Large herbivores in the wildwood and in modern naturalistic grazing systems

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Large herbivores in the wildwood
and modern naturalistic grazing systems

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‘…let us again recur to Nature. The process by which she forms woods and forests is as follows. Seeds are scattered indiscriminately by winds, brought by waters and dropped by birds. They perish, or produce, according as the soil and situation upon which they fall are suited to them: and under the same dependence, the seedling or sucker, if not cropped by animals (which Nature is often careful to prevent by fencing it about with brambles or other prickly shrubs) thrives, and the tree grows, sometimes single, taking its own shape without constraint, but for the most part compelled to conform itself to some law imposed upon it by its neighbours.’

William Wordsworth, 1835, *A guide through the District of the Lakes*

“The beautiful British countryside ….. is maintained by farming and other land management practices. Without dedicated work the countryside would degenerate into scrub, even threatening the survival of those species that depend on cultivation or grazing and obscuring beautiful views and archaeological features”.

Preface

This report stems from work commissioned by English Nature into the role of large herbivores in the post-glacial landscape of Britain and the potential for using free-ranging grazing animals to create and maintain diverse landscape mosaics in modern conditions.

Some aspects may be disputed or considered controversial; it is an active field of research. Therefore we stress that the views expressed are those of the authors at the current time. Subsequent research may confirm our views or lead us to modify them.

We hope they will be useful in future discussions, both within English Nature and in conservation land-management circles more generally.

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Summary

English Nature’s interest in the role of large herbivores in forest systems
K.J.Kirby

- Frans Vera’s book *Grazing Ecology and Forest History* challenges our views on the nature of the former natural landscape in Britain. English Nature therefore commissioned a review of the nature and current state of the debate on his hypothesis and its relevance to future conservation practice.

- Understanding the role of grazing in past forests is relevant to current work on improving the management of wood-pasture systems, but also to proposals to encourage landscape-scale conservation programmes.

- Debates about Vera’s hypothesis have however been hampered by different interpretations of the words used to describe wooded and unwooded landscapes; and different ‘visions’ of what sort of landscape the Vera hypothesis or its alternatives might produce.

- Two separate questions need to be addressed: (i) were large herbivores the main drivers of the landscape, and, if so, (ii) did they produce half-open landscapes?

The Vera model of post-glacial landscapes in Europe: a summary of the debate
K.H. Hodder & J.M. Bullock

- Responses to the ideas put forward in Frans Vera’s book *Grazing History and Forest Ecology* are summarised.

- Vera argues that, if the natural forest (before significant human impact) is assumed to consist only of closed-canopy conditions, then the light demanding species, oak and hazel, should not be so well represented in the fossil record. He uses ecological, palynological, etymological and historical arguments to propose a ‘half-open’ park-like landscape for the lowlands of Central and Western Europe in the pre-Neolithic, Atlantic era, c7,000 years ago.

- There has been an enthusiastic welcome to the notion that wood pasture systems may be more representative of the original-natural landscape than closed high forest, and should therefore be given high conservation priority. However, the degree of landscape openness and the mechanisms by which clearings may be generated are the subject of much debate. Vera argues that large herbivores were an essential driving force behind the cyclical vegetation dynamics that resulted in shifting mosaic systems. Other authors suggest that abiotic disturbance such as fire and windthrow may also have important roles.

- Reviewers accept that there can be considerable bias in interpretations of the fossil pollen record, but note that analyses based on combinations of pollen and macrofossil remains, which tend to lead to similar conclusions, can be much more robust.

- Problems caused by the paucity of large mammal remains are harder to solve. In fact the debate about the scale and impacts of past ungulate-vegetation interactions is unlikely to be fully resolved until more is known about past ungulate population sizes.

- The picture that emerges is one of a mixed landscape including areas with vegetation cycles and others with more permanent vegetation. The difference between the closed forest hypothesis and Vera’s alternative of cyclical dynamics may be a matter of degree. While there is general agreement that the original-natural forest may have been more open than was previously thought,
this is not equivalent to saying that a wood-pasture landscape would necessarily dominate the landscape. The balance of opinion is towards predominance of closed forest with localised, longer lasting openings. Shifting vegetation mosaics may have operated on fertile floodplains, and open vegetation may have been frequent on floodplains, infertile soils, limestone and poor sandy soils.

- One of the major problems involved in applying Vera’s ideas in conservation is that there is no clear idea of spatial or temporal scale. Degrees of openness are likely to vary in different soil and topographic (and climatic) conditions, but at present there is no guidance on the patterns that might be expected. Therefore, a key area for future research is to understand the factors influencing temporal and spatial patterns of the grassland-forest matrix in the full range of environmental conditions.

**Palaeoecological evidence for the Vera hypothesis**

P.C. Buckland

- The model put forward by Frans Vera is examined in the light of the palaeoecological record for the Holocene and previous Late Quaternary interglacials. Previous reviews have largely dealt with the data available from pollen diagrams, and so this chapter concentrates upon the fossil beetle (Coleoptera) evidence, utilising the extensive database of Quaternary insect records, BUGS.

- The insect record is much less complete than the pollen one, but there are clear indications of open ground taxa being present in the ‘Atlantic forest’. The extent of open ground and dung faunas during the Neolithic suggests that many of these elements were already present (although not necessarily abundant) in the natural landscape before agriculturalists began extensive clearance during the late sixth millennium BP.

- In the palynological literature there is something of a dichotomy between those working in the uplands and lowlands, with the former being more inclined to credit Mesolithic hunter/gatherers with deliberate modification of the forest cover, usually utilising fire, sometimes leading to the expansion of blanket bog and in the lowlands the creation of heath. The concept of a natural forest, without human interference, in the present interglacial in Britain is doubtful.

- The role of natural fire tends to be underplayed by both groups. The presence of pyrophilic elements in the British beetle fauna and the frequency of charcoal in bog and soil profiles imply that fire is part of the natural system, although the gaps between major fires in deciduous forests may be long. Fire should be considered as a useful and natural management tool in the creation of forest clearings.

- The extent to which natural grazers formed part of the pre-forest clearance system has tended to be underestimated, partly as a result of the relatively poor mid-Holocene fossil record of large herbivores. Aurochs, *Bos primigenius*, however, is not infrequent. As a herd animal it probably maintained some areas of open ground, not necessarily on the floodplains, as the megaherbivores of previous interglacials did, but on the higher ground of the Chalk and other limestone outcrops.

**Naturalistic grazing and conservation**

K.H. Hodder & J.M. Bullock

- The implications of naturalistic grazing for conservation practice in Britain are reviewed through the use of case study sites.

- Naturalistic grazing does not have a formal definition; consequently the term tends to be used loosely. In this report we have attempted to clarify the issue by defining the differences between naturalistic and other forms of extensive grazing for conservation.
The principal of linking or expanding sites in order to avert the ecological problems, which are often associated with small isolated reserves, is not in question; nor is the utility of extensive grazing for the management of large sites.

The defining difference between naturalistic grazing and other large, extensively grazed conservation management is in the role of ‘natural processes’. In the naturalistic approach, there is no specified grazing density, instead herbivore populations are resource-limited. Rather than managing towards targets for habitat and species composition, direct management intervention is reduced to a minimum and the natural process is seen as an aim in itself.

The principal issue raised by the naturalistic grazing concept is the unpredictability of outcomes: if the conservation of natural processes becomes the goal, it is then difficult to define targets and to evaluate development of wild areas. The lack of defined goals is incompatible with current management aims based on targets for species and habitats of conservation concern, which are guided by Biodiversity Action Plans, in order to fulfil obligations agreed in the Convention on Biological Diversity (1992).

It is not realistic for proponents of naturalistic or wilderness grazing to assume that biodiversity benefits of naturalistic grazing can be forecast by describing the habitats and species found in the landscape that they assume will emerge. In fact there is little theoretical or empirical knowledge allowing prediction of the outcomes of any naturalistic grazing regime.

Management within ‘acceptable limits to change’ may therefore be more realistic than complete non-intervention, but in areas with high biodiversity this may differ little, if at all, from managing to targets.

Limits could be set by taking account of both ecological and cultural factors, as well as those imposed on site managers, such as reserve size and ‘completeness’ (ie the range of habitats available), climate change and airborne pollutants. These latter factors impose a limit to how ‘natural’ a system can be, because it will unavoidably be affected by inadvertent human actions.

Legislative changes would be needed to allow the use of resource-limited herds, and even then, there would be important limits to their potential ‘naturalness’. There are unlikely to be adequately large and networked nature reserves to allow seasonal migration, and the absence of large predators has important consequences for grazing behaviour, and hence ecosystem development.

It is likely to be very difficult to impose a wilderness ideology on the busy cultural landscapes of Britain, particularly lowland areas. Even in upland areas, it may be the sense of wilderness or ‘naturalness’ that is sought by the public and site managers. This goal is one of landscape management, rather than naturalistic management, because the main aim is to fulfil a deep psychological need for access to places that appear to be in a state of wilderness. Active management, such as the maintenance of unobstructed views will often be necessary to achieve this aim, and this requirement may conflict with stepping back from intervention.

Respondents to the case study questionnaires often expressed an interest in moving away from highly prescriptive target-lead management for their landscape-scale projects; however, the potential loss of biodiversity or highly valued habitats was rarely seen as acceptable, and this lead to an impasse for groups and even individuals.

More progress was made when accepting that management is for multiple aims, including active conservation of biodiversity and also landscape management to maintain a sense of wilderness. Confusing these separate objectives may make it more difficult to grasp the exciting opportunities...
we now have for developing large interconnected nature reserves for the benefit of plants, animals and people.

Was the wildwood closed forest or savannah and does it matter for modern nature conservation – some conclusions
K.J. Kirby

- Large herbivores could have been a significant factor in shifting the balance towards oak and away from more shade-tolerant species.

- The Atlantic period landscape did contain open areas, but trees and woodland appear to predominate. There is no direct evidence for a half-open landscape; nor is this high level of openness a requirement for oak regeneration and cyclical vegetation turnover.

- Cyclical vegetation turnover, driven by grazing, seems less likely than more complex patterns. There is evidence that other disturbance factors were at least locally important. Most parts of the landscape were probably driven by more than one disturbance agent and the relative importance of these might vary over time.

- Parts of the Atlantic forest may have looked like a modern wood-pasture and there might have been some permanently open areas; but the majority seems likely to have been relatively closed high forest, with a component of temporary and permanent glades.

- This research has also emphasised the need for clear objectives as to what naturalistic grazing is intended to achieve in modern landscapes. Even if we wished we cannot re-create the Atlantic period landscape and the grazing regime that operated then.

- We can use the ‘ideal, but impossible to achieve’ naturalistic grazing model as a guide to how we approach the management of real systems. Where a choice exists we can look for the option that, within the particular constraints, is closest to our understanding of the natural situation, the option that involves the least direct human intervention.

- Encouraging a naturalistic approach to grazing has the potential to change the way that we practise large-scale conservation, but it must be based on sound ecological and animal management principles.
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1. English Nature’s interest in the role of large herbivores in forest systems

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1.1 Summary

• Frans Vera’s book *Grazing Ecology and Forest History* challenges our views on the nature of the former natural landscape in Britain. English Nature therefore commissioned a review of the nature and current state of the debate on his hypothesis and its relevance to future conservation practice.

• Understanding the role of grazing in past forests is relevant to current work on improving the management of wood-pasture systems, but also to proposals to encourage landscape-scale conservation programmes.

• Debates about Vera’s hypothesis have however been hampered by different interpretations of the words used to describe wooded and unwooded landscapes; and different ‘visions’ of what sort of landscape the Vera hypothesis or its alternatives might produce.

• Two separate questions need to be addressed: (i) were large herbivores the main drivers of the landscape and, if so, (ii) did they produce half-open landscapes?

1.2 Background to the project

Frans Vera’s book *Grazing ecology and forest history* was published in English in 2000. He proposes that the former natural vegetation of much of north-west Europe, about 7,000 years ago was a ‘half-open park-like landscape’. This shifting mosaic of open grassland, scrub and closed tree-cover was created and maintained by large herbivores, particularly aurochs (wild ox), ponies and bison. As a consequence shade-intolerant species such as oak *Quercus* spp and hazel *Corylus avellana* were able to survive competition from species such as beech *Fagus sylvatica*. This landscape, and the grazing processes that shaped it, provide the origin of much of the flora and fauna that we seek to conserve. We could therefore, as the Dutch are doing in Oostvaardersplassen, establish large reserves with free-ranging, unmanaged grazing animals, as an alternative (in places) to the current emphasis of trying to combine conservation with modified agricultural systems.
Vera’s ideas have generated a lot of interest, not least because they appeared at a particularly opportune time. English Nature, and the conservation movement more generally, were showing increased interest in wood-pastures, in allowing more scope for natural processes to operate in conservation areas, and in landscape-scale management of the countryside. Soon after I had read the book I went across to meet Frans and had a very stimulating discussion with him.

Nevertheless his arguments could be, and were being, challenged. English Nature needed to establish its position, both with respect to the role of large herbivores in the former post-glacial ‘natural’ landscapes, and in relation to proposals to use large herbivores to create and maintain large-scale landscapes with a mix of habitats. We did not wish to dismiss what might prove to be a paradigm shift in scientific thinking, just because it went against previously accepted ideas of the wildwood; however, equally we needed to know that the ideas were soundly based and appropriate for British conditions.

English Nature therefore commissioned a study, under the general heading ‘Fresh Woods and Pastures New’, in summer 2003:

- to summarise the current state of debate concerning Vera’s ideas with respect to the past-natural landscape of Britain: would large herbivores have had the impact that he proposes;
- to review evidence for ‘openness’ in the past-natural landscape, in particular using fossil insect records which were not considered in Vera (2000).
- to set out the issues involved in the use of naturalistic grazing regimes in future conservation schemes.

The main work was carried out by the Kathy Hodder and James Bullock of the Centre for Ecology and Hydrology, and by Paul Buckland (Bournemouth University) working through the Sheffield University Consultancy ECUS. The study involved literature searches, a website forum, some new analyses of fossil beetle assemblages and much discussion with colleagues in both Britain and The Netherlands.

We publicised the project at the start to encourage ideas and views from both supporters and critics of Vera’s hypothesis. The various chapters were sent to a range of specialists both internally and externally for comment. We are grateful for their contributions. Some comments were contradictory, but we have tried to incorporate them as far as possible.

Some of the report, particularly that dealing with the past role of large-herbivores, may apply as much to Scotland and Wales as it does to England. The section on modern use of grazing is however focussed on English conditions.

The views expressed throughout are our understanding of the state of the debate and the issues. This is however still a very active area of debate. We hope this report is a useful contribution to the discussions and would welcome further comment or criticism.

Subsequent chapters deal with each of the main objectives of the study in turn. Prior to that however I explore some of the work that had been already underway in relation to woodland grazing, ‘re-wilding’ and landscape-scale conservation. I also discuss how we are using terms such as ‘forest’ or ‘grove’; and what pictures people may have as to the structure of a
‘Vera-type’ landscape or the ‘traditional’ closed forest model. Often debate on these ideas founders because the two sides are talking about different things.

1.3 Wood-pastures and the structure of the wildwood

Wood-pastures – the remnants of former Royal Forests, old parks and common lands - were identified as a important type of ancient woodland by Peterken (1977), particularly because of their rich epiphytic lichen and saproxylic invertebrate communities (Harding and Rose 1986). The combination of large old trees, often gnarled and twisted, with open space between them maintained by grazing, makes them very attractive: indeed many of the most famous woods in England are (or were) wood-pastures – Epping Forest, the New Forest, Windsor Great Park and Sherwood Forest.

From the late 1980s there has been increasing interest in how to manage these areas, both in terms of the trees themselves (Mitchell 1989; Read 1991, 2000), but also the grazing system around them (Kirby and others 1995). The combination of old trees, open glades and patches of scrub created and maintained by cattle, ponies or sheep has been recognised as important for many species. In 1998 a Habitat Action Plan for wood-pastures and parkland was published (English Nature 1998).

The open structure of many wood-pastures has been seen as a product of management, quite distinct from the conventional closed-forest view of what most natural woodland would have been like in Britain. Rackham (1998) suggested that there might be a role for ‘savannah’ in parts of Europe, and Tubbs (1996) suggested that the abundance of non-woodland species in our wildlife pointed to more open landscapes in the past. However, while open space has increasingly been recognised as a component of the original-natural forests (Peterken 1996), the prevailing view has been that the trees were dominant.

Wood-pastures, as they exist today in most of Britain, are a cultural landscape feature. They tend to have survived only on certain soil types and locations. The old trees nearly always show signs of having been cut many times (usually by pollarding); the numbers and types of grazing animals, and hence the patterns of vegetation, are, and have been for centuries controlled to a greater or lesser degree. However Vera (2000) has proposed that the characteristics of wood-pastures might be closer to the structure of the past-natural forests than the closed-forest model.

Vera’s argument is that large herbivores such as aurochs, wild horse and bison, created and maintained a half-open park-like landscape; over most of the lowlands of Europe he suggests that the vegetation went through cycles of open grassland, scrub and closed tree cover (Figure 1). This idea is important since, if correct, it affects our views on how the landscape and current species assemblages have evolved. It is also very relevant to discussions on the use of extensive grazing to manage conservation areas at a landscape-scale.
1.4 Extensive grazing and re-wilding

Many species in England are associated with habitats and landscapes that have been grazed as parts of traditional agricultural systems, for example chalk downland, heathland, or upland moors. Agricultural intensification over the last 50 years has led to the loss of many valuable areas (NCC 1984): in the uplands stock numbers have tended to increase and important sites are being damaged by over-grazing; in the lowlands the problem is often the converse. It is no longer economic to graze areas of lowland pasture or heath and they are at risk through becoming overgrown (English Nature 2003; Townshend and others 2004). The changes to the Common Agricultural Policy may affect patterns of grazing, but do not currently seem likely to resolve these problems. Consequently there is interest in English Nature in developing appropriate low-intensity grazing regimes (eg Lake and others 2001; Tolhurst & Oates 2001) that could be applied in currently under-grazed sites in the lowlands or over-grazed sites in the uplands.

Separate, but related, strands of work within English Nature are considering the need to promote conservation at landscape-scale and to try to work more with natural processes (Kirby and others 2004). There are debates about ‘re-wilding’ parts of the uplands (eg Harvey 2002; Taylor 2005) and the potential for new ‘wildwoods’ (Worrell and others 2002; Rogers & Taylor 2003). On the continent there is much interest in the work that the Dutch have been doing at Oostvaardersplassen (Vera 2000), where herds of cattle, ponies and red deer are allowed to graze 2000 ha of reclaimed polder with management limited to humane intervention when required for animal welfare reasons (Wigbels 2001).

Vera’s ideas are thus relevant to English Nature’s (and others’) interests in the use of naturalistic grazing regimes in large-scale landscape conservation schemes. Such regimes
could, however, only be adopted once all the relevant issues (including animal welfare and safety considerations) have been properly considered. They would form only one approach to conservation: elsewhere target-orientated management of habitats would still be practised.

1.5 What words do we use to describe the past-natural landscape?

The debate on the Vera hypothesis has at times been hampered by different interpretations of what a landscape driven by large herbivores would actually have looked like. Some people may be imagining an open savannah with very low levels (<30%) of tree cover, whilst others have a picture of a mainly wooded landscape (>70%) but with bigger, shifting glades than would be expected under small-gap regeneration models (Vines 2002).

Frans Vera (2000) comments on the problems that can arise through using terms, such as ‘forest’ or ‘woodland’, that conjure-up particular landscape images. So for example:

- In Britain the word ‘forest’ will to most people mean an extensive area of trees, probably conifers, managed commercially for timber. In medieval times it meant an area to which particular laws applied with respect to the deer (or other game). The current international definition of forests however can apply to any area of tree-covered land where the canopy cover is more than 20%.

- Park, similarly, had a quite specific meaning in medieval times to do with the emparking (within a fence) of game, again not necessarily anything to do with trees. Currently it is widely used to mean an open area with scattered trees; but in towns it may simply mean any area of public open-space.

- A grove, the term adopted by Vera (2000) to represent the tree-covered part of his vegetation cycle, is defined by the dictionary as ‘a (small) wood, a clump of trees’. Most people would therefore expect his groves to be small, but Vera (2000) (p151) notes that New Forest 'groves' might be up to 250-500 ha.

Within this report we try to stick to the following conventions and meanings.

- ‘forest’ – generic term for extensive areas with trees, where the canopy cover is more than 20%. The open space, ie no canopy cover, between the trees, counts as part of the forest. There is no implication about whether the trees are coniferous or broadleaved. Where the medieval use of a place with deer is necessary we will follow Rackham’s convention and use Forest (capital F), or refer to ‘royal forests’ or ‘hunting forests’.

- ‘woodland’ – generic term for areas where tree cover predominates although there may still be small permanent or temporary gaps such as rides or glades and areas where the canopy has been removed, eg by felling or disturbances such as windthrows. Typically in modern woodland in the UK such gaps occupy 10-20% of the area.

- ‘wood’ – a specific defined patch of woodland.

- ‘park’ – an area in which tree cover is less than 20% and the trees are mainly as scattered individuals or small groups, similar to Rackham’s (1998) ‘savannah’. We note however that Vera (2000) uses the term ‘park-like landscape’ to include both such open areas and the other phases of his cycle, including the closed-canopy groves.
•  ‘grove’ – only used for the tree-covered part of Vera’s regeneration cycle; grove in this specific sense does not mean just small patches of trees, but can be of any size.

•  ‘wood-pasture’ – a generic term used for areas with a mixture of trees and open habitats, where large herbivores are the key factor driving the overall structure and composition of the landscape.

Similar consideration needs to be given to the words used to describe the open areas in the landscape.

•  **Glades** - Open patches, i.e. without canopy cover, within a woodland matrix usually less than 1 ha in extent. Such small areas, and the species found in them will be strongly affected by the shade of the surrounding trees. They may be temporary or permanent.

•  **Open grassland** etc – areas of more than 1 ha, either as patches within a woodland matrix; or forming the matrix within which the trees occur. In the context of discussion of the Vera cycle of vegetation turnover (Figure 1), it is convenient to refer to the open phase as ‘grassland’, even though on more acid soils the open phase of the cycle might have been dominated by bracken or heathland species.

### 1.6 Patterning and scale in the landscape affect interpretation of evidence

There is no dispute that some large herbivores were present in Britain in the post-glacial landscape and undoubtedly in some places they were critical to the way the landscape functioned. The debate is about over how much of the landscape structure and function they influenced, in comparison, say, to fire, wind or flooding.

Peterken (1996) is often presented as the antithesis of the Vera hypothesis, but refers to the importance of open space in natural forests (page 197).

> ‘Although one readily envisages natural forests as unbroken massifs of tree-covered land, openings of various kinds form a permanent and sometimes common component. Individual gaps and other disturbance-generated openings are individually transitory but, collectively, gaps are permanent, in the sense that new gaps form somewhere in the landscape almost every year. Other openings are permanent in a more direct sense, i.e. they retain indefinitely their individual identity, even if they fluctuate around the margins and trees occasionally become established within them.’

The key question is not therefore whether a herbivore-driven regeneration cycle *can* occur, but

(a) whether it was the dominant mechanism for landscape regeneration; and

(b) if so what were the temporal and spatial scales for the different elements of the cycle – would it necessarily produce a half-open park-like landscape?

Figure 2 illustrates four hypothetical landscapes: two contain substantial open areas and in two large herbivores drive the landscape structure. In Vera’s book, and in much of the
subsequent debate, attention has been focussed on the contrast between the open landscape driven by large herbivores (Figure 2d) and the traditional closed-forest model (Figure 2a). However other possibilities (Figure 2b,c) exist and should be considered when looking at the evidence.

One other cause of the openness in Figure 2b might be human activity. There is debate as to the degree to which Mesolithic peoples modified the landscape, either directly or through their impact on their prey, including large herbivores. Indeed some suggest that the ‘closed forest’ model of Figure 2a might itself be the result of earlier human elimination of elephants and other mega-herbivores, such as existed in the previous interglacial period.

Such debates may affect whether we regard the pre-Neolithic, Atlantic period landscape as natural or not (depending on our definition of natural). However they do not affect the interpretation of what it was like, only of how it functioned. Since Vera (2000) considers that the openness of the landscape was created and maintained by wild herbivores (not including elephants) this is also the starting point in this report, although some reference to early human activities is made. A generalised chronology for the Holocene period is given in Annex 1 at the end of this chapter.

The evidence available to us, whether from pollen analysis, fossil beetles, or historical analysis, is limited and biased. That is unavoidable. We can only compare it with what we might expect under different scenarios, both in terms of variation in space – differences between sites – and changes at a site over time. As far as England is concerned, the landscape had already been heavily modified by the Roman period, to the extent that most fossil insect faunas from this period are not dissimilar to those from the nineteenth century: in many places clearance must have been much earlier. The distribution, composition and structure of both the woodland and open habitats from Roman times onward cannot provide much indication as to what the former more natural landscape was like. The critical changes are therefore from the time when the landscape is agreed to have been open in the immediate post-glacial period through to when it started to be increasingly open again with the expansion of agriculture in the Neolithic, Iron Age and Roman periods.
Most managed woodland in Britain contains 10-20% open space in the form of permanent rides and glades and temporary regeneration gaps. This may be helpful in envisaging the degree of openness in the closed forest models below.

