

# 'Islands' in Holocene forests: Implications for Forest Openness, Landscape Clearance and 'Culture-Steppe' Species

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## Abstract

Human activity has undoubtedly had a major impact on Holocene forested ecosystems, with the concurrent expansion of plants and animals associated with cleared landscapes and pasture, also known as 'culture-steppe'. However, this anthropogenic perspective may have underestimated the contribution of autogenic disturbance (e.g. wind-throw, fire), or a mixture of autogenic and anthropogenic processes, within early Holocene forests. Entomologists have long argued that the north European primary forest was probably similar in structure to pasture woodland. This idea has received support from the conservation biologist Frans Vera, who has recently strongly argued that the role of large herbivores in maintaining open forests in the primeval landscapes of Europe has been seriously underestimated. This paper reviews this debate from a fossil invertebrate perspective and looks at several early Holocene insect assemblages. Although wood taxa are indeed important during this period, species typical of open areas and grassland and dung beetles, usually associated with the dung of grazing animals, are persistent presences in many early woodland faunas. We also suggest that fire and other natural disturbance agents appear to have played an important ecological role in some of these forests, maintaining open areas and creating open vegetation islands within these systems. More work, however, is required to ascertain the role of grazing animals, but we conclude that fossil insects have a significant contribution to make to this debate. This evidence has fundamental implications in terms of how the palaeoecological record is interpreted, particularly by environmental archaeologists and palaeoecologists who may be more interested in identifying human-environment interactions rather than the ecological processes which may be preserved within palaeoecological records.

**Keywords:** FOSSIL BEETLES, FOREST OPENNESS, ECOSYSTEM DYNAMICS, EARLY HOLOCENE

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## Introduction

The idea that non-anthropogenic processes may have played an important role in the structure of primeval European forest ecosystems has recently been highlighted by Frans Vera (2000), who has questioned many assumptions concerning the natural ecological state of 'wildwood' (*Urwald*). In particular, he suggests that the role of large herbivores has been seriously underestimated playing an important part in maintaining substantial open areas in the forests of primeval Europe. Vera's ideas have generated intense discussion amongst conservationists, biologists and palaeoecologists (Blumer

2002; Eriksson *et al.* 2002; Sutherland 2002; Svenning 2002; Bradshaw *et al.* 2003; Kirby 2003; Rackham 2003). Vera debunks the widespread idea that the 'wildwoods' of Britain and the rest of Europe were a dense, continuous canopy (*cf.* Rackham 1986; Peterken 1996) and suggests it may have been 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

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wildwood have been made by several modern entomologists (e.g. Harding and Rose 1986) and some palaeoecologists, who have drawn attention to the role of grazing in affecting vegetation structure (Buckland and Edwards 1984; Bradshaw and Hannon 1992; Bradshaw and Mitchell 1999; Robinson 2000). However, Vera fundamentally challenges traditional interpretations of vegetational history, ideas of succession and climax and the role of disturbance, suggesting we need to understand more fully the role of other agents, particularly animals, within these woodland systems and examine more carefully how we identify and interpret 'disturbances' within the palaeoecological record.

Palaeoecologists have argued that many such 'disturbances' are the result of anthropogenic activities from the early Mesolithic onwards in some areas of the British Isles (c. 10000–5000 BP) (e.g. Evans 1975; Williams 1985; Simmons 1996). These early clearances have been identified palaeoecologically in fluctuations of tree pollen, an increase in certain open taxa and, frequently, an increased occurrence of microscopic charcoal particles. The latter, in particular, have been seen to be the result of the use of fire to burn forests for clearance, and to encourage grazing animals for hunting (e.g. Mellars 1976; Simmons and Innes 1987; Edwards 1990; Simmons 1996; 2001). These ideas put people firmly at the centre of any identified disturbance of woodland ecosystems within the archaeological and palaeoecological literature, despite obvious problems with some of these models (e.g. Rowley-Conwy 1981; Bogaard 2002). In contrast, others highlight the range of autogenic and allogenic woodland processes, in addition to anthropogenic activities which may be preserved within palaeoecological records (e.g. Bennett *et al.* 1990; Bradshaw and Hannon 1992; Whitehouse 2000) raising questions about the interpretation of some of these so-called anthropogenic 'activities' evident within the pollen record (*cf.* Tipping 1994). From a palaeoecological and archaeological perspective, Vera's work highlights that the nature of early-mid Holocene landscapes may require re-thinking, and suggests that an understanding of the full range of anthropogenic, autogenic and allogenic processes affecting woodland ecosystems is needed to make sense of the palaeoecological record. Finally, his ideas challenge concepts of how people may have moved through these wooded landscapes and used available resources.

