

# Can the pre-Neolithic provide suitable models for re-wilding the landscape in Britain?



A scene from Oostvaardersplassen, in The Netherlands, with Heck cattle, but could the landscape of Britain in the pre-Neolithic have resembled this? Ruben Smit/www.rubensmit.nl

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Palaeoecologists have been encouraging us to think about the relevance of the Holocene fossil record for nature conservation for many years (e.g. Buckland 1993) but this information seems slow to filter through to the conservation community. Indeed, Willis *et al.* (2005) report that recently published biodiversity reports and policy documents rarely look back more than 50 years and may ignore the historical context entirely. This has been a lost opportunity for understanding ecological systems. Many natural processes occur over timescales that confound our

attempts to understand them, so the vast temporal perspective provided by palaeoecological studies can provide important guidance for nature conservation (Willis & Birks 2006).

However, accurate vegetation mapping is difficult enough in modern landscapes (Cherrill & McLean 1999), so the challenge of describing prehistoric environments is immeasurably greater. Nevertheless, pioneering work in the mid 20th century showed that pollen and spores extracted from peat bogs were so perfectly preserved that they could be used to demonstrate sequences

**Box 1 Evaluation of the New Forest ecosystem using the Ratcliffe criteria (*Nature Conservation Review* Ed. Ratcliffe 1977)**

**Naturalness:** with 5,000 years of recorded human interventions, the New Forest can hardly be regarded as natural in the sense of virgin wilderness. However, those interventions have maintained a wood pasture/heathland system which is likely to have continuity with prehistoric lowland Britain. Woodlands will have existed on many of the ancient woodland sites in the forest since those times, and canopy gaps will have supported grassland and heathland communities in a mosaic of mire and swamp, maintained by large wild grazing animals. Vera (2000) questions the widely held belief that a climax vegetation of closed forest covered the lowlands in prehistoric times before the onset of agriculture. He argues that vegetation communities were governed by the activities of large herbivores creating a prehistoric parkland landscape

consisting of grasslands, scrub, solitary trees and groves bordered by a mantle and fringe vegetation. This is arguably analogous to the situation in the [New] Forest today, though in a greatly modified form, with commoners' animals having replaced wild herbivores.

(Extract from the *New Forest SAC Management Plan Part 2* (2001) <http://www.newforestlife.org.uk/life2/part2.PDF>)



**Ponies grazing in the New Forest, Hampshire.** Andrew Branson

of vegetation change since the last glaciation (Godwin 1956). Since then, the science has burgeoned: ancient deposits of beetles, snails, fungal spores and plant macrofossils add to the picture, as does the chemistry of ancient lake sediments (Bell & Walker 2004).

Many questions still remain to be answered by this fascinating research and one aspect has received considerable attention in the last decade. This concerns the nature of the 'primeval' landscapes, in other words our understanding of natural systems prior to significant human impact. The debate was kindled by a thesis by the Dutch forest ecologist Frans Vera in 2000 (see also Vera & Buissink 2007). Vera effectively challenged established views about the primeval landscapes and argued that the refutation, and the resulting alternative landscape models, had critical importance for modern conservation practice.

Vera's thesis is focused on the pre-Neolithic (*ca* 8000-5000BP) landscape in the lowlands of

central and western Europe, with the assumption that this period represents an almost pristine or 'natural' state which should provide a suitable conservation benchmark. Vera contends (i) that this landscape was not closed woodland but a relatively open park-like mosaic of wood and grassland, and (ii) that large wild herbivores were an essential driving force behind woodland-grassland vegetation cycles. The advocacy in his argument and the timing of the publication, when grazing was seen as increasingly important in conservation in Europe, have combined to raise the profile of this issue. If Vera is correct, the open park-like landscapes were inherited rather than created by people; this may have implications for conservation practice in Europe.

The rapid adoption of Vera's ideas into conservation management plans in the UK (see Box 1) gives an indication of the influence that this work has had. Indeed, Vera's ideas have been described as a 'challenge to orthodox thinking' (Miller

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2002) and considerable debate has been stimulated centering on the ecological validity of Vera's hypothesis and its relevance for modern conservation. In this article, we attempt to address these issues on the basis of results from a literature review, web-debate and discussions with Dutch and British ecologists, prepared for English Nature with a view to informing conservation strategies (Hodder & Bullock 2005a).

### Key assumptions and arguments considered

- The pre-Neolithic period provides a suitable benchmark for conservation.
- The pre-Neolithic landscape was a relatively open park-like mosaic rather than closed forest. This is supported in Vera's thesis, using evidence from ecology, history, the pollen record and the history of language.
- Large wild herbivores were an essential driving force behind woodland-grassland vegetation cycles. These species drove a shifting mosaic in which tree seedlings were able to survive in the protection of thorny scrub.
- The established wisdom supports a dominance of closed-canopy forest in central and western Europe.

### Does the pre-Neolithic period provide a suitable benchmark for conservation?

Although 'biodiversity baselines' are often encouraged as useful tools for planning conservation (e.g. Royal Society 2003), the idea of using any past landscape to guide action in a changing world needs caution (Egan & Howell 2001; Lunt & Spooner 2005; Willis *et al.* 2005). If the distant past is taken as a benchmark for conservation through a desire to achieve a more 'natural' landscape, the qualities of 'naturalness' proposed by Peterken (1996) are useful. He describes future-naturalness as the state that would prevail in areas where human influence is reduced or removed, as distinct from the original-naturalness of the pre-Neolithic forest. Differences in these states are inevitable because climate and soils have changed, as well as biotic changes such as extirpation of large predators and introduction of invasive alien species. Original-naturalness, of course, becomes more difficult to define if the influence of Mesolithic peoples is considered significant (Innes & Blackford 2003; Simmons 2003), but this is an issue whichever model (open or closed forest) is considered for the pre-Neolithic landscape.