<table>
<thead>
<tr>
<th>Herbivores major driver of change</th>
<th>Landscape low openness (&lt;25%)</th>
<th>Landscape high openness (&gt;50%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) ‘Traditional’ closed forest model</td>
<td>Large herbivores present, but wind, fire and flood assumed to be main factors driving regeneration</td>
<td>Other factors, eg fire or flooding produce an open landscape. Large herbivores are present but not a key driver.</td>
</tr>
<tr>
<td>(c) Closed forest model, driven by grazing</td>
<td>Large herbivores are the main driver, but the outcome is not an open landscape - see Kirby (2003, 2004) for how this could occur.</td>
<td>Large herbivores are the main factor driving regeneration and produce an open park-like landscape.</td>
</tr>
</tbody>
</table>

**Figure 2.** Hypothetical landscape structures resulting from different regeneration models
As a supplement to evidence from the past, modern sites have been used as analogues for some of the processes and landscapes that may once have existed. Three in particular come up frequently in the debates: Oostvaardersplassen (the Netherlands), the New Forest (southern England) and Bialowieza Forest (Poland) (Box 1).

**Box 1 Modern sites often used as analogues for elements of original-natural landscapes**

<table>
<thead>
<tr>
<th>a. Oostvaardersplassen, The Netherlands 5,600 ha (Vera 2000; Wigbels 2001). This was a polder created in 1968, originally intended for industrial use which never materialised, and subsequently became a nature reserve. It consists of marsh and grassland, with some woodland and scrub that developed in the first 10 years. Heck cattle (developed in the 1930s by crossing various primitive breeds) and Konik horses were introduced in the 1980s. On about 2,000 ha of the reserve they live as resource-limited herds, with minimal intervention. Red deer are also abundant on the site. Approximate numbers in 1999 were 500 cattle, 450 horses, 400 red deer.</th>
</tr>
</thead>
<tbody>
<tr>
<td>b. The New Forest, England, 38,000 ha (Tubbs 2001) The New Forest was established as a royal Forest, primarily for hunting, by William the Conqueror, c1079 AD. It is a mixture of woodland, heath, mires and grassland, with extensive grazing by cattle and ponies. Both wooded and non-wooded habitats are managed to varying degrees, for example parts of the Forest have been enclosed at various times, bracken used to be regularly harvested, locally grasslands have been improved and mires drained. The animals are a valuable resource and have been for centuries, albeit the nature of the stock has varied: in the past many of the cattle were dairy animals; whereas now they are mainly store cattle. Deer, particularly fallow, are also abundant. Putman (1986) gives estimates of about 2,500 deer, 2,750 ponies and 1,750 cattle on c20,000 ha of open Forest for the period 1965-1981.</td>
</tr>
<tr>
<td>c. Bialowieza Forest, Poland, c125,000 ha (Falinski 1986) This is a mixed, predominantly broadleaved lowland forest with a high forest structure. The forest was protected in the past as a hunting reserve, but with grazing by stock. In the last 200 years much of the area has been partly cleared and managed for timber. The National Park area within the forest covers c4700 ha and has been strictly protected since 1921. The forest contains a good range of large wild herbivores - bison, elk, red and roe deer and wild boar. However it no longer has wild ox or wild horse and there is some winter feeding of the bison. The national park area is largely dense woodland, but temporary open gaps occur following windthrow and more permanent open space occurs on small mires and alongside the river.</td>
</tr>
</tbody>
</table>

Oostvaardersplassen (Box 1,a) illustrates how it is possible to set up areas with free-ranging herbivores; but it has been in existence for less than 40 years and no conclusions can therefore be drawn as to whether or not Vera’s cyclical vegetation dynamic will operate.
there. Vera himself (pers. com) suggests that, because of the fertility of the soils it may remain more-or-less open for a long time.

The New Forest (Box 1.b) is an ancient wood-pasture system and it shows the main elements of the cycle shown in Figure 1. However the grazing animals are managed, their numbers adjusted across the year; much of the openness of the Forest is maintained by other management such as heather-burning. Its composition has changed considerably over the last 1000 years (Tubbs 2001) but there is little evidence for large scale shifts in the distribution of wooded areas as proposed under the shifting vegetation mosaic hypothesis.

‘Minimum intervention’/near-natural woodland reserves (old growth stands in the eastern United States), such as Bialowieza in Poland (Box 1.c), usually show signs of previous interventions or lack key components of original-natural conditions (such as some of the large herbivores). Therefore they do not provide a perfect match for the ‘closed forest’ model.

1.7 Conclusion

The evidence for what the past was like is far from perfect; this report is a contribution to the debate, but many areas would benefit from further research. Nevertheless, I feel that the evidence presented in the following chapters is sufficient to make some suggestions as to where the balance of probabilities may lie and I will return to this in the final chapter of the report.

1.8 References


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VERA, F.W.M. 2000. *Grazing ecology and forest history*. Wallingford, CABI.


Adapted from Yalden (1999) *The History of British Mammals* Poyser, and http://www.abdn.ac.uk/mammal/history.shtml

<table>
<thead>
<tr>
<th>T&lt;sup&gt;14&lt;/sup&gt;C Dates Years BP</th>
<th>Pollen Zones</th>
<th>Archaeological periods</th>
<th>Latest recorded dates on extinct mammals in Britain</th>
<th>Vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1000</td>
<td>VIII</td>
<td>Historical</td>
<td>Wolf - 300 BP Wild Boar -500 BP Beaver - 700 BP Lynx - 800 BP Brown Bear - 1500 BP</td>
<td>Increasingly open landscape with little unmanaged woodland</td>
</tr>
<tr>
<td>2000</td>
<td></td>
<td></td>
<td>Aurochs - 3250 BP Moose (Elk) - 3400 BP</td>
<td></td>
</tr>
<tr>
<td>3000</td>
<td>VIIB</td>
<td>Iron Age</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4000</td>
<td></td>
<td>Bronze Age</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5000</td>
<td></td>
<td>Neolithic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6000</td>
<td>VIIA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7000</td>
<td></td>
<td>Mesolithic</td>
<td>Reindeer 8300 BP Giant deer <em>Megaloceros giganteus</em> - 9225BP Horse - 9330 BP</td>
<td>Maximum woodland cover dominated by lime in the lowlands with oak, alder, hazel, and elm. Half-open parkland according to Vera’s ‘alternative hypothesis’.</td>
</tr>
<tr>
<td>8000</td>
<td>VI</td>
<td></td>
<td></td>
<td>Pine-birch woodland; hazel and oak becoming more common towards the end.</td>
</tr>
<tr>
<td>9000</td>
<td>V</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10000</td>
<td>IV</td>
<td></td>
<td></td>
<td>Spread of pine-birch woodland. Willow in wetter areas.</td>
</tr>
<tr>
<td>11500 BP</td>
<td>III</td>
<td>Late Upper Palaeolithic</td>
<td>Saiga antelope - 12400 BP Mammoth - 12500 BP</td>
<td>Open tundra with dwarf birch and willow</td>
</tr>
</tbody>
</table>
2. The ‘Vera model’ of post-glacial landscapes in Europe: a summary of the debate

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NERC Centre for Ecology and Hydrology

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Implications for conservation policy and practice
Conclusions
References

2.1 Summary

- Considerable interest has been generated by Frans Vera’s book *Grazing ecology and forest history*. This chapter summarises published reviews and relevant research post-dating publication of the book, along with additional material from unpublished reports, web-sites, and discussions with experts.

- Vera argues that, if the natural forest (before significant human impact) is assumed to consist only of closed-canopy conditions, then the light demanding species, oak and hazel, should not be so well represented in the fossil record. He uses ecological, palynological, etymological and historical arguments to propose a ‘half-open’ park-like landscape for the lowlands of Central and Western Europe in the pre-Neolithic, Atlantic era.

- There has been an enthusiastic welcome to the notion that wood pasture systems may be more representative of the *original-natural* landscape than closed high forest, and should therefore be given high conservation priority. However, the degree of landscape openness and the mechanisms by which clearings may be generated are the subject of much debate. Vera argues that large herbivores were an essential driving force behind the cyclical vegetation dynamics that resulted in shifting mosaic systems. Other authors suggest that abiotic disturbance such as fire and windthrow may also have important roles.

- Reviewers accept that there can be considerable bias in interpretations of the fossil pollen record, but note that analyses based on combinations of pollen and macrofossil remains, which tend to lead to similar conclusions, can be much more robust.

- Problems caused by the paucity of large mammal remains are harder to solve. In fact the debate about the scale and impacts of past ungulate-vegetation interactions is unlikely to be fully resolved until more is known about past ungulate population sizes.
The picture that emerges is one of a mixed landscape including areas with vegetation cycles and others with more permanent vegetation. The difference between the closed forest hypothesis and Vera’s alternative of cyclical dynamics may be a matter of degree. While there is general agreement that the original-natural forest may have been more open than was previously thought, this is not equivalent to saying that a wood-pasture landscape would necessarily dominate the landscape. The balance of opinion is towards predominance of closed forest with localised, longer lasting openings. Shifting vegetation mosaics may have operated on fertile floodplains, and open vegetation may have been frequent on floodplains, infertile soils, limestone and poor sandy soils.

One of the major problems involved in applying Vera’s ideas in conservation is that there is no clear idea of spatial or temporal scale. Degrees of openness are likely to vary in different soil and topographic (and climatic) conditions, but at present there is no guidance on the patterns that might be expected. Therefore, a key area for future research is to understand the factors influencing temporal and spatial patterns of the grassland-forest matrix in the full range of environmental conditions.

2.2 Introduction

This review explores the interest and debate generated by the publication, in English, of ‘Grazing Ecology and Landscape History’ by Frans Vera¹, an expanded version of his PhD thesis ‘Metaphors for the wilderness - Oak, hazel, cattle and horse’. Vera challenges the widely held belief that prior to significant human impact the lowlands of Central and Western Europe were dominated by closed forest (Bradshaw & Mitchell 1999; Pott 2000; Yalden 1999).

The central problem addressed in Vera’s study is the poor regeneration of pedunculate and sessile oak (*Quercus robur* and *Q. petraea*) and hazel *Corylus avellana* under the canopy of modern woodland. According to Vera, this conflicts with evidence from fossil pollen, which indicates the continuous existence of these light-demanding species in Central and Western Europe since their range expansion following the end of the last glaciation (~10,000 years ago). Vera argues that if the Atlantic forest is assumed to consist mainly of closed canopy forest, with regeneration only in small gaps created by disturbance, then oak and hazel should not be so well represented in the fossil record. He also notes that it is difficult to differentiate between closed and open forest structures using pollen spectra.

Vera uses ecological, palynological, etymological and historical arguments to propose an alternative ‘half-open’ park-like landscape for the pre-Neolithic Atlantic period (see timeline at end of previous chapter). A cyclical turnover of vegetation types operates in this landscape leading to the development of a shifting mosaic of open grassland, scrub and woodland groves. Crucially, he argues that wild grazers such as aurochs *Bos primigenius*, horse *Equus przewalski gmelini*, bison *Bison bonasus*, elk *Alces alces*, red deer *Cervus elaphus*, and roe deer *Capreolus capreolus* played an essential role in this cycle.

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Figure 1. The Vera model of forest dynamics as envisaged by Kirby (2003, 2004).
Note that Vera (2000) refers to only three phases because he does not specifically separate out the ‘Scrub phase’: he describes the whole cycle as contributing to ‘a park-like landscape’.

The work has been described as a ‘challenge to orthodox thinking’ (Miller 2002), and an attempt to ‘demolish’ fundamental scientific assumptions. However, Vera is not the first author to suggest that landscapes in Europe north of the Alps may not have been dominated by closed forest, but may have been more open in the Atlantic period. The potential for large wild herbivores to create open areas by grazing, browsing and trampling has been raised in the literature on several occasions in recent decades (Chatters & Sanderson 1994; Knapp 1971; Tubbs 1996). Harding & Rose (1986) argued that the large proportion of species found in modern woodland that are adapted to relatively well lit conditions may indicate that the wildwood (minimally modified by humans) was closer to a pasture-woodland type landscape than it was to dense forest. In a paper discussing ‘Savannah in Europe’ Oliver Rackham noted the ‘thin but continuous record of dry-land plants of open ground’ throughout Holocene records in England. He concluded that although real savanna was unlikely in England, there was clearly more to wildwood than just forest (Rackham 1998).

The importance of Vera’s review is, however, in its wide-ranging nature, the advocacy in his argument and the timing of the publication when grazing is increasingly important in conservation in Europe (see chapter 4 on Naturalistic grazing and conservation). These have combined to raise the profile of this issue and stimulate considerable debate. If Vera is correct, and the open park-like landscapes were inherited rather than created by people, this may have consequences for conservation practice in Europe.

This chapter is based on a literature search, web-debate and discussions with Dutch and British ecologists (including a visit to key sites and individuals in the Netherlands). The aim was a short summary of the main issues and the current state of the debate about the ecological validity of Vera’s hypothesis and its relevance for modern conservation, rather than an exhaustive review of all of the evidence surrounding the ‘Vera debate’. The authors...
have endeavoured to remain neutral and represent all relevant views, with particular emphasis on those supported by empirical, and particularly published, data. The more speculative comments received and those for which there is little empirical evidence have not been included.

2.3 Vera’s ‘hypothesis’

The issues addressed in Vera’s thesis are expressed as a null hypothesis based on the assumption that the lowlands of Western and Central Europe (see Figure 1.5 in Vera (2000)) were covered with closed canopy forest and still would be if there had been no human intervention. The hypothesis states that ‘pedunculate and sessile oak survive in a closed canopy forest and regenerate in canopy gaps, and that large herbivores did not have any natural influence on forest succession and regeneration.’

As an alternative hypothesis he proposed that ‘the natural vegetation consists of a mosaic of large trees and 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 for this landscape.’

In his final conclusion Vera rejects the null hypothesis and states that ‘the original vegetation in the lowlands of Europe is a park-like landscape where the succession of species of trees is determined by large herbivorous mammals and birds such as the jay’. He does, however, make clear that not all areas would be subject to cyclical dynamics, and some may be vegetated by more permanent closed forest (p. 378).

Although phrased as a single hypothesis by Vera, it is easier to examine the issues raised in his thesis by splitting it into three separate elements.

(i) The pre-Neolithic landscape in the lowlands of central and western Europe was not closed woodland but a relatively open park-like mosaic of wood and grassland.

(ii) Large wild herbivores were an essential driving force behind woodland-grassland vegetation cycles.

(iii) Rewilding is the optimal conservation strategy for the maintenance and restoration of biodiversity in Europe (see Vera’s Epilogue p. 379).

Issues (i) and (ii) are addressed in this chapter and (iii) in the chapters 4 and 5.

2.3.1 Cyclical succession and shifting mosaics

Cyclical succession and resulting mosaic patterns of vegetation have been observed for many decades and given systematic treatment in a seminal paper by Watt (1947). The major contribution of Frans Vera and colleagues is to assert that large herbivores are key drivers of such cyclic processes at the landscape scale involving transitions between woodland and grassland.

There are three stages in the cyclical turnover of vegetation described in Vera’s book:

(i) grassland with patches of unpalatable scrub / tree seedlings (these have been separated in Figure 1 above);
(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 (Vera 2000, p 379).

More detail of the processes involved in cyclic patch dynamics, and the resulting shifting mosaics of vegetation, are given in a paper to which Vera contributed (Olff and others 1999). This paper stresses the importance of plant facilitation and competition found in grazed and browsed mixtures of palatable and unpalatable plants.

Cyclic succession in the presence of large herbivores is driven by the alternation of positive (associational resistance) and negative (competitive) interactions between plant species. Short unpalatable forbs facilitate the establishment of thorny scrub, which in turn facilitates the growth of palatable trees. The trees shade out the shrubs that facilitated them, then eventually degenerate leading to a dynamic cycle of vegetation turnover (Figure 2).

Regeneration does not occur within the closed canopy grove (A) because grazing animals attracted to the woodland for shelter prevent establishment of seedlings by grazing and trampling. Any seedlings that do germinate are consumed by the large herbivores. Even without herbivores, light-demanding trees and herbaceous plants fail to regenerate because of the shade provided by the closed canopy. Exceptions may occur where fallen trees protect seedlings from grazing in the so-called called ‘branch cage’ effect (1). Eventually, the trees in the closed canopy grove degenerate and die leading to the break-up phase (2) where the canopy opens out. The increase in light allows grasses to establish, attracting grazing animals and preventing the establishment of shrubs and trees. A few trees may remain within this open landscape (B).

Deposition of dung or soil disturbance by animals such as wild boar provides windows of opportunity for invasion by non-palatable herbaceous species (C). Where the density of herbivores is high, these patches of forbs are grazed back to short grass (3), but if these patches become established there is the potential for establishment of scrub within them (4). These scrub patches (D) may then expand with a fringe of unpalatable forbs (eg nettles *Urtica dioica*) offering protection to young stems of thorny plants (eg blackthorn *Prunus spinosa*). The patches of scrub shield palatable tree seedlings from grazers. Eurasian jays *Garrulus glandarius* may aid the recruitment of oak *Quercus* spp. by caching acorns in the scrub. Once they reach a certain height, the trees shade out the scrub creating a grove within the patch of scrub (E), which eventually develops into closed canopy woodland completing the cycle (6 A).

The different elements of this process or variations on them (such as bracken shielding birch and oak in the New Forest) can be seen at many sites (Bakker and others 2004). The key question is not therefore whether such a regeneration cycle can occur, but (a) whether it was the dominant mechanism for landscape regeneration and (b) if so what were the temporal and spatial scales for the different elements of the cycle.
2.4 Landscape history and ecology: evidence for openness

2.4.1 Palynology, plant macrofossils and invertebrates

Whilst the continuous and abundant pollen record from oak and hazel is crucial to Frans Vera’s thesis, he questions the potential for palynology to detect vegetation openness. Sub-fossil pollen from peat, soil and freshwater sediments has commonly been used to estimate past vegetation openness by comparing the percentage of arboreal to non-arboreal pollen (NAP) (Svenning 2002), and NAP percentages of \( \leq 10\% \) have conventionally been interpreted as closed forest (Vera 2000, p.68). In his chapter 3, Vera reviews the pollen-based evidence for the closed forest hypothesis and concludes that palynology has a poor record for detecting open spaces within woodland, because of weaknesses in the techniques of pollen analysis.

Mitchell (2001) suggests that the evidence used in Vera’s book relies largely on early pollen references. For instance, the exclusion of hazel and herbs from pollen records has been discontinued for 40 years. Recent research also shows that data from small hollows are far more sensitive to open forest conditions than traditional sites (lakes and bogs) for pollen analysis (Bradshaw and others 2003). Lakes and bogs may collect pollen from tens of kilometres, whereas small hollows tend to be dominated by local pollen rain (Mitchell 1998). 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 small hollows tend to support the closed forest hypothesis (Bradshaw 2002; Mitchell 2001, 2005).

Simulation models have been developed to estimate landscape openness from pollen records, and these can currently provide a rough approximation of openness (Sugita 1994; Sugita and others 1999). However, there is still a need for better empirical validation of model parameters, such as pollen productivity and fall speeds of non-arboreal species (Sugita and others 1999). For example, Broström and others (2004) have made empirical estimates of herb and tree species pollen productivity in heterogeneous landscapes in southern Sweden. In addition the European Pollen Monitoring Programme has been set up to aid the interpretation of pollen spectra from peat and soil profiles. This programme aims to use pollen traps to monitor pollen deposition across vegetation transitions from closed forest to open situations under as natural conditions as possible as a basis for interpreting fossil pollen spectra (http://www.ngdc.noaa.gov/paleo/pmp/guide.html).

Early results on spatial variation in arboreal pollen deposition, concentrating on pinpointing tree-lines, show that there is potential to achieve this. However, the authors suggest that many more years of data collection will be required to draw firm conclusions because fossil assemblages from comparable terrestrial situations may represent anything from 5-50 years. Other preliminary results indicate that the long distance component of the pollen assemblage may be much greater than previously thought, but also that cereal pollen penetrated surprisingly well into forest traps. The latter could lead to overestimates of openness (Hicks and others 2001). Despite analytical problems associated with palynological assessment of past vegetation openness, such as noisy and non-linear data, NAP percentages from interglacial sites correlate well with vegetation openness estimated independently from beetle, mollusc and /or plant macrofossils (Svenning 2002).

Modern landscapes and pollen data have been used as analogues to deduce past vegetation openness from pollen records. Broström and others (1998) contend that cultivated land, open land and deciduous forest are ‘reasonably well reflected’ in modern pollen assemblages from surface sediments on small Swedish lakes. They combine data from a study in open agricultural land with data from a forested region to conclude that ‘background pollen’ has an important effect, so that palynological analyses of openness at a local level should use analogues from the same broad habitat. The study also indicated that landscape openness may be ‘difficult to reconstruct in patchy half-open landscapes’. Although their Figure 9 indicates an increase in landscape openness with greater NAP%, this is achieved by combining cultivated and other open land. In fact, they found a positive correlation between percent cultivated land and NAP, but not for other non-cultivated open land (their Figure 8) and it is this lack of ‘direct relationship’ that is noted by Vera (p. 94). More recently Mitchell (2005) concludes that pollen records from small hollows can distinguish at least half-open from largely closed forest landscapes.

Bradshaw (2002) agrees with Vera that the pollen record ‘tells us more about trees than undergrowth’ but cites several arguments in favour of the utility of palynology for accurately detecting openness in the landscape. Grass pollen is well represented in palynological records, and he suggests that Vera’s argument that grasses may be poorly represented in deposits from wood-pasture type landscapes because of heavy grazing of the flowering heads, is ‘not the most parsimonious’. Bush (1993) provides an example of detection of openness in Mesolithic landscape in the Yorkshire wolds. Tree species were present as macrofossils but ‘failed to dominate the pollen spectrum’. Weeds of disturbed ground were found and also
beetles characteristic of open grassland. Given the large numbers of Mesolithic settlements in the area, the authors speculated that early humans may have been responsible for creation of openness by disturbance, and that in the absence of evidence for burning this may have been achieved by tree-felling or ring barking.

The European pollen record clearly shows increased proportions of grasses and herbaceous species with increasing evidence of Neolithic human activity. Peterken (2001) suggests that the shift in balance between grass and tree pollen (ie greater NAP) in the Neolithic era could be explained under Vera’s hypothesis as a greater area of under-grazed grassland which would therefore produce more pollen from ungrazed flowering grasses without there being a shift in openness. However, there is supporting data from macrofossils, lake sediment and chemistry which does suggest that the landscape became more open under human influence, so that invoking a putative increase in flowering of grasses is not necessary.

A similar increase in grass and herb pollen accompanied by a decrease in tree pollen has also been documented following European settlement in North America (Foster and others 2002). Motzkin and Foster (2002) collated pollen records from across a wide swathe of New England and compared percent grass and weed pollen from Pre-European settlement times, the peak of forest clearance post-settlement and modern times (when the forest cover has regenerated over wide areas): the pre-settlement levels of grass and weed pollen are in all cases lower than the most recent records, suggesting that tree cover was at least as great as present.

Vera suggests that shelter provided by the mantle and fringe vegetation would minimise pollen dispersal from open grassy areas to mires. Presumably, this shelter effect would depend on the proportion of the landscape occupied by trees and scrub; it could be explored through sampling modern pollen deposition (see details above on the European Pollen Monitoring Programme).

Many of the shrubs making up the mantle vegetation (eg hawthorn *Crateagus* spp or blackthorn *Prunus spinosa*) are insect pollinated and therefore should remain ‘entirely or almost entirely invisible’ to palynology according to Vera (p.86). Rackham (2003) refutes this, noting that hawthorn and blackthorn are ‘not negligible pollen producers’ although their pollens are not very distinctive. He contends that there ought to be a regular pollen record for these species if they occurred in the ‘quantities that Vera required.’ Records of hawthorn, blackthorn and bramble *Rubus fruticosus* pollen from floodplain sites in the previous interglacial (the Ipswichian) show that this mantle vegetation is in fact visible in palynological studies (Svenning 2002).

Vera argues that hazel pollen in the palynological record indicates open landscapes because it would not flower or regenerate in closed canopy forest. Rackham (2003) agrees that hazel flowering stops when it is shaded by taller neighbours. This is however challenged by Bobiec (2002) based on observations in Bialowieza forest. He describes abundant hazel in the mesic and riparian communities and notes that the hazel flowers two months before the tree leaves emerge and hence would not be shaded. The difference between these views may be due in part to differing interpretations of what is ‘closed forest’: a small study at Wytham Woods (Box 1) suggests that, while flowering is much reduced where the canopy cover is greater than 50%, flowering does commonly occur in relatively small canopy gaps (cover 25-50%). Bobiec also feels that Vera’s ideas cannot be ‘uncritically extrapolated’ from a relatively warm oceanic climate to the boreo-nemoral zone of the Bialowieza forest.
Box 1. Flowering of hazel bushes in relation to overhead cover at Wytham Woods, Oxfordshire.
110 bushes were examined in late March 2005. Canopy cover above the bushes was estimated in broad percentage cover bands and flowering estimated on a four-point scale. K J Kirby unpublished.