We discuss the grazing debate in the light of the published fossil beetle record and examine whether these indicate open 'islands' of vegetation in these woodlands. Beetles are powerful proxies for reconstructing a range of habitats and environmental conditions, including the reconstruction of forest

and disturbance histories (*cf.* Whitehouse 1997; 2000; Boswijk and Whitehouse 2002). We concentrate on records covering the early-mid Holocene, the period most representative of true wildwood, mostly free from anthropogenic activities.

## The Grazing Debate

Vera (2000) suggests that the original vegetation in the lowlands of Europe was a park-like landscape where the succession of trees is determined by large grazing herbivores. Grasslands develop as a result of grazing, but patches of hawthorn, blackthorn and holly would form thorny scrub. Seedlings of light-demanding trees become established on the fringes of this scrub, protected against the browsing of herbivores by these thorny shrubs and develop into wooded groves. The woodland shades out the thorny scrub and light-demanding trees, followed by more shade-tolerant species. Eventually the wooded grove breaks up as the trees age and decline, and the cycle starts all over again. Vera (2000, 9) thus suggests that: "The natural vegetation consists of a mosaic of large and small grasslands, scrub, solitary trees and groups of trees, in which the indigenous fauna of large herbivores is essential for the regeneration of the characteristic trees and shrubs of Europe. The wood-pasture can be seen as the closest modern analogy of this landscape".

Vera draws upon the palynological record of these early woodlands and highlights the high levels of *Quercus* and *Corylus* – both light-demanding trees – found regularly in pollen diagrams at this time, suggesting that these could indicate an increased role for light-demanding trees and a reduced role for shade-bearing taxa such as *Fagus*, *Tilia* and *Ulmus*. Additionally, he suggests that pollen diagrams have been interpreted to indicate closed canopy forest *because* of an uncritical expectation that wildwood was indeed thus. For instance, many pollen investigations often only reflect changes in arboreal taxa rather than whole woodland assemblage of shrubs and grasses (see also Rackham 2003, 501–2 for further comments). This is because many of these investigations are based on relatively limited pollen counts, which do not always register the full range of open indicator taxa or because these taxa have been excluded from the percentage calculations. Furthermore, modelling and empirical data suggest that relationships between non-arboreal pollen percentages (NAP) and vegetation openness can be non-linear (*cf.* Sugita *et al.* 1999). This is compounded in patchy landscapes such as those proposed by Vera (Broström *et al.* 1998; Bunting 2002; 2003). There are also some issues concerning the taphonomy and interpretation of pollen data,

particularly from lakes and bogs, suggesting ambiguity in some of these records (Bunting 2002; 2003). To circumvent some of these problems Bradshaw (1988) and Mitchell (1988; 1990) highlight the use of forest hollows as excellent sedimentary archives to study forest histories. However, even here, records indicate that arboreal taxa have dominated woodland assemblages throughout the Holocene (F. Mitchell pers. comm. 2003).