### Was the pre-Neolithic landscape a relatively open park-like mosaic?

#### Regeneration failure of oaks and Hazel in modern forests

Vera's (2000) key argument lies in the well-known paucity of regeneration of oaks *Quercus* and Hazel *Corylus avellana* under unmanaged forest canopies. Vera argues that if the mid-Holocene landscape consisted mainly of such closed-canopy forest, these species should not be so well represented in the fossil record. He concludes that oaks and Hazel thrived in the primeval landscape because there were large open areas for regeneration and because grazing animals reduced competition from more shade-tolerant species such as Beech *Fagus sylvatica*.

What may be underplayed is the influence of soil conditions and topography on the shade-intolerance that often prevents oaks from developing from seedlings to larger trees. In some situations oaks may be able to maintain themselves even where more shade-tolerant species are present (Mitchell & Cole 1998). On acid sandy soils, oaks were able to regenerate successfully within gaps in pine stands (Mosandl & Kleinert 1998; Paluch & Bartkowicz 2004). Oak competes well on very acid, nutrient-poor soils and in regions subject to summer drought, while Hazel can survive on steep slopes and floodplains (Coppins *et al.* 2002; Svenning 2002).

Also, in large parts of Britain, the absence of some shade-tolerant species such as Hornbeam *Carpinus betulus* and Beech during the mid-Holocene (Huntley & Birks 1983) may have provided a wider potential niche for oaks than would have been found on the Continent.

Lastly, the presence of Hazel pollen in the fossil record does not necessarily indicate large canopy gaps. Although very open conditions are generally necessary for full flowering of Hazel, substantial flowering, and so pollen production, can be frequent in very small gaps (K J Kirby unpublished data, in Hodder & Bullock 2005a).

So, although the poor regeneration of the light-demanding trees and shrubs in modern forests is cited as a major issue for the closed-forest hypothesis (Bradshaw 2002), there are explanations that do not require a half-open landscape or a major role for large herbivores.

### Can the study of fossil pollen detect vegetation openness and thorny scrub?

Vera (2000) questions the potential for palynology to detect vegetation openness. Although it is accepted that models available in 1999 gave only a rough approximation of openness, and require improved testing (Sugita *et al.* 1999), the case against palynological insights may be overstated by Vera's reliance on early references. Many of the methodological weaknesses critiqued in Vera's thesis have largely been solved in more recent work (Mitchell 2001) and small-scale openness in some landscapes can now be recognised (Fyfe 2007).

For instance, studies of small hollows are excluded, yet these are far more sensitive to open-forest conditions because they tend to be dominated by local pollen rain, as opposed to data from lakes and bogs, which may collect pollen from tens of kilometres away (Bradshaw *et al.* 2003). Estimates of the source area for small-hollow sites vary from 20-30m (Bradshaw 1981; Mitchell 1988) to 50-100m (Sugita 1994), and observations from such sites tend to indicate a closed pre-Neolithic forest (Bradshaw 2002; Mitchell 2001, 2005). Any further debate on past forest openness should also be informed by the recent advances in pollen mapping and data model comparisons for vegetation dynamics and climatic change (e.g. Bradshaw 2008).

Vera (2000) also seeks to explain why the open-ground plants, such as grasses, and thorny scrub, which his thesis suggests should be very common, are rare in the pollen records. Obstruction provided by woodland-edge vegetation would minimise pollen dispersal from open grassy areas in forests to mires. This argument is, however, valid only if either woody vegetation grew preferentially around mire edges or the proportion of woody vegetation in the landscape was high.

It is also suggested that grass pollen deposits may have been uncommon in wood-pasture landscapes because of heavy grazing of the flowering heads. However, grass pollen can be well represented in palynological records; for instance, the European pollen record clearly shows increased proportions of grasses and herbaceous species with increasing evidence of Neolithic human activity, and grazing undoubtedly occurred during this period.

The contention in Vera's thesis that hawthorns

*Crataegus* and Blackthorn *Prunus spinosa* are 'entirely or almost entirely invisible' to palynology also needs consideration. Insect-pollinated shrubs making up the marginal vegetation of open spaces in forest are proportionately poorly represented in pollen diagrams (Godwin 1956), but pollen from such scrubby species is recorded from floodplain sites in the previous interglacial (the Ipswichian) (Svenning 2002), demonstrating that it is certainly visible in ancient records.

### What do other fossil and subfossil records tell us about landscape openness?

Non-pollen evidence has been used less frequently for interpreting past landscapes, but a combination of data sources may be used to add confidence to landscape models. Non-tree pollen records from interglacial sites correlate well with vegetation openness estimated from beetle, mollusc and/or plant macrofossils (Svenning 2002). In Svenning's review the various information sources pointed to predominant forest in the pre-agricultural Holocene of north-west Europe, with some open vegetation on floodplains, on some calcareous or poor sandy soils and in the continental interior. Whitehouse & Smith (2004) criticise Svenning's interpretation of the fossil beetle data, but in a review of data from two English Holocene sites, their conclusions are not radically different from Svenning's. They reported open woodland, but little sign of grazing animals, on a calcareous site in southern England, and primary forest, including a large proportion of old trees and dead wood, with few open taxa/dung beetles on a floodplain in the English Midlands.