<table>
<thead>
<tr>
<th>Canopy cover over the bush</th>
<th>No flowers seen</th>
<th>A few catkins only</th>
<th>Some branches with some catkins</th>
<th>Most branches with many catkins</th>
<th>Total no of bushes</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-25%</td>
<td>0</td>
<td>1</td>
<td>8</td>
<td>15</td>
<td>24</td>
</tr>
<tr>
<td>26-50%</td>
<td>2</td>
<td>2</td>
<td>9</td>
<td>3</td>
<td>16</td>
</tr>
<tr>
<td>51-75%</td>
<td>2</td>
<td>8</td>
<td>6</td>
<td>1</td>
<td>17</td>
</tr>
<tr>
<td>76-100%</td>
<td>22</td>
<td>21</td>
<td>8</td>
<td>2</td>
<td>53</td>
</tr>
</tbody>
</table>

Although NAP percentages may provide a ‘fairly robust’ indication of past vegetation openness, the debate needs to be informed from a wider variety of data sources on the nature of the pre-Neolithic, Atlantic landscape (Svenning 2002). More evidence may be obtained from fossil beetle assemblages, and to date, beetles found in pre-Neolithic deposits are predominantly tree living species rather than dung beetles and other grassland indicators (Rackham 2003). Molluscs are also good indicators of the openness of forest habitat (Mitchell 2001). However, evidence from snail faunas may lack the degree of resolution required for detailed landscape reconstruction, and they may be poor discriminators between scrub and ‘true forest’ (Buckland 2005, chapter 3 of this report). Insect records, particularly beetles, are a promising tool for interpreting past landscapes, particularly when applied in a multidisciplinary approach. Valuable insights could also be obtained from other sources such as soil pedogenesis under closed and open conditions (Mitchell 2001).

Svenning’s detailed review, summarised in Box 2, combines data from a variety of pollen and macrofossil sources to evaluate vegetation openness in the pre-agricultural Holocene of NW Europe (Svenning 2002). Although Vera’s work dealt with lowland areas, the upland landscape categories have been included for a more complete picture. Svenning concludes that forested conditions were predominant and that open vegetation in the pre-agricultural Holocene would mainly be present on some floodplains, calcareous or poor sandy soil and in the continental interior of NW Europe.

Whitehouse and Smith (2004) criticise Svenning’s methods and conclusions. However their findings are not radically different: they suggest evidence for open woodland, but little sign of grazing animals in Holywell Combe, Kent (by the chalk downs) during in the early Holocene (<8690 BP) (no data are available for later at this site); and a landscape of primary forest, including a large proportion of old trees and dead wood, with only a low level of open taxa/dung beetles during the mid-Holocene at Bole Ings (a flood plain in the Trent valley).
Box 2. Conclusions from Svenning (2002) for different landscape types

(i) Fertile uplands
In upland sites with oceanic climates, relatively fertile soils and no flooding by rivers, sub-
fossil pollen from lakes and small forest hollows indicated a landscape dominated by closed 
forest. Evidence from beetle and plant macrofossils from lake sites supported this argument. 
However, scattered pollen of herbs such as *Rumex* spp, *Plantago lanceolata* and *Artemisia* 
spp indicated either distant or localised open vegetation. Pollen and plant macrofossil data 
from small hollows indicated generally closed forest. However plant macrofossils suggested 
open wet conditions immediately above the hollows which could perhaps have been created 
by beavers *Castor fiber*. Overall, Svenning concludes that closed forest was predominant in 
the upland landscape. Localised open patches with characteristic meadow plants may 
indicate maintenance by large herbivores.

(ii) Floodplains
Pollen and macrofossil remains from the last interglacial suggest widespread open conditions 
with NAP percentages often > 40%. However, evidence from the pre-agricultural Holocene 
in England indicates relatively forested conditions with NAP records between 10-20% (≤ 
10% has been interpreted as closed forest (Vera 2000)). Beetle assemblages varied; some 
contained few dung fauna and more saproxylic species, at others dung beetles were relatively 
frequent. One coleopteran study indicated open marsh, grassland and closed woodland all 
within 2-3km.

(iii) Chalk uplands
Bush (1993) has argued that continuous chalk grassland existed in East Yorkshire since the 
late glacial. He suggested that tree clearance by early hunters may have arrested succession to 
forest. More recent work at a site in the eastern South Downs, England (ca. 7100 to ca. 3800 
cal. yr BP) indicated well-wooded slopes, however, scrub and grassland species were also 
regularly recorded indicating that there must also have been some open habitat. Species 
specific to chalk grassland only appeared from 6000 BP onwards, so their presence could 
have been related to human activity. Such communities are most likely to have occupied the 
steepest slopes, although the processes that maintained them are unclear (Waller & Hamilton 
2000). Svenning (2002) notes that in the absence of charcoal remains to indicate 
anthropogenic burning, poor edaphic conditions combined with grazing by large herbivores 
may be a likely alternative explanation.

(iv) Infertile uplands
NAP percentages of ≥ 10-20% indicate fairly open conditions on sandy infertile uplands in 
the pre-Neolithic Holocene in Denmark and England. The pollen records indicate open heath 
or grass vegetation and lightly shaded woodland (*Quercus* spp., *Betula* spp., *Alnus glutinosa*, 
*Corylus avellana*, *Tilia cordata* and sometimes much *Pinus sylvestris*). At one site, pollen, 
plant macrofossils and beetles indicated a mixture of fairly open *P. sylvestris* forest grassland 
and marsh. Svenning (2002) concludes that the mixture of open forest heath and grass was 
caused by a ‘synergistic effect with fire and perhaps large herbivores’. A high fire frequency 
would be caused by the dry soil conditions and fire promoting plants (*Calluna* and *Pinus*). 
Bracken *Pteridium aquilinum* and cow wheat *Melampyrum* are frequently well represented 
and have been suggested as indicators of grazed forest; they also benefit from fires.
2.4.2 Large herbivores

In the last interglacial (the Ipswichian), floodplain sites in NW Europe generally show rich fossil faunas of large herbivorous mammals, abundant dung faunas and plant remains characteristic of disturbed ground (Svenning 2002). In comparison, floodplains of the early Holocene show reduced open conditions which may be related to changes in the herbivore fauna, notably the lack of mega-herbivores (eg elephant and rhinoceros). Hunting pressure from humans may also have affected grazing pressure by reducing population densities of the surviving herbivores (Svenning 2002). Bird and mammal faunal assemblages from previous interglacials support the occurrence of open or semi-open habitats (at least in certain landscapes) (Svenning 2002). However, climatic differences between the present interglacial and preceding ones may limit the usefulness of this evidence.

The British herbivore fauna of the Atlantic era is thought to have included aurochs, red deer, and roe deer and wild boar. The giant Irish deer *Megaloceros giganteus* was recorded early in the Mesolithic period but probably became extinct prior to the Atlantic era (Yalden 1999, 2003). The failure of giant deer to re-expand its European range in the Holocene (as it had in previous interglacials) raises the question of whether early humans may have played a role (Stuart and others 2004). The moose *Alces alces* was, until recently, thought to have become extinct in the British Isles during the early Holocene, but carbon dating of an antler from the River Cree in Scotland has given a much later date of 3,900 BP for Scotland (Kitchener & Bonsall 1997).

There is a very long gap in the British fossil record for horse between the Mesolithic and the early Neolithic. Although some teeth and bones have been recorded in archaeological sites in this gap, dating of these specimens may not be secure; it is therefore considered unlikely that there are any direct descendents of British wild horse in our modern fauna. There is no evidence for the European bison *Bison bonasus* in Britain following the last glacial maximum (Yalden 1999, 2003).

The carrying capacity for large herbivores in the Atlantic period is unknown. However, it is possible that spores of dung fungus in sediments might be used to understand something of past species densities (Mitchell 2001). High frequencies of the obligate dung fungus *Sporormiella* have been used to infer high herbivore numbers in the Late Quaternary in N. America and Europe (Innes & Blackford 2003). In modern closed European forests the large herbivore carrying capacity has been estimated as one individual of each species (wild boar, red deer, moose, bison, aurochs, and horse) in 10km². The social behaviour of these species makes this figure unrealistic, but a forest mosaic, including open areas, could support much higher densities, but with very unequal spatial distribution (Remmert 1991). Such a patchy distribution reduces the chances of uncovering large herbivore remains in the fossil record.

WallisDeVries (1998) notes that despite limitations (assumption of ecosystem stability, spatial scale factors and other complications) the concept of carrying capacity may be useful to give an approximate range of herbivore densities in specific conditions. Estimates for temperate zones though, are hampered by a lack of data from areas not managed by people, only North American studies describe relatively undisturbed areas. He cites data from various habitats in N. America and Europe with much higher carrying capacity than suggested by Remmert (1991) for closed forest.
The paucity of good bone assemblages (especially the wild component) from the pre-
Neolithic period limits the reliability of conclusions about the diversity of fauna of this era
(Bradshaw & Hannon 2004). In this context the absence of evidence is not the same as
evidence of absence. Equally the incompleteness of the fossil record cannot be used to infer
presence, and particularly not high abundance of the missing species. Nevertheless,
Bradshaw and Hannon (2004) argue that the Irish Holocene fauna is so well studied, that the
absence of remains of aurochs can be relied upon as a real difference from the fauna of
mainland Britain, where sub-fossil remains of this herbivore are widespread. Pollen diagrams
from the two regions during the Holocene are ‘remarkably similar’ in terms of indications of
vegetation openness, and the relative importance of light-demanding trees. They conclude,
therefore, that ungulate grazing pressure ‘alone’ cannot account for the early to mid Holocene
 persistence of light-demanding trees in north-west Europe, ‘although it may be a contributory
factor’.

Mitchell (2005) develops this idea further. He suggests that the scarcity of red deer remains
(compared to wild boar) may indicate that this herbivore may have been absent or rare in
Ireland in the early Holocene. The earliest radio-carbon date for this species in Ireland is
4000 BP. Ireland could therefore be considered an ‘early Holocene grazing exclosure albeit
containing wild boar and possibly some isolated red deer populations’. Mitchell compares
the pollen profiles from Ireland with those from the continent and concludes that the presence
or absence of large herbivores does not significantly alter the patterns. From this he
concludes that large herbivores were not a major factor driving the forest composition.

2.5 Evidence for cyclical vegetation turnover: pattern and process

2.5.1 Succession and vegetation cycles

Vera devotes Chapter 2 of his work to a critical assessment of succession theory and A.S.
Watt’s gap-phase model. He goes back to the early literature to unravel the basis for the
assumption that the pre-Neolithic vegetation of Central and Western Europe was closed
canopy forest. He also examines the role of large herbivores in forest succession.

Mitchell (2001) notes that Vera ‘appears to suggest that Clements’ concept of climax
woodland encapsulates his null hypothesis’. However, successional theory has moved away
from climax towards more ‘complex and stochastic models’ in the last 50 years. In particular,
successional pathways have been shown to vary strongly among sites with apparently similar
starting points (eg sand dunes, or glacial forelands), showing different sequences of species
and vegetation types and varying rates of succession. Such ‘multiple successional pathways’
have been linked to variation among sites in abiotic conditions such as soil nutrients or
moisture, and to differences in local species pool available to colonise sites (Bullock and
others 2002).

There is also emerging evidence that the Holocene climate may have been far more dynamic
than previously realised. Hence, dynamic changes as a result of climate fluctuations could
allow establishment of light demanding tree species (oak and hazel) without ‘transposing the
landscape into parkland’ (Mitchell 2001). Pontailler and others (1997) note that the
’supremacy’ of beech in Fontainebleau forest is dependent on current climatic conditions, and
that oak could be in a good position to benefit from predicted increases in temperature, unless
accompanied by a significant increase in rainfall. Even A.S. Watt considered that the ‘normal
cycle of change’ in beech woods would include a phase dominated by another tree species (e.g., oak, ash, or birch), and this phase could occupy small or large areas (Watt 1947).

Rackham (2003) considers the possible effects of different dominant tree species on cyclic dynamics (Figure 2) and suggests that beech-dominated landscapes may be a special case. Indeed the ‘very efficient closure’ of forest gaps in Fontainebleau forest was mainly due to beech trees (Pontailler and others 1997). Where long-lived trees dominate, such as lime in the lowlands of England in the Atlantic period, landscapes may be less dynamic, particularly when trees are able to prolong their life span by self-coppicing or suckering. Peterken (2001) similarly felt that Vera’s work might not adequately cover the ‘wide range of site types, and stand composition, which makes up temperate lowland forest’.

### 2.5.2 The role of large herbivores and their predators

Vera concludes that large herbivores are essential for creating semi-open park-like landscapes. Rose (2002) agrees that the role of large herbivores has been under-emphasised in forest ecology, and states that they must have been a major driving force creating and maintaining open habitats. Yalden (1999) also suggested that the size and feeding requirements of a large bovid, such as the auroch, would allow it to at least maintain, if not create, forest clearings.

Other reviewers are more circumspect. Mitchell (2001) writes that the case for dense closed forest in the pre-Neolithic, Atlantic era may be overstated, but he is not convinced that herbivores dictated the structure of the forest. The reverse could occur. For instance, a climate downturn could lead to severe herbivore mortality, followed by an expansion of tree cover. Remaining herbivores would then have to reduce tree cover to restore more open conditions and this would be far more challenging in temperate Europe, than in climates where soil moisture is limiting. Bradshaw and others (2003) conclude that grazing animals are unlikely to have been responsible for opening up the forest and that other physical factors such as climatic differences between interglacials are responsible for the ‘primary habitat structure’.

Mitchell (2005) notes that palaeoecologists have tended to ignore the potential impact of herbivores in the past because of the difficulty of quantifying herbivore density, but that this problem is beginning to be addressed. He concludes that large herbivores would not have affected landscape structure, but would have influenced species composition. This supposition is based partly on a review of European data, which showed similar pollen records for *Quercus* and *Corylus* in areas inhabited by large herbivores and in Ireland in the early Holocene where large herbivores appear to have been scarce or absent (see earlier).

Mitchell (2005) also cites two previous papers which demonstrate an influence of grazing on tree species composition but not on forest structure. On a small lake island in Killarney, pollen records over the last two hundred years showed that the response to gap creation in oak woodland depended on the grazing regime as reported in historical records. During grazing by cattle, holly *Ilex aquifolium* invaded a canopy gap, later after grazing had ceased a gap was filled by yew *Taxus baccata* (Mitchell 1990). In Białowieża, analysis of pollen from small hollows revealed an increase in the proportion of less palatable conifers when herbivore densities were high when the forest was used for hunting, and in contrast, an increase in records for more palatable broadleaved taxa when herbivores were very scarce due to poaching during World War I (Mitchell & Cole 1998).
There is, however, evidence that large herbivores can maintain open areas in modern landscapes. Deer maintain grassy glades in British upland forests (Peterken 1996); beaver can create locally open patches, and elk _Alces alces_ appears to prevent woodland succession in fenland sedge communities in Poland (Svenning 2002). Cattle grazing in nature reserves in the Veluwe in the Netherlands appeared to encourage the development of grass lawns in woodland gaps created by storms. They suppressed tall woody vegetation in the gaps by browsing and trampling and encouraged development of grassland plants by nutrient and seed transfer (Bokdam 2003).

The ability of large herbivores to open up the vegetation may be greater on poorer soils (Svenning 2002). On the other hand, aurochs may have needed to graze on fertile soils in order to obtain sufficient food, and this could have been available on floodplains at least for part of the year. Cattle grazing on phosphorous deficient heathland do not thrive, but their condition improves with access to riverine grasslands (WallisDeVries 1996).

Rackham (2003) writes that in English wood-pastures there is ‘some correlation between oak regeneration and grazing’; however, he also notes that oaks do regenerate within woodland in the absence of grazing and cites a generation of oaks from Hayley wood, Cambridgeshire dating from 1840. His argument that increased grazing of woodland (by fallow deer) did not ‘bring back the oaks’ does not really contradict Vera’s hypothesis, because in the cyclical turnover system, oak regenerates in the open areas and _not_ within the wood.

Plant macrofossil evidence from the large island of Zealand in Denmark suggests that in some circumstances oak, hazel and pine (_P. sylvestris_) can occur in a lime-dominated forest in the apparent absence of _Bos primigenius_ and _Alces alces_, which became extinct on this island 7-8000 years ago. This left only ‘larger grazers’ _Cervus elaphus, Capreolus capreolus, Sus scrofa_ and _Castor fiber_. Svenning (2002) concludes from this that Vera’s hypothesis may not be necessary to explain the past occurrence of oak, hazel and pine on ‘fertile’ uplands. However, the ability of deer to maintain open areas in forests in upland regions (Peterken 1996) may undermine this conclusion.

The role of the nationally extinct predators of the large herbivores (wolf _Canis lupus_ and lynx _Lynx lynx_) must also be considered in discussions of large herbivores as potential drivers of forest ecology. The interaction between vegetation structure, predator hunting behaviour and herbivore response to predation risk is likely to be profound, variable and complex (White and others 2003). The influence of predators is only briefly mentioned by Vera (p. 349) where he concludes that ‘Whatever the influence the large predators had, the densities [of large herbivores] that are required for the regeneration of oak and hazel must have been the result’. This, of course, assumes that the reader has accepted Vera’s conclusions about the role of large herbivores.

### 2.5.3 Defence guilds

The protection of oak (and other palatable tree) seedlings from browsing by large herbivores by a mantle of thorny or unpalatable plants (eg _Rubus, Ilex, Crataegus, Ulex, Prunus spinosa_) has often been described (Kelly 2002; Shaw 1974; Watt 1919). In fact in the New Forest, spiny shrubs were historically seeded around young trees for protection (Flower 1980). This associational resistance may be more likely to operate in areas grazed by bulk feeders (cattle and horses) rather than more selective feeders such as sheep or goats (Rousset & Lepart
However, even in sheep-grazed chalk grasslands, young *Buxus* seedlings were able to survive in areas dominated by other unpalatable plants (Rousset & Lepart 2003). The facilitative effect is likely to be dependent on the age of the scrub; for instance in the Causse du Larzac plateau in southern France, *Buxus* scrub did not protect downy oak *Quercus humilis* from grazing by sheep, until the scrub reached about 20 years of age (Rousset & Lepart 2000).

Very high grazing pressure may negatively affect succession to scrub, and Vera cites several examples where heavy grazing has a detrimental effect on the recruitment of thorny shrubs (p.343). In the Castor Hanglands NNR, near Peterborough, browsing by fallow deer *Dama dama* was particularly severe on blackthorn *Prunus spinosa*. Deer-damage to brambles *Rubus fruticosus* and gorse *Ulex europaeus* was less severe, and these species were able to nurse the more palatable woody plants. Shorter plants were defended by a fringe of tall grasses, but were browsed once they reached > 30cm (Ward and others 1994). Similarly, fallow deer grazing in the New Forest, caused the destruction of the shrub layer and failure of trees to recruit (Putman and others 1989) in some circumstances. However, elsewhere in the New Forest, birch and oak establish in the presence of grazing, for example amongst bracken patches.

Protection from grazing should not be confused with other benefits provided by shrubs around young seedlings, such as protection from abiotic stress. In arid environments the ‘nurse effect’ of shrubs may be due to the shade provided, which gives a suitable microclimate for seedling survival. For instance, shade was beneficial to *Quercus douglasii* in California, but protection from herbivores alone did not substantially improve long-term survival of seedlings of this species (Callaway 1992). Abiotic nurse effects are also seen in the UK. For example in Dorset, moderate heather *Calluna vulgaris* cover protects Scots pine *Pinus sylvestris* seedlings from low temperatures (winter) and low humidity (summer) (J. Bullock, unpublished data). Ideally, grazed and ungrazed study sites should be compared, to determine whether shrub facilitation is through protection from grazing (Rousset & Lepart 1999).

The effects of small mammalian grazers should also be considered. Does seed or seedling predation *within* thorny scrub affect the efficacy of the defence or do the small mammals graze on the thorny scrub itself preventing or limiting establishment? Rabbits *Oryctolagus cuniculus*, of course, were not present in NW Europe in the Atlantic period, but their influence has to be considered in most modern landscapes in the region. Bakker (2003) showed that although thorny scrub protected young palatable trees (oaks) on Dutch floodplains grazed by cattle, this associational resistance broke down when rabbits were present in high densities. In those circumstances the rabbits grazed both the young trees and young ramets of blackthorn. When myxomatosis caused rabbit population crashes, thorny scrub was able to establish. In contrast, wood mouse *Apodemus sylvaticus* and bank vole *Clethrionymus glareolus* ‘although ubiquitous’ were of ‘little or no importance’ to oak regeneration in Wales (Shaw 1974), and *A. sylvaticus* in Killarney, Ireland failed to limit oak regeneration (Kelly 2002).

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2 Stage 3 of the cycle illustrated in Figure 1.
2.5.4 The role of fire, storms, and drought

There is an extensive literature on forest structure and regeneration patterns generated by disturbances other than grazing, e.g., Björkman & Bradshaw (1996); Björse & Bradshaw 1998; Cowling and others 2001; Hannon and others 2000; Lindbladh & Bradshaw 1998; Lindbladh and others 2000; Mountford 2004; Peterken 1996.

Fire does not feature in Vera’s landscape model, he states that ‘fire did not play a decisive role in the regeneration and permanent presence of oak’ (p. 368). British deciduous woods have been credited with the ability to burn like ‘wet asbestos’ (Rackham 1986), and hence fire is generally not considered important in the removal of woods in British lowlands in the Holocene (Moore 2000), although Miller (2002) disagrees. Abundant dead wood (see next chapter by Buckland (2005)) or a high build up of dry grass in open woodland might increase the significance of fire. However, major grass build-up would imply low grazing pressures, and should lead to a much higher proportion of non-arboreal pollen in the sub-fossil record than has been described (Rackham 2003).

Fire has been proposed as an alternative means of maintaining open areas and ensuring the continued success of light-demanding species (Bradshaw & Hannon 2004; Svenning 2002). Indeed, Simmons (2003) argues that fire was routinely used to manipulate the landscapes of the British uplands by Mesolithic peoples. Oak, hazel, and Scots pines are all favoured, relative to their more shade-giving competitors, by fire. Thick bark makes large oaks and Scots pines likely to survive fires, and strong re-sprouting ability should benefit hazel, and possibly oak (Svenning 2002). Rackham (2003) also argues that open areas of heath, bracken or moorland could conceivably be maintained by fire, but that species of these habitats lack a fossil record; however published evidence e.g., (Svenning 2002), indicates the existence of fossil evidence (spores and pollen) for heath and moorland species, as does Buckland (in press) for fossil heathland invertebrates.

A pollen and charcoal study from Germany showed a 250-year successional cycle from Corylus avellana and Fraxinus excelsior to Quercus to Ulmus and Tilia and finally Fagus sylvatica. This cycle was accompanied by forest fires probably occurring at 250 year intervals. Throughout the British Isles, Holocene Pinus sylvestris macrofossils are frequently associated with charcoal, or are charred themselves, and sometimes found with the remains of fire-adapted pinicolous beetles (Whitehouse 2000). Fires could therefore have contributed to the maintenance of light demanding trees, and shrubs, in the temperate upland vegetation of NW Europe (Svenning 2002). This may also be true of North America (Abrams 2003, Peterken 1996), where oak species are thought to be ‘fire persistent’ compared to many associated species, possibly due to the concentration of dormant buds near the root collar (Johnson and others 2002).

The relative importance of anthropogenic and natural fires is unclear (Svenning 2002), but the ‘majority of archaeologists and palaeoecologists’ would interpret charcoal in natural profiles as evidence of fire setting by early peoples (Buckland 2002, Moore 2000). The return period of ancient Holocene pine forest fires recorded in the peat at Thorne and Hatfield moors in Yorkshire may fit in with a natural cycle of regeneration and suggests that lightning struck fires could be responsible (Buckland 2002, Whitehouse 2000). Bradshaw & Hannon (2004) argue that charcoal records from temperate southern Sweden indicate the existence of a natural fire regime from 6000 to 4000 BP, which was followed by regular anthropogenic burns.
In lowland Scotland reductions in charcoal frequency in the upper Mesolithic were associated with a shift to drier soil conditions suggesting a climatic origin (Tipping & Milburn 2000). However, it is not known when fire setting by early people began and it is not possible to distinguish natural and anthropogenic fires from charcoal remains (Behre 1988). The possibility that Mesolithic peoples had significant impacts on vegetation communities is more widely accepted than it was previously, and although the majority of records of disturbances are from upland areas, an increasing proportion are reported for lowland sites (Innes & Blackford 2003). In addition to fire setting to improve hunting opportunities, the possibility that fire could have been used to manipulate the acorn supply for Mesolithic people has been discussed in recent literature (Mason 2000). Hence, charcoal deposits, like palynological data, are best interpreted in a holistic framework (Moore 2000).