Studies in other regions, however, have found indicators of open vegetation throughout the Holocene – for instance, chalk grassland in the Yorkshire Wolds, at Willow Garth, England (Bush and Flenley 1987; Bush 1988; 1989), and western Jutland, Denmark (Odgaard 1994). In the former case, Bush (1988) suggests that grasslands were present from the early post-glacial in some chalkland areas, replacing the earlier tundra with temperate grassland taxa. Thomas (1989) later argued that some of this 'grassland' pollen may have derived from marshland plants, but failed to appreciate the importance of fossil beetle evidence described by Bush (1988) in his evaluation. Fossil beetles from the same levels as the grassland pollen included species typical of open grassland (*Phyllopertha horticola* (L.), *Cantharis rustica* Fall. and *Serica brunnea* L.). This suggests that grassland is indeed represented during the period of interest and highlights that the pollen record alone cannot be used to elucidate the grazing debate.

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 woodland composition, and hence structure, changes over the Holocene (cf. Birks 1989) or the changing climatic backdrop against which these changes were being played. Both succession and progressive climate change are likely to have impacted upon the forest ecosystem structure, either directly or indirectly. Millennial-scale climate variability resulting from solar forcing (Bond *et al.* 1997; 2001) and additional rapid, short-term climatic shifts reflecting changes in the strength of the North Atlantic Thermohaline Circulation occur during this early part of the Holocene (Broecker *et al.* 1989; Clark *et al.* 2001). Climate variability will have impacted on 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). Occasional severe winters, with a long period of snow cover, may also have an impact on ungulate populations (Kramer *et al.* 2003).

The assumption that animals and grazing pressure were distributed evenly across the landscape is open to question (cf. Buckland and Edwards 1984) – indeed, ungulate species vary in their impacts of forest environments with distinct forest types being favoured by different grazers (Latham 1999) – but more fundamentally, the role of humans in affecting animal distributions is not considered (e.g. Blumer and Bryne 1991; Martin and Szuter 1999). Vera's model requires high populations of large herbivores, an aspect which is difficult to address from the palaeontological evidence alone (Bradshaw *et al.* 2003). It is pertinent that whilst mainland Europe supported populations of his key grazers, both Britain and Ireland were different. In Britain, bison may not have re-colonised during the Holocene and large mammals – with the exception of wild pig – appear not to have been part of the native Irish fauna during the early Holocene (Woodman *et al.* 1997; Bradshaw *et al.* 2003). Vera's model, therefore, may be problematic in these areas. Most significantly, he does not properly consider the role of other disturbance factors in affecting the European wildwood structure – these include wind-throw of trees, dead trees and wood, pest attack, flooding and fires, all components known to have been active within these forested ecosystems (Zackrisson 1977; Patterson and Backman 1988; Whitehouse 2000; Bradshaw *et al.* 2003).

In an attempt to refute Vera's hypothesis, Svenning (2002) considered palaeoecological evidence from oceanic interglacial sites from northwestern Europe. He examined published pollen records, particularly non-arboreal pollen percentages, against estimates of vegetation openness inferred from beetle, molluscan and plant macrofossil remains. Svenning (2002) suggests that all the proxies indicate that the wildwood was indeed closed in character during the last interglacial, showing that palynological reconstructions of closed wildwood are correct. He concludes that Vera's assumption of open wildwood during the Holocene is not supported by any of the palaeoecological proxies. Where some open areas existed in the landscape, Svenning highlights the role of other disturbance factors, including forest fires in creating openings in the landscape, rather than grazing animals.

Although Svenning's (2002) idea of testing vegetation openness in previous interglacials from a range of proxies is an interesting one, there are several problems with some of his assumptions and arguments. In particular,

- the well understood differences in both climate and prevailing vegetation between the present and previous interglacial period;
- a basic lack of consideration of the difficulty of dating and correlating interglacial sites;



Figure 1. Location map showing sites discussed in text.

- the low sample resolution obtainable from interglacial sites due to deposit compression which makes the reconstruction of forest histories extremely challenging.

In addition, the comparative figures are largely meaningless, certainly those derived from beetle data. This is because it is not presently possible to estimate percentages of landscape openness/closedness from beetle records. Palaeoentomologists routinely provide indications of percentages of open taxa represented within an assemblage. These, however, reflect abundances within assemblages and are not intended to indicate *direct proportions of associated habitat* (Kenward 1975; 1978; Whitehouse 2004).