Buckland (2005) has reviewed the fossil-insect evidence for Britain in more detail in relation to Vera's ideas, utilising the BUGS Coleopteran Ecology Package of fossil record, habitat and distribution (Buckland & Buckland 2002, 2006). He concludes that, as in previous interglacials, species associated with dead wood were very frequent in the early to mid Holocene, but declined, often to regional extinction, from the Neolithic onwards. Species associated with grassland and other components of 'open habitats' occurred but were rare in the mid-Holocene, suggesting that there were open areas but that such habitats formed a limited part of the overall landscape. However, open-habitat species do become more common at the time that Neolithic humans are likely to have

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opened up the landscape, and an apparently rapid diversification of dung-beetle faunas during the Neolithic suggests an increase in their food supply. As Britain was an island from about 7500BP (Preece 1995), it seems probable that much of this beetle fauna was already in residence. This would suggest that prior to the Neolithic clearances, wild herbivores were widespread but rare. Buckland (2005) also noted the occurrence of pyrophilic (fire-loving) species in the pre-Neolithic landscape, which indicates that fire, either natural or anthropogenic, is likely to have been a significant factor in creating and maintaining open conditions.

Macrofossils from trees may also be used to help understand the nature of past forests, although there is inevitable difficulty in interpretation of the small samples of these records. The park-like landscape postulated by Vera (2000) would be expected to include open-grown trees with low, spreading branches. However, tree remains from lowland bogs and fens generally have the characteristics of having grown in closed-canopy conditions: straight trunks, narrow girth and lack of low branches (Rackham 2003).

### Can the abundance of modern open-ground assemblages inform us about the pre-Neolithic environment?

The abundance of species associated with open conditions in modern landscapes in Britain has been put forward as evidence that the primeval landscape must also have been open. For instance, Rose (2002) stresses the diversity of vascular plants, epiphytic bryophytes and lichens and butterflies found among woodland edges and clearings, and Miller (2002) points out that birds, such as the Corncrake *Crex crex* must have evolved to need grassland before human clearances for agriculture.

However, there is a logical flaw and a risk in extrapolating from where species occur today. In modern Swedish landscapes many saproxylic species associated with dead wood are more abundant when old trees are open-grown (Rannius & Jansson 2000). However, most sites where old trees grow at present are former wood-pastures, i.e. the trees grew in open conditions. Equivalent populations of invertebrates from 400-year-old trees that grew in closed forest can be compared only by use of the fossil record, because such

stands no longer exist.

Also, limited understanding of the distribution, dispersal abilities and population characteristics of many species/organisms confound interpretations of landscape history. Motzkin & Foster (2002) note that in North America many butterfly and moth species thought to be grassland-indicators may also be common in woodland. The Heath Hen *Tympanuchus cupido cupido* has been used to document former abundance of grasslands and other open habitats in eastern North America, but most historical descriptions cite woodland or 'bushy plains' as the primary habitat for this species. Many 'woodland' bird species have different patterns of habitat use in Britain and mainland Europe, and changes in habitat use have occurred over time (Fuller 1995).

In Britain, species that depended on continuous closed forest would be expected to have declined in the last 5,000 years because woodland cover was reduced to about 5% by 1900, whereas conditions for species of open ground have generally increased (Kirby 2003), and this is abundantly clear from the fossil insect record ([www.BugsCEP.com](http://www.BugsCEP.com)). Open-ground species may previously have been restricted to small 'refuges' such as cliff-tops during the pre-Neolithic period and then spread to the rest of Britain. Given continuous openness in marginal habitats, dispersal would need to happen only occasionally for species to survive (Marks 1983).

Arguments against spread from refugia, based on the poor dispersal of old-growth species under current conditions (Alexander 2004), may underestimate the significance of chance rare events and the role of large herbivores in long-distance dispersal (Schmidt *et al.* 2004; Eycott *et al.* 2004). It is also easy to under-estimate the scale of past movement of flora and fauna in ships' ballast (Buckland *et al.* 1995; Lindroth 1957), or even on human feet (Wichmann *et al.* 2009). This may well have influenced species' dispersal during the Neolithic migration.

### Were large wild herbivores an essential driving force behind woodland-grassland vegetation cycles?

Cyclic succession and resulting mosaic patterns of vegetation have been observed for many decades and were given systematic treatment in a seminal paper by Watt (1947). The major contribution of Frans Vera and colleagues is to assert that large





What role did the large herbivores of the Mid-Holocene play in wooded landscapes? John Davis

herbivores, such as the Aurochs, would have been key drivers of such cyclic processes at the landscape scale, involving transitions between woodland and grassland (Olf *et al.* 1999). There are three stages in the cyclical turnover of vegetation that they propose: (i) grassland with patches of unpalatable scrub where tree seedlings can establish and grow because they are protected from grazing; (ii) groves of trees which eventually shade out the scrub, and harbour large ungulates which prevent regeneration; (iii) a break-up phase where trees in the centre of the grove decay, allowing light to enter, and grasses and herbs to establish – leading back to the first stage.

Olf *et al.* (1999) have elaborated the mechanism by which such vegetation cycling could occur, and different elements of the process can be seen at many sites, for example in the New Forest in southern England (Bakker *et al.* 2004). The question is not, therefore, whether such a regeneration cycle could have occurred, but whether it was the dominant mechanism for landscape regeneration and what temporal and spatial patterns it might have produced.