The creation of gaps by windthrow is another mechanism that might explain the past success of light-demanding tree species (Bradshaw & Hannon 2004; Svenning 2002). Small gaps created by the loss of single, or small groups of trees, tend to be filled by shade-tolerant species, or even closed by expansion of the canopy. Quercus spp. may regenerate to small trees in gaps of ≥ 0.05 ha, but development of such trees to maturity seems unlikely in beech-dominated forests. For instance in Fontainebleau forest, about 95% of oak seedlings in clearings of 100m² or less died after four years growth (Pontailler and others 1997).

The effects of storms may also differ depending on tree species and the age of the stand. High winds in the New Forest in the 1980s caused the loss of large swathes of beeches whereas oaks and other broadleaved species were relatively unaffected (Tubbs 2001). Many modern semi-natural forests consist of relatively dense stands of fairly young trees. This is largely due to the cessation 50-200 years ago of traditional management, such as coppicing, which kept them open. Larger gaps may have been created in the distant past when there were more old growth stands containing groups of senescent trees (Svenning 2002). Bradshaw & Hannon (2004) however see no evidence that windthrow has decreased in importance in recent decades in north-west Europe, and windthrow monitoring in spruce plantations in the UK revealed a gap size distribution that was ‘intriguingly’ similar to that found in studies of ‘natural’ forests (Quine & Bell 1998). The monitoring studies also showed that wind speeds only slightly higher than ‘experienced regularly’ could cause catastrophic damage (Quine & Bell 1998).

A combination of drought and storms can lead to the production of substantial gaps in modern forests, such as those recorded in the permanent transects in Denny Wood, in the New Forest (Mountford 2001) and changes in the competitive ability of forest dominants (e.g. Peterken and Jones 1987). Long term studies in Denmark have also indicated the importance of wind in the creation of large gaps (Bradshaw & Hannon 2004). Although these events may be exceptional, Miller (2002) suggests that catastrophic windblow which could create gaps large enough for regeneration of light-demanding species, is ‘highly likely’ in the life-time of an oak.

2.5.5 Spatial and temporal detail

Differences in edaphic conditions such as soil fertility and water table depth are certain to influence the vegetation structure (Bradshaw & Hannon 2004). Rackham (2003) suggests that limits to spatial shifts in areas of grassland and woodland may be imposed by ‘even the
gentlest topography’. He observes a tendency for trees to occupy the higher ground, and grass
the valleys, both in English wood-pastures and in many other situations worldwide. The holly
‘holms’ or ‘hats’ of the New Forest, Hampshire, so called because of their propensity for
occupying hilltops, are a good example (Tubbs 2001). This pattern might leave ‘little room for
manoeuvre’ for the shifting mosaics. However, there may still be scope for shifting
vegetation mosaics to operate in riverine areas (Bakker, in press). Thus, the Atlantic
landscape of Europe may have been mixed, including areas where vegetation types cycle as
proposed by Vera and also areas of more permanent grass or forest (Kirby 2003, 2004).
Indeed Vera (2000) acknowledges that not all geographic areas would be subject to cyclical
dynamics (p. 378).

There is a lack of spatial and temporal detail in the cyclical turnover of vegetation as
presented by Vera. There is no indication of how long the cycle might take on any one patch
of land or how large the patches might be except that wooded groves might extend for several
hundred hectares and could often be 40-80 ha. Kirby (2003) developed a model based on
Vera’s ideas to try and predict what sort of spatial and temporal patterns might occur if
Vera’s alternative hypothesis applied to a significant area of Great Britain. The model used a
hypothetical uniform landscape of one hectare cells which move through phases of the ‘Vera
cycle’. It was run in a number of ways to investigate the effects of variable extents of
different vegetation stages as the starting point, variable cycle times for different cells and
variable cycles in different sections. Some of the landscapes generated by the model were
consistent with the half-open park like landscape proposed by Vera but equally, relatively
closed landscapes could be produced.

2.6 Tree autecology - regeneration and shade-intolerance

2.6.1 Regeneration of oak, hazel and pine

One of the major difficulties with the closed forest hypothesis is the lack of regeneration of
the light demanding trees and shrubs, particularly oak *Quercus* and hazel *Corylus* in modern
forests (Bradshaw 2002). Vera reviews the literature on the effects of light on the
regeneration of a number of tree species in European forest reserves and concludes that there
is no regeneration of oak and hazel under forest canopies and that these species disappear
from a closed forest in just one or a few generations.

A pollen diagram from Bialowieza National Park in Poland, however, indicates the existence
of continuous *Quercus*-dominated canopy for 600 years which suggests that oak has been
able to regenerate here for more than one generation (Mitchell & Cole 1998). The apparently
‘conflicting reports’ of oak regeneration in Bialowieza forest (Falinski 1986) that are
reported by Vera p. 264, in fact appear to refer to differences between the two oak species.
Regeneration failure is noted for *Q. robur* (Falinski p.88 & p. 228), whereas regeneration in
certain reserves (Falinski p. 61) is noted for *Q. petraea*. However more recent observation
indicates that that there are many young oaks (mainly *Q. robur*), not only seedlings, that "die
soon after", but also well developed saplings and young trees. Most of these are associated
with disturbed areas, mainly gaps created by windblown spruce. The gap size varies from ca.
0.03 ha to more than one hectare (mean about 0.12 hectare), and there does not appear to be
any influence of gap size on the oak regeneration. More rigorous evidence is required on oak
regeneration in Bialowieza to confirm or refute these observations (A. Bobiec pers. comm.).
Pinus sylvestris also experiences regeneration problems in closed temperate forest (Peterken 1996). However, fossil records (plant macrofossils, pollen from small hollows and pinicolous beetles) indicate that pine occurred in mixed, otherwise deciduous, forest and was abundant in mires in the early and middle Holocene (Svenning 2002).

Humphrey & Swaine (1997) report experiments by Jarvis (1964) which demonstrated that light is the major limiting factor for Q. petraea and Q. robur regeneration. However, shade tolerance may be influenced by climate (Kelly 2002) and the effects of shade cannot be simplified to a contrast between canopy and clearing. Successful regeneration of Q. petraea in the Pennines occurred under a canopy of the same species; this woodland had an unusually favourable light regime: a purely deciduous canopy of only 5-12m with a south-easterly aspect (Pigott 1983). In contrast, there was no regeneration of Q. petraea under the canopy in the oakwoods of Killarney: here light levels were impeded by the persistent cloud of the oceanic climate and a dense evergreen understorey (Kelly 2002). Other environmental factors are also likely to influence shade tolerance. Svenning (2002) concluded that Quercus spp and Corylus avellana are not poor competitors with shade trees such as Tilia and Fagus sylvatica under all edaphic-topographic conditions. Oak competes well on very acid, nutrient poor soils and on soils subject to summer drought, hazel can survive on steep slopes and floodplains and Scots Pine may remain on localised acid bogs.

Ellenberg (1988) similarly notes that on certain dry soil types, but also on some wet soils, oak is the commonest dominant in the ‘natural’ vegetation. On acid sandy soils it is able to regenerate successfully within gaps in pine stands (Mosandl & Kleinert 1998; Paluch & Bartkowicz 2004). In Britain some shade-tolerant species such as hornbeam and beech, that otherwise replace oak, appear to have been late colonists (Rackham 2003) and are absent from large parts of the country during the mid-Holocene; lime regeneration from seed is often irregular because of its requirement for hot summers (Pigott & Huntley 1978). Therefore it is possible that the niche for oak as a dominant in the former natural landscape would have been wider in Britain than on the continent, even if large herbivores played no part in the regeneration cycle. Similarly high levels of hazel pollen in samples from the more exposed parts of Britain may indicate dense hazel scrub as a ‘climax’ woodland type; stands that appear to match this are still found in places on the west coast of Scotland (Coppins, Coppins and Quelch 2002).

Oak (Quercus spp) can grow up just outside the canopy limits of its parent tree, for example in windthrow gaps of $\geq 0.05$ ha (Svenning 2002), although whether the oaks can grow to maturity in these gaps may be questionable (Vera 2000). According to Miller (2002), however, oak can regenerate under canopy, and there is evidence of regeneration of oak in both uniform and group shelterwood systems. Rackham’s (2003) study of medieval timbers shows that house-builders of that time used ‘millions of oaks less than 70 years old’: these were obtained from islands of woodland in farmland that were heavily fenced to exclude grazing. He concludes that oaks must have regenerated freely in medieval woods under canopy [and in competition with coppice regrowth]. Bobiec (2002) indicates that there are numerous anecdotal and photographic accounts ‘that contradict the theory of regeneration failure in the preserved forest’ at Białowieża. However, Bobiec (pers comm.) notes that more detailed research is required to provide solid evidence for this. Thus, the possibility of oak surviving within continuous forest may exist – at least in some areas.
2.6.2 Oak mildew

Vera was criticised by Rackham (2003), and Peterken (2001) for failing to discuss the possible role of the fungal pathogen oak mildew *Microsphaera alphitoides*. This fungus was probably introduced from North America to Europe in 1907 and has been credited with the ability to have a deleterious impact on oak regeneration (Kelly 2002). Rackham (2003) suggests that infection with this pathogen may cause oak seedlings to fail to survive in a degree of shade in which they would formerly have survived. The action of *M. alphitoides* is likely to be related to climate, through increasing the susceptibility to abiotic stresses such as drought, and hence in the moist mild climate of Killarney, Ireland *M. alphitoides* was not a significant deterrent to oak regeneration (Kelly 2002).

2.7 Adaptation of modern flora and fauna to relatively open woodland

The abundance and frequency of species associated with open habitats, mosaics or scrub has commonly been used to argue that the pre-agricultural landscape of Britain would have been more open. For instance, Rose (2002) writes that the greatest biodiversity in European woodlands is found among edges and rides, and this is not just true of vascular plants but also of epiphytic bryophytes and lichens which require light to flourish, as do many forest birds and butterflies. Rackham (2003) asks why many British birds - blackbird, buzzard, robin, sparrowhawk, rook etc. are not ‘really woodland or grassland species but flourish best with combinations of grassland and trees’? Miller (2002) points out that birds, such as the corncrake *Crex crex*, must have evolved to need grassland before human clearances for agriculture. Similar points have been made for North American species, although it is commonly (but not exclusively – eg Cronon 1983) thought that prior to European settlement there was continuous forest between the Atlantic and the Great Plains (Foster & Motzkin 2002). Three grassland bird species have Eastern sub-species, indicating long isolation, and there are several endemic species of grassland plant in the east (Sutherland 2002).

These arguments do not however provide direct support for Vera’s hypothesis (Kirby 2003).

- There are unlikely to have been many major evolutionary changes since the last glaciation and most species had to re-invade the British Isles. Therefore, conditions under which species evolved cannot be used as support for the occurrence of habitats in the Atlantic era. Even red grouse may have occurred under more scrubby conditions than the open moorland with which it is now associated. If evolutionary change since the last glaciation is presumed, then we cannot use the occurrence of species as surrogates for habitat presence.

- The abundance and niche range of woodland versus non-woodland species in the modern landscape does not predict these factors in previous landscapes. We should expect species dependent on continuous closed forest to have declined, given that they have had to survive 3000 years in which the vast majority of woodland was cleared. Over the same period, since the dawn of agriculture, conditions for stenotypic species of open ground have steadily improved.

- Stenotypic species of open ground could have existed at low levels in the Atlantic period and then spread from refuges such as cliff-tops to the rest of Britain even if there was a closed forest in Atlantic times. The survival of light-demanding species in ‘nooks and crannies’ (steep slopes, wetland margins, etc.) in an otherwise closed forest has also been postulated for N. America. Despite poor seed dispersal for many
open field species considered in his study, Marks (1983) suggests that given continuous openness in marginal habitats, dispersal would only need to happen occasionally for species survival (Peter Marks pers. comm. 2004).

- Care must be taken in interpreting estimates of current mobility/immobility of species since these under-estimate the significance of chance very rare events. Modern estimates of ancient woodland species movement of about 1m a year (eg Brunet and von Oheimb 1998) would not cover the current range of these species in Britain, let alone permit spread back from post-glacial refuges in southern Europe. Cain and others (1998) demonstrated that the understorey herb *Asarum canadense* showed rates of spread in N. America in the Holocene that were much faster than would be predicted by modern dispersal distances. They suggested extremely rare events, such as attachment to large animals, could have transported seeds very long distances.

- In modern landscapes saproxylic species are more abundant when old trees are open grown. However most sites where old trees grow are present or former wood-pastures, ie they grew up in open conditions; equivalent populations for comparison of 400 year-old trees that grew in closed forest without human interference do not now exist.

Motzkin and Foster (2002) note that limited understanding of the distribution, dispersal abilities and population characteristics of many taxa confound interpretations of landscape history in North America. Many lepidopteran species thought to be grassland indicators may also be common in woodlands. The heath hen *Tympanuchus cupido cupido* has been used to document former abundance of grasslands and other open habitats in eastern North America: however, most historical descriptions cite woodland or ‘bushy plains’ as the primary habitat for this species, and there is ‘considerable uncertainty’ about the pre-European abundance of this species. Many ‘woodland’ bird species also have different patterns of habitat use in Britain and mainland Europe, and changes in habitat use have also been recorded over time (Fuller 1995). This indicates a need for caution when attempting to interpret landscape history on the basis of current species distributions or population characteristics.

### 2.8  Etymology and history

Vera uses historical texts in many European languages in his Chapter 4 to examine the use of the term ‘wilderness’ in Europe between the Middle Ages and 1900. He argues that words such as ‘silva’, ‘Forst’, ‘forest’, ‘Wald’, ‘wold’, ‘woud’, ‘wood’, did not necessarily indicate closed forest, and hence ‘Medieval’ wilderness areas were likely to have been relatively open. He suggests that the range of uses of these single terms shows that the wilderness consisted of a mosaic of grassland, scrub, trees and groves. Rackham (2003) feels that the meanings of these terms and the way they change between languages were not fully investigated. He gives one example directly from Vera’s book: ‘underwood’ which in English does not mean shrubs, and is not the same as brushwood. Rackham also suggests that analysis of the meanings of place names would be pertinent but is little utilised by Vera. For instance, the implications of names such as La Tillaie, place of limes, in the Fôret de Fontainebleau and Lyndhurst, or lime grove, in the New Forest are not discussed in Vera’s book. Tubbs (2001) notes that lime occurred in several of the early pollen records from the New Forest but then declines in the last 1,000 years.

Vera apparently also misinterprets Rackham’s earlier work to support the thesis that oak ceases to regenerate in English woods when grazing stops: in fact, Rackham wrote, not about
abolition of grazing, but about the destruction of commons, which would not affect the woods – see Vera p. 274 and Rackham (2003) p. 500. Rackham feels that Vera’s vision of large wilderness areas out of which the medieval landscape was created ‘does not transfer’ from Central Europe to England. With a denser population than central Europe, England had lost a great deal of its wildwood by the Iron Age, and many of the wooded areas of medieval England contain evidence of earlier settlement.

Vera uses historical texts to argue that grazing by domesticated animals in medieval wood-pastures maintained their openness and it was only in the eighteenth century that increased timber demands led to active protection of woods for grazing. This may help to explain why there are so many old oaks in forests today (Mitchell 2001) and why heavily branched oaks, characteristic of open grown trees, are found within modern closed canopy forest. However, this does not prove that the wildwood was necessarily open, because there is no separate evidence to indicate that that the structure of medieval wood-pastures mimicked that of the wildwood.

### 2.9 Implications for conservation policy and practice

Setting goals and targets in conservation requires the use of ecological reference points to inform management goals. Where conservation is aimed at managing cultural landscapes, the goals can be relatively easily defined as the particular habitat or species population as it existed in (say) the 1930s or the mid-nineteenth century. If however, the distant past is taken as a template for conservation, through a desire to achieve a more natural landscape, it is imperative to seek similar clarity of aims. Some practical implications of this debate for modern conservation are considered in detail using case studies in Chapter 4 (Hodder & Bullock 2005).

A good definition of ‘natural’ is required, and here, the qualities of naturalness proposed by Peterken (1981,1996) 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 Atlantic 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 to be significant (Innes & Blackford 2003; Simmons 2003), but this is an issue whichever model (open or closed forest) is considered most likely for the pre-Neolithic, Atlantic landscape.

Large herbivores and fire were likely to have been ‘key agents’ in the creation of diverse original-natural landscapes (alongside those traditionally considered such as wind, disease and drought). Even in a landscape where closed forest predominated however, open woodland, grasslands, scrub and heaths were likely to have had a significant presence in NW Europe (Peterken 2001). The herbivores could have had an influence both as grazers / browsers and as dispersers of plant seed (Poschlod & Bonn 1998). They also create important microhabitats for fire and dung dependent species, many of which are currently rare or threatened in NW Europe (Svenning 2002). The impact of large predators is also likely to be important and the implications of this for conservation management are dealt with in more detail in Chapter 4 (Hodder & Bullock 2005).

Fire and large herbivores could therefore be important in future-natural landscapes, whether or not the original-natural landscape was dominated by closed old-growth forest or was
more open. On this basis, Vera (2000), Svenning (2002) and others advocate reestablishment of native large herbivores and natural fire regimes, and using management by domestic grazing, mowing or prescribed burning to mimic their effect where near-natural regimes are not possible.

Vera reviews the pervasive influence that the assumption of closed natural forest has had on attitudes in conservation (Peterken 2001). However, uncritical acceptance of Vera’s alternative landscape structure also harbours many pitfalls. Bakker (2005) cautions against *laissez-faire*, when creating new areas of wilderness and establishing free-ranging herbivores in near-natural grazing systems. If the conservation of natural processes becomes the goal, as opposed to conservation of particular patterns of habitat and species distribution, it becomes difficult to define targets and to evaluate development of wild areas. The cessation of human activities in semi-natural landscapes may result in closed forest with losses of highly-valued open habitats and species.

Vera’s book reinforces the desirability of a large-scale approach to conservation (Peterken 2001), not least because areas of 100-1000km² may be required for the restoration of viable populations of large herbivores Bakker (2005). However, there is no consensus on the use of near-natural grazing in conservation even in the Netherlands where the ideas were pioneered, ‘It remains an open question whether the current strategy of releasing free-ranging large grazers in former agricultural areas will really counteract the ongoing loss of biodiversity’ (Olff and others 1999).

### 2.10 Conclusions

Reviewers agree that Vera has produced a comprehensive, in-depth and thought provoking study (Bradshaw 2002; Miller 2002; Mitchell 2001; Peterken 2001; Rackham 2003; Rose 2002). Criticism of the accuracy of citations (Bradshaw 2002; Peterken 2001; Rackham 2003) may weaken the strength of some arguments but does not undermine the effect that the book has had. The book is ‘unlikely to win many total converts but it does challenge convention and will change thinking’ (Miller 2002).

Vera’s null hypothesis and its alternative both contain several elements, and it is not necessary to accept either all or none of the elements in each. Thus, oak may require large gaps for regeneration, but creation of these gaps may not necessarily depend on large herbivores but could instead be formed by fire or windthrow etc. Similarly, large herbivores could have influenced original-natural landscapes but this may not have resulted in ‘half-open park-like’ landscapes or shifting mosaics of vegetation proposed by Vera (2000).

Reviewers accept that there can be considerable bias in interpretations of the palynological record but note that analyses based on combinations of pollen and macrofossil remains, which tend to lead to similar conclusions, can be much more robust. Problems caused by the paucity of large mammal remains and uncertainties about their behaviour (herd size, migratory patterns etc) are harder to solve (van Vuure 2002). In fact the debate about the scale and impacts of past ungulate-vegetation interactions is unlikely to be fully resolved until more is known about past ungulate population sizes.

Simulation models of ungulate-vegetation interaction based on information about past vegetation composition and parameterised from present day studies could provide some indication of the range of ungulate population densities and their impact on the vegetation...
(Bradshaw and others 2003). However, as noted by Vera, there may be some danger of circularity in this approach, and this risk depends on our confidence in the available data on early Holocene vegetation.

There has been an enthusiastic welcome, in some quarters, to the notion that wood pasture systems may be more representative of the original-natural landscape than closed high forest, and should therefore be given high conservation priority (Alexander 2002; Rose 2002). However while there is more general agreement that the original-natural forest may have been more open than was previously thought, this is not equivalent to saying that a wood-pasture landscape would necessarily dominate the landscape (Miller 2002; Mitchell 2001; Peterken 2001; Sutherland 2002). There is also no certainty that the pre-Neolithic landscape can be classified as original-natural. Early humans may have had a significant affect on their environment either through using fire, or through the postulated “overkill” of large mammals in the Late Pleistocene (Brook & Bowman 2004; Stuart and others 2004).

The original questions were whether a vegetation cycle driven by large herbivores was the dominant mechanism for landscape regeneration and if so what were the temporal and spatial scales for the different elements of the cycle.

The balance of opinion among active researchers in this field is probably more towards closed old growth forest with open grassland restricted to environments which restricted tree growth (Prins 1998; Bakker 2005; Svenning 2002). Shifting vegetation mosaics may have operated on fertile floodplains (Bakker 2005; Olff and others 1999; Svenning 2002); open vegetation including some long-lasting clearings may also have been frequent on infertile soils, chalkland, and in continental and sub-Mediterranean areas (Svenning 2002). Closed forests may also have existed in some areas that the large herbivores could not reach (Vera 2000).

Herbivores can generate clearings but high tree cover could mitigate against them and reduce populations. There are thus at least two possible feedback loops, one leading to Vera’s park-like landscape and the other to closed high forest. The degree to which these processes operate may also depend on the site type, ie soil fertility and moisture, and topography. For instance in Denny Wood, New Forest, deer and pony grazing maintains wood pasture, but closed high forest persists in the core of Bialowieza National Park despite grazing by deer and bison (Peterken 2001). Differences between these two sites may however, also depend on site management, eg fluctuations in grazing pressure, both in the present and historically (Vera 2000). Windthrow may also have been locally important and there is general agreement that fire may have played an important and perhaps under-rated role in maintaining open landscapes and light-demanding woody species in some landscapes.

The picture that emerges from this review is one of a mixed landscape, including areas with cyclical turnover of the vegetation and others with more permanent vegetation (both open and closed). The difference between the closed forest hypothesis and Vera’s alternative of cyclical dynamics 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 Vera’s ideas in conservation is that there is no clear idea of spatial or temporal scale. Degrees of openness are likely to vary in different edaphic and topographic (and climatic) conditions, but at present there is no guidance on the patterns that might be expected. Therefore, a key area for future research is to understand the
factors that would influence temporal and spatial patterns of this matrix in the full range of environmental conditions.

2.11 Acknowledgements

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243-251.
3. Palaeoecological evidence for the Vera hypothesis?

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Assisted by: Philip Buckland, Dept. of Archaeology & Sami Studies, University of Umeå &
Damian Hughes – ECUS, University of Sheffield

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3.1 Summary

- Frans Vera has produced a model of the mid-Holocene woodland as a dynamic system driven by herbivore grazing pressure, in a cycle from high forest, through die-back to open pasture, with regeneration taking place along the margins of open areas in places protected from heavy grazing by spinose and unpalatable shrubs. This has attracted much interest, not least because it offers support for current moves towards a hands-off approach to nature conservation and the employment of ‘natural grazers’.

- The model is here examined in the light of the palaeoecological record for the Holocene and previous Late Quaternary interglacials. Previous reviews have largely dealt with the data available from pollen diagrams, and so this chapter concentrates upon the fossil beetle (Coleoptera) evidence, utilising the extensive database of Quaternary insect records, BUGS.

- The insect record is much less complete than the pollen one, but there are clear indications of open ground taxa being present in the ‘Atlantic forest’. The extent of open ground and dung faunas during the Neolithic suggests that many of these elements were already present (although not necessarily abundant) in the natural landscape before agriculturalists began extensive clearance during the late sixth millennium BP.

- In the palynological literature there is something of a dichotomy between those working in the uplands and lowlands, with the former being more inclined to credit Mesolithic hunter/gatherers with deliberate modification of the forest cover, usually utilising fire, sometimes leading to the expansion of blanket bog and, in the lowlands,
the creation of heath. The concept of a natural forest, without human interference, in the present interglacial in Britain is doubtful.

- The role of natural fire tends to be underplayed by both groups. The presence of pyrophilic elements in the British beetle fauna and the frequency of charcoal in bog and soil profiles imply that fire is part of the natural system, although the gaps between major fires in deciduous forests may be long. Fire should be considered as a useful and natural management tool in the creation of forest clearings.

- The extent to which natural grazers formed part of the pre-forest clearance system has tended to be underestimated, partly as a result of the relatively poor mid-Holocene fossil record of large herbivores. Aurochs, *Bos primigenius*, however, is not infrequent. As a herd animal it probably maintained some areas of open ground, not necessarily on the floodplains, as the megaherbivores of previous interglacials did, but on the higher ground of the Chalk and other limestone outcrops.