Robinson (1991) has suggested that values of up to 20% for wood and tree beetle taxa are indicative of closed woodland and less than 2% are indicative of largely open landscapes. Figures of 1% pasture/dung are suggested for closed woodland, whilst 10% pasture/dung is seen as largely pastoral. These figures are largely intuitive, however, are not based on any taphonomic study of the landscapes concerned, and should be viewed with considerable caution. Svenning (2002) does not allude to these figures. Aside from the problems of extrapolating vegetation openness from coleopteran data, Svenning (2002) does not publish details of his analysis, nor explain species habitat requirements. We conclude his comparison between pollen and beetle data as undertaken in this publication is misleading in the extreme, although the premise of using beetles and other proxies to examine vegetation openness clearly has potential, as we discuss below.

### Does the Fossil Beetle Record Throw any Light on this Debate?

Having provided a review of some of the issues concerning the grazing debate, we turn our attention to the fossil beetle record itself. It is important to note that there is a scarcity of published early Holocene fossil insect assemblages to draw upon and our conclusions are necessarily tentative. Fig. 1 shows the location of sites discussed.

Hollywell Coombe in Kent, England, is one of the earliest Holocene deposits investigated for its fossil insect fauna (Coope 1998). Several high forest beetles are already present within deposits spanning the first thousand years of the Holocene. Additionally, there is a community of beetles associated with open ground and light woodland, probably living in early successional habitats. An absence of dung beetles suggests that grazing mammals were not common. Fig. 2 shows the percentage contri-

bution of taxa associated with wood and trees, open ground and dung, within the limits of the published chronology, as classified by the authors from the original species list (Coope 1997). Open taxa represent high proportions (c. 20%) during the very early phases of the Holocene, but decline to c. 10% over the next thousand years, with a concurrent increase in woodland species, from c. 3% to 30%. Abundances of dung species remain mostly constant through the period.

What do these figures mean in real landscape terms? Open taxa do indeed decrease, but still contribute c. 10% of the assemblage, equal to one third of the woodland component at its highest levels. Using Robinson's (1991) percentages, we suggest the figures could indicate high forest, but with some significant open areas, either with patches of open landscape or woodland with an open aspect. Given the rather local nature of environmental reconstruction inferred from fossil beetles, we believe the latter interpretation may be more correct rather than the former, otherwise the high number of high forest inhabitants would be absent. How much grazing animals contributed to this openness is more difficult to judge, particularly given the low numbers of dung beetles in the assemblage. The relatively open nature of the woodland may have more to do with the fact that this is early successional woodland, where the

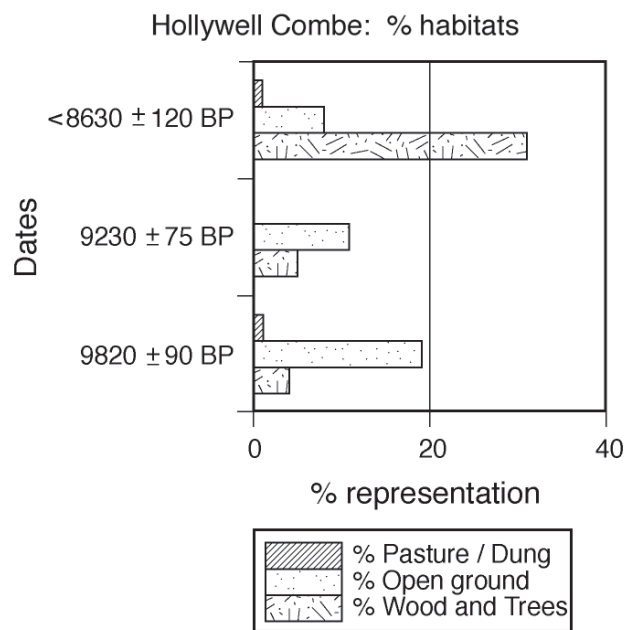


Figure 2. Percentages of selected beetle habitat groups from Hollywell Coombe, Kent, England. Data from Coope (1997), assigned to categories by the authors.

mixture of open woodland trees (*Betula*, *Pinus*, *Corylus*) and developing soils would have ensured the canopy of the woodland was maintained relatively open.