The mechanism does, of course, assume the presence of large herbivores in sufficient numbers to undertake this dominant role. The likelihood of this is difficult to address due to the paucity of

good bone assemblages from the early to middle Holocene. This lack of evidence limits direct conclusions about the diversity and particularly the abundance of the large-herbivore fauna and its predators (Bradshaw & Hannon 2004; Vera 2000; Yalden 1999).

This leaves circumstantial evidence that can be surmised by comparison with modern populations of large herbivores. This is emphasised by Fenton (2004), who argues that the main limitation on herbivores was food supply, and that, if current landscapes (such as the Scottish Highlands) can be kept open by grazing, so might have those in prehistory. It may be that the role of large herbivores has been under-emphasised in forest ecology. For instance, it is known that deer can maintain small-scale grassy glades in British upland forests (Peterken 1996) and Elk *Alces alces* appear to prevent woodland succession in fenland sedge-communities in Poland (Svenning 2002). Rooting by Wild Boar *Sus scrofa* provides suitable places for trees and shrubs to become established, but equally damage to roots and bark may lead to the demise of trees through subsequent disease. One problem is that this ignores possible impacts of predators. Vera (2000) simply assumes that ‘Whatever the influence the large predators had, the densities [of large herbivores] that are required



Factors such as fire and disease would have had a significant impact on the nature of the landscape. John Davis

for the regeneration of oaks and Hazel must have been the result.’ which illustrates the level of speculation affecting this debate.

In recent years there have been fascinating insights into predator effects on the landscape, which should at least warn us to beware of assumptions about past environments based on limited data. For instance, the interactions between vegetation structure, predator hunting behaviour and herbivore response to predation risk are complex (White *et al.* 2003; Laundré *et al.* 2001; Hebblewhite *et al.* 2002). Ecologists in Yellowstone National Park were able to demonstrate how the reintroduction of Wolves to overgrazed forest generated a ‘landscape of fear’ by modifying the behaviour of grazing animals. At sites of high predation risk (e.g. low visibility or escape barriers), the riparian vegetation was released from browsing by Red Deer *Cervus elaphus*, whereas at low-risk sites (open areas) riparian vegetation was still suppressed (Ripple & Beschta 2003). Lynx *Lynx lynx* are also reported to have a significant impact on the distribution and behaviour of Roe Deer *Capreolus capreolus* in Switzerland, which could similarly lead to reduced deer impact on vegetation (Hetherington 2006, 2008).

We also need to improve our understanding of the extirpated herbivores before coming

to firm conclusions. The Aurochs may not have required large open areas in the landscape (Van Vuure 2005). In fact, isotope research on Auroch bones indicates that these bovids had an essentially woodland diet (Noe-Nygaard *et al.* 2005). It remains to be seen whether further research with samples from a range of sites support these results.

To apply Vera’s thesis specifically to British conditions, we need to allow for a reduced suite of large herbivores compared with that on the Continent. There is a very long gap in the British fossil record for ‘horse’ between the Mesolithic and the early Neolithic, and there is no convincing evidence for Elk after the Early Holocene, despite the one late date from the Cree River in Scotland (Kitchener *et al.* 2004). The European Bison *Bison bonasus* did not return to Britain during the present interglacial (Yalden 1999, 2003). Large herbivores were even more restricted in Ireland, where Aurochs were absent and Red Deer scarce or absent. Bradshaw & Hannon (2004) and Mitchell (2005) have therefore compared the pollen profiles from Ireland with those from Britain and the Continent. They conclude that the presence or absence of large herbivores does not significantly alter the vegetation patterns, and that large herbivores were therefore not the major factor driving forest composition. Erik Buchwald

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(pers. comm.) has, however, pointed out that shade-bearing trees such as Beech and limes *Tilia* were also absent from Ireland; oaks and Hazel might thrive in Ireland in the absence of large herbivores, whereas in the presence of shade-tolerant competitors some grazing may be required for them to become well established.

While we know that large herbivores can influence forest structure, there are huge areas of uncertainty and speculation about wild populations of these animals in prehistoric times. Whether their behaviour or abundance, both of which are difficult to reconstruct, could have enabled them to be the dominant driver of landscape composition in pre-Neolithic Europe remains open to debate.

### Does evidence from literary sources inform us about the primeval landscape?

Early writings provide information about forest cover and wilderness and so give clues as to the ancient landscape. In terms of modern conservation decisions, it is therefore important to know what the medieval concept of wilderness entailed and whether it can be related to the pre-Neolithic landscape. Vera uses historical texts to argue that words such as 'silva', 'Forst', 'forest', 'Wald', 'wold', 'weald', 'woud' and 'wood' in classical and medieval texts did not necessarily indicate closed forest, and hence 'medieval' wilderness areas were relatively open. He assumes that these wildernesses may reflect the condition of the pre-Neolithic landscape.

Van Vuure (2005) argues against Vera's suggestion that the Latin 'silva' refers to a 'mosaic of groves and grassland', and he considers that closed forest is more consistent with the descriptions of German forests in classical accounts, although these texts themselves are not without bias. The 'Great Wilderness' in East Prussia in the medieval period, described as 'wald', was an area of extensive and closed forest, interspersed by marshes, despite retaining populations of Wild Horse, European Bison and Aurochs (Van Vuure 2005).

