtiere* from their mainland European refugia (*cf.* Bennett and others 1991).

The fossil beetle record also provides us with valuable insights into the nature of these forests. There is strong evidence to suggest that they were subject to a range of natural disturbances including forest fires, storm damage, and floods, creating open, sun-exposed places with a considerable amount of dying and dead wood (Whitehouse 1998, 2000). Occasionally, insect attack and pathogens would also have caused defoliation and extensive tree damage *(cf.* Patterson and Backman 1988). Such small-scale disturbances are part of the natural system within forests (Kaila and others 1997) and opened up the canopy of the woodland, creating clearings, and generating a build-up of fuel upon the forest floor, thus making the forest more susceptible to fire (Danks and Foottit 1989). Early Holocene and later sediments often contain abundant charcoal indicating frequent fires (Huntley 1993, Patterson and Backman 1988, Patterson and others 1987). Local non-forest vegetation patches may have emerged quite frequently, creating semi-permanent open spaces and breaking up the canopy of the woodland.

The structure of these forest ecosystems has recently been the subject of fierce discussion, most notably by Frans Vera (2000), who has questioned many assumptions about the natural ecological state of "wildwood". Vera's ideas have generated intense discussion amongst conservationists, biologists and palaeoecologists (e.g., Bakker and others 2004; Blumer 2002; Bradshaw and Hannon 2004; Bradshaw and others 2003; Eriksson and others 2002; Kirby 2003, 2004; Mitchell 2005; Rackham 2003; Sutherland 2002; Svenning 2002; Whitehouse and Smith 2004). In particular, Vera suggests that the role of large herbivores in these wildwoods has been seriously underestimated and that they played an important part in maintaining substantial open areas in the forests of primeval Europe. He debunks the widespread idea that the "wildwoods" of Europe were a dense, continuous canopy (*cf.* Peterken 1996, Rackham 1986). Moreover, Vera suggests these woodlands may have been much more open, rather similar in structure to wood pasture and parkland. These concepts underpin much of our current attitude to the management of woodland and parkland and, if correct, imply that the current conservation policies of regenerating closed woodland may be flawed.

Similar arguments concerning the openness of wildwood and its comparison to pasture woodland have been made by several modern entomologists (e.g., Harding and Rose 1986) and some palaeoecologists, who have long drawn attention to the role of grazing in affecting vegetation structure (Bradshaw and Hannon 1992, Bradshaw and Mitchell 1999, Buckland and Edwards 1984, Mitchell 1990, Robinson 2000). A recent review by Whitehouse and Smith (2004) argues that whilst Vera (2000) undoubtedly challenges many traditional interpretations of vegetational history, he underestimates the complexity of the physical landscape and environmental backdrop of the wildwood, creating a model which is at times simplistic, especially when considering the diversity across Europe (*cf.* Rackham 2003). For instance, he fails to consider that forest composition, and hence structure, changes over the Holocene (*cf.* Birks 1989) or the changing climatic backdrop against which these changes were being played (e.g., Bond and others 1997, 2001). Climate variability will have impacted forests in several different ways, including making it more susceptible to disturbance and affecting the frequency and occurrence of forest fires (Bradshaw and Hannon 1992). Moreover, the assumption that animals and grazing pressure were distributed evenly across the landscape is open to question (*cf.* Bradshaw and Hannon 2004, Buckland and Edwards 1984), but more fundamentally, the role of humans in affecting animal distributions is not considered (Whitehouse and Smith 2004).

Whitehouse and Smith (2004) considered the published fossil insect data from the early Holocene to investigate whether fossil beetle data could throw any light on this debate. They concluded that, within the limits of the published record, some early-mid Holocene forest was at least partly open in character or included open areas, whilst species usually associated with the dung of grazing animals, although in small numbers, are persistent. They stress, however, that the role of grazing animals in creating these openings is far from clear on the present evidence and that new research is required to address this point. Moreover, they suggest that other disturbance agents, such as forest fires are likely to have been equally important. Similar points are made by Bradshaw and Hannon (2004), who consider the pollen, plant macrofossil and charcoal record from several Danish and Swedish sites and additionally draw attention to the role of flooding and wind-throw in the structure of "wildwood".

Human Impacts and Loss of Biodiversity

By 8,000-4,000 cal BC there appears to be some evidence for the disturbance of primary forest indicated within the pollen and charcoal record (e.g., Edwards 1996; Smith 1970, 1981). However, there is far clearer unequivocal evidence for human disturbance during the move to agriculture in the Neolithic, *c.* 5,000 cal BC, when we know from the archaeological record that humans were starting to clear the landscape, but also managing forest areas through coppicing and pollarding (Rackham 1986, Rasmussen 1990). These changes can be observed in detail through the fossil beetle record from several archaeological sites. For instance, at West Heath, Hampstead, London, Mesolithic deposits indicate a largely undisturbed landscape, with a diverse range of undisturbed forest indicators (*Urwaldtiere*) including the lime feeder, the RDB1 *Ernoporus caucasicus* Lind. and two taxa which no longer live in Britain, *Pycnomerus tenebrans* Ol. (a species which displays a very scarce, sporadic distribution in mainland Europe, where it is considered a relict species of old forest), and *Isorhipis melasoides* (Lap.) (another ancient forest inhabitant often found in dry beech wood (Reitter 1911)). Within a relatively short period of time, perhaps 500-1,000 years, the beetles indicate a chiefly managed landscape (Girling 1989). Similarly, at Runnymede, Surrey, investigations over a decade cover a sequence of at least 6,000 years, one of the longest Holocene insect sequences studied in Britain (Robinson 2000). The Mesolithic (*c.* 7,000-5,000 cal BC) until the late Neolithic deposits (*c.* 4250-3650 cal BC, 5100 ± 100 BP, BM-3039) are characterised by an insect fauna with a strong wildwood element. By the Late Bronze Age the insect fauna reflects a largely agricultural landscape (Robinson 1991, 2000). At Wilsford, in the British Midlands, at *c.* 1880-1430 cal BC (3330 ± 90 BP, NPL-74) Osborne (1969) records a fauna that indicates grazing animals in an almost treeless landscape. These transitions from forested to cleared landscape have been observed at several other sites in Britain (e.g., Dinnin 1997), Ireland (Caseldine and others 1997) and elsewhere in Europe (e.g., Ponel and others 2001) with the result that by about 2,500 years ago mature forest beetle species, at least on the islands of Britain and Ireland, appear to represent an insignificant faunal element. Significant inroads had also been made into the forested areas almost throughout Europe. By 2,000 to 1,000 years ago it is doubtful whether anything more than patches of secondary forests remained in the lowlands, over most of the Mediterranean and parts of western Europe accessible to cultivation (Greig 1982, Speight 1989). By the onset of the scientific period when Linnaeus started to give animals and plants Latin names, Europe's forest areas had been reduced to their smallest extent since the last glaciation. Across the Atlantic, in America, massive scales of human impact are noticeable within a few centuries of the arrival of Europeans, with concurrent dramatic environmental impacts (e.g., Baker and others 1996, Schwert 1996), although populations of earlier human colonists had far greater impacts on the environment that has sometimes been commonly recognised (Cronon 1983, Russell 1997).