A site covering the period of interest is Bole Ings, Trent Valley (Dinnin 1997; Brayshay and Dinnin 1999; Dinnin and Sadler 1999), which covers over 6,000 years of environmental history, from c. > 8240±60 BP to after 2690±100 BP. It is very difficult to have a good understanding of how the components of the fauna change, except in a very broad sense, because of the limitations imposed by the site chronology. Division of the faunas over periods is hampered by this (Fig. 3). Chronology at this site is based on just five radiocarbon dates and we have made no attempt to interpolate ages between dated horizons. One age inversion suggests that the dates should be treated with caution, especially since all except one date are based on organic mud rather than identified plant macrofossils (*cf.* Turney *et al.* 2000); additionally, the deposits suffered from drying between c. 5000–3600 BP, affecting the quality of the palaeoecological record for this period. Despite these problems, the associated palaeoecological record itself is excellent and provides

one of a very few beetle sequences covering such a long period.

The insect and pollen data from the site indicate a landscape of primary forest, including a large proportion of old trees and an abundance of dead wood habitats. These are reflected in the high proportion of beetle taxa associated with wood and trees (Fig. 3), representing up to 25% of the assemblage, whilst open taxa represent c. 7–5%, decreasing to just c. 2% sometime around 5300–5000 BP, rising again during later periods, presumably due to anthropogenic opening of the landscape. It is interesting that these latter abundances are at similar levels to those found during the first 4,000 years of the Holocene and suggest that some open habitats were persistent features in these floodplain areas during this early period, maintained and expanded upon later by anthropogenic activities. Levels of pasture/dung beetles appear to fluctuate significantly and perhaps reflect differing levels of grazing animals across the floodplain, but are generally lower, at about 1–3%, apart from an anomalous higher period during 6300–5000 BP. The relatively high proportions of open ground taxa may reflect the creation of a steady supply of early successional