### 3.2 Introduction

The nature and form of lowland woodland in Northwest Europe during the mid-Holocene, before extensive forest clearance have been the source of much discussion, largely based upon the palynological evidence. Much of this has concerned the processes of immigration and differential expansion and contraction of individual taxa (eg Tallantire 1992; Bennett 1995), leading to the development of a closely wooded landscape, the ‘Atlantic forest’. The image of the early medieval landscapes of closed forest lacking any substantial open spaces, of the ‘massed tree trunks of the primeval forest still waiting the axe’, to quote Hoskins’ evocative phrase (1977), has been challenged. Archaeologists have had problems relating archaeological evidence to the palynology (cf. Rowley-Conwy 1982) and some palynologists have seen Mesolithic hunters as having significant impact on their environment (eg Simmons 1996).

More recently Frans Vera (2000) has proposed that the forest before extensive clearance began in the Neolithic was a much more varied landscape. He envisages an open park-like landscape of old trees, open areas, maintained by natural grazing pressure, and structurally more complex forest boundary communities in a dynamic cycle of death and regeneration. Vera’s hypothesis has lead to extensive review of the nature of the mid-Holocene landscape, largely by palynologists and woodland historians responding to the challenges contained in the hypothesis (cf. Bradshaw & Mitchell 1999; Hodder & Bullock 2005 (this volume); Rackham 2003). An entire issue of the journal *Forest ecology and management* was devoted to its implications. Svenning (2002) provides the most extensive consideration of the nature of the European evidence, whilst Bradshaw, Hannon and Lister (2003), combining data from the vertebrate record with pollen and plant macrofossil evidence, attempt a compromise between Vera’s hypothesis and the traditional closed canopy model. More recently, Mitchell (2005) has compared the pollen record from Ireland, not reached during the Holocene by large vertebrates other than boar and possibly red deer, with that from elsewhere in western Europe. He concludes that the impact of grazing on the overall landscape structure was negligible.

The relevance of the debate is not purely academic, in that if conservation is to be guided by the inherited history embedded in any landscape, then the nature of the trajectory which resulted in its present form needs to be considered. Whilst it is impossible to return to the
past, reasonable approximations to past landscapes may be achieved by managed or unmanaged grazing regimes, just so long as it is known what we are aiming for.

3.3 Dating

3.3.1 The Late Quaternary

The present interglacial, the Holocene, has to be seen in the context of the last 2.4 million years, the Quaternary. In this light it is only the most recent of numerous oscillations between extended cold periods, glacials, sometimes accompanied by actual glaciation, and shorter warm periods. The warm periods are termed interglacials when sufficiently long to allow temperate forest to extend into northern Europe, or interstadials when of shorter duration (Bell & Walker 2004).

The British sequence has recently been reviewed (Bowen 1999) and correlations offered with the more continuous sequence derived from the isotope record from ocean cores. These have been numbered in a sequence which begins with the present interglacial, the Holocene, as stage 1 and extends back, such that cold periods have even numbers and warmer ones odd. The complexities of some periods have necessitated sub-divisions indicated by letters. Thus deposits ascribed to the last interglacial, the Ipswichian or Eemian of previous terminology, can be shown to belong to two discrete events with similar pollen signatures, Isotope stages 5e and 7, with type sites at Bobbitshole, Ipswich and Stanton Harcourt in Oxfordshire. A similar refinement of the stratigraphy has also divided the earlier Hoxnian (Holsteinian) deposits into stages 9 and 11.

There are difficulties in dating deposits beyond the range of radiocarbon, > c.45,000 years, but the present, Holocene, interglacial, stage 1, lies well within this range and conventionally begins at the rapid upswing in temperature dated to c.10,000 BP. This date because of the vagaries of $^{14}$C production in the upper atmosphere, equates with c.11,670 calendar years, as counted in the annually deposited layers of snow in the Greenland ice cores (Mayewski & White 2002). Both fossil insect (Brooks & Birks 2000) and ice core data combine to show that the transition between stages 2 and 1 was marked by a short period of rapid warming, followed by cooling first to subarctic conditions and then a return to glacial conditions over the period c.13,500 to 10,000 radiocarbon years, a phase collectively known as the Lateglacial. By the time birch forest was developing in Britain, conditions were already cooling into the terminal cold phase of the Loch Lomond Stadial or Younger Dryas, named from its characteristic plant macrofossil in the Scandinavian sequence. Whilst arctic and eurythermal elements survived this cooling event, the bulk of the present biota has arrived in Britain since the beginning of the Holocene; it is unlikely that any higher plants or animals survived the maximum of the last glaciation between c.18,000 and 14,500 BP.
Table 1. The Late Quaternary sequence (Dates after Bassinot and others 1994).

<table>
<thead>
<tr>
<th>Geological</th>
<th>Pollen Zones</th>
<th>OIS</th>
<th>Dates B.P.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holocene</td>
<td>IV-VIII</td>
<td>1</td>
<td>0-10,000</td>
</tr>
<tr>
<td>Lateglacial</td>
<td>I-III</td>
<td></td>
<td>13,500-10,000</td>
</tr>
<tr>
<td>Devensian</td>
<td>2-5d</td>
<td></td>
<td>122,000-10,000</td>
</tr>
<tr>
<td>Ipswichian</td>
<td>5e</td>
<td></td>
<td>127,000-122,000</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td></td>
<td>186,000-127,000</td>
</tr>
<tr>
<td>Stanton Harcourt</td>
<td>7</td>
<td></td>
<td>242,000-186,000</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td></td>
<td>301,000-242,000</td>
</tr>
<tr>
<td>Hoxnian</td>
<td>9</td>
<td></td>
<td>334,000-301,000</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td></td>
<td>364,000-339,000</td>
</tr>
<tr>
<td>Swanscombe</td>
<td>11</td>
<td></td>
<td>427,000-364,000</td>
</tr>
<tr>
<td>Anglian</td>
<td>12</td>
<td></td>
<td>478,000 - 427,000</td>
</tr>
</tbody>
</table>

3.4 The Holocene

The terminology for subdivision of the present interglacial, the Holocene, or Flandrian, derives from examination of the plant macrofossil evidence from bogs in Scandinavia by Blytt and Sernander, in which they noted oscillations between continental (= Boreal) and oceanic (= Atlantic) assemblages (Godwin 1975). Their climatic inferences have been largely superseded, but the terms are still widely used, and references to mid-Holocene ‘Atlantic forest’ derive ultimately from these sources. The subdivision of the interglacial based upon pollen zones IV-VIII, originates from von Post’s work, again in Scandinavia, but was refined in terms of the British sequence essentially by Godwin (1975). Zone boundaries initially reflect the progressive immigration and expansion of species of tree to the British Isles (IV-VIIa) and then the modification of that woodland cover by human activity (VIIb-VIII). Whilst there is some variation across the country, and regional or local assemblage zones have tended to replace the traditional nomenclature in recent work, the outline of dates for zonal boundaries have been fixed by radiocarbon, using the bog at Red Moss in Lancashire as the type site (Hibbert & Switzur 1976).

Table 2. Subdivision of the Holocene (Flandrian)

<table>
<thead>
<tr>
<th>Pollen Zone</th>
<th>Flandrian Zone</th>
<th>Blytt &amp; Sernander</th>
<th>Commencing Date BP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Late Holocene</td>
<td>VIIb</td>
<td>FIII</td>
<td>Sub-Atlantic</td>
</tr>
<tr>
<td>Mid Holocene</td>
<td>VIa</td>
<td>FII</td>
<td>Atlantic</td>
</tr>
<tr>
<td>Early Holocene</td>
<td>V-VI</td>
<td>F1b-d</td>
<td>Boreal</td>
</tr>
<tr>
<td></td>
<td>IV</td>
<td>F1a</td>
<td>Pre-Boreal</td>
</tr>
</tbody>
</table>

For the purposes of this review, a tripartite division of the present interglacial has been adopted as a framework:

a) the Early Holocene during which the major forest trees immigrated from their refugia in the south of Europe (pollen zones IV – VI),
b) the mid-Holocene with mixed deciduous woodland, the so-called Atlantic forest (pollen zone VIIa), and
c) the Late Holocene, the post-Elm Decline landscapes of clearance and increasing human impact.
3.5 The Vera Hypothesis

The publication of an English translation of Frans Vera’s (1997) doctoral dissertation (Vera 2000) resulted in renewed interest in the nature of what Rackham (1976) has termed the Wildwood, the Holocene forest with minimal human intervention. Whether human intervention really was minimal is a separate debate, but both Vera and Rackham assume that pre-agricultural impacts were not that significant.

Vera argues that the poor natural regeneration of oak, both Quercus robur and Q. petraea, and hazel Corylus avellana under the closed canopy of modern woodland implies that earlier Holocene forests had sufficient open areas where these trees were able to set seed and regenerate successfully. Both oak and hazel provide a significant proportion of the pollen rain of the mid-Holocene, but, he argues, because of differing productivity and poor modern analogues, it is difficult, if not impossible to translate pollen spectra into woodland structure. Using a broad range of data, including historical as well as palaeoecological sources, he proposes a model of a much more open mid-Holocene landscape, maintained by wild grazers, in northern and central Europe, aurochs, Bos primigenius, bison, Bison bonasus, horse, Equus przewalski, elk, Alces alces, red deer, Cervus elaphus, and roe deer, Capreolus capreolus. Closed forest areas, which died back as a result of natural processes of aging, wind-throw and other disturbance, would give way to open pasture, as a result of natural grazers being attracted to new growth stimulated by light reaching the forest floor. These herbivores would suppress new tree growth, which would only be possible where thorn and other unpalatable shrubs acted as nurseries for the renewed growth of forest trees, essentially along the margins of the opened up areas.

In the British Isles, several of the large herbivores, bison, horse, and probably elk, are absent from the mid-Holocene record, but this does not mean that the remaining large herbivores, (plus wild boar, Sus scrofa, and beaver, Castor fiber) did not still influence woodland succession. However the question remains as to whether there is sufficient palaeoecological evidence to support Vera’s hypothesis, particularly in terms of whether there is:

- evidence that open areas were a significant part of the landscape in the Atlantic period;
- evidence that at any one point there is alternation of open and closed conditions; and
- evidence that large herbivores were driving the system.
1. Park (Temperate Savannah)

The open or Park phase: largely open landscape with a thin scatter of trees left from the previous grove; mainly grassland or heath.

2. Scrub

Scrub phase: spread of thorny shrubs excludes herbivores; young trees grow up with the shrubs and eventually overtop them.

3. Grove (Forest)

Grove: tree-dominated phase of the cycle; closed canopy shades out shrubs; herbivores return preventing regeneration.

4. Break-up

Break-up: period during which the canopy opens out as trees die; vegetation shifts from woodland to grassland.

Figure 1. The Vera model of forest dynamics as envisaged by Kirby (2003, 2004)

Note that Vera (2000) refers to only three phases because he does not specifically separate out the ‘Scrub phase’; he describes the whole cycle as contributing to ‘a park-like landscape’.

3.5.1 Evidence types

There is a plethora of Holocene pollen diagrams from the British Isles (summarised in Chambers 1996; Greig 1996; Tipping 1995), but other lines of evidence have been less effectively explored. Vera (2000) is correct to note the potential circularity of argument in much of the older palynological literature. Rackham (2003) criticises Vera’s use of historical sources, but he concedes that the mid-Holocene forest was more varied than often indicated. This is a point previously made on palynological grounds by Smith (1970), and recently emphasised on fossil beetle evidence from Skåne, southern Sweden by Lemdahl (2002).

Part of the problem lies in the paucity of good mid-Holocene vertebrate assemblages from Britain, and the continued compartmentalisation of complementary disciplines. Vera (2000), for example, virtually ignores the importance of fire in succession and Rackham (2003) maintains its insignificance at least for broadleaved woodland. However archaeologists and palynologists, particularly those working in the uplands (e.g. Edwards & Whittington 2000; Moore 1993; Simmons 2003), see vegetation manipulation by burning as a prime factor in forest structure, encouraging hazel, initiating peat formation and by maintaining an open browse-rich canopy, allowing higher herbivore populations.

The different types of palaeoecological evidence are now considered in turn.

3.5.2 Pollen and spores

Until perhaps thirty years ago, pollen diagrams were largely constructed on the basis of varying percentages of tree pollen (AP), usually excluding hazel, with non-tree pollen (NAP) being expressed as percentages over the basic count of AP (Birks & Birks 1980). The use of
proportional counts in most recent work provides a better indication of changes in forest composition.

Correction factors have been applied in an attempt to allow for the varying productivity of trees and shrubs (Andersen 1970), and these enable a more accurate estimate of forest composition to be obtained (Broström 2002) (although the corrections are criticised by Vera (2000) as unjustified). Correction factors have been particularly influential in terms of adjusting models of the frequency of lime, *Tilia* spp, which is insect-pollinated (Pigott 1991) and therefore a low pollen producer, in the mid-Holocene forest. Greig (1982), who also used plant macrofossil evidence, has shown this to be the dominant tree in the lowland mid-Holocene forest.

Vera (2000) argues that pollen records from grazed open forests cannot be distinguished from closed forest areas. This may be true, but records from the New Forest do indicate increases in *Calluna*, bracken and Gramineae in post-Atlantic period landscapes following human disturbance from the Bronze Age onward (Dimbleby 1965; Barber 1975; Tubbs 2001) suggesting that large-scale openness in a ‘wood-pasture type’ landscape should be detectable.

Outside of the Fens and larger river estuaries sites suitable for pollen analysis are much rarer across southeast England, particularly on the better drained soils. On the heathlands there is some evidence available from soil pollen (Dimbleby 1962), but its interpretation is often difficult, if not disputed (cf Tipping and others 1999).

### 3.5.3 Plant macrofossils

The recovery and study of plant macrofossils has a long history back into the nineteenth century, but their examination has rarely been applied to the elucidation of the nature of mid-Holocene forest. There have been numerous individual identifications, most recently reviewed, species by species, by Godwin (1975). Integrated with dendrochronology (cf. Chambers and others 1997) and dendroecology, it is the most effective technique for examining the nature of the Atlantic forest, but preservation imposes severe taphonomic restraints upon interpretation. Most sites where such integrated work is possible are inevitably lowland and wetland, with excellent sites preserved by rising sea level in the Fens, Humberhead Levels, Severn Estuary, and Lancashire/Cheshire lowlands. They provide little evidence for the nature of woodland away from wetlands, however, and knowledge of the drier areas of woodland remains slight.

Clarke (1988) studied the macro-fossils in peat cores from a number of New Forest mires. Some of these show ‘open vegetation’ remains throughout. Where peat initiation post-dates the Bronze Age, this is not evidence of openness in the Atlantic period, but at Cranes-Moor there does appear to be longer-term continuity of open vegetation. This may have been localised to the mire surface, as pollen records also suggest woodland within the vicinity.

### 3.5.4 Charcoal

The frequency of both macroscopic and microscopic charcoal in peat and soils has long been noted, although the systematic counting of the material in pollen preparations is a relatively recent development (cf. Edwards 1990; Edwards & Whittington 2000). Moore (1973; 1993) and Simmons (1996; 2003), in particular, have argued that anthropogenic burning of forest lies at the origin of much upland blanket bog. Lowland bogs similarly often show evidence
of fire both in underlying soils and within the peat (cf. Buckland 1979; Smith 2002). Archaeologists (eg Jacobi and others 1976; Mellars 1976) have tended to interpret all evidence of fire as a result of landscape scale modification, but palynologists and other palaeoecologists have often been more circumspect, either stressing the contribution from domestic fires (Edwards 1998) or allowing, contra Rackham (2003), natural fire as a significant factor in forest history (Moore 2000; Whitehouse 2000). Multiple pollen and charcoal profiles provide some possibilities of answers to these questions, but the problem is most easily examined in those areas where there is extensive macrofossil preservation (Chambers and others 1997), and these places, usually former peatlands with pine woodland again tend not be typical of the landscape as a whole.

3.5.5 Vertebrate fossil record

Over much of upland Britain, acid soils preclude the preservation of animal bone. The few assemblages available from the early to mid-Holocene, largely from caves in the Carboniferous and Permian limestones, are often of doubtful stratigraphic integrity. The early Holocene is dominated by the relatively large bone groups from archaeological sites at Star Carr in the Vale of Pickering, north Yorkshire, (Fraser & King 1954) and Thatcham in Berkshire (King 1962). Bones from red deer form a significant proportion of both groups, but aurochs, elk, horse, roe deer, boar and beaver are also present. These sites provide lists of species, but they are a poor index of animal frequency in contemporary landscapes; attempts to estimate population densities of herbivores (eg Marroo & Yalden 2000) from them must remain purely speculative. Much has been made of European deer-based Mesolithic economies (Jarman 1972), but more recent work, beginning with Clark (1978) has been much more sceptical. The mid-Holocene is even less well served with vertebrate remains and individual finds have been reviewed by Yalden (1999). When the record becomes more complete, in post-forest clearance Neolithic assemblages, such as that from Windmill Hill in Wiltshire (Smith 1965), the range of species does not change, but there are remarkably few wild mammals alongside the domestics.

3.5.6 Mollusca

Research, principally by John Evans (1972), on terrestrial snail faunas from sites on the Chalk and limestones of southern England has been instrumental in modifying a previous view of the chalklands. Whereas these had been seen as something approaching edaphic steppe, which was transformed into cultursteppe by early Neolithic agriculturalists, the mollusc records suggest more of a forested landscape, a viewpoint which Tansley (1939) had arrived at on theoretical grounds. Limestones occupy roughly a quarter of the land surface of England and over most of the outcrop of calcareous rocks, palaeoenvironmental evidence is essentially restricted to snails. These are incapable of providing the degree of resolution required for detailed landscape reconstructions, although their study can often supplement other lines of evidence from adjacent sites with better preservation (cf. French and others 2003). Whilst there are often problems with the taphonomy of assemblages, relatively discrete faunas occupy arable or other disturbed ground, stable grassland and shaded habitats (Carter 1990). They are, however, poor discriminators between closed scrub and true forest, although a few species might be regarded as old forest indicators (eg Cameron 1973).
3.5.7 Insects

Insects are the most frequent multicellular animal fossils in Quaternary deposits (Elias 1994), and often attributable to very specific habitats. Thus they are potentially the most useful group for the reconstruction of past environments. They may be preserved in any anaerobic sediment and the extraction techniques are relatively simple, if time-consuming (Coope & Osborne 1968). The aquatic larvae of the Chironomidae have proved particularly useful in reconstructing the changing climate of the Late-glacial and Holocene (Brooks & Birks 2000). However the Coleoptera, the beetles, which are virtually ubiquitous in terrestrial and fresh to brackish water habitats, are most useful in examining wider landscapes, both natural and archaeological.

Nearly forty years ago, Osborne (1965) pointed out the frequency of old forest beetles, several of them either no longer found in Britain or restricted to relict communities in a few localities, in assemblages from mid- to late Holocene sediments. His list of extirpations was considerably expanded by Buckland and Kenward (1973), Girling (1982a), and more recently by Whitehouse (Boswijk & Whitehouse 2002). Virtually all local extinctions concern forest species, for which the German term Urwaldrelikt, is most appropriate. This term was first used by K. Dorn for one of the species, *Rhysodes sulcatus*, which has since been found as a fossil at several Holocene sites in England (Figure 2).

![Figure 2](image-url)

**Rhysodes sulcatus (F.)**

**Holocene Fossil Localities:**

- **D** = Church Farm, Davenham, Cheshire, \(~9200\) BP (Hughes et al. 2000).
- **B** = Baker Site, Somerset Levels, \(~4950\) BP (Girling 1980).
- **NS** = North Sea Floor? Early Holocene (Blair 1935).
- **S** = Shustoke, Warks, \(~4830\) BP (Kelly & Osborne 1965).
- **T** = Thorne Moors, S. Yorks, \(~3000\) BP (Buckland 1977).

Figure 2. Holocene fossil record and modern distribution of the archetypal Urwaldtiere *Rhysodes sulcatus*
There are a number of taphonomic problems in interpreting insect assemblages and interpretation, as in any field, is much the stronger when a multidisciplinary approach is adopted. (Taphonomy is the study of processes involved in the decay and fossilisation of buried plant and animal material.) Nevertheless beetle assemblages provide a strong line of evidence that is independent of the dominant technique of palynology. Both studies of change within the Holocene and comparison between the Holocene and previous interglacials are instructive.

The provision of a database for virtually the whole of the Quaternary fossil beetle record for northern Europe, with habitat and distribution data provides a powerful tool for comparing past environments (Buckland & Buckland 2002; <www.bugs2000.org>). It should be stressed, however, that so far only the beetles have been subjected to intensive study, and that the distribution of sites examined both spatially and temporally remains patchy.

3.5.8 Sediments

One of the major problems in reconstructing past landscapes is estimating the nature and extent of changes in soils. The former mantle of cryoturbated Late Devensian loess (Catt 1978) would have provided a fertile base for forest development in the early Holocene, but the tendency of soils on this base to lessivage and acidification could have resulted in at least local development of heathland communities (cf. Thomas 1960), probably long before large scale human interference in the landscape. In the uplands and on nutrient-poor substrates, the development of podzolisation has been widely examined (Limbrey 1975); Fenton (2004) argues that the openness of much of the Scottish highlands is a natural consequence of climatic change and grazing, only marginally affected by anthropogenic clearances. However, the extent of soil and sediment loss over much of the lowlands has only been realised through examination of floodplain sediments (Shotton 1978; Robinson & Lambrick 1984) and sections across dry valleys on the Chalk (Bell 1983). Much of this erosion appears to be Roman or later, perhaps a reflection of the widespread availability of a plough at last able to cut the root mat created by domestic grazers (Buckland 2002). However, close dating and evidence for the duration of erosion events is often lacking because of the intermittent nature of the sediment record.

3.5.9 Archaeology

Over much of Britain, acid soils lead to poor preservation of bone, and the only evidence of early to mid-Holocene human activity may consist of a few charred hazel nuts and a scatter of flint or chert artefacts. This Mesolithic material was catalogued by Wymer (1977) and there have been several regional updates. Late Mesolithic, narrow blade, implements and debitage, partly at least contemporary with the Atlantic forest, are widespread. The bias towards sites on light acid soils is probably more a reflection of relative ease of recovery and erosion of soils from much of the limestone outcrop rather than a real difference in actual site distribution. More systematic field-walking and collecting certainly indicate use of the Chalk outcrop in areas where the Mesolithic was previously unknown (cf. Hayfield and others 1995). This increase in artefactual evidence to cover a further three thousand years, however, often comes from sites at which there would have been many individual occupations. It is therefore of limited use in examining human impact on the forest in the absence of palaeoecological data. In addition, where such links have been made, the connection between archaeology and palaeoecology is often tenuous (eg Radley and others 1974).
Whilst the study of individual groups of micro- and macrofossils provides important data, each has its own taphonomic problems, and it is necessary to evaluate several lines of evidence in order to obtain a balanced picture of any palaeoenvironment. Unfortunately this has rarely been achieved, and differential preservation, as well as available funding, usually imposes limitations on such studies. The value of such integrated research is illustrated by a number of recent projects, including that of French and others (2003) on the Dorset Chalk.

3.6 Evolution of the Holocene landscape

Despite some arguments to the contrary (eg Stewart & Lister 2001), it is unlikely that any significant elements in the British biota survived the Last Glacial Maximum. From ca. 13,500 BP onward the present flora and fauna immigrated from refugia in southern and south eastern Europe (Hewitt 1999; Willis & Whittaker 2000). The return to high arctic conditions for about 1000 years between ca.11,000 and 10,000 BP temporarily curtailed these processes, but a fully temperate insect assemblage, although not the associated trees, was already present at Lea Marston in Warwickshire by ca. 9500 BP (Osborne 1974a). The rapidity of Lateglacial warming immediately into a Holocene at least as warm as present day, was first indicated on insect faunas from sites at Church Stretton, Shropshire (Osborne 1972), Glanlynnau, Gwynedd (Coope & Brophy 1972), and Red Moss, Lancashire (Ashworth 1972). Osborne’s (1980) well dated site at West Bromwich, near Birmingham, in particular, shows a rapid transition that can be measured in decades rather than centuries; this rapid climate change was confirmed by the annual record from the Greenland ice cores, over twenty years later (Alley and others 1993).

The Early Holocene is marked by the progression from birch to pine and birch woodland, followed by the immigration of other forest trees, with hazel forming a remarkable early expansion. Oak is followed by elm and lime; alder makes a marked expansion in the mid-Holocene; whilst hornbeam and beech woodland only become extensive in the South East after human impact had largely cleared earlier forest. Applying correction factors for pollen productivity to the major tree taxa provides a picture of the Atlantic woodlands, with lime dominant over much of the lowlands, north at least as far as East Yorkshire (Greig 1982; 1996). Lime dominance may have been favoured by the former extent of loess soils over much of the limestone and Chalk outcrop; oakwood probably extended over much of the heavier ground, extending into the uplands, whilst oak-alder carr occupied most of the wetlands away from expanding areas of raised mire. This provides the generally accepted view amongst palynologists, but the interest lies in the detail: just how closed was this forest, and was its structure dictated by large herbivores, fire, human activity or purely vegetative processes?