Associated with these enormous changes to the landscape and forest clearance, was the concurrent decline of its invertebrate inhabitants. Fossil beetle work spanning several decades of research from archaeological and palaeoecological sites suggests that Britain and Ireland have lost a large portion of their original old-growth forest Coleoptera, particularly the saproxylic species, coinciding with the loss of primeval and semi-natural forests and forests. The few studies that have examined natural successions indicate that it is still really too early to quantify the number of extirpations in Britain and Ireland. To date, 40 pre-Linnean (i.e., not including recent 18th-19th century extinctions) extirpations have been recorded amongst British Holocene Coleoptera, whilst 15 have been recorded in Irish deposits (Buckland 1979; Dinnin and Sadler 1999; Whitehouse 1997a, in press). Assessing true numbers is compounded by problems associated with the identification of species that cannot be identified on characteristics recoverable from the fossil record (i.e., based upon their head, thoraces or elytra), and some of the difficulties of identifying specialist species where modern comparative specimens are increasingly difficult to track down. These factors would suggest that these identified extirpated fossils represent a tiny proportion of the range of species which formerly lived in Ireland and Britain (Whitehouse, in press). Of the complete list, over 60 percent of species (25) are from saproxylic taxa associated with old and dead wood, with the rest coming from beetles representing a variety of threatened habitats, including those associated with wetlands and meadowland. An example of one of these species is shown in figure 3, the ostomid *Temnochila coerulea* West, with its modern distribution shown in figure 4. This species is typical of the "extirpated" taxa recovered in fossil records, being today found in central Europe, associated with ancient forest and considered an "*Urwaldrelikt*".

In addition to the "extirpations", many saproxylics which are today extremely rare or endangered are remarkably common in the fossil record. For instance, investigations of the raised mires of Thorne and Hatfield Moors, in the Humberhead Levels, for their fossil insect record include 49 rare or threatened saproxylics in addition to 18 extinct taxa (Boswijk and Whitehouse 2002; Buckland 1979; Smith and Whitehouse 2005; Whitehouse 1997a, 1997b, 2004). Here, the forest fauna is dominated by two categories of saproxylics: those that are predators of primary invaders of freshly dead trees and species that live in well-rotted, dead, fungoid wood. There is also the notable presence of species apparently associated with burnt forest, particularly pinewood (*cf.* Whitehouse 2000). The rarest species tend to be the predators, highlighting that species at the top of the food chain are often the first affected by and endangered by habitat change and manipulation.

A review of the published literature (Smith and Whitehouse 2005) for its ancient forest fauna across a series of assemblages from Britain representing different forest types suggests,

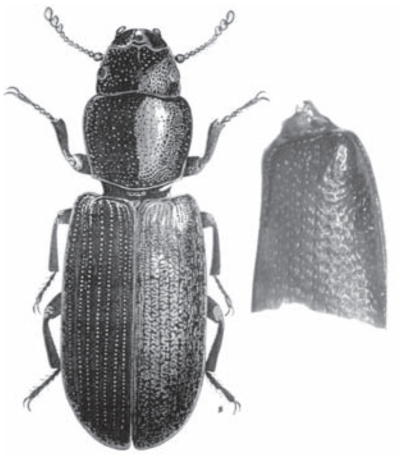

Figure 3—*Temnochila coerulea* West: on left, drawing of modern beetle by Peter Skidmore and on right fossil specimen of elytra. © Peter Skidmore (modern beetle drawing), with permission. The fossil was recovered from wood peat within the basal deposits of the bog at Thorne Moors, England (Roper 1996, Whitehouse 1997b).