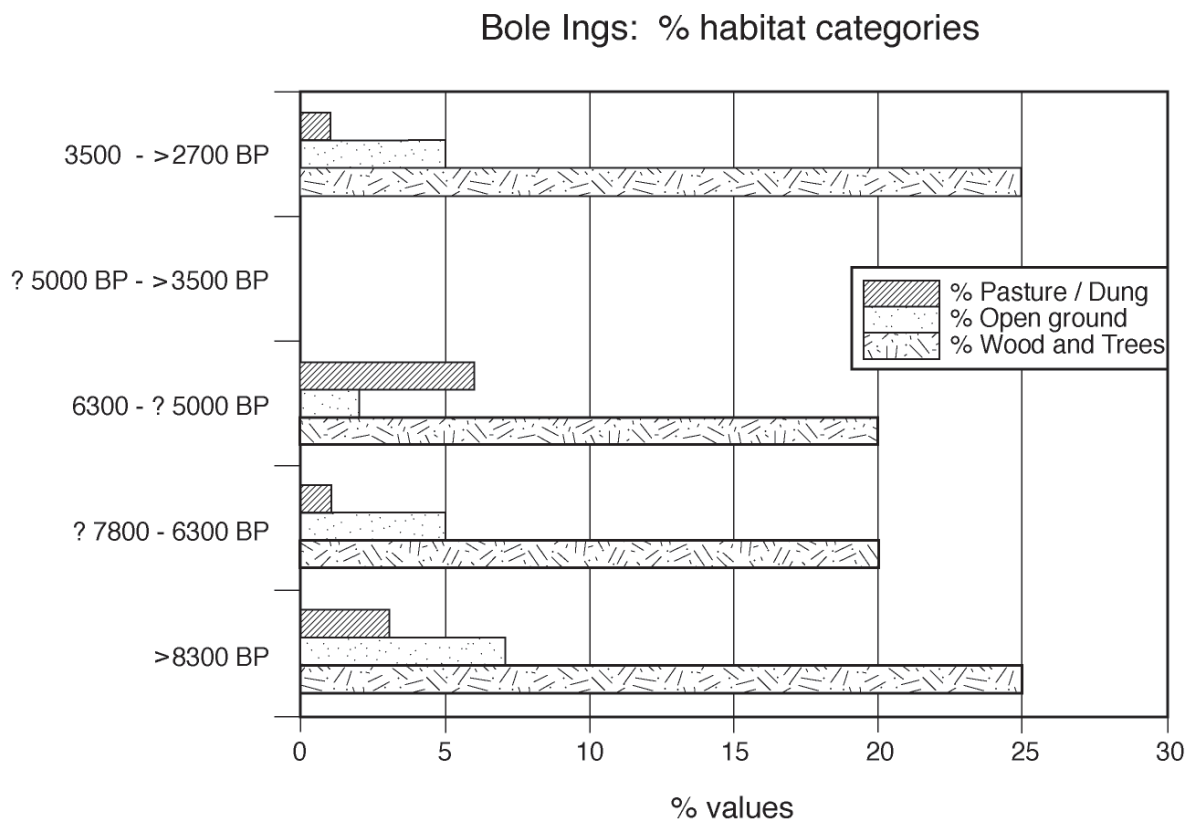


Figure 3. Percentages of selected beetle habitat groups from Bole Ings, Trent Valley, England. Data from Dinnin (1997), using categories from Dinnin and Sadler (1999).

habitats in unstable floodplain landscapes (Dinnin 1997).

The persistent presence of these open indicator taxa suggests that the floodplain continued to provide some open habitats for a considerable time. Other floodplain assemblages of slightly later date from elsewhere on the Trent (Howard *et al.* 1999; Greenwood and Smith in press; Smith and Whitehouse in press; Smith *et al.* in press) and Thames Valleys (Robinson 1991; 2000) indicate that species typical of open grassland are persistent in many of these floodplain faunas.

The above two examples do hint at the wider importance of open areas within these early Holocene woodlands, but the role of grazing animals in maintaining open areas cannot really be addressed within the context of the data set and resolution offered by existing studies. It is unclear how truly representative these two sites are of other woodland types (*cf.* Smith and Whitehouse in press) or different regions. Svenning (2002) suggests that floodplain deposits will inevitably include dung beetles and open indicators because of the activities of herbivores on the floodplain, perhaps attracted to water sources. Brown (1997) has highlighted that the natural state of many lowland rivers during the earlier Holocene would have been as flood plain wide multi- rather than single-channel rivers. Thus, the results could relate to river dynamics in conjunction with herbivore activity and may explain the relative abundance of open indicators at Bole Ings and other floodplain sites.

Dinnin and Sadler (1999) have provided a useful review of changes across habitat groups over the Holocene. During the early Holocene, many sites contain an average of 10–20% woodland species, with pasture/dung species at low levels, at c. 3–5%. Given that 1% of pasture/dung species is what might be expected for closed woodland and 10% for a largely pastoral landscape (Robinson 1991), this suggests some limited background grazing. Open ground taxa generally represent up to 5–6% of the assemblage, again suggesting some open areas. The woodland component from most sites is clearly important, but it is interesting to note that numerically speaking, open-terrain and dung beetles remain reasonably constant across the early Holocene (Mesolithic) period. Effectively, increases in percentage values of woodland species are the product of the enhanced range and diversity forming the forest ecosystem and do not reflect declines in the number of taxa associated with open and pasture habitats. We believe these increases are caused by the availability of the full range of forest habitats at different successional stages and the final arrival of the highly specialised *Urwaldtiere* from their mainland European refugia (Whitehouse 1998).

## Discussion

This limited review provides evidence that some of these early-mid Holocene woodlands were at least partly open in character or included open areas. The role of grazing animals in creating these openings is not clear on the present evidence, although we believe that the study of fossil beetles has significant potential to provide answers through targeted sampling.