3.7 Palynological and charcoal evidence

Greig (1996) provides regional palaeoecological summaries of the Lateglacial and Holocene vegetation, based upon the pollen evidence for the various regions of England. Wales (Chambers 1996) and Scotland (Birks 1996) and much of the rest of Europe (Berglund and others 1996) are also covered in the same volume. Tipping (1995) provides a further review of the Scottish evidence. The mid-Holocene landscapes of lowland England were dominated by lime forest (Greig 1982), giving way to oak and elm to the west, oak and alder on wetter soils, and to oak hazel woodland in the uplands. The continuous trace for pine on the poorer, more acid soils and its presence in the plant macrofossil record from lowland bogs into the Late Holocene (eg Legeard and others 2001) suggest that pine woodland may have been a
component of forest heath landscapes, like the Surrey heaths, as well as raised mires (Chambers 1997).

Some palynologists working in the uplands and with archaeologists (eg Edwards 1998; Simmons 1996) have argued that significant human impacts upon vegetation occurred through both the early and mid-Holocene; controlled burning to encourage new browse for natural grazers was often seen as an essential, if ultimately deleterious element of Mesolithic economies (cf. Mellars 1976). Evidence for the early impact of fire extends at least to the Isle of Man, but it is less evident in Ireland, where the absence of several of the herbivores, including aurochs, made such management of resources by hunter/gatherers less appropriate (Innes and others 2003). Mitchell (2005) argues that the similarity between Irish and mainland European pollen evidence would support the hypothesis of a largely continuous closed canopy mid-Holocene landscape. In southeast England, Dimbleby (1962, 1965), using the evidence of pollen preserved in acid soils on the Mesolithic sites of Oakhanger and Iping on the Sussex heaths, suggested that the progression towards heathland had begun as a result of late Mesolithic burning, which he also correlated with evidence for soil erosion. Bush and Flenley (1987) and Bush (1988) argue on palynological evidence that human impact on the Chalk of the Yorkshire Wolds was sufficiently continuous from the Early Holocene to have maintained open areas, perpetuated by grazing through to the more extensive clearances of the Neolithic. Bush’s research engendered some debate (Thomas 1989, and response by Bush 1989), but the prevailing picture still appears to be one of closed forest on the Chalklands (eg Waton 1986), although Scaife (in French and others 2003) has recently reopened the argument.

Whilst most of the evidence for early ‘openness’ in the landscape comes from the uplands, there are several diagrams from eastern England which show short-term intervals of small temporary clearances in the Atlantic forest (eg Smith and others 1989; Sims 1978). Buckland and Edwards (1984) have suggested that such features may reflect the prolongation of anthropogenic clearances by natural grazers. Smith (1970; 1984) argued that the early expansion of hazel and the later rise in alder related to human manipulation of the succession. Whilst others (eg Edwards 1990; Huntley 1993) are more circumspect, the concept of a ‘natural forest’, whatever its structure, if this is taken as totally without human influence, may be inappropriate to the Holocene.

Svenning (2002), following Stuart (1991), has suggested that it might be possible to estimate large herbivore densities on the frequency of dung fungi in sediments. Although several herbivores have the habit of creating latrines and also of ‘yarding’ in inclement weather, thereby creating potential dung ‘hot spots’, and the distribution of such evidence is likely not to be random, Innes and Blackford (2003) have been able to use fungal spore frequency, along with the pollen evidence, to show increased grazing pressure in a post-fire clearance during the mid-Holocene on the North York Moors.

In reviewing the evidence for the nature of Atlantic forest in Europe, Svenning (2002) compares the pollen record with that from previous interglacials. He suggests that ‘normal uplands’, which includes all sites beyond the floodplains, including those close to sea level like Hatfield Moors in south Yorkshire (Whitehouse 2000), would be predominantly closed forest. A more varied landscape would however occur in places with ‘open woodland, scrub, woodland glades, dry and calcareous grassland, marshes and bare disturbed ground’. Open ground would be particularly likely to occur on floodplains, and calcareous or poor sandy soils. Fossil insect evidence (see later), however, implies that many floodplains were not
only the most densely forested areas, but also those on which closed woodland survived longest.

3.8 The vertebrate record

The species composition and frequency of large vertebrates in the mid-Holocene landscape has been recently reviewed by Yalden (1999) and Marroo and Yalden (2000). The problem is bedevilled by the paucity of good bone assemblages, and the wild component of archaeological assemblages from early Neolithic sites is relatively small. There are sizeable early Holocene groups, associated with archaeological sites, such as the much discussed bones from Star Carr in the Vale of Pickering, Yorkshire (Fraser & King 1954; Legge & Rowley-Conwy 1988; Rowley-Conwy 1998), but few mid-Holocene bone groups, largely because many Mesolithic sites lie on acid soils which are not conducive to bone preservation. None of those that do exist are substantial. The impact of large grazers and browsers in this period may therefore have been underestimated, and as a consequence changes in the forest pollen spectra ascribed to other either climatic or anthropogenic causes.

The early Holocene herbivore assemblage from Star Carr includes aurochs, elk, red deer, and roe deer. Wild boar and beaver are also present (Legge & Rowley-Conwy 1988) and need to be considered, as they are also likely to have had a significant impact on the landscape (Coles & Orme 1983; Coles and others 2003). Schadla-Hall (1988) adds horse from the nearby site of Seamer Carr, and this assemblage is repeated at the only other reasonably secure and sizeable Mesolithic assemblage, at Thatcham in Berkshire (King 1962). Although Gonzalez and others (2000) have published radiocarbon dates for Irish deer, *Megaloceros giganteus*, suggesting survival down to ca. 9250 BP in the Isle of Man and SW Scotland, Pastor and Moen (2004) have recently re-evaluated the evidence and suggest a Late-glacial extinction.

Elk and horse probably disappeared during the early Holocene (Yalden 1999). Horse, like Irish deer, might be regarded as animals essentially of the open steppe with only a slim hold on north-west Europe, but much of Scotland in the mid-Holocene would not be significantly different from areas of Scandinavia where elk continues to thrive. There are two possible late Holocene dates for elk. The Roman record of elk, a brow tine from Newstead in the Borders, has recently been re-examined and shown to be an aberrant red deer (Kitchener and others 2004), and the radiocarbon date from Cree River in Galloway, south-west Scotland (Kitchener & Bonsall 1997), is on an old find requiring confirmation; its extinction is probably of Early Holocene date. Unless human populations and predation were greater than the archaeological record suggests, this group of extinctions may reflect the short, cold snap at ca. 8200 BP, the most significant climatic downturn during the Holocene (Mayewski and others 1996; Alley and others 1997; Klitgaard-Kristensen and others 1998), perhaps causing stress as a result of a significant reduction in carrying capacity.

Grigson (1978) notes the relatively high frequency of aurochs in mid-Holocene deposits of England and Wales and individual finds from wetland locations, sometimes of complete skeletons, are widespread. By analogy with modern feral cattle then these animals may represent bulls marginalised from the herd during contests for dominance over breeding cows. Extrapolating from the fossil record is hazardous, but aurochs appear to have been not uncommon during the mid-Holocene; they are likely to have moved about in herds and must have had some impact on the forest.
3.9 Soil, snails and erosion

The work of Catt (1978) in reviewing the former extent of loess soils in England and of Evans (1972) on evidence for shaded habitats derived from snail faunas have substantially revised views of the Chalk outcrop, from one of open edaphic steppe on thin rendzina soils to one of closed forest on deeper loess-based soils. Forest clearance, however, has lead to extensive and continuing erosion of such soils (cf. Bell and Boardman 1992). Catt (1979) suggests that over a metre of sediment has been lost to Late-glacial and Holocene erosion, whilst Fisher (1991), from work on Cranborne Chase in Dorset, provides a much more conservative estimate of 180mm, a point further emphasised by a recent multidisciplinary study of the same area (French and others 2003). This evidence serves to stress the patchy nature of aeolian deposition and later erosion, but as work on valley sediments has shown (eg Bell 1983), most of the soil and sediment loss, whatever its extent, is post-Neolithic. The *in situ* palaeoecological record is confined to truncated profiles beneath archaeological features (French 2003) and the arcuate scars of tree pits. The latter seem not to be as frequent as might be expected from dense woodland (Cheetam, pers. comm.), but, as the 1987 storm showed, species differ in their reaction to wind, with some species tending to snap or drop branches rather than blow over (Kirby & Buckley 1994).

3.10 Fossil insect evidence

Although there had been some earlier work, notably by Henriksen (1931) and Lindroth (1948) in Scandinavia, it was only with the discovery of fossil beetles in organic silts at Upton Warren, Worcestershire (Coope and others 1961) and Chelford, Cheshire (Coope 1959) that detailed research upon Quaternary insect assemblages began. Holocene forest faunas were first examined by Osborne at Shustoke in Warwickshire (Kelly & Osborne 1965). Deadwood species of Coleoptera (beetles), were identified including species now either extinct or extremely rare in Britain (Osborne 1965, 1972), Buckland and Kenward (1973) extended this list with material from Thorne Moor in South Yorkshire, at ca. 3000 BP, still the most recent Old Forest (*Urwald*) insect assemblage from Britain (Buckland 1979).

With the work by Roper (1996) and Whitehouse (1997, 2004), the peats of the Humberhead Levels now have the longest list of nationally extinct species from any region; all are associated with dead wood habitats. Elsewhere Girling (1982a) has added species from the Somerset Levels, and Robinson (2000) has specifically targeted the Mesolithic/Neolithic transition, at ca.5200 yrs BP. Whitehouse and Smith (2004) have recently reviewed the Holocene fossil insect record in the light of the Vera hypothesis, although their sample is essentially restricted to two published sites, Holywell Coombe, near Folkestone, Kent (Coope 1998), and Bole Ings, near Gainsborough, Lincolnshire (Dinnin 1997).

Earlier sites, away from direct evidence of human occupation, such as several of Girling’s (1984; 1985) in the Somerset Levels, give some hint of a natural, relatively undisturbed landscape, with forest faunas dominated by Urwald species, and closed woodland survived into the Late Bronze Age, ca. 3000 BP at Thorne (Buckland 1979). However, it is apparent from sites like Pilgrim Lock at Bidford-on-Avon, Warwickshire (Osborne 1988), and the Wilsford shaft in Wiltshire (Osborne 1969; 1989) that much of the later prehistoric landscape was already largely cleared and managed. The Roman countryside has several large assemblages from both urban and rural wells (eg Coope & Osborne 1968; Girling 1989a), as well as some natural assemblages (eg Osborne 1996). Long lists of fossil insects for the ninth to eleventh centuries AD have been put together from York (Hall and others 1983; Kenward & Hall 1995), but rural landscapes of that period are less well served, although recent work at
Conisbrough in south Yorkshire shows a wood pasture landscape during the early seventh century (Buckland and others in prep.)

A critical period is the pollen zone VIIa/b boundary (Table 2), coincident with the first evidence of clearance and farming activity. Osborne’s (1972) series of sites along the edge of the Longmynd at Church Stretton is particularly useful, and West Heath Spa on the edge of London (Girling 1989b) gives an indication of the nature of the first impacts upon the fauna of the forest by early agriculturalists. The latter site has been the basis of much discussion because of the presence of Scolytus scolytus, the elm bark beetle, in deposits predating the classic Elm Decline, one of the parameters used to define the VIIa/b boundary (Girling & Greig 1985; Girling 1988; Moore 1984; Robinson 2000). Clark (2002; Clark & Edwards 2004) has recently recorded multiple occurrences of this species in pre-Elm Decline sediments in north east Scotland. Table 3 lists the sites (Figure 3), which have produced beetle faunas which cover the period from the Early Holocene to the Neolithic.

Table 3. Early Holocene – Neolithic (Late Holocene) sites with insect faunas

<table>
<thead>
<tr>
<th>Site</th>
<th>Range</th>
<th>Date from</th>
<th>Date to</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glanllynnau, Gwynedd</td>
<td>LG-EH</td>
<td>Coope &amp; Brophy (1972)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Church Stretton, Salops.</td>
<td>LG-MH</td>
<td>VIIb</td>
<td>Osborne (1972)</td>
<td></td>
</tr>
<tr>
<td>Holywell Coombe, Kent</td>
<td>LG-EH</td>
<td>&gt; 9900 ± 100</td>
<td>Coope (1998)</td>
<td></td>
</tr>
<tr>
<td>West Bromwich, Warks.</td>
<td>LG-EH</td>
<td>9080 ± 455</td>
<td>Osborne (1980)</td>
<td></td>
</tr>
<tr>
<td>Mingies Ditch, Oxon</td>
<td>LG-MH</td>
<td>6540 ± 80</td>
<td>Robinson (1993)</td>
<td></td>
</tr>
<tr>
<td>Rodbaston, Staffs.</td>
<td>LG-EH</td>
<td>&gt; 10300 ± 170</td>
<td>Ashworth (1973)</td>
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<tr>
<td>Church Farm, Chesh.</td>
<td>LG-EH</td>
<td>7900 ± 50</td>
<td>Hughes and others (2000)</td>
<td></td>
</tr>
<tr>
<td>Red Moss, Lanes.</td>
<td>LG-EH</td>
<td>&gt; 9800 ± 700</td>
<td>Ashworth (1972)</td>
<td></td>
</tr>
<tr>
<td>Leicester</td>
<td>EH</td>
<td>9450 ± 90</td>
<td>Osborne (1974)</td>
<td></td>
</tr>
<tr>
<td>Lea Marston, Warks.</td>
<td>EH</td>
<td>2750 ± 60</td>
<td>Howard and others (2000)</td>
<td></td>
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<tr>
<td>Ripon, Yorks.</td>
<td>EH</td>
<td>8240 ± 60</td>
<td>Dinnin (1997)</td>
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<tr>
<td>Bole Ings, Notts.</td>
<td>E-LH</td>
<td>&gt; 8500 ± 90</td>
<td>Robinson (1999)</td>
<td></td>
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<tr>
<td>Little Stretton, Salops.</td>
<td>EH</td>
<td>6930 ± 380</td>
<td>Shotton and others (1977)</td>
<td></td>
</tr>
<tr>
<td>Church Stretton RS2, Salops</td>
<td>EH-MH</td>
<td>VIIa</td>
<td>Osborne (1972)</td>
<td></td>
</tr>
<tr>
<td>Alcester, Warks.</td>
<td>EH</td>
<td>9700 ± 60</td>
<td>Robinson (1977)</td>
<td></td>
</tr>
<tr>
<td>Norwich</td>
<td>EH</td>
<td>4960 ± 90</td>
<td>Robinson (1999)</td>
<td></td>
</tr>
<tr>
<td>Etton, Cambs.</td>
<td>EH</td>
<td>&lt;= 3980 ± 100</td>
<td>Robinson (1999)</td>
<td></td>
</tr>
<tr>
<td>West Heath Spa</td>
<td>M-LH</td>
<td>VIIa</td>
<td>Girling (1989b)</td>
<td></td>
</tr>
<tr>
<td>Runnymede, Surrey</td>
<td>M-LH</td>
<td>&gt; ca.3950</td>
<td>Robinson (1991)</td>
<td></td>
</tr>
<tr>
<td>Abbot's Way, Somerset</td>
<td>M-LH</td>
<td>5900 ± 100</td>
<td>Girling (1976)</td>
<td></td>
</tr>
<tr>
<td>Baker Track, Somerset</td>
<td>M-LH</td>
<td>4530 ± 110</td>
<td>Robinson (1997)</td>
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</tr>
<tr>
<td>Rowland's Track, Somerset</td>
<td>M-LH</td>
<td>4210 ± 90</td>
<td>Girling (1977)</td>
<td></td>
</tr>
<tr>
<td>Stileway, Somerset</td>
<td>LH</td>
<td>4470 ± 70</td>
<td>Girling (1985)</td>
<td></td>
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<tr>
<td>Silbury Hill, Wilts.</td>
<td>LH</td>
<td>4830 ± 100</td>
<td>Kelly &amp; Osborne (1965)</td>
<td></td>
</tr>
<tr>
<td>Sweet Track, Somerset</td>
<td>LH</td>
<td>4054 ± 45</td>
<td>Buckland and others (2001)</td>
<td></td>
</tr>
<tr>
<td>Breiddin, Clwyd</td>
<td>LH</td>
<td></td>
<td>Warsop (2000)</td>
<td></td>
</tr>
<tr>
<td>Eilean Domhnuill a Spionnadh, N Uist</td>
<td>LH</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Key: LG = Lateglacial ~13,500-10,000 BP; EH = Early Holocene ~10,000-7000 BP; MH = 7000-5000 BP; LH = 5000- present day
In reviewing the species lists from these sites, the dominance of saproxylic species is immediately apparent (cf. Buckland & Dinnin 1993). As Elton (1966) perceptively noted, however, most species which spend their larval development in dead wood are reliant upon the nectar of flowers, often umbellifers and shrubs like blackthorn and hawthorn, to provide the necessary fuel for imaginal dispersal; such would be in short supply in a totally closed forest, as often envisaged on the palynological evidence. Keith Alexander (personal communication) therefore cautions that an abundance of species associated with old trees does not necessarily indicate the presence of closed woodland. Many such species do best where the old trees are in open sunny conditions (Rannius and Jannson 2000).

In a detailed review of the saproxylic fauna of southern Sweden, Thure Palm (1959) tabulated their habitat requirements. Most species were found in both sunny and shaded locations, although a few, particularly amongst the Cerambycids and Scolylids, specialised in the more exposed places (Figure 4). Inevitably his data are biased towards captures of imagines, and insects often rely on direct insolation to warm up muscles for flight (eg Fisher (1940) on the death-watch beetle Xestobium rufovillosum (Deg.)).

The availability of some sunny locations in the mid-Holocene landscape is therefore evident. However closed forest is not without temporary and permanent clearings (Peterken 1996). Even if the open space occupied only 5% of the landscape veteran trees and open glades might be no more than 100m apart across most of the landscape (Keith Kirby personal communication, based on a model landscape approach similar to that used in Kirby (2003)).

Figure 3. Sites with mid-Holocene fossil insect faunas in the UK (Sites referred to in the text are indicated)
The changes in the biota during the present interglacial can be compared with those of previous ones, where there is no or at least little human interference in the succession. Given the problems of survival in disparate refugia and differing patterns of post-glacial expansion, it might be expected that each interglacial would have a unique signal. However nature does occasionally deal what, in terms of palynological signature, appears to be the same hand at least twice. In pollen terms sites previously regarded as all belonging to the last interglacial, the Ipswichian, can be shown to belong to two separate events, better labelled using the numbered sequence derived from the major swings in climate apparent in the deep sea core sequence as Isotope Stages 5e and 7, and the preceding Hoxnian deposits belong to 9 and 11 (Table 1). Similar elements of the Old Forest (Urwald) fauna appear in all these stages. Coope (2001) has recently suggested, however, that there may be unique elements in particular interglacial insect faunas. The Holocene might be said at least in the Lowland Zone to be characterized by the lime bark beetle *Ernopus caucasicus*, almost a zone fossil for the mid-Holocene, and discovered by Osborne (Kelly & Osborne 1965) as a fossil before A. A. Allen (1969) added it to the modern British List. Isotope Stage 5e, the Ipswichian, on the pollen evidence dominated by *Carpinus*, should perhaps have the hornbeam scolytid *Scolytus carpini* as characteristic, although this is currently only known from two sites (Gaunt and others 1972; Keen and others 1999).
3.10.1 Extinctions – Man or climate change?

Table 4 summarises the present position with regard to extirpations from the British insect fauna during the Holocene. Decisions as to what to include have inevitably been somewhat arbitrary, and some species currently known only as fossils may yet be added to the British list. Several species with a few doubtful nineteenth century records have been omitted as have probable casual imports, such as the cerambycid Hesperophaenades fasciculatus from Roman Alcester (Osborne 1971). Others, like the dung beetle Onthophagus fracticornis, a relatively frequent fossil (e.g. Osborne 1969), but which might just be surviving in a few localities (Hyman 1992; 1994), have also been excluded.

Much of the deadwood fauna, having perhaps evolved in a Tertiary landscape of more continuous habitat availability, appears much the same whenever mature temperate mixed forest is reassembled, and the same species occur in several interglacials (cf. Dinnin 1992). Having co-evolved in this landscape, these species would be under particular threat as tree cover and especially the abundance of old trees declined, hence the importance attached to dead wood habitats and their continuity in modern conservation (cf. Harding & Rose 1986; Kirby & Drake 1993; Speight 1989).

Table 4, however, includes a number of species, where the woodland association is slight. For several wetland and dung species, either extirpated or in steep decline, their disappearance has been recent (Foster 2000; Hyman 1992), and it is difficult to dissect out the impact of habitat destruction from climate; Osborne (1997b) and Wagner (1997) present opposing views. The evidence from the Greenland ice cores suggests that between the short, dramatic downturn in temperatures at ca. 8200 BP and the late medieval period there were no similarly major changes in the climate of Western Europe (Mayewski and others 1996). This does not mean, however, that oscillations between oceanic and more continental regimes, even particularly severe individual years, did not have impact on the biota. The evidence is often contentious. Bas van Geel and others (1998) in particular have presented evidence for a major change at ca. 850 BC, the Sub-Boreal Sub-Atlantic transition, although van den Bogaard and others (2002) are sceptical of the synchroneity of the change. Most of the extirpations from the British insect fauna concern species which currently have a more continental distribution, and this is as much apparent in the dung and open ground fauna as in the Urwald (Table 4). Girling (1984) has argued that the colder temperatures of the post-medieval Little Ice Age contributed to the loss of the whirligig beetle Gyrinus colymbus (but see Buckland & Wagner 2001).

Several of these species are relatively southern and eastern in their present distributions and Palm’s table of habitat preferences has to be supplemented from other sources (Table 5).

The extinctions amongst the saproxylics, however, are not restricted to the closed forest or its deep litter, as Keith Alexander has pointed out. An association with lowland pine forest, which had largely disappeared from Britain by the late Bronze Age, may have impacted on some species. Several – Porthmidius autriacus, Isorhipis melasoides, Buprestis rustica, Pycnopus tenebrans, Stagetus pilula, Cerambyx cerdo and Rhynocoris punctulatus – would appear to prefer exposed sunny locations, whilst others show no such preference.

On balance, the fossil insect data would suggest that the mid-Holocene and at least the earlier part of the Late Holocene were more continental than the present oceanic regime – summers
were warmer and winters colder, even if annual temperatures appear the same, and this has some implications for management.