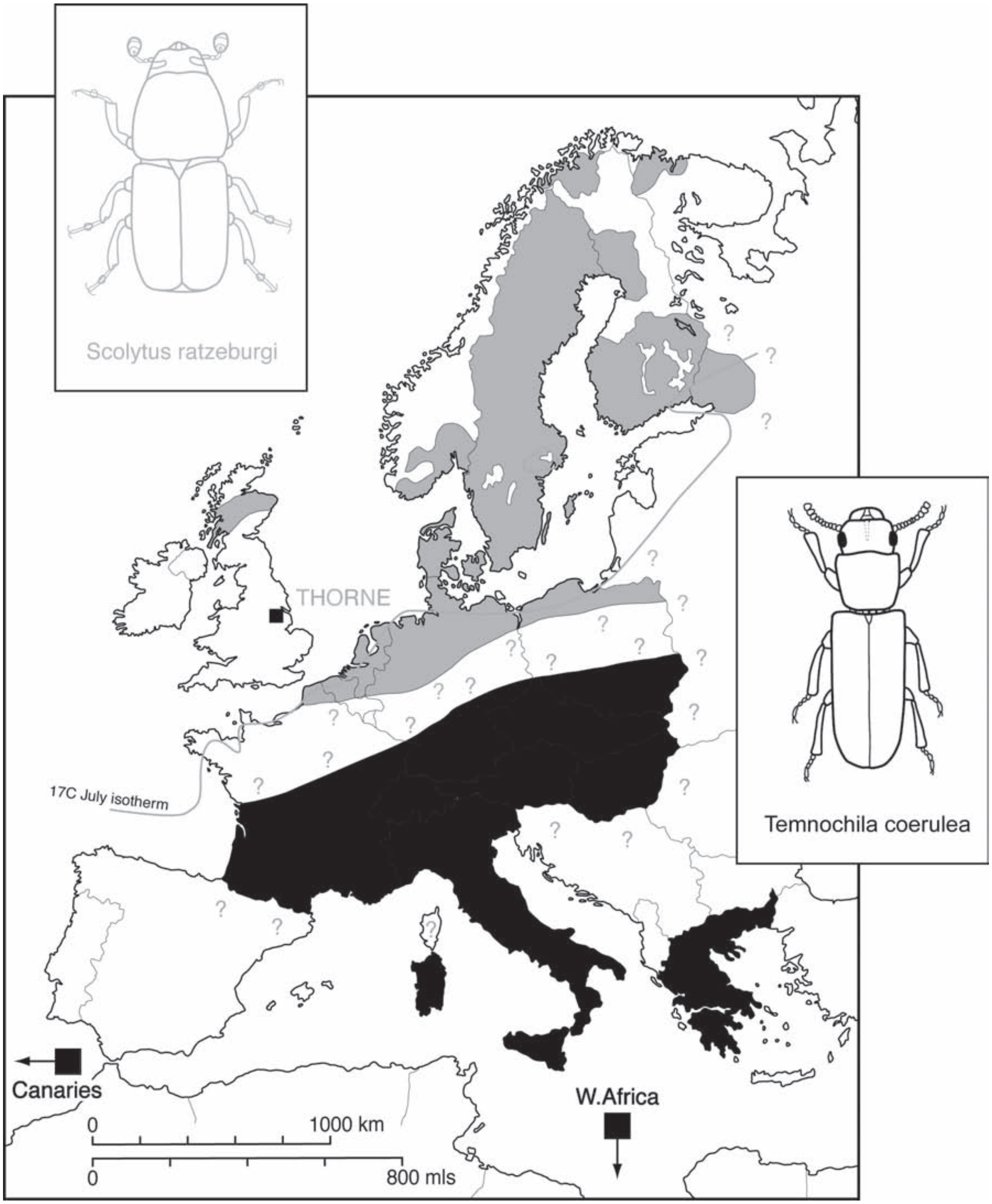

Figure 4—Modern distribution of *Temnochila coerulea* Westw (black) and *Scolytus ratzeburgi* Jans (grey), which were found together in the same deposit at Thorne Moors, Humberhead Levels, England. Arrowed boxes indicate find spots in Africa and the Canary Islands for *T. coerulea*. Redrawn with permission after an original by P.I. Buckland. © P.I. Buckland.

from the range of taxa present at many sites and the variety of niches they potentially exploited, that many of these forests were ecologically diverse and complex. For many sites, the 'woodland' component (this includes 'ancient woodland' taxa as well as other species associated with trees) accounts for *c.* 15-20 percent or higher of the terrestrial fauna present, a figure usually taken to indicate closed canopy forest (Robinson 1981). Such high levels are particularly evident at particular sites, such as woodland mires and floodplains, but this is not the case everywhere. Indeed, not all sites in the survey included large numbers of extinct, endangered or rare species, despite containing substantial forest faunas (Smith and Whitehouse 2005). Smith and Whitehouse (2005) conclude that it may sometimes be difficult to assess the extent to which individual species of beetle were rare or common in the past and therefore the extent they have declined by the present day. Nevertheless, certain groups appear to have suffered greater declines than have others—namely those associated with boreal forests (particularly pinicolous taxa, see Whitehouse 1997a, for further details) and mire forest habitats, because their habitats have declined, at least in the British Isles. More recently, large numbers of these species have declined in the boreal forests of Fennoscandia (Heliövaara and Väisänen 1984, Kaila and others 1997), following increased felling and grazing in the latter part of the 21st century (Peterken 1996). Many of the species showing contractions in populations are associated with the later stages of wood decomposition, and whilst the biology of many of these species is qualitatively well-known, quantitative information concerning the micro- and macro-habitat requirements of individual species is still scarce (Kaila and others 1997).

It is still unclear when many of these species decline or disappear from the fossil record. At least a sizeable proportion probably disappears with primary clearance during the prehistoric period, although at least some taxa survive into the medieval period (Dinnin 1997; Whitehouse, in press). There are hints that there are differences in the records between Britain and Ireland, although our knowledge of the latter's record is still very limited (Whitehouse, in press). In particular, it appears that some taxa may survive in Ireland up until the medieval period, but that high levels of post-medieval woodland clearance caused the further eradication of other less specialised taxa. The use of wood in urban areas and house structures in towns may have provided important refugia for some species during this period. In contrast, the establishment of Forests, Chases and the practises of traditional woodland management in England ensured the continued survival of some of the species which sadly have contracted in Ireland (Whitehouse, in press).

DISCUSSION: IMPLICATIONS FOR FOREST MANAGEMENT

What are the implications of this research for the management of forested areas? There are, broadly speaking, three different areas where fossil beetle research has important insights to provide the forest managers with. Firstly, the research can provide valuable insights into the structure of native forest; secondly, it provides an insight into species decline and causes of decline and therefore ways in which loss of biodiversity may be halted and even reversed; finally, it provides insights into how the forest can best be managed to ensure survival of saproxylics and encourage their return.

In terms of forest structure, forest managers need to be clear about what they are trying to achieve. The current debate concerning the level of open-ness of forests and the role of grazing animals may be particularly pertinent and it may no longer be appropriate to aim for the development of closed canopy forest. Indeed, many forest invertebrates require a mixed mosaic landscape rather than full canopy forest (Alexander 1999, Palm 1959, Ranius and Jansson 2000), whilst Similä and others (2002) have drawn attention to the high numbers of threatened insect species belonging to early successional forest. These habitats, often in glades and on forest edges, provide significant nectar sources near breeding habitat (Harding and Rose 1986). Other taxa appear to require sunny, open habitats with large amounts of dead wood, the type of habitat offered by pasture woodland suggested by Vera (2000) for past forests. As Alexander (1999, 2002) has pointed out, ancient wood pastures and parklands provide some of the most valuable habitats for many saproxylics rather than closed forest. Moreover, if the "wildwood" was uniformly dense, where did all the many light-demanding species of plants and invertebrates evolve? Eriksson and others (2002) draw attention to the fact that an explicit consideration of the original habitats of semi-natural grassland species has been overlooked in the closed forest hypothesis and highlight that many such species already existed in the landscape. The mixture of different species found in the fossil record during the early Holocene, periods when forests were largely free of human disturbance, suggests that substantial open areas did indeed exist although their extent may have varied across different forest types and areas.