Vera (2000) interprets Eichwald's 1830s map of the Bialowieza Forest in Poland as showing that it was composed of groves interspersed with open grassland areas. Van Vuure produces a near-contemporary map (1826) which, while appearing also to show relatively open conditions, is accompanied by a written description that emphasises the closed nature of the forest. He concludes that

the maps were an artist's interpretation, rather than a realistic depiction of the forest vegetation. So both pictorial and written accounts can be untrustworthy and social context may be crucial to interpretation.

Even if some shadows of the 'wildwood' survived into historic times on the Continent, in Britain, wilderness, waste and forest in the medieval sense cannot be equated with the state of the mid-Holocene landscape. Most of Britain had, by this time, been subject to some form of agricultural use for hundreds, if not thousands of years. Medieval wilderness or waste was strongly influenced by human management (grazing, burning, cutting of wood and bracken, etc) (Rackham 1986, 2003). Pollen and archaeological evidence increasingly point to the demise of major uncleared landscapes in Britain by the late Iron Age, which renders the literary debate somewhat futile.

### Does the established wisdom support a dominance of closed-canopy forest in central and western Europe?

Although it is not difficult to find references to the 'widely held belief that a climax vegetation of closed forest covered the lowlands in prehistoric times' (Box 1), closer inspection of the literature reveals that this view has not necessarily been supported by experts in the field. While predominant tree-cover may be posited, vegetation dynamics and structural variation is clearly recognised. As early as 1945, Jones had suggested that 'climax forest' may be a 'concept only', never existing in practice, and Remmert (1991) introduced the concept of cyclical mosaics to forest ecology. Peterken (1996) concluded that in natural woodland, openings of various kinds form a permanent and sometimes common component.

### Conclusions and discussion

Vera's (2000) work has stimulated an exciting debate. Unfortunately, the argument has often polarised around the false dichotomies that either the landscape was half-open and large herbivores were important or the landscape was completely closed and herbivores were not important at all. This ignores other possibilities such as that the landscape was open, but not herbivore-driven, or closed, but with large herbivores playing a significant role. The difference between the closed-forest hypothesis and the alternative of cyclical dynam-





**A glade in Bramshaw Wood in the New Forest, with ancient Beech pollards forming the canopy. Some might describe this view as classic 'high forest' with a closed canopy, but compared to many modern, managed woodlands it also has a 'half-open' aspect.** Andrew Branson

ics may be a matter of degree. Miller (2002), for example, asks whether the grassland or the forest provides the matrix in which the other may be found.

One of the major problems involved in applying the ideas in conservation is that there is no clear idea of spatial or temporal scale. Vera refers to a 'half-open' landscape but does not give any justification for this particular level of openness. Kirby's (2003, 2004) model, based on Vera's description of the phases in his cycle, shows that many different combinations of open and closed conditions could potentially occur.

Degrees of openness are likely to vary in different topographic, climatic and soil conditions, but at present there is no guidance on the patterns that might be expected. Future research may reveal more about the factors that influence temporal and spatial patterns of vegetation in the full range of environmental conditions. A focus on large herbivores as a single factor driving landscape structure is also rather limiting. Given the highly variable topography and geology that exists in Britain, a more realistic approach may be to consider that over much of the landscape

there would have been several disturbance factors (grazing, flood, fire, disease, wind, human activity), all driving change to differing extents, the significance of which could also vary over time. In Britain, deciduous forest may rarely burn, but one rare lightning strike leading to extensive wildfire may have been sufficient to modify succession for long periods.

We agree that the openness of the landscape and the role of large herbivores have both been underplayed in past discussions, but conclude that Vera's argument – that the bulk of the lowland landscape was half-open and driven by large herbivores – is not currently supported by the evidence. Multi-disciplinary studies of fossil and sub-fossil assemblages supported by studies of fossilisation, which help us to interpret this buried evidence, may eventually solve this problem.

Finally, does this debate have relevance for modern nature conservation? Is the pre-Neolithic landscape appropriate as a 'template' or guidance? The merits and limits of using any past landscapes in conservation planning have deservedly received significant attention (e.g. Andel & Aronson 2006, Egan & Howell 2001, Higgs 2003) and certain



conceptual and practical issues emerge repeatedly. How do you select the correct ‘template’ and how meaningful is this reference to the past in a world where biophysical conditions constantly change. Nature reserves in Britain are the product of their history, particularly the last 13,000 years since the *tabula rasa* of the last glaciation. Every accident of fire, disease or overgrazing has left a subtle mark on subsequent landscapes. It would seem reasonable to assume that no one really believes that past landscapes can be restored exactly, but that invaluable lessons may be learned by looking back, and that we can strive towards, but never reach, a future natural state.

There is, however, increasing interest in creating landscapes that are driven more by natural disturbance processes than by agricultural or forestry practices. Grazing by large herbivores has a role to play in such attempts, but not to the exclusion of other factors. In some cases, this may involve the descendants, albeit much modified both morphologically and behaviourally, of species that were present in the pre-Neolithic period; in other cases, a wider range of animals may be used. The outcomes of such efforts are by definition uncertain and unpredictable (Hodder & Bullock 2005b), and none of us will live long enough to see the outcome of these attempts to create new ‘wildwood’ or ‘wild-parkland’.