**Table 4.** Extinctions from the British Holocene insect fauna, the fossil evidence, compared with earlier interglacial records. Species with 19th C records but now regarded as extinct are included. * indicates a species lacking woodland association.
(For key to sites, see Appendix 1)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Site</th>
<th>Interglacial</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chlaenius sulcicollis</em></td>
<td>ST; MH;</td>
<td>TS; Itt (5e); Ave (7)</td>
</tr>
<tr>
<td><em>Oodes gracilis</em></td>
<td>ST; AW; Go;</td>
<td>TS; Ips; Itt; Shr; De; TCP (5e)</td>
</tr>
<tr>
<td><em>Gyrinus natator</em></td>
<td>Co; Cald; Bri;</td>
<td></td>
</tr>
<tr>
<td><em>G. colymbus</em></td>
<td></td>
<td>Lei</td>
</tr>
<tr>
<td>Rhysoedes sulcatus</td>
<td>Dav; Shu; BS; TM; Nsea</td>
<td>De; (5e)</td>
</tr>
<tr>
<td>Batrisus formicarius</td>
<td>Stil</td>
<td></td>
</tr>
<tr>
<td>Porthmidius austriacus</td>
<td>World;</td>
<td></td>
</tr>
<tr>
<td>Dromaeolus barnabita</td>
<td>Boi; Run;</td>
<td></td>
</tr>
<tr>
<td>Isorhhipis melasoides</td>
<td>WHS; BS; Mist; TM</td>
<td>TCP (5e)</td>
</tr>
<tr>
<td>Buprestis rustica</td>
<td>TM</td>
<td></td>
</tr>
<tr>
<td><em>Dermestes laniarius</em></td>
<td>Wil</td>
<td>TS (5e)</td>
</tr>
<tr>
<td>Zimioma grossum</td>
<td>Run; TM</td>
<td></td>
</tr>
<tr>
<td><em>Airaphilus elongatus</em></td>
<td>Wils; Rip; CS; ST; Sto; Dro;</td>
<td>Ips; Max (5e); HL (12)</td>
</tr>
<tr>
<td>Prostomis mandibularis</td>
<td>ST; TM</td>
<td></td>
</tr>
<tr>
<td>Cryptolestes corticinus</td>
<td>HM;</td>
<td></td>
</tr>
<tr>
<td>Pycnoderus terebrans</td>
<td>WHS; Min; Stil;</td>
<td>TCP (5e)</td>
</tr>
<tr>
<td>Bothriderus contractus</td>
<td>Stil; TM;</td>
<td>Au (5e)</td>
</tr>
<tr>
<td>Mycetina cruciata</td>
<td>TM</td>
<td></td>
</tr>
<tr>
<td>Rhopalodontus bauderi</td>
<td>TM</td>
<td></td>
</tr>
<tr>
<td><em>Leucohimatium sp.</em></td>
<td>LeaM</td>
<td></td>
</tr>
<tr>
<td><em>Anthicus gracilis</em></td>
<td>ST; AW; RT; Mea;</td>
<td></td>
</tr>
<tr>
<td>Tenebroides fuscus</td>
<td>HM;</td>
<td></td>
</tr>
<tr>
<td>Stagetus pilula</td>
<td>TM</td>
<td></td>
</tr>
<tr>
<td><em>Caccobius schreberi</em></td>
<td>SS;</td>
<td>TS; Ips; Els; Shr; Wool; De (5e)</td>
</tr>
<tr>
<td><em>Onthophagus taurus</em></td>
<td>Run; Pil; Flag;</td>
<td>TS; Ips; Els; De (5e);</td>
</tr>
<tr>
<td><em>O. verticicorins</em></td>
<td>Wil; Pil; Ming; Ast;</td>
<td>TS; Els; Wool; De (5e)</td>
</tr>
<tr>
<td><em>Aphodius quadriguttatus</em></td>
<td>Wil;</td>
<td></td>
</tr>
<tr>
<td><em>A. scrofa</em></td>
<td>WHS;</td>
<td></td>
</tr>
<tr>
<td><em>A. varians</em></td>
<td>Run; Min;</td>
<td></td>
</tr>
<tr>
<td><em>Rhyssesus germanus</em></td>
<td></td>
<td>TS; Shr; Wool; (5e)</td>
</tr>
<tr>
<td><em>Pleurophorus caesus</em></td>
<td></td>
<td>TS; De; (5e)</td>
</tr>
<tr>
<td><em>Polyphilla fullo</em></td>
<td>Hib;</td>
<td></td>
</tr>
<tr>
<td>Valgus hemipterus</td>
<td>SS;</td>
<td>TS; Ips; Itt; Shr; TCP; De (5e)</td>
</tr>
<tr>
<td>Platycerus caraboides</td>
<td>Melt;</td>
<td></td>
</tr>
<tr>
<td>Strangalia attenuata</td>
<td>ST;</td>
<td></td>
</tr>
<tr>
<td>Cerambyx cerdo</td>
<td>Isle; Rams;</td>
<td></td>
</tr>
<tr>
<td><em>Cathingicus validiscapulus</em></td>
<td>Al;</td>
<td>SG (7);</td>
</tr>
<tr>
<td><em>Cytpholeon trisulcatus</em></td>
<td>LeaM</td>
<td></td>
</tr>
<tr>
<td>Rhyncolus elongatus</td>
<td>HoC; World; TM;</td>
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</tr>
<tr>
<td>R. sculpturatus</td>
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<td></td>
</tr>
<tr>
<td>R. strangulatus</td>
<td>World;</td>
<td></td>
</tr>
<tr>
<td>R. punctulatus</td>
<td>Stil; TM; HM;</td>
<td></td>
</tr>
</tbody>
</table>
Table 5. Habitat preference for saproxylics present in the Holocene fossil record and extirpated from the British Isles.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat preference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhysodes sulcatus</td>
<td>damp places (Silvferberg 1985)</td>
</tr>
<tr>
<td>Batrisus formicarius</td>
<td>In deciduous woodland (Koch 1989)</td>
</tr>
<tr>
<td>Pormtidius austriacus</td>
<td>On warm slopes (Koch 1989)</td>
</tr>
<tr>
<td>Isorhopis melasoides</td>
<td>Swarming in mid-day heat (Horion 1953)</td>
</tr>
<tr>
<td>Dromaeolus barnabita</td>
<td>In old deciduous woods (Koch 1989)</td>
</tr>
<tr>
<td>Buprestis rustic</td>
<td>In pines in hot sun (Harde 1984)</td>
</tr>
<tr>
<td>Temnochila coerulce</td>
<td>On pine (Koch 1989)</td>
</tr>
<tr>
<td>Zimioma grossum</td>
<td>Prefers sun but not exclusively (Palm 1959)</td>
</tr>
<tr>
<td>Cryptolestes corticinus</td>
<td>Under pine bark (Koch 1989)</td>
</tr>
<tr>
<td>Prostomis mandibularis</td>
<td>In damp wood (Palm 1959)</td>
</tr>
<tr>
<td>Pycnoderus tenebrans</td>
<td>Mostly in sunny places (Koch 1989)</td>
</tr>
<tr>
<td>Bothrioderes contractus</td>
<td>No preference (Palm 1959)</td>
</tr>
<tr>
<td>Mycetina cruciata</td>
<td>Prefers shade but not exclusively (Palm 1959)</td>
</tr>
<tr>
<td>Rhopalodontus baudueri</td>
<td>In parks (Koch 1989)</td>
</tr>
<tr>
<td>Stagetus pilula</td>
<td>Prefers sun (Palm 1959)</td>
</tr>
<tr>
<td>Platycerus carahoides</td>
<td>No preference (Palm 1959)</td>
</tr>
<tr>
<td>Cerambyx cerdo</td>
<td>Prefers sun but not exclusively (Palm 1959)</td>
</tr>
<tr>
<td>Rhyncolus elongatus</td>
<td>No preference (Palm 1959)</td>
</tr>
<tr>
<td>Rhyncolus strangulatus</td>
<td>On pine (Hoffmann 1958)</td>
</tr>
<tr>
<td>Rhyncolus punctulatus</td>
<td>Only in sun (Palm 1959)</td>
</tr>
</tbody>
</table>

3.10.2 Species associated with open ground in the mid-Holocene

Old, unimproved grasslands are perhaps even more under threat than woodland - most sites having been either ploughed or heavily fertilised over the past century. Their insect faunas, however, having evolved to be more mobile because of the transient nature of much of their habitat, annual plants and dung, are perhaps less likely to regional extinction. If clearings in the post-glacial forest were also widespread, if transient habitats, then their insects, should appear in the fossil record alongside the dead wood faunas. They should also occur in peat successions remote from woodland localities. Most species, however, largely disappear between the open ground of the warmer parts of the Late-glacial and Early Holocene and the extensive opening up of the Urwald by people. Some, like the thermophilous steppe genus Leucoclimatium sp. and the weevil Cyphocleonus trisulcatus, feeding on Chrysanthemum leucanthemum, present at Lea Marston in Warwickshire during the Early Holocene (Osborne 1974a), probably also the warmest and most continental part of the present interglacial (cf. Tzedakis 1999) do not return. Others become characteristic of the open landscapes, particularly of the Chalk and limestones, from the Bronze Age onwards, although many had to wait until the Roman period to gain assisted passage to the British Isles. This is the fauna of what Hammond (1974) has termed the cultursteppe. Much of this fauna had also been present during the warmer periods of open ground conditions during Isotope Stage 3 (Coope 2002), but the last Glacial Maximum (Isotope stage 2) is likely to have resulted in a tabula rasa on to which the present biota rapidly immigrated with ameliorating conditions.

Several species which one would regard as primarily inhabitants of old established grassland, do appear to maintain a continuous trace through the Holocene, whilst becoming more common in post-clearance landscapes. The large elaterid Agrypnus murina occurs in pasture
and on woodland margins, where its larvae are predatory on those of Melolontha spp., Phyllopertha horticola and other root feeders in grassland (Horion 1953). It is present in the earliest Holocene at Lea Marston (Osborne 1974a) and West Bromwich (Osborne 1980), both in Warwickshire, and later at Westward Ho in Devon (6810±140 BP) (Girling & Robinson 1987), Bole Ings, Nottinghamshire (<6290±70) (Dinnin 1997), and Church Stretton in Shropshire (pollen zone VIIa) (Osborne 1972) (Table 6). The cockchafer, Melolontha melolontha, whose larvae develop on the roots of grassland in clearings in woodland, is present at West Heath Spa on Hampstead Heath in north London during pollen zone VIIa (Girling 1989b) and at Bole Ings in the Lower Trent valley (Dinnin 1997).

Others fail to maintain a continuous trace, although this might relate to the patchy nature of the fossil record. The heather beetle Lochmaea suturalis is recorded in the late-glacial, but then not again until the late Holocene. The weevil Micrelus ericae has several records from the early Holocene, but then nothing until the Neolithic (Buckland in press).

Osborne (1972), interpreted the insect assemblage from the pollen zone VIIa landscape around the Church Stretton site as one in which “Large herbivores must have been present and it is suggested that this locality was occupied by grassland.” He preferred to regard this as evidence of early human impact, but the associated dung fauna, largely Aphodius spp., extends back to early in the pollen zone, when it is unlikely there were settled human populations. The pollen diagram from the same site (Rowlands & Shotton 1971) is too summary to provide much additional information, and the absence of 14C dates casts some doubts on the exact position of the zonal boundaries. However, the major fluctuations in Arboreal Pollen/Non-Arboreal Pollen ratios before the decline in elm support Osborne’s
contention and are matched in a diagram from Marton, 11 miles NW of Church Stretton. In
terms of fossil insect assemblages, this group of sites, lying immediately east of the
Longmynd, is unique in that they provide an indication of the pre-clearance uplands away
from the developing landscapes of large floodplains and upland and lowland raised mires,
where most faunas have been examined (cf. Dinnin 1997; Panagiotakopulu 2004).

Table 6. Open ground species from the mid-Holocene (Carabid habitat data from Andersen
2000)

(For key to sites, see Appendix 1)

<table>
<thead>
<tr>
<th>Species</th>
<th>Mid-Holocene</th>
<th>Interglacial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carabus granulatus</td>
<td>Ming</td>
<td>De (OIS5e); SG (OIS7)</td>
</tr>
<tr>
<td>Nebria brevicollis</td>
<td>CS</td>
<td>Wool (OIS5e); Camb; SH (OIS7)</td>
</tr>
<tr>
<td>Loricera pilicornis</td>
<td>CS; Bol; Ming</td>
<td>TS; Itt; Wool; TCP; Aust (OIS5e); SG; Mar; UppS (OIS7)</td>
</tr>
<tr>
<td>Patrobus atrorufus</td>
<td>Ming</td>
<td>Itt (OIS5e); Ave; Cam; Mar; UppS; TT (OIS7)</td>
</tr>
<tr>
<td>Pterostichus niger</td>
<td>West</td>
<td>TS; Shr; Wool (OIS5e); Mars; TT (OIS7)</td>
</tr>
<tr>
<td>Harpalus sabulicola</td>
<td>West</td>
<td></td>
</tr>
<tr>
<td>Agriotes obscurus</td>
<td>Bol</td>
<td></td>
</tr>
<tr>
<td>Agrypnus marina</td>
<td>West; Bol; CS</td>
<td>TS; Els; Itt; Shr; De (OIS5e); Ave (OIS7)</td>
</tr>
<tr>
<td>Cantharis rustica</td>
<td>WilG</td>
<td>Ave; Mar (OIS7)</td>
</tr>
<tr>
<td>Serica brunnea</td>
<td>WilG</td>
<td>Ave; Mar (OIS7)</td>
</tr>
<tr>
<td>Phyllopertha horticola</td>
<td>WilG</td>
<td>Ave; Mar (OIS7)</td>
</tr>
<tr>
<td>Otiorhynchus ligustici</td>
<td>CS</td>
<td></td>
</tr>
<tr>
<td>Alyphus triguttatus</td>
<td>CS</td>
<td>Shr (5e); Cam; Mar; SH; US (OIS7)</td>
</tr>
<tr>
<td>Ceuthorhynchidius troglodytes</td>
<td>Bol</td>
<td></td>
</tr>
</tbody>
</table>

In the uplands, Simmons (1975; 1996) has long argued that Mesolithic hunters had significant
impact on the vegetation, and Bush (1988) has advanced similar arguments for the Chalk of
East Yorkshire, incorporating insect evidence in the presence of the grassland scarabaeids
Phyllopertha horticola and Serica brunnea and the cantharid Cantharis rustica with data
from pollen and plant macrofossils. It is unfortunate however, that there is a major hiatus in
Bush’s Willow Garth succession between ca. 8290±80 and 3970±50 BP, so that habitat
continuity from the early Holocene cannot be demonstrated; the insect faunas were also not
examined in detail. Another large chafer beetle, Valgus hemipterus, appears in Neolithic
deposits at the South Stanwick long barrow in Northamptonshire, where Robinson (2000)
thinks that it may have been breeding in the decaying stumps of a recently cleared landscape.
Now extinct in Britain, it is likely to have formed part of the natural fauna of forest clearings.

Despite largely intuitive attempts by Robinson (1991) to interpret faunas in terms of
percentage habitat represented, it remains difficult to view insect assemblages in the same
manner as pollen diagrams (Smith and Whitehouse 2005), but see Figures 5, 7 & 8. The fossil
insect faunas, however, do suggest high levels of open ground in the early Holocene and from
the Neolithic onwards, with a limited presence during the mid-Holocene.
3.10.3 The dung fauna

The insect fauna of herbivore dung is widely dispersed, and provides a trace for the large herbivores in the absence of a direct fossil record. Many species, however, are able to exploit analogous accumulations of rotting plant debris, and occasional records of these have to be treated circumspectly. The scarabaeoid beetles which feed in dung are specific to the depositional environment of the faeces, rather than the vertebrate species of origin. Thus, whilst *Aphodius zenkeri* is normally found in deer droppings, it is the shaded habitat provided by forest or pasture woodland that is being exploited. The species is as likely to be in sheep, pony or cattle dung when these domestic animals are grazed in woodland localities (Landin 1961). Its present apparent expansion in range may relate to increasing deer populations providing more dung habitats in shaded locations (Skidmore, pers. comm.).

Most of the scarabaeoid dung fauna first appear in the Neolithic, and the record is thereafter heavily biased towards research upon samples from archaeological sites. The earliest Holocene records for *Aphodius zenkeri* for example, are from the Late Holocene at Langford in Nottinghamshire, *ca.* 4000 BP (Howard and others 1999) and Stileway in the Somerset Levels, *ca.* 4470 ± 70 BP (Girling 1985). The large assemblage recovered by Osborne (1969; 1989) from the Late Bronze Age well at Wilsford, is one of the few assemblages from the Chalk, and adds several members of the dung fauna to the list, including large numbers of individuals of *A. quadriguttatus*, now extinct in Britain. A few sites, have mid-Holocene records at the generic level for *Aphodius sp*, including Church Stretton in Shropshire where there is a continuous trace through pollen zones V1c and V1a (Osborne 1972). However, at the species level, only *Aphodius rufipes*, has been recorded between the Lateglacial and the Neolithic, at Mingies Ditch in Oxfordshire in deposits of 6540±80 BP (Robinson 1993). Jessop (1986) records *A. rufipes* as a cuckoo parasite of *Geotrupes spiniger*, and so it is probable that this species was also present. *A. rufipes* is however fairly eurytopic and flies readily, but it avoids open ground. Koch (1989) notes it particularly from clearings in woodland and on pastures near woods, so it may suggest a small-scale mosaic of woodland and grassland rather than extensive open areas.
Table 7. Earliest Holocene and Interglacial records for the scarabaeoid dung fauna
For key to sites, see Appendix 1

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Holocene</th>
<th>Interglacial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Typhaeus typhoeus</td>
<td>Wil – 3060 BP (LBA)</td>
<td></td>
</tr>
<tr>
<td>Geotrupes mutator</td>
<td></td>
<td></td>
</tr>
<tr>
<td>G. spiniger</td>
<td>ST – 5150 BP</td>
<td></td>
</tr>
<tr>
<td>G. stercorarius</td>
<td>TatT – 2350 BP (IA)</td>
<td></td>
</tr>
<tr>
<td>G. stercorosus</td>
<td>SLoch – Mid Holocene?</td>
<td></td>
</tr>
<tr>
<td>G. vernalis</td>
<td>ST – 5150 BP</td>
<td></td>
</tr>
<tr>
<td>G. pyrenaenus</td>
<td>ST – 5150 BP</td>
<td></td>
</tr>
<tr>
<td>+ Caccobius schreberi</td>
<td>SS – ~ 4500 BP</td>
<td>TS; Ips; Els; Shr; Wool; De (5e)</td>
</tr>
<tr>
<td>Onthophagus taurus</td>
<td>Run - &lt; 5400 BP (Neol.)</td>
<td>TS; Ips; Els; De (5e)</td>
</tr>
<tr>
<td>O. verticicornis</td>
<td>Wil – 3160 BP (LBA)</td>
<td>TS; Els; Wool; De (5e)</td>
</tr>
<tr>
<td>O. joannae</td>
<td>ST – 5150 BP</td>
<td></td>
</tr>
<tr>
<td>O. nuchicornis</td>
<td>TatT – 2350 BP</td>
<td>TS (5e)</td>
</tr>
<tr>
<td>O. vacca</td>
<td>Wil – 3160 BP (LBA)</td>
<td>TS; Wool; TCP (5e)</td>
</tr>
<tr>
<td>O. fracticornis</td>
<td>Sil – 4750</td>
<td></td>
</tr>
<tr>
<td>O. similis</td>
<td>CS – Zone VIIb</td>
<td></td>
</tr>
<tr>
<td>O. coenobia</td>
<td>Wil – 3160 BP (LBA)</td>
<td>TCP (5e)</td>
</tr>
<tr>
<td>Onthophagus sp.</td>
<td>CS – Zone VIIa</td>
<td>Max; Wool; TCP (5e)</td>
</tr>
<tr>
<td>Aphodius fuscor</td>
<td>Sil - 4750 BP</td>
<td>TS; Itt; De (5e); SG; SH; US;</td>
</tr>
<tr>
<td>A. haemorrhoidalis</td>
<td>Run - &lt; 5400 BP (Neol.)</td>
<td></td>
</tr>
<tr>
<td>A. brevis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. arenarius</td>
<td>Wil – 3160 BP</td>
<td></td>
</tr>
<tr>
<td>*A. rufipes</td>
<td>Ming – 6540 BP</td>
<td>Itt; De (5e)</td>
</tr>
<tr>
<td>A. juridus</td>
<td>ST – 5150 BP</td>
<td></td>
</tr>
<tr>
<td>A. depressus</td>
<td>West – 4840 BP</td>
<td>Shr; (5e) SH (7)</td>
</tr>
<tr>
<td>A. zenkeri</td>
<td>Lang – 4000 BP</td>
<td></td>
</tr>
<tr>
<td>A. pusillus</td>
<td>Sil – 4750 BP</td>
<td></td>
</tr>
<tr>
<td>A. coenosus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>+A. quadrigruttatus</td>
<td>Wil – 3160 BP</td>
<td></td>
</tr>
<tr>
<td>A. quadririmaculatus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. sticticus</td>
<td>Bol - &lt; 6290 BP</td>
<td></td>
</tr>
<tr>
<td>A. consparcatus</td>
<td>Brigg – 3000 BP</td>
<td></td>
</tr>
<tr>
<td>A. distinctus</td>
<td>Wil – 3160 BP</td>
<td></td>
</tr>
<tr>
<td>A. paykulli</td>
<td>Bart – Late Roman</td>
<td></td>
</tr>
<tr>
<td>A. obliteratus</td>
<td>TatT – 2350 BP (IA)</td>
<td></td>
</tr>
<tr>
<td>A. contaminatus</td>
<td>Pil – 2900 BP</td>
<td></td>
</tr>
<tr>
<td>A. sphacelatus</td>
<td>Sil – 4750 BP</td>
<td></td>
</tr>
<tr>
<td>A. prodromus</td>
<td>Sil – 4750 BP</td>
<td></td>
</tr>
<tr>
<td>A. consputus</td>
<td>ST – 5150 BP</td>
<td>TS; Shr; De (5e)</td>
</tr>
<tr>
<td>A. porcus</td>
<td>Run - &lt; 5400 BP</td>
<td>De; TCP (5e)</td>
</tr>
<tr>
<td>A. scrofa</td>
<td>WHS – Zone VIIa/b</td>
<td></td>
</tr>
<tr>
<td>A. merdarius</td>
<td>TatT – 2350 BP (IA)</td>
<td></td>
</tr>
<tr>
<td>A. foetidus</td>
<td>Run - &lt; 5400 BP</td>
<td></td>
</tr>
<tr>
<td>A. lapponum</td>
<td>SLoch - ?Mid Holocene</td>
<td></td>
</tr>
<tr>
<td>A. finetarius</td>
<td>LS – Zone VIIa</td>
<td>Shr (5e)</td>
</tr>
<tr>
<td>A. foetens</td>
<td>Brigg – 3000 BP</td>
<td></td>
</tr>
<tr>
<td>A. fasciatus</td>
<td>TinT – 3060 BP</td>
<td>SH (7)</td>
</tr>
<tr>
<td>A. ater</td>
<td>TatT – 2350 BP (IA)</td>
<td></td>
</tr>
<tr>
<td>A. constans</td>
<td>Wil - 3160 BP (LBA)</td>
<td></td>
</tr>
<tr>
<td>A. borealis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. mentalis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. sordidus</td>
<td>TinT-3060 BP</td>
<td></td>
</tr>
<tr>
<td>A. ictericus</td>
<td>Wil – 3160 BP (LBA)</td>
<td></td>
</tr>
<tr>
<td>A. rufus</td>
<td>ST – 5150 BP</td>
<td></td>
</tr>
<tr>
<td>A. plagius</td>
<td>Go - (IA)</td>
<td></td>
</tr>
<tr>
<td>A. niger</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. varians</td>
<td>Run – (BA)</td>
<td></td>
</tr>
<tr>
<td>A. lividus</td>
<td>Emp – (Rom)</td>
<td></td>
</tr>
<tr>
<td>A. granarius</td>
<td>ST – 5150 BP</td>
<td></td>
</tr>
<tr>
<td>+ Aphodius sp.</td>
<td>CS</td>
<td></td>
</tr>
</tbody>
</table>
Table 8. Earliest Holocene records of other species associated with dung (probable Roman or later introductions excluded)

For key, see Appendix I

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Earliest Holocene</th>
<th>Interglacial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cercyon atomarius</td>
<td>Run - &lt; 5400 BP</td>
<td></td>
</tr>
<tr>
<td>C. haemorrhoidalis</td>
<td>Run - &lt; 5400 BP</td>
<td></td>
</tr>
<tr>
<td>C. melanocephalus</td>
<td>Wil – 3160 BP (LBA)</td>
<td>Itt; Shr (5e); Ave; Cam; SG; Mars; SH; US (7)</td>
</tr>
<tr>
<td>C. lateralis</td>
<td>Drag – (Rom)</td>
<td></td>
</tr>
<tr>
<td>C. atricapillus</td>
<td>Run – (LBA)</td>
<td></td>
</tr>
<tr>
<td>C. terminatus</td>
<td>Run – (LBA)</td>
<td></td>
</tr>
<tr>
<td>C. pygmaeus</td>
<td>Run - &lt;5400 BP</td>
<td></td>
</tr>
<tr>
<td>Megasternum boletophagum</td>
<td>CS zone VIIa</td>
<td>Itt; Shr; Wool; De; TCP (5e); Ave; Cam; Mars; US; TT (7)</td>
</tr>
<tr>
<td>Cryptopleurum minutum</td>
<td>CS zone VIIa</td>
<td>Itt; Shr; De (5e); Ave; Cam; SG; Mars; US;</td>
</tr>
<tr>
<td>Sphaeridium bipustulatum</td>
<td>Run - &lt;5400 BP</td>
<td>TS; Shr; Wool; De (5e); SG (7)</td>
</tr>
<tr>
<td>Hister bisexstriatus</td>
<td>Run &lt; 5400 BP</td>
<td></td>
</tr>
<tr>
<td>Oxytelus piceus</td>
<td>BS – (BA)</td>
<td>Wool (5e);</td>
</tr>
<tr>
<td>O. laqueatus</td>
<td>CS – zone VIIa</td>
<td></td>
</tr>
<tr>
<td>Anotylus sculpturatus</td>
<td>ST – 5150 BP</td>
<td>TS (5e); US (7)</td>
</tr>
<tr>
<td>A. complanatus</td>
<td>Bol - &lt; 6290</td>
<td>SG (7)</td>
</tr>
<tr>
<td>A. tetracarinatus</td>
<td>Brigg – 2600 BP</td>
<td></td>
</tr>
<tr>
<td>Platystethus arenarius</td>
<td>Ming – 6540 BP</td>
<td>De; TCP (5e); Cam; SG; Mars; US (7);</td>
</tr>
<tr>
<td>Leptacinus batychrus</td>
<td>Run – (BA)</td>
<td></td>
</tr>
<tr>
<td>Gyrohypnus punctulatus</td>
<td>Shu – 4830 BP</td>
<td>TS (5e); SG (7)</td>
</tr>
<tr>
<td>G. fracticornis</td>
<td>Shu – 4830 BP</td>
<td></td>
</tr>
<tr>
<td>G. angustatus</td>
<td>Run - &lt; 5400</td>
<td>Au (5e)</td>
</tr>
<tr>
<td>Xantholinus glabratus</td>
<td>Sil – 4750 BP</td>
<td></td>
</tr>
<tr>
<td>Philonthus laminatus</td>
<td>Brigg – 2600 BP</td>
<td></td>
</tr>
<tr>
<td>P. politus</td>
<td>Eil – (Neo.) (then Rom.)</td>
<td></td>
</tr>
<tr>
<td>Ontholestes tesselatus</td>
<td>Fish – (IA)</td>
<td></td>
</tr>
<tr>
<td>O. marinus</td>
<td>Cald – zone VII</td>
<td></td>
</tr>
<tr>
<td>Platydraucus fulvipes</td>
<td>TM - &lt; 4500 BP</td>
<td></td>
</tr>
<tr>
<td>P. stercorarius</td>
<td>Abb – (Neo.)</td>
<td></td>
</tr>
<tr>
<td>P. pubescens</td>
<td>Wil – 3160 BP (LBA)</td>
<td></td>
</tr>
<tr>
<td>Quedius fuliginosus</td>
<td>TM - &lt; 4500 BP</td>
<td></td>
</tr>
<tr>
<td>Tachinus signatus</td>
<td>Shu – 4830 BP</td>
<td></td>
</tr>
<tr>
<td>T. marginellus</td>
<td>Shu – 4830 BP</td>
<td></td>
</tr>
<tr>
<td>Autalia rivularis</td>
<td>TM – 3000 BP</td>
<td></td>
</tr>
<tr>
<td>Tinotus morion</td>
<td>Brigg – 2600 BP</td>
<td></td>
</tr>
</tbody>
</table>

For the remainder of the essentially obligate dung fauna, the Church Stretton borehole provides the most hints of the presence of large herbivores in the mid-Holocene. The histerid Onthophilus striatus, appears in a sample spanning the pollen zone VIIa/b boundary, and in the absence of any evidence for proximity of human occupation, it seems likely to be related to dung from wild herbivores; Skidmore (1991) records it largely from horse dung in Britain, although it is known from a wider range of habitats on the Continent (Koch 1989; see also Donisthorpe 1939). The more eurytopic hydrophilid Megasternum boletophagum, which Skidmore (1991) notes in large numbers in herbivore dung, also occurs early in zone VIIa at
Church Stretton, with *Cryptopleurum minutum*, also often in dung, from the overlying sample.