From a management perspective, it is therefore crucial that forest managers are aware of the history of a forest area and its current status. They should manage the area in the most appropriate way for the species which are present, whilst being aware of opportunities for species colonisation from nearby sites and potential to create new habitats. Any management activities and their impacts on invertebrates should be monitored to ensure that biodiversity is not adversely impacted by management activities. Where it is established that the species mix is such that pasture woodland would be beneficial, managers may allow the development of open glades as well as areas with a more closed canopy. In this scenario, allowing some level of grazing by wild or domesticated animals as a management tool is likely to be beneficial, although stock levels may need to be controlled in terms of their density, by season and their effects monitored to ensure that over-grazing does not occur (Mountford and Peterken 2003). A consideration of baseline flora and fauna prior to the introduction of grazing will be essential, followed up by survey at intervals after the introduction of grazing. The use of animals as a management tool has often been perceived in negative terms by forest managers, but the development of the grazing debate and ongoing experimental work indicates the potential of this sort of approach, particularly in the management of large reserves, allowing managers to help maintain structural and species diversity within forest and encourage regeneration of light-demanding taxa (Bakker and others 2004). Current large scale ecological projects where this approach has proven beneficial include the Oostvaardersplassen reserve in the Netherlands (Kampf 2002) and the New Forest, Hampshire, UK (Kirby 2004, Mountford and Peterken 2003).

It is likely that a range of other disturbance factors, in addition to animal grazing, played equally important roles in creating open areas. Forests in the past appear to have been subject to a range of natural disturbances such as forest fires and storm damage, often creating open, sun-exposed places with considerable amounts of dying and dead wood (Kirby 2004; Whitehouse 1998, 2000). Forest fires, in particular, appear to have played an important role in maintaining an open character in at least some early Holocene forests, especially where dominated by flammable pine and birch (Bradshaw and Hannon 2004, Whitehouse 2000). Indeed, substantial numbers of the boreal insect fauna are fire-favoured (Wikars and Schimmel 2001), and this faunal element may represent the closest modern analogue for some of the early Holocene beetle assemblages which have been examined in Great Britain. As a result of such fires, local vegetation patches and islands may have emerged locally quite frequently, creating semi-permanent open spaces and opening up the canopy of the forest. Again, whilst many foresters are understandably cautious about forest fires, from an ecological perspective they can be extremely useful and add to ecosystem diversity. Moreover, ecologists are increasingly recognising that natural fires may have played a more important part than previously assumed in maintaining areas of open landscape in the past (Kirby 2004). Emulation and controlled use of these natural dynamics may be one key area in which managers may increase ecosystem structure, range and biodiversity.

Forest managers may also find it beneficial to consider the causes of saproxylic insect decline which can be seen clearly in the fossil insect record. The demise of many of the species of *Urwaldtire* has been attributed to the combined loss of undisturbed forest habitats and particularly of dead wood. Elton (1966) pointed out that if dead wood is removed from the forest ecosystem, the system is impoverished of a fifth or more of its invertebrate fauna. The apparent poor mobility of many of these saproxylic species (*cf.* Warren and Key 1991) appears to have played an important part in their decline and/or extirpation in the British Isles (Buckland and Dinnin 1993, Whitehouse 1997b), particularly with the onset of forest fragmentation and the loss of continual forest corridors. Forest history, management and temporal continuity of habitat also appear to have been significant components in the maintenance and survival of many of these saproxylic communities (Whitehouse, in press), whilst increasing geographic isolation in areas such as raised mires and other wetlands appears to have played an important role in isolating relict populations. The loss of particular types of forest, such as pinewood and its associated habitats, either through successional competition, decline in forest fires and/or the development and expansion of peatlands, seem to have all been important contributory factor for some species (Whitehouse 1997a, 2000). There is strong evidence to support the idea that climate change may also have played an important role in some local extirpation. This may have been related to changes in temperature, but also a move from a more continental climate to a wetter, more oceanic one (Buckland 1979; Dinnin and Sadler, 1999; Whitehouse and others 1997, in press). However, it is clear that extirpations are the result of a complex interplay between climate changes on the one hand and human impact on the ecosystem on the other.

From a management perspective, it is clear that managers must ensure that forests include a variety of dead, frassy wood habitats in a range of different conditions and levels of moisture, leaving wind-throws and upstanding dead wood to die in situ. Although forest managers are commonly concerned that this may encourage forest “pests” into an area which may attack healthy trees, the fossil record indicates that populations are commonly kept in check by predators of primary invaders of wood. Moreover, the availability of suitable habitats for predators is likely to ensure that any pests affecting healthy trees are more likely to be controlled because predators are provided with suitable habitats.

Continuity of habitat appears to be crucial as does ensuring that habitats are not overly isolated and fragmented; corridors of suitable habitat appear to be important. Traditional management practices including pollarding and coppicing can create the necessary diversity and range of different successional habitats for many saproxylics. This management approach may be particularly desirable where it can be established that these traditional management practises have been used in the past and therefore will be beneficial to and contributed towards the current species mix. Where there is no history of these traditional practises it may still be worthwhile considering using these approaches, depending upon the overall aims of forest management and the current species mix. Under these circumstances, managers may wish to undertake any such management under controlled conditions during initial stages and with invertebrate monitoring to establish any impacts on existing site fauna.

In some types of forests, allowing forest fires to occur on a regular basis is likely to be beneficial not only in facilitating the regeneration of some trees (e.g., *Pinus sylvestris*), but encouraging a wide range of fire-adapted and pyrophilous invertebrates (Whitehouse 2000), as well as discouraging major build-ups of forest litter layers which commonly lead to major devastating conflagrations.

CONCLUSIONS

The fossil insect record indicates that it has many useful contributions to make to any debate concerning ecosystem conservation and draws attention to the long term changes which sites have undergone. In particular, it highlights the major changes which have impacted on forest invertebrates, mostly through the activities of humans, and emphasises that we are still some way from having a good understanding of what forest ecosystems in high northern latitudes may have looked like in their ‘natural’ state.