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### References and further reading

- Alexander, K N A 2004 Landscapes with ancient trees: invertebrate mobility and population viability. In: R Smithers (ed) *Landscape ecology of trees and forests* pp 107-114. IALE, UK
- Alexander, K N A 2005 Wood decay, insects, palaeoecology, and woodland conservation policy and practice – breaking the halter. *Antennae* 29: 171-178
- Andel, J V, & Aronson, J 2006 *Restoration Ecology: the New Frontier*. Blackwell Science Ltd, London
- Bakker, E S, Olf, H, Vandeneberghe, C, De Maeyer, K, Smit, R, Gleichman, J M, & Vera, F W M 2004 Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. *Journal of Ecology* 41: 571-582
- Bell, M G 1983 Valley sediments as evidence of prehistoric land-use on the South Downs. *Proceedings of the Prehistoric Society* 49: 119-150
- Bell, M, & Walker, M J C 2004 *Late Quaternary Environments. Physical & Human Perspectives* (2nd ed). Pearson Prentice Hall, Harlow
- Bokdam, J 2003 *Nature conservation and grazing management. Free ranging cattle as a driving force for cyclic vegetation succession*. PhD thesis, Wageningen University, Wageningen
- Bradshaw, R H W 1981 Modern pollen-representation factors for woods in south east England. *Journal of Ecology* 69: 45-70
- Bradshaw, R H W 2002 *Forest Ecology and Management [Review of Grazing Ecology and Forest History]*. *Forest Ecology and Management* 165: 327-329
- Bradshaw, R H W 2008 Detecting human impact in pollen record using data-model comparison. *Vegetation History and Archaeobotany* 17: 597-603
- Bradshaw, R H W, & Hannon, G 2004 The Holocene structure of north-