A range of other disturbance factors, in addition to animal grazing, are likely to have equally played important roles in creating open areas. Forests appear to have been subject to a range of natural disturbances and catastrophes, such as forest fires and storm damage, often creating open, sun-exposed places with considerable amounts of dying and dead wood (Whitehouse 1998; 2000). Early successional habitats during the early Holocene and the nature of the woodland, dominated by tree taxa which require open conditions, may also partially explain some of the open indicator taxa evident. Forest fires, in particular, appear to have played an important role in maintaining an open character in at least some of these early Holocene forests, especially where dominated by flammable *Pinus* and *Betula* (Whitehouse 2000). Indeed, substantial numbers of the boreal insect fauna are fire-favoured (Wikars and Schimmel 2001), the closest modern analogue for some of these early Holocene beetle assemblages. As a result local vegetation patches and islands may have emerged locally quite frequently, creating semi-permanent open spaces and opening up the canopy of the woodland.

It is also pertinent to note that many woodland invertebrates require a mixed mosaic landscape rather than full canopy woodland (Palm 1959; Alexander 1999; Ranius and Jansson 2000). Similä *et al.* (2002) have drawn attention to the high numbers of threatened insect species found in the early stages of the woodland succession. Early successional habitats seem to be important, providing significant nectar sources near breeding habitats, in glades and on woodland edges (Harding and Rose 1986). Many of these species appear to require the sunny, open habitats with large amounts of dead wood, the type of habitat offered by pasture woodland indicated by Vera's reconstruction.

Lindbladh *et al.* (2003) have drawn attention to several *Pinus* and *Betula* dependent beetle species connected to open forests that have become extinct in southern Sweden. The fossil beetle record indicates such faunal changes are not new; a considerable suite of *Pinus*-loving species have disappeared from British and Irish forests during the Holocene (Whitehouse 1997; Boswijk and Whitehouse 2002; Smith and Whitehouse in press). The extinction of

these species has been viewed as primarily, although not exclusively, linked to the decline of *Pinus* habitats. This review suggests that we may need to think more carefully about the causes of such extinctions and consider the possibility that the *open structure* of many of these forests may have been equally crucial to some of these species' survival.

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. If the primeval forest was uniformly dense, where did all the numerous light-demanding species of plants and invertebrates evolve? Eriksson *et al.* (2002) have highlighted that an explicit consideration of the original habitats of semi-natural grassland species has been overlooked in the closed forest hypothesis and draw attention to the fact that many such species already existed in the landscape. From an invertebrate perspective, it raises further questions concerning the origins and development of 'culture-steppe' species (*cf.* Hammond 1974), a research area which remains largely unstudied, but which could be a useful new avenue in this debate.

## Conclusions

Frans Vera (2000) has provided an important new starting point with which to understand the mosaic of different landscapes operating across Europe during the Holocene, although his model is at times simplistic when compared with the full range of palaeoecological evidence. The fossil insect evidence, within the limits of the available data, hints that beetles associated with open taxa are a constant feature in these early Holocene assemblages, whilst species usually associated with the dung of grazing animals, although in small numbers, are persistent. Whilst it is not possible to evaluate fully the contribution of grazing animals in creating these rather more open forests, it clearly draws attention to the role of autogenic and allogenic factors. It seems likely that fire and dead wood as well as a range of other disturbance factors, including grazing, may have been important contributory factors in creating open areas. We suggest this has important implications in terms of how the palaeoecological record is interpreted, particularly by environmental archaeologists and palaeoecologists who may be more interested in identifying human-environment interactions rather than the ecological processes which may be preserved within palaeoecological records.

We believe fossil beetle specialists have an important role to play in further exploring the structure of European 'wildwood', principally

through the analysis of woodland assemblages from a range of woodland contexts and comparing results from a range of sites from Ireland, Britain and mainland Europe. Crucial to any such work will need to be an understanding of the taphonomy of such assemblages and a clear appreciation of the differences between 'open' and 'closed' woodland faunal signatures (*cf.* Kenward and Hall 1997).

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