Future research needs to take several different directions. First, many of the records discussed above come from the British Isles. We need to have a much clearer understanding of the wider context of these faunas and examine similar fossil faunas from across Europe. Is what we see in the fossil record in Britain and Ireland unique or is it just part of a wider, complex, European picture? A series of comparative sites across Europe would provide a much-needed context to these studies. Our understanding of the early “wildwood” is relatively poor, despite its potential to provide valuable answers, particularly concerning the arrival and development of the forest fauna. Our knowledge of records covering the last thousand years is surprisingly poor; this is at least partially because of a paucity of suitable peat deposits which relate to this period, but there are a variety of deposits—such as in-filled forest hollows, in-filled palaeochannels and shallow lakes—which could all be suitable for investigation and which could provide valuable insights into this period. Any such investigations would provide valuable insights into the impacts of the modern era upon many saproxylics and their implications for long term management of sites.

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LITERATURE CITED

Alexander, K. 1999. Should deadwood be left in sun or shade? British Wildlife 10: 342.

Alexander, K.N.A. 2002. The invertebrates of living and decaying timber in Britain and Ireland Peterborough. English Nature.

Andrieu-Ponel, V.; Ponel, P.; Bruneton, H. [and others]. 2000. Palaeoenvironments and cultural landscapes of the last 2000 years reconstructed from pollen and Coleopteran records in the Lower Rhône Valley, southern France. The Holocene 10: 341-355.

Ashworth, A.C. 2004. Quaternary Coleoptera of the United States and Canada. Developments in Quaternary Science 1: 505-517.

Atkinson, T.C.; Briffa, K.R.; Coope, G.R. 1989. Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. Nature 325: 587-592.

Baker, R.G.; Bettis, E.A.; Schwert, D.P. [and others]. 1996. Holocene palaeoenvironments of northeast Iowa. Ecological Monographs 66(2): 203-234.

Bakker, E.S.; Olff, H.; Vandenberghe, C. [and others]. 2004. Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. Journal of Applied Ecology 41, 571-582.

Bennett, K.D.; Tzedakis, P.C.; Willis, K.J. 1991. Quaternary refugia of north European trees. Journal of Biogeography 18: 103-115.

Birks, H.H.; Battarbee, R.W.; Birks, H.J.B. 2000. The development of the aquatic ecosystem at Kråkenes Lake, western Norway, during the late-glacial and early-Holocene—a synthesis. Journal of Palaeolimnology 23: 91-114. [Contributions by Bradhsaw, E.G.; Brooks, S.J.; Duigan, C.A.; Jones, V.J.; Lemdahl, G.; Peglar, S.M.; Solem, J.O.; Solhøy, T. and Stalsberg, M.K.]

Birks, H.J.B. 1989. Holocene isochrone maps and patterns of tree-spreading in the British Isles. Journal of Biogeography 16: 503-40.

Biström, O.; Väisänen, R. 1988. Ancient forest invertebrates of the Pyhän-Häkki National Park in central Finland. Acta Zoologica Fennica 185: 1-69.

Blumer, M.A. 2002. Review of Grazing ecology and forest history. Environmental History 7: 687-9.

Böcher, J. 1986. Boreal insects in northernmost Greenland: palaeoentomological evidence from the Kap Kobemhavn Formation (Plio-Pleistocene) Peary Land. Fauna Norvegica B36: 37-43.

Böcher, J. 1997. History of the Greenland insect fauna with emphasis on living and fossil beetles. Quaternary Proceedings 5: 35-48.

Bond, G.; Kromer, B.; Beer, J. [and others]. 2001. Persistent solar influence on North Atlantic climate during the Holocene. Science 294: 2130-6.

Bond, G.; Showers, W.; Chesby, M. [and others]. 1997. A pervasive millennial-scale cycle in North Atlantic Holocene and glacial climates. Science 278: 1257-1266.

Boswijk, G.; Whitehouse, N.J. 2002. *Pinus* and *Prostomis*: a dendrochronological and palaeoentomological study of a mid-Holocene woodland in eastern England. The Holocene 12: 585-96.

Bradshaw, R.; 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.; Mitchell, F.J.G. 1999. The palaeoecological approach to reconstructing former grazing-vegetation interactions. Forest Ecology and Management 120: 3-12.

Bradhsaw, R.H.W.; Hannon, G.E. 2004. The Holocene structure of north-west European temperate forest induced from palaeoecological data. In Honnay, O.; Verheyen, K.; Bossuyt, B. and Hermy, M. (eds) Forest Biodiversity: lessons from history for conservation. Wallingford, Oxfordshire: CABI Publishing, 11-26.

Bradshaw, R.H.W.; Hannon, G.E.; Lister, A. 2003. A long-term perspective on ungulate-vegetation interactions. Forest Ecology and Management 181: 267-80.

Brooks, S.J.; Birks, H.J.B. 2000. Chironomid-inferred late glacial air temperatures at Whitrig Bog, southeast Scotland. Journal of Quaternary Science 15 (8): 759-764.

Brooks, S.J.; Lowe, J.J.; Mayle, F.E. 1997a. The Late Devensian Lateglacial palaeoenvironmental record from Whiting Bog, SE Scotland. 2. Chironomidae (Insecta: Diptera). Boreas 26: 297-308.

Brooks, S.J.; Mayle, F.E.; Lowe, J.J. 1997b. Chironomid-based lateglacial climatic reconstruction for southeast Scotland. Journal of Quaternary Science 12 (2): 161-167.

Buckland, P.C. 1979. Thorne Moors: a palaeoecological study of a bronze age site; a contribution to the history of the British insect fauna. Birmingham: Dept. of Geography, University of Birmingham, Occasional Publication Number 8.

Buckland, P.C.; Amorosi, T.; Barlow, L.K. [and others]. 1996. Bioarchaeological and climatological evidence for the fate of Norse farmers in medieval Greenland. Antiquity 70: 88-96.

Buckland, P.C.; Coope, G.R. 1991 A bibliography and literature of Quaternary entomology. University of Sheffield: J.R. Collis Publications.

Buckland, P.C.; Dinnin, M.H. 1993. Holocene woodlands, the fossil insect evidence. In: Kirby, K.J. and Drake, C.M. (eds.) Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain. Peterborough: English Nature, 6-20.

Buckland, P.C.; Edwards, K. 1984. The longevity of pastoral episodes of clearance activity in pollen diagrams; the role of post-occupation grazing. Journal of Biogeography 11: 243-9.