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- west European forest induced from palaeoecological data. In: O Honnay and others (eds) *Forest Biodiversity: Lessons from History for Conservation*. IUFRO, Leuven
- Bradshaw, R H W, Hannon, G, & Lister, A 2003 A long-term perspective on ungulate-vegetation interactions. *Forest Ecology and Management* 181: 267-280
- Buckland, P C 1979 *Thorne Moors: a palaeoecological study of a Bronze Age site*. Dept of Geography, University of Birmingham
- Buckland, P C 1993 Peatland archaeology: a conservation resource on the edge of extinction. *Biodiversity and Conservation* 2: 513-527
- Buckland, P C 2005 Palaeoecological evidence for the Vera hypothesis. In: *Large herbivores in the wildwood and modern naturalistic grazing systems*. English Nature Research Report 648, pp 62-116, Peterborough
- Buckland, P C, Ashworth, A C, & Schwert, D 1995 By-passing Ellis Island. Insect immigration to North America. In: R Butlin & N Roberts (eds) *Human impact and adaptation: ecological relations in historical times*, pp 226-244. Institute of British Geographers, Blackwell, Oxford
- Buckland, P I, & Buckland, P C 2002 How can a database full of Bugs help reconstruct the climate? In: G Burenhult & J Arvidsson (eds) *Archaeological informatics: pushing the envelope*, CAA 2001. Computer applications and quantitative methods in archaeology. Proceedings of the 29th conference, Gotland, April 2001. *British Archaeological Reports* S1016: 453-462
- Buckland, P I, & Buckland, P C 2006 *Bugs Coleopteran Ecology Package*. www.bugs2000.org
- Bunting, M J 2002 Detecting woodland remnants in cultural landscapes: modern pollen deposition around small woodlands in north-west Scotland. *The Holocene* 12: 291-301
- Catt, J A 1978 The contribution of loess to soils in lowland Britain. In: S Limbrey & J G Evans *The effect of man on the landscape: the Lowland Zone*. Council for British Archaeology Research Report 21: 12-20
- Cherrill, A & McClean C 1999 The reliability of 'Phase 1' habitat mapping in the UK: the extent and types of observer bias. *Land-use and urban planning*. 45:131-143
- Coppins, A, Coppins, B, & Quelch, P 2002 Atlantic Hazelwoods. *British Wildlife* 14: 17-26
- Cronon, W 1983 *Changes in the land. Indians, Colonists, and the ecology of New England*. Hill & Wang, New York
- Egan, D, & Howell, E A 2001 *The Historical Ecology Handbook: a Restorationists' Guide to Reference Ecosystems*. Island Press, Washington DC
- Ellenberg, H 1988 *The vegetation ecology of central Europe*. Cambridge University Press, Cambridge
- Elton, C S 1966 *The pattern of animal communities*. Methuen, London
- Evans, J G 1972 *Land snails in archaeology*. Seminar Press, London
- Eycott, A E, Watkinson, A R, & Dolman, P M 2004 Deer as vectors of plant dispersal in woodland networks. In: R Smithers (ed) *Landscape ecology of trees and forests*, pp 50-57. IALE, UK
- Fenton, J 2004 Wild thoughts . . . a new paradigm for the uplands. *ECOS* 25: 2-5
- Foster, D R, & Motzkin, G 2002 Interpreting and conserving the open land habitats of coastal New England: insights from landscape history. *Forest Ecology and Management* 185: 127-150
- Foster, D R, Hall, B, Barry, S, Clayden, S, & Parshall, T 2002 Cultural, environmental and historical controls of vegetation patterns and the modern conservation setting on the island of Martha's Vineyard, USA. *Journal of Biogeography* 29: 1381-1400
- French, C, Lewis, H, Allen, M J, Scaife, R G, & Green, M 2003 Archaeological and palaeo-environmental investigations of the Upper Allen valley, Cranborne Chase, Dorset (1998-2000): a new model of earlier Holocene landscape development. *Proceedings of the Prehistoric Society* 69: 201-234
- Fuller, R J 1995 *Bird life of woodland and forest*. Cambridge University Press, Cambridge
- Fyfe, R 2007 The importance of local-scale openness within regions dominated by closed woodland. *Journal of Quaternary Science* 22: 571-578
- Godwin, H 1956 *History of the British flora*. Cambridge University Press, Cambridge
- Goodburn, D 1999 An image of ancient English woodland. *British Archaeology* (March 1999) 10-11
- Greig, J R A 1982 Past and Present Lime Woods of Europe. In: M Bell & S Limbrey (eds) *Archaeological Aspects of Woodland Ecology*. British Archaeological Reports S146: 23-56
- Harding, P T, & Rose, F 1986 *Pasture-woodlands in lowland Britain*. Institute of Terrestrial Ecology, Huntingdon
- Hebblewhite, M, Pletscher, D H, & Paquet, P C 2002 Elk population dynamics in areas with and without predation by recolonizing Wolves in Banff National Park, Alberta. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 80: 789-799
- Hetherington, D 2006 The lynx in Britain's past, present and future. *ECOS* 27: 66-74
- Hetherington, D A 2008 The history of the Eurasian Lynx in Britain and the potential for its reintroduction. *British Wildlife* 20: 77-86
- Higgs, E 2003 *Nature by design: People, Natural Process, and Ecological Restoration*. MIT Press, Cambridge, MA
- Hodder, K H, & Bullock, J M 2005a The Vera model of post-glacial landscapes in Europe: a summary of the debate. In: *Large herbivores in the wildwood and modern naturalistic grazing system*. English Nature Research Report 648, pp30-61. Peterborough
- Hodder, K H, & Bullock, J M 2005b Naturalistic grazing and conservation. In: *Large herbivores in the wildwood and modern naturalistic grazing systems*. English Nature Research Report 648, pp 117-168. Peterborough
- Huntley, B, & Birks, H J B 1983 *An atlas of past and present pollen maps for Europe 0-13000 years ago*. Cambridge University Press, Cambridge
- Innes, J, & Blackford, J 2003 The ecology of late mesolithic woodland disturbances: Model testing with fungal spore assemblage data. *Journal of Archaeological Science* 30: 185-194
- Jones, E W 1945 The structure and reproduction of the virgin forest of the north temperate zone. *New Phytologist* 44 130-48
- Kirby, K J 2003 *What might a British forest landscape driven by large herbivores look like?* English Nature Research Report 530. Peterborough
- Kirby, K J 2004 A model of a natural wooded landscape in Britain driven by large-herbivore activity. *Forestry* 77: 405-420
- Kitchener, A C, Bonsall, C, & Bartosiewicz, L 2004 Missing Mammals From Mesolithic Middens: A Comparison Of The Fossil And Archaeological Records From Scotland. In: A Saville *Mesolithic Scotland and its neighbours. The Early Holocene prehistory of Scotland, its British and Irish context, and some North European perspectives*, pp 73-82. Society of Antiquaries of Scotland, Edinburgh
- Laundré, J W, Hernández, L, & Atendorf, K B 2001 Wolves, elk and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79: 1401-1409
- Lindroth, C H 1957 *The faunal connections between Europe and North America*. John Wiley & Sons, New York
- Lunt, I D, & Spooner, P G 2005 Using historical ecology to understand patterns of biodiversity in fragmented agricultural landscapes. *Journal of Biogeography* 32: 1859-1873
- Marks, P L 1983 On the origin of the field plants of the North-eastern United States. *The American Naturalist* 122: 210-228
- Mason, S L R 2000 Fire and Mesolithic subsistence – managing Oaks for acorns in northwest Europe? *Palaeogeography Palaeoclimatology Palaeoecology* 164: 139-150
- Mellanby, K 1968 The effects of some mammals and birds on the regeneration of Oak. *Journal of Applied Ecology* 5: 359-366.
- Miller, H G 2002 Review of F W M Vera. *Grazing Ecology and Forest History*. *Forestry* 75: 212-213
- Mitchell, F J G 1988 The vegetational history of the Killarney Oakwoods, SW Ireland: evidence from fine spatial resolution pollen analysis. *Journal of Ecology* 76: 415-436
- Mitchell, F J G 2001 Is the natural vegetation cover of lowland Europe really parkland rather than closed forest? [Review of *Grazing Ecology and Forest History*]. *Journal of Biogeography* 28: 409-411
- Mitchell, F J G 2005 How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology* 93: 168-177
- Mitchell, F J G, & Cole, E 1998 Reconstruction of long-term successional dynamics of temperate woodland in Bialowieza Forest, Poland. *Journal of Ecology* 86: 1042-1061
- Mosandl, R, & Kleinert, A 1998 Development of Oaks (*Quercus petraea* (Matt.) Leibl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus silvestris* L.) stands. *Forest Ecology and Management* 106: 35-44
- Motzkin, G, & Foster, D R 2002 Grasslands, heathlands and shrublands in coastal New England: historical interpretations and approaches to conservation. *Journal of Biogeography* 29: 1569-1590

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- Noe-Nygaard, N, Price, T D, & Hede, S U 2005 Diet of Auroch and early cattle in southern Scandinavia: evidence from 15N and 13C stable isotopes. *Journal of Archaeological Science* 32: 855-871
- Olf, H, Vera, F W M, Bokdam, J, Bakker, E S, Gleichman, J M, De Maeyer, K, & Smit, R 1999 Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biology* 1: 127-137
- Osborne, P J 1972 Insect faunas of Late Devensian and Flandrian age from Church Stretton, Shropshire. *Philosophical Transactions of the Royal Society of London B* 263: 327-367
- Palm, T 1959 Die Holz- und Rinden-käfer der süd- und mittelschwedischen Laubbäume. *Opuscula Entomologica*, Suppl. 16
- Paluch, J G, & Bartkowiak, L E 2004 Spatial interactions between Scots pine (*Pinus sylvestris* L.), common Oak (*Quercus robur* L.) and silver birch (*Betula pendula* Roth.) as investigated in stratified stands in mesotrophic site conditions. *Forest Ecology and Management* 192: 229-240
- Peterken, G F 1996 *Natural Woodland: ecology and conservation in northern temperate regions*. Cambridge University Press, Cambridge
- Pigott, C D, & Huntley, J P 1978 Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. *New Phytologist* 81: 429-441
- Preece, R C 1995 *Island Britain: A Quaternary Perspective*. Geological Society, London
- Rackham, O 1986 *The History of the Countryside: the classical history of Britain's landscape, flora and fauna*. J M Dent, London
- Rackham, O 1998 Savannah in Europe. In: K J Kirby & C Watkins (eds) *The Ecological History of European Forests*, pp 1-24. CABI, Wallingford
- Rackham, O 2003 *Ancient Woodland: its history, vegetation and uses in England*. Castlepoint Press, Dalbeattie
- Rannius, T, & Jansson, N 2000 The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old Oaks. *Biological Conservation* 95: 85-94
- Remmert, H 1991 The mosaic cycle concept of ecosystems – an overview. In: H Remmert (ed) *The mosaic cycle concept of ecosystems. Ecological Studies Vol 85*. Springer, Berlin
- Ripple, W J, & Beschta, R L 2003 Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184: 299-313
- Robinson, M A 1991 The Neolithic and Late Bronze Age Insect Assemblages. In: S Needham *Excavation and Salvage at Runnymede Bridge 1978: The Late Bronze Age waterfront site*, pp 277-326. British Museum Press, London
- Rose, F 2002 Review of grazing ecology and forest history. *Watsonia* 24: 119-120
- Royal Society 2003 *Measuring biodiversity for conservation*. Policy report 11/03. <http://www.marinebiodiversity.ca/en/pdfs/royalsoc.pdf>
- Schmidt, M, Sommer, K, Kriebitzsch, W-U, Ellenberg, H, & Oheimb, G 2004 Dispersal of vascular plants by game in Northern Germany. Part 1: Roe Deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). *European Journal of Forest Research* 123: 167-176
- Simmons, I G 2003 *Moorlands of England and Wales – an environmental history 8,000 BC-AD 2,000*. Edinburgh University Press, Edinburgh
- Sinclair, A R E, & Norton-Smith, M 1979 *Serengeti, dynamics of an ecosystem*. The University of Chicago Press, Chicago
- Smout, T C 2003 *People and Woods in Scotland*. Edinburgh University Press, Edinburgh
- Struik, J 2001 *Pollen rain research within parkland landscapes*. University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics, Internal Report 329
- Sugita, S 1994 Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology* 82: 881-897
- Sugita, S, Gaillard, M J, & Brostrom, A 1999 Landscape openness and pollen records: a simulation approach. *Holocene* 9: 409-421
- Sutherland, W J 2002 Openness in management. *Nature* 418: 834-835
- Svenning, J C 2002 A review of natural vegetation openness in north-western Europe. *Biological Conservation* 104: 133-148
- Tansley, A G 1939 *The British Islands and their Vegetation*. Cambridge University Press, Cambridge
- Taylor, P 2005 *Beyond conservation – a wildland strategy*. Earthscan and BANC, London.
- Van Vuure, C 2005 *Retracing the Auroch*. Pensoft, Sofia-Moscow
- Vera, F W M 2000 *Grazing Ecology and Forest History*. CABI International, Wallingford
- Vera, F, & Buissin, F 2007 *Wilderness in Europe. What goes on between the tree and the beasts*. Tirion, Baarn, The Netherlands
- Watt, A S 1947 Pattern and process in the plant community. *Journal of Ecology* 35: 1-22
- White, C A, Feller, M C, & Bayley, S 2003 Predation risk and the functional response of elk-aspen herbivory. *Forest Ecology and Management* 181: 77-97
- Whitehouse, N J 1997 Silent witnesses: an 'Urwald' fossil insect assemblage from Thorne Moors. *Thorne & Hatfield Moors Papers* 4: 19-54
- Whitehouse, N J, & Smith, D N 2004 'Islands' in Holocene forests: implications for forest openness, landscape clearance and 'culture-steppe' species. *Environmental Archaeology* 9: 199-208
- Wichmann, M C, Alexander, M J, Soons, M B, Galsworthy, S, Dunne, L, Gould, R, Fairfax, C, Niggemann, M, Hails, R S, & Bullock, J M 2009 Human mediated dispersal of seeds over long distances. *Proceedings of the Royal Society B-Biological Sciences* 276: 523-532
- Willis, K J, Gyllson, L, Brncic, T M, & Figueroa-Rangel, B L 2005 Providing baselines for biodiversity measurement. *Trends In Ecology and Evolution* 20: 107-108
- Willis, K J, & Birks, H J B 2006 What is natural? The need for a long-term perspective in biodiversity conservation. *Science* 314: 1261-1265
- Yalden, D W 1999 *The History of British Mammals*. T & A D Poyser, London
- Yalden, D W 2003 Mammals in Britain – an historical perspective. *British Wildlife* 14: 243-251

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