Buckland, P.I.; Yuan Zhuo, D.; Buckland, P.C. 1997. Towards an expert system in palaeoentomology. Quaternary Proceedings 5: 67-78.

Caseldine, C.; Gearey, B.; Hutton, J. [and others]. 2001. From the wet to the dry: palaeoecological studies at Derryville, Co. Tipperary, Ireland. In Raftery, B. and Hickey, J. (eds) Recent Developments in Wetland Research. Dublin: Dept. of Archaeology, University College Dublin, 99-115.

Coope, G.R. 1970. Interpretations of Quaternary insect fossils. Annual Reviews of Entomology 15: 97-120.

Coope, G.R. 1977. Fossil Coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (last) cold stage. Philosophical Transactions of the Royal Society of London Series B 280: 313-340.

Coope, G.R. 1978. Constancy of insect species versus inconstancy of Quaternary environments. In L.A. Mound and N. Waldoff (eds.) Diversity of Insect Faunas (Symposia of the Royal Entomological Society of London 9). London: Blackwell, 176-187.

Coope, G.R. 1994. The response of insect faunas to glacial-interglacial climatic fluctuations. Philosophical Transactions of the Royal Society of London, Series B, 344: 19-26.

Coope, G.R. 1995. Insect faunas in ice age environments: why so little extinction? In Lawton, J.H. and May, R.M. (eds.) Extinction rates. Oxford: Oxford University Press, 55-74.

Coope, G.R. 1998. Insects. In Preece, R. C. and Bridgland, D. R. (eds.), Late Quaternary Environmental Change in North-West Europe: Excavations at Hollywell Coobe, South-East England. London: Chapman and Hall, 213-33.

Coope, G.R. 2004. Several million years of stability among insect species because of, or in spite of, ice age climatic instability? Philosophical Transactions Royal Society London B 359: 209-214.

Coope, G.R.; Brophy, J.A. 1972. Late glacial environmental changes indicated by a Coleopteran succession from North Wales. Boreas 1: 97-142.

Coope, G.R.; Lemdahl, G. 1995. Regional differences in the late-glacial climate of northern Europe based on Coleopteran analysis. Journal of Quaternary Science 10(4): 391-395.

Coope, G.R.; Lemdahl, G.; Lowe, J.J.; Walkling, A. 1998. Temperature gradients in northern Europe during the last glacial-Holocene transition (14-9^{14}C kyr BP) interpreted from Coleopteran assemblages. Journal of Quaternary Science 13 (5): 419-433.

Coope, G.R.; Osborne, P.J. 1968. Report on the Coleopterous fauna of the Roman well at Barsley Park, Gloucestershire. Transations of the Bristol and Gloucershire Archaeological Society 86: 84-87.

Coope, G.R.; Shotton, F.W.; Strachan, I. 1961. A late Pleistocene fauna and flora from Upton Warren, Worcestershire. Philosophical Transactions of the Royal Society of London, B244: 379-421.

Cronon, W. 1983. Changes in the land; Indians, colonists and the ecology of New England. New York: Hill and Wang.

Danks, H.V.; Foottit, R.G. 1989. Insects of the boreal zone of Canada. Canadian Entomologist 121: 626-674.

Dinnin, M. 1997. Holocene beetle assemblages from the lower Trent floodplain at Bole Ings, Nottinghamshire, U.K. Quaternary Proceedings 5: 83-104.

Dinnin, M.H.; Sadler, J.P. 1999. 10,000 years of change: the Holocene entomofauna of the British Isles. Quaternary Proceedings 7: 545-62.

Edwards, K.J. 1996. A Mesolithic of the Western and Northern Isles of Scotland? Evidence from pollen and charcoal. In Pollard, T. and Morrison, A. (eds.) The early prehistory of Scotland. Edinburgh: Edinburgh University Press, 23-38.

Elias, S.; Anderson, K.H.; Andrews, J.T. 1996. Late Wisconsin climate in Northeastern USA and Southeastern Canada, reconstructed from fossil beetle assemblages. Journal of Quaternary Science 11 (5): 417-421.

Elias, S.A. 1996. Late Pleistocene and Holocene seasonal temperatures reconstructed from fossil beetle assemblages in the Rocky Mountains. Quaternary Research 46: 311-318.

Elias, S.A. 1997. The mutual climatic range method of palaeoclimate reconstruction based on insect fossils: new applications and inter-hemispheric comparisons. Quaternary Science Reviews 16: 1217-1225.

Elton, C. 1966. Dying and dead wood. In Elton, C. (Ed.), The Pattern of Animal Communities. London : Methuen, 279-305.

Elton, C.S. 1966. The pattern of animal communities. London: Methuen.

Eriksson, O.; Cousins, S.A.O.; Bruun, H.H. 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. Journal of Vegetation Science 13: 743-8.

Franklin, J.F. 1988. Structural and functional diversity in temperate forests. In Wilson, E. O. (ed.) Biodiversity. Washington: National Academy Press, 166-75.

Girling, M. 1989. Mesolithic and later landscapes interpreted from the insect assemblages of West Heath Spa, Hampstead. In: Collins, D. and Lorimer, D. (eds.) Excavations at the Mesolithic site on West Heath, Hampstead 1976-1981 (British Archaeological Reports 217), York: British Archaeological Reports, 72-89.

Girling, M.A. 1976. Fossil Coleoptera from the Somerset Levels: the Abbot's Way. Somerset Levels Papers 2: 28-33.

Greenwood, M.T.; Agnew, M.D.; Wood, P.J. 2003. The use of caddisfly fauna (Insecta: Trichoptera) to characterise the late-glacial River Trent, England. Journal of Quaternary Science 18(7): 645-662.

Greig, J. 1982. Past and present lime woods in Europe. In: Bell, M. and Limbrey, S. (eds.) Archaeological Aspects of Woodland Ecology (British Archaeological Reports International Series 146), Oxford: British Archaeological Reports, 23-55.

Harding, P.T.; Rose, F. 1986. Pasture-woodlands in lowland Britain. Peterborough: Institute of Terrestrial Ecology, NERC.

Heliövaara, K.; Väisänen, R. 1984. Effects of modern forestry on north-western European forest invertebrates: a synthesis. Acta Forestalia Fennica 189: 1-32.

Kaila, L.; Martikainen, P.; Puttila, P. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodiversity and Conservation 6: 1-18.

Kampf, H. 2002. Nature conservation in pastoral landscapes: challenges, chance and constraints. In Redecker, B.; Finck, P.; Hardtle, U.; Riecken, U. and Schroder, E. (eds) Pasture landscapes and Nature Conservation. Berlin: Springer-Verlag, 15-30.

Kenward, H.K. 1975. Pitfalls in the environmental interpretation of insect death assemblages. Journal of Archaeological Science 2: 85-94.

Kenward, H.K. 1978. The analysis of archaeological insect assemblages: a new approach. York: York Archaeological Trust.

Kenward, H.K.; Hall, A.R. 1995. Biological evidence from 16-22 Coppergate, York (Archaeology of York: The Environment 14/7). York: York Archaeological Trust,

Kirby, K.J. 2003. What might a British forest-landscape driven by large herbivores look like? (Research Report 530). Peterborough: English Nature.

Kirby, K.J. 2004. A model of a natural wooded landscape in Britain as influenced by large herbivore activity. Forestry 77 (5): 405-420.

Klinger, L.F.; Elias, S.A.; Behan-Pelletier, V.M.; Williams, N.E. 1990. The bog climax hypothesis: fossil arthropod and stratigraphic evidence in peat sections from south-east Alaska, U.S.A. Holarctic Ecology 13: 72-80.

Lucht, W.H. 1987. Katalog. Die Käfer Mitteleuropas. Krefeld: Goecke and Evers.

Marra, M.J.; Smith, E.C.G.; Schulmeister, J.; Leschen, R. 2004. Late Quaternary climate change in the Awatere Valley, South Island, New Zealand using a sine model with a maximum likelihood envelope on fossil beetle data. Quaternary Science Reviews 23: 1637-1650.

Matthews, J.V., Jr. 1970. Two new species of Micropeplus from the Micropeplinae of western Alaska with remarks on the evolution of Coleoptera: Staphylinidae. Canadian Journal of Zoology 48: 779-788.

Mitchell, F.J.G. 1990. The impact of grazing and human disturbance on the dynamics of woodland in sw Ireland. Journal of Vegetation Science 1: 245-54.

Mitchell, F.J.G. 2005. How open were European primeval forests? Hypothesis testing using palaeoecological data. Journal of Ecology 93: 168-177.

Morgan, A.V.; Morgan, A. 1987. Palaeoentomology—towards the next decade. Episodes 10 (1): 38-40.

Mountford, E.P.; Peterken, G.F. 2003. Long-term change and implications for the management of wood-pastures: experience over 40 years from Denny Wood, New Forest. Forestry 76 (1): 19-43.

Osborne, P.J. 1969. An insect fauna of late bronze age date from Wilsford, Wiltshire. Journal of Ecology 38: 555-566.

Osborne, P.J. 1972. Insect faunas of Late Devensian and Flandrian age from Church Stretton, Shropshire Philosophical Transactions of the Royal Society of London 263: 327-367.

Osborne, P.J. 1974. An insect assemblage of early Flandrian age from Lea Marston, Warwickshire, and its bearing on the contemporary climate and ecology. Quaternary Research 4: 471-486.

Osborne, P.J. 1980. The Late Devensian-Flandrian transition depicted by serial insect faunas from West Bromich, Staffordshire, England. Boreas 9: 139-147.

Osborne, P.J. 1988. A late bronze age insect fauna from the River Avon, Warwickshire, England: its implications for the terrestrial and fluvial environment and for climate. Journal of Archaeological Science, 15: 715-727.

Osborne, P.J. 1995. An insect fauna of Roman date from Stourport, Worcestershire, U.K. and its environmental implications. Circaea (The Journal of the Association for Environmental Archaeology) 12 (2): 183-189.

Palm, T. 1951. Die Holz und Rindenkäfer der nordschwedischen Laubbaume. Meddelelser Statens Skögsfors.-instituten, 40, no. 2.

Palm, T. 1959. Die Holz und Rindenkäfer der Sud- und Mittelschwedischen Laubbäume. (Opuscula Entomologica Supplementum 16) Lund: Entomologiska Sallskapet.

Panagiotakopulu, E. 2004. Dipterous remains and archaeological interpretation. Journal of Archaeological Science 31: 1675-1684.

Patterson, W.A.; Backman, A.E. 1988. Fire and disease history of forests. pp. 603-32 in Huntley B. and Webb, T. (eds.), Vegetation History. New York: Kluwer Academic.

Patterson, W.A.; Edwards, K.J.; Maguire, D.J. 1987. Macroscopic charcoal as a fossil indicator of fire. Quaternary Science Reviews 6: 3-23.

Pearson, G.W.; Pilcher, J.R.; Baillie, M.G.L. [and others]. 1986. High precision ^{14}C measurement of Irish oaks to show the natural ^{14}C variation from AD 1840-5210 BC. Radiocarbon 28(2B): 911-934.

Peterken, G.F. 1996. Natural woodland: ecology and conservation in northern temperate regions. Cambridge: Cambridge University Press.

Ponel, P.; Andrieu-Ponel, A.; Parchoux, F. [and others]. 2001. Lateglacial and Holocene high-altitude environmental changes in Vallée des Merveilles (Alpes-Maritimes, France): insect evidence. Journal of Quaternary Science 16: 795-812.

Rackham, O. 1986. The history of the countryside. London: J. M. Dent and Sons Ltd.

Rackham, O. 2003. Ancient woodland. Its history, vegetation and use in England. (New Edition). Dalbeattie: Castlepoint Press.

Ranius, T.; Jansson, N. 2000. The influence on forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation 95: 85-94.

Rasmussen, P. 1990. Pollarding of trees in the Neolithic: often presumed—difficult to prove. In: D. E. Robinson (ed.) Experimentation and reconstruction in environmental archaeology. (Symposia of the Association of Environmental Archaeologists 9) Oxford: Oxbow Books, 139-148.

Reiss, R.; Ashworth, A.C.; Schwert, D.P. 1999. Molecular genetic evidence for the post-Pleistocene divergence of populations of the artic-alpine ground beetle *Amara Alpina* (Paykull) (Coleoptera: Carabidae). Journal of Biogeography 26: 785-794.

Reitter, E. 1908-12. Fauna Germanica-Die Käfer des Deutchen Reiches. Stuttgart.

Ribera, I.; Vogler, A.P. 2004. Speciation of Iberian diving beetles in Pleistocene refugia (Coleoptera, Dytiscidae). Molecular Ecology 13: 179-193.

Robinson, M. 1981. Appendix I: the use of ecological groupings of Coleoptera for comparing sites. In M. Jones and G. Dimbleby (eds.) The Environment of Man: the Iron Age to the Anglo-Saxon Period. London: British Archaeological Reports, 279-281.

Robinson, M.A. 1991. The Neolithic and late bronze age insect assemblages. In Needham, S. (ed.), Excavation and Salvage at Runnymede Bridge, 1978: the Late Bronze Age Waterfront Site. London: British Museum, 277-325.

Robinson, M.A. 2000. Middle Mesolithic to late bronze age insect assemblages and an early Neolithic assemblage of waterlogged macroscopic plant remains. In Needham, S. P. (ed.), The Passage of the Thames: Holocene Environment and Settlement at Runnymede. (Runnymede Bridge Research Excavations: Volume 1). London: The British Museums Press, 146-67.

Roper, T. 1996. Fossil insect evidence for the development of raised mire at Thorne Moors, near Doncaster. Biodiversity and Conservation 5: 503-521.

Russell, E. 1997. People and land through time. Linking Ecology and History. New Haven, Connecticut: Yale University Press.

Schwert, D.P. 1996. Effect of Euro-American settlement on an insect fauna: paleontological analysis of the recent chitin record of beetles (Coleoptera) from northeastern Iowa. Ecology and Population Biology 89: 53-63.

Shirt, D.B. 1987. British red data books: 2. Insects. Peterborough: Nature Conservancy Council.

Similä, M.; Kouki, J.; Martikainen, P.; Uotila, A. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation 106: 19-27.

Skidmore, P. 1995. A dipterological perspective on the Holocene history of the North Atlantic area. Unpublished PhD thesis, University of Sheffield, England.

Smith, A.G. 1970. The influence of Mesolithic and Neolithic man on British vegetation: a discussion. In: D. Walker and R.G. West (eds.), Studies in the Vegetation History of the British Isles. Cambridge: University Press, 81-96.

Smith, A.G. 1981. Palynology of a Mesolithic-Neolithic site in county Antrim, N. Ireland. Lucknow: Proceedings of the IVth International Palynology Conference (1976-1977), 248-257.

Smith, D.; Whitehouse, N.J. 2005. Not seeing the woods for the trees; a palaeoentomological perspective on woodland decline. in Brickley, M., Smith, W. and Smith, D.N. (eds.), 'The Fertile Ground'; Papers in Honour of Susan Limbrey. Oxford: Oxbow Books.

Smith, D.N.; Howard, A.J. 2004. Identifying changing fluvial conditions in low gradient alluvial archaeological landscapes: can Coleoptera provide insights into changing discharge rates and floodplain evolution? Journal of Archaeological Science 31: 109-120.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. (Nature and Environment Series No 42). Strasbourg: Council of Europe,

Sutherland, W.J. 2002. Conservation biology: openness in management. Nature 418: 834-5.

Svenning, J.-C. 2002. A review of natural vegetation openness in north-western Europe. Biological Conservation 104: 133-48.

Vandenberghe, J.; Coope, R.; Kasse, K. 1998. Quantitative reconstructions of palaeoclimates during the last interglacial-glacial in western and central Europe: an introduction. Journal of Quaternary Science 13 (5): 361-366.

Vera, F.W.M. 2000. Grazing ecology and forest history. Oxfordshire: CABI Publishing.

Walker, I.R.; Mott, R.J.; Smol, J.P. 1991. Allerød-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. Science 253: 1010-1012.

Walker, M.J.C.; Coope, G.R.; Lowe, J.J. 1993. The Devensian (Weichselian) Lateglacial palaeoenvironmental record from Gransmoor, East Yorkshire, England. Quaternary Science Reviews 12: 659-680.

Warren, M.S.; Key, R.S. 1991. Woodlands: past, present and potential for insects. In Collins, N.M. and Thomas, J.A. (eds.) The conservation of insects and their habitats (15th Symposium of the Royal Entomological Society of London, 14-15 September 1989). London: Academic Press, 155-211.

Whitehouse, N.J. 1997a. Insect faunas associated with *Pinus sylvestris* L. from the mid-Holocene of the Humberhead Levels, Yorkshire, U.K. Quaternary Proceedings 5: 293-303.

Whitehouse, N.J. 1997b. Silent witnesses: an “Urwald” fossil insect assemblage from Thorne Moors. Thorne and Hatfield Moors Papers 4: 19-54.

Whitehouse, N.J. 1998. The evolution of the Holocene wetland landscape of the Humberhead Levels from a fossil insect perspective. Unpublished PhD thesis, University of Sheffield.

Whitehouse, N.J. 2000. Forest fires and insects: palaeoentomological research from a sub-fossil burnt forest. Palaeogeography, Palaeoclimatology, Palaeoecology 164: 231-46.

Whitehouse, N.J. [In press]. The Holocene British and Irish ancient woodland fossil beetle fauna: implications for woodland history, biodiversity and faunal colonisation. Quaternary Science Reviews.

Whitehouse, N.J.; Boswijk, G.; Buckland, P.C. 1997. Peatlands, past, present and future; some comments from the fossil record. In: Parkyn, L.; Stoneman, R. and Ingram, H.A.P. (eds.) Conserving Peatlands. Wallingford, Oxfordshire: CAB International, 54-64.

Whitehouse, N.J.; Smith, D.N. 2004. “Islands” in Holocene forests: implications for forest openness, landscape clearance and “culture-steppe” species. Environmental Archaeology 9(2): 199-208.

Wikars, L.-O.; Schimmel, J. 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. Forest Ecology and Management 141: 189-200.

Wilkinson, B.J. 1984. Interpretation of past environments from subfossil caddis larvae. In Morse, J.C. (ed.) Proceedings of the 4th International Symposium on Trichoptera. The Hague: W. Junk, 447-452.

Willis, K.J. 1996. Where did all the flowers go? The fate of temperate European flora during glacial periods. Endeavour 20: 110-114.