The dung beetles therefore support the presence of large herbivores, possibly locally abundant, but also indicate that they became more abundant from the Neolithic onward.

### 3.10.4 The carrion fauna

Another index of the presence of large mammals would be a fauna associated with their dead. No significant elements of the large carrion fauna have been recorded from deposits, which pre-date extensive forest clearance (Table 9), but even previous interglacials, despite their more abundant large herbivore record, do not include a rich carrion assemblage. Whether the dermestid *Dermestes laniarius* should be regarded as part of this fauna is doubtful, since it occurs in both carrion and vegetable debris on open and arable ground (Koch 1989). Now extinct in Britain, it is recorded from Late Bronze Age Wilsford in Wiltshire (Osborne 1969) and the last interglacial site at Trafalgar Square in London (Coope 2001). Its present distribution tends to be more continental and it is probable that it is a victim of the oscillation towards a more oceanic climate during the Late Holocene. Its presence, however, raises an interesting question with regard to its origin – anthropochorous or survivor from the early Holocene steppe fauna?

**Table 9.** Earliest Holocene records of large carrion fauna

For key, see Appendix I

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Earliest Holocene</th>
<th>Interglacial</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nicrophorus humator</em></td>
<td>Whit – (Rom)</td>
<td></td>
</tr>
<tr>
<td><em>Necrodes littoralis</em></td>
<td>Brigg – 2600 BP</td>
<td></td>
</tr>
<tr>
<td><em>Thanatophilus rugosus</em></td>
<td>Wil – 3160 BP (LBA)</td>
<td></td>
</tr>
<tr>
<td><em>T. simatus</em></td>
<td>Wil – 3160 BP (LBA)</td>
<td></td>
</tr>
<tr>
<td><em>Dermestes lardarius</em></td>
<td>Run - (BA)</td>
<td></td>
</tr>
<tr>
<td><em>Omosita discoidea</em></td>
<td>Run – (BA)</td>
<td></td>
</tr>
<tr>
<td><em>O. colon</em></td>
<td>Run – (BA)</td>
<td></td>
</tr>
<tr>
<td><em>Nitidula bipunctata</em></td>
<td>Wil – 3160 BP (LBA)</td>
<td></td>
</tr>
</tbody>
</table>

### 3.10.5 The interglacial record

In terms of analogues for a warmer Holocene, the previous interglacial, the Ipswichian (Eemian), Isotope Stage 5e, with summer temperatures of the order of 3°C warmer than present on the fossil beetle evidence (Coope & Beesley 1987), provides interesting parallels (Figure 6). In contrast with the interglacial before that, Isotope Stage 7, there is no evidence for the presence of hominids in the British Isles, yet abundant evidence of open ground taxa at the period of maximum warmth and forest expansion. Species which are particularly favoured by human activity, such as the ground beetles *Calathus fuscipes* and *Pterostichus melanarius*, are present, and there is a remarkable suite of dung beetles, including the presently Sicilian ‘endemic’ *Onthophagus massai*, from several sites. The invertebrate fauna and the flora in part reflect the presence of large herbivores, elephant, rhinoceros and hippopotamus (Turner 1975), which fail to return in the present interglacial, but the warmer nature of the maximum is also apparent. Rackham’s (1998) view of temperate savannah is more appropriate for this interglacial; the frequency of the dung fauna and the large chafer *Valgus hemipterus* indicate a parkland landscape rather than closed forest.
In the present interglacial, the open ground taxa are less evident in the early – mid-Holocene record, although in part this may reflect the paucity and nature of sites examined. Continuous sequences through much of the Holocene are only available from Church Stretton (Osborne 1972) and Bole Ings (Dinnin 1997). These sites have problems because of the limited sample size from the available boreholes. The trace, however, is sufficient to provide some support for Vera’s hypothesis on the variegated nature of Holocene forests, but the incidence of natural fire, particularly in regions on poor soils still dominated by pine, rather than Mesolithic pyromania, should also be reconsidered.

**Figure 6.** Interglacial sites with insect faunas (Sites referred to in the text are labelled).
3.10.6 Insect evidence for fire

Although openness associated with major wind-throw or disease events may not be easily defined in the palaeoecological record, fire is often evident in the charcoal record, and there are elements in the insect fauna which specialise in burnt-over woodland. Tidy deciduous forest with little dead wood may not be particularly flammable, but return the dead wood with many standing moribund trees and the recipe for occasional lightning-struck fires becomes available (Moore 1996). This would provide habitat for a range of insects, which have evolved to exploit this transient habitat.

Whitehouse and Eversham (2002) have recently discussed the fossil record of the pyrophilic carabid *Pterostichus angustatus* from Hatfield Moors, South Yorkshire, and pointed out the problems of habitat continuity for such species through the mid-Holocene, a point equally valid for even more fire-dependent species (*cf.* Wikars 1992), such as the buprestid *Melanophila acuminata* (Danks & Footit 1989; Palm 1951), apparently now largely restricted to the Surrey heaths in Britain (Levey 1977; Alexander 2002), yet omitted from the Red Data Book lists (Hyman 1992; 1994). The absence of fire-related species from previous interglacials may be significant in terms of the extent of human interference in the landscape in the Holocene.

Table 10. Fossil record of species associated with burnt woodland, habitat data from Lundberg (1984) and Wikars (1992)

(For key to sites, see Appendix 1)

<table>
<thead>
<tr>
<th>Species</th>
<th>Holocene</th>
<th>Interglacial</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pterostichus oblongopunctatus</em></td>
<td>HoC; Ming.</td>
<td></td>
</tr>
<tr>
<td><em>P. angustatus</em></td>
<td>Hat.</td>
<td></td>
</tr>
<tr>
<td><em>Dromius spilitus</em></td>
<td>Bol.</td>
<td></td>
</tr>
<tr>
<td><em>Micropeplus tesserula</em></td>
<td>LeaM.</td>
<td></td>
</tr>
<tr>
<td><em>Henoticus serratus</em></td>
<td>World.</td>
<td></td>
</tr>
<tr>
<td><em>Litargus connexus</em></td>
<td>Lang.</td>
<td></td>
</tr>
<tr>
<td><em>Synchita humeralis</em></td>
<td>West.</td>
<td></td>
</tr>
<tr>
<td><em>Ditoma crenata</em></td>
<td>LeaM.</td>
<td></td>
</tr>
<tr>
<td><em>Salpingus ater</em></td>
<td>Bol.; SLoch</td>
<td></td>
</tr>
<tr>
<td><em>Rhinocinus planirostris</em></td>
<td>Bol.;</td>
<td></td>
</tr>
<tr>
<td><em>Schizotus pectinicornis</em></td>
<td>HoC.</td>
<td></td>
</tr>
<tr>
<td><em>Platystomos albino</em></td>
<td>Ming.</td>
<td></td>
</tr>
</tbody>
</table>

3.10.7 Taphonomic problems

Vera (2000) has argued that there are serious taphonomic issues in the interpretation of the mid-Holocene pollen record, including the nature of modern analogues used in interpretation. Suppression of flowering of grasses by intensive grazing pressure and the poor pollen productivity of many understorey shrubs, would lead to an under-representation of the open ground components. His arguments have been vigorously countered by some palynologists and woodland historians (*cf.* Bradshaw & Mitchell 1999; Rackham 2003), but there remain several issues, which also affect the insect record. The Neolithic and later record is heavily biased towards archaeological sites and therefore the dung fauna, associated with domestic stock is strongly represented. Those sites which sample the fauna away from the archaeology of occupation sites, however, like Late Holocene Thorne and Hatfield Moors in south...
Yorkshire, for example (Buckland 1979; Roper 1996; Boswijk & Whitehouse 2002; Whitehouse 2004), contain few dung beetles or open ground indicators. In the Late Holocene, as these sites evolved from poor fen to raised mire (Buckland & Smith 2003), the faunas show little if any evidence of the adjoining landscapes, whereas the pollen record from the bogs and aerial photographic evidence shows extensive clearance taking place by the Iron Age (Riley 1980; Smith 2002).

At least in part this problem must be related to the fact that dispersal for most species, which are not passively part of the aerial plankton (sensu Crowson 1981) is not a random process: sites where accumulation takes place need not reflect places where open ground is likely to occur. There are currently no pre-Neolithic sites, for example, actually on Chalk, Carboniferous, Permian or Jurassic limestone outcrops for comparison. In a series of fossil insect studies in Skåne, southern Sweden, Lemdahl (2002) has examined a range of Holocene sites and noted the varied nature of the woodland at each, although the detail has yet to be published. In Britain, Smith (1970) had come to similar conclusions on palynological grounds (see also Smith & Whitehouse 2005).

Short of funding and sampling a wider range of sites there is no way round this problem. Either we work with the data we have, being aware of the limitations, or we reject the approach altogether. It is not reasonable to pick and choose accepting results which fit one scenario while simultaneously rejecting as biased as all those that do not.

![Figure 7](image.png)

**Figure 7.** Habitat groups for the insect faunas from beneath the Neolithic mound at Silbury Hill, Wiltshire. Sample number is indicated on the left, most recent at the top, oldest at the bottom. The horizontal axis represents the percentage of each habitat grouping (R1-R13) reflected in the faunas. Where a species occurs in more than one habitat grouping, the percentage is apportioned accordingly. The right hand column gives the number of individuals in each sample.

### 3.11 Other factors

During the mid-Holocene, wind damage, outbreaks of insect pests and disease, and occasional flood events may have been effective in opening up the canopy.
Dendrochronology has some potential in examining major storm events, although this has rarely been linked with other studies. Allen (1992) has looked at the direction of wind thrown trees in mid-Holocene foreshore sediments in the Severn Estuary, and related these to storminess. In North America, a massive die-back in hemlock during the mid-Holocene has been linked to insect attack (Bhiry & Filion 1996). In Western Europe, the Elm Decline around the Mesolithic Neolithic transition continues to excite discussion (Parker and others 2002; Clark & Edwards 2004; Buckland and others 2004), with an explanation, which relies upon climatic stress, perhaps drought, leading to increased vulnerability of elms to scolytid attack, followed by human opportunism in moving into the naturally opened up areas, appearing the most probable. Flood events, related to either increased runoff as a result of clearance in the upper reaches of catchments or to raised water tables leading to paludification, are not uncommon in the Holocene record, and Buckland (1979; Buckland & Sadler 1985; Buckland & Smith 2004) has suggested that lowland raised mires at Thorne Moors, and elsewhere, may owe their origins to such processes, although again the driving force is likely to have been anthropogenic (see also Simmons 1996).

3.12 Biogeographic considerations

The main island of Britain ceased to be a part of the Continent at roughly the time that Atlantic forest (whether open or closed) became the dominant vegetation form (Preece 1995). Thereafter, additions to the insect fauna were increasingly restricted to those taxa able to fly (or be blown) across the Channel, and those able to travel as uninvited guests with human colonists and traders (Hammond 1974; Buckland 1991). ‘Rafts’ of logs and vegetation washed out by floods would also have been much more common that at present. Although few sites have been examined, the Neolithic insect record shows that open and disturbed ground species start to appear immediately after forest clearance (Robinson 2000). Most of these species probably already formed part of the native biota, rather than being introduced in the boats of the first settlers, although their previous abundance may have been low. Andersen (2000) has argued that much of the ground beetle, Carabidae fauna, which has been able to exploit man-made habitats originated in ephemeral wetlands, bare ground at the edge of rivers and lakes, and such habitats would have been present, if more restricted before forest clearance. This is evident in the mid- to Late Holocene assemblages from Runnymede, on the Thames in Berkshire (Robinson 1991). The extent of the dry, open ground fauna beneath the Neolithic mound at Silbury Hill in Wiltshire at 4530 ± 110 (Robinson 1997) (Figure 7) also suggests that much of this element is indigenous, rather than anthropochorous. Although the number of sites examined remains small, the evidence from West Heath Spa on Hampstead Heath, summarised in Figure 8, indicates the scale of immediate impact of Neolithic clearance on the native Coleopterous fauna.
Figure 8. Changes in insect faunal composition across the Pollen Zone VIIa/b boundary at West Heath Spa, Hampstead Heath, London. Sample number is indicated on the left, most recent at the top, oldest at the bottom. The horizontal axis represents the percentage of each habitat grouping (R1-R13) reflected in the faunas. Where a species occurs in more than one habitat grouping, the percentage is apportioned accordingly. The right hand column gives the number of individuals in each sample.

Table 11: Species first recorded in the Neolithic

For key to sites, see Appendix 1
Approaching from a different viewpoint, Piper and Compton (2003) have described both genetic and ecological differences in isolated populations of several species of the chrysomelid genus *Cryptocephalus*. Most appear to have limited dispersal ability, despite their transient habitat, and are restricted to the ecotone between grassland and woodland. This could be interpreted in support of the Vera hypothesis, several species requiring virtually continuous edge habitats in the mid-Holocene forest to achieve their present distribution pattern, but it is equally probable that most species were able to disperse widely during the warmer part of the early Holocene, when such habitats were virtually continuous, and that their genetic divergence reflects population fragmentation by mature forest expansion. As in the case of the xerophilous heathland carabid *Pterostichus kugelanni*, recently discussed by Buckland (in press), however, some relatively permanent forest edge and open ground localities must have existed through much of the Holocene close to their present refuges. Unfortunately none of the key sites have a Holocene fossil insect record, and only three species of *Cryptocephalus*, *C. hypochaeridis* (L.) from Iron Age deposits at Mingies Ditch in Oxfordshire (Robinson 1993) *C. labiatus* (L.) from Lateglacial Low Wray Bay in Cumbria (Coope 1977) and *C. moraei* (L.) from Lateglacial Rodbaston in Staffordshire (Ashworth 1973) and Late Bronze Age Runnymede in Surrey (Robinson 1991), have been found as fossils.

The fine detail of present distributions often appears random, the chances of survival being related to individual site histories, about which often little is known, and the fossil record often throws up unexpected changes in distribution and frequency. An example is provided by the Maybug, *Melolontha melolontha*. Its congener *M. hippocastani*, now rare and restricted in Britain to the uplands of the west and north (Hyman 1992), appears in the Early Holocene in the Midlands (Osborne 1974a, 1980) and then in the Bronze Age at Wilsford in Wiltshire (Osborne 1969), Iron Age in Lincolnshire (Chowne and others 1986) and early medieval period at Conisbrough, south Yorkshire (Buckland and others in prep.). The larvae of both species are root feeders in old grassland, and both might be expected to survive in unploughed wood pasture. Horion (1953), however, provides a clue as to why *M. hippocastani* might have declined. Oviposition preferably takes place in loose, recently disturbed ground. Could its decline be related to the disappearance of wild boar and free-range feral pig?

### 3.13 Conclusions

#### 3.13.1 Implications for modern landscape management for nature conservation

Much has yet to be learnt about the nature of ‘natural’ woodland, and a more integrated approach to the fossil record is the best approach, based upon a sound knowledge of the present ecology of species. Palaeoecology can also inform decisions on conservation issues, although managers of present reserves rarely have access to the knowledge of the long term past trajectories of their landscapes. It is a problem which needs addressing. Whilst sites like Thorne and Hatfield Moors have been extensively researched for their Late Holocene Coleoptera record (most recently, Whitehouse 2004), similar studies of apparently less damaged habitats, like the New Forest for example, are lacking.

Bakker and others (2004) found that it may not be possible to achieve the necessary levels of regeneration of oak in blackthorn ‘nurseries’ protected from large grazers in the presence of rabbits, an animal introduced to Britain after the Norman Conquest (Yalden 1999). It is
never possible to go back to the past, only to create something new, which can at least be
guided by knowledge of the historical trajectory of individual sites.

This does not mean however that the dynamic nature of the forest system of death and re-
growth, influenced by ‘natural’ grazers and browsers, can be ignored. The insect record does
provide some support for the Vera hypothesis, but the picture is not one of warm temperate
savannah, as appeared in the last interglacial. The reasons for this difference are complex,
but the relative warmth of the Ipswichian, perhaps accompanied by seasonal drought may
have concentrated herbivores on the floodplains, where inevitably most palaeoecological
samples come from. The extinction from the European fauna of elephant, rhinoceros and
hippopotamus would have had a significant impact on the nature of wetland forest, whereas
deer, aurochs and boar in the mid-Holocene were unable to have similar impact.
Anthropogenic impact, if this is the reason for Late Pleistocene overkill of large mammals
rather than climatic impacts, had already started by the early Holocene. The Atlantic forest,
in itself further modified by fire, had perhaps more trees than that of previous interglacials.

The fossil insect evidence in relation to the Vera hypothesis indicates that:

- Species associated with dead wood are common in the early to mid-Holocene, but
decline from the Neolithic onwards.
- Species associated with grassland and other components of ‘open habitats’ do occur,
but are rare in the mid-Holocene, suggesting that there were open areas, but that such
habitats formed a limited part of the overall landscape.
- Open habitat species become more common as humans open up the landscape.
- In comparison with previous interglacials, open habitat species were less common in
the mid-Holocene, because of the absence of mega-herbivores, which may have been
more effective in creating and maintaining open areas.
- The record of pyrophilic species suggests that fire, with or without large herbivores,
may have been a significant factor in creating and maintaining open conditions
- To what extent the incidence of fire reflects natural or human impact remains
uncertain.

3.14 Further research

In terms of examining the nature of the mid-Holocene forest utilising fossil insect faunas, the
major problem is the patchy distribution of sites, and as Vera (pers. comm.) has observed, the
bias of sites towards floodplain and mire localities. The remarkable nature of the few faunas
from the Chalk, with the exception of the Early Holocene sites at Holywell Coombe, near
Folkestone (Coope 1998) and Willow Garth in East Yorkshire (Bush 1988), all post-forest
clearance, implies continuity with earlier faunas, rather than large scale introduction by
Neolithic colonists, who must initially have been relatively few. Pollen diagrams have been
constructed from a number of dolines in the Chalk and others are available from adjacent
sites on Tertiary or older Mesozoic bedrocks (egWatton 1982; 1986; Waller & Hamilton
2000). The problems of the nature of the mid-Holocene forest would perhaps best be served
by a return to these sites to recover more extensive samples for insect and other macrofossil
analysis.
3.15 Acknowledgements

This review results from a reading of Frans Vera’s book and subsequent discussions with him and Keith Kirby of English Nature, to both of whom primary acknowledgment is made. The research was funded by English Nature through ECUS at the University of Sheffield as part of their project to examine ‘naturalistic grazing regimes’, and was designed to provide the longer term framework for management projects. The review is here largely limited to the fossil insect data, and will later be extended to other sources of evidence. The comments of Keith Alexander, Damian Hughes (ECUS), Tim Darvill, Mark Dinnin, James Greig, Eva Panagiotakopulu, Jon Sadler, Philip Buckland (who also prepared the diagrams) and Frans Vera on previous drafts of the text are also acknowledged.

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Appendix I: Key to site name abbreviations

AW = Abbot’s Way, Somerset (Girling 1976)
Al = Alcester, Warks. (Shotton and others 1977)
Ast = Aston Mills, Worcs. (Whitehead 1989)
Au = Austerfield, Notts. (Gaunt and others 1972)
Ave = Averley, Essex (Coope 2001)
Bart = Barton Court Farm, Oxon. (Robinson and others 1984)
BoI = Bole Ings, Notts. (Dinnin 1997)
Brigg = Brigg, Lincs. (Buckland 1981)
BS = Baker Site, Somerset (Girling 1980)
Bre = Breiddin, Clwyd (Buckland and others 2001)
Cald = Caldicott, Gwent (Osborne 1997)
Cam = Histon Road, Cambridge (Coope 2001)
CS = Church Stretton, Salops. (Osborne 1972)
Co = Cowick, W Yorks. (Hayfield & Greig 1989)
Dav = Church Moss, Davenham, Ches. (Hughes and others 2000)
De = Deeping St. James, Lincs. (Keen and others 1999)
Drag = Dragonby, Lincs. (Buckland 1996)
Dro = Droitwich, Worcs. (Osborne 1974b)
Eil = Eilean Domhnuill a Spionnaidh, N Uist (Warsop 2000)
Els = Elsing, Norfolk (Coope 2001)
Emp = Empingham, Rutland (Buckland 1986)
Fish = Fisherwick, Staffs. (Osborne 1979)
Flag = Flag Fen, Cambs. (Robinson 1992)
Go = Goldcliff, Gwent (Smith and others 1997)
Hib = Hibaldstow, Lincs. (Girling, unpubl.)
HL = High Lodge, Suffolk (Coope 1992)
HM = Hatfield Moors, S Yorks. (Whitehouse 2004)
HoC = Holywell Coombe, Kent (Coope 1998)
Ips = Bobbitshole, Ipswich, Suffolk (Coope 2001)
Isle = Isleham, Cambs. (Duffy 1968; Buckland & Kenward 1973)
Itt = Itteringham, Norfolk (Coope 2001)
Lang = Langford, Notts. (Howard and others 1999)
LeaM = Lea Marston, Warks. (Osborne 1974a)
Lei = Leicester (Girling 1984b)
LS = Little Stretton, Salops. (Osborne 1972)
Mar = Marsworth, Bucks. (Murton and others 2001)
Max = Maxey, Cambs. (Davey and others 1991)
Mea = Meare, Somerset (Girling 1979)
Melt = Melton, E Yorks. (Wagner, in Constantine 1994)
MH = Meare Heath, Somerset (Girling 1982c)
Min = Minsterley, Salops. (Osborne 1972)
Ming = Mingies Ditch, Oxon. (Robinson 1993)
Mist = Misterton Carr, Notts (Osborne, in Girling 1982a)
NSea = North Sea floor (Blair 1935)
Pil = Pilgrim Lock, Bidford-on-Avon, Warks. (Osborne 1988)
Radley = Radley, Oxon. (Robinson 1996)
Rams = Ramsey Heights, Cambs. (Harding & Plant 1978)
Rip = Ripon, N Yorks (Howard and others 2000)
RT = Rowland's Track, Somerset (Girling 1977)
Run = Runnymede, Surrey (Robinson 1991)
SG = Stoke Goldington, Bucks. (Green and others 1996)
SH = Stanton Harcourt, Oxon. (Briggs and others 1985)
Shr = Shropham, Norfolk (Coope 2001)
Shu = Shustoke, Warks. (Kelly & Osborne 1965)
Sil = Silbury Hill, Wilts. (Robinson 1997)
SLoch = South Lochboisdale, S Uist, Outer Hebrides (Dinnin 1996)
SS = South Stanwick, Northants. (Robinson 2000).
ST = Sweet Track, Somerset (Girling 1984a)
Stil = Stileway, Somerset (Girling 1985)
Sto = Stourport, Worcs. (Osborne 1996)
TatT = Tattershall Thorpe, Lincs. (Chowne and others 1986)
TCP = Tattershall Castle Pit, Lincs. (Girling 1980b)
TinT = Tinney’s Track, Somerset (Girling 1982)
TM = Thorne Moors, S Yorks. (Buckland 1979; Roper 1996; Whitehouse 1997)
TS = Trafalgar Square, London (Coope 2001)
TT = Tattershall Thorpe, Lincs (Coope 2001)
US = Upper Stensham, Worcs. (de Rouffignac and others 1995)
West = Westward Ho, Devon (Girling & Robinson 1987)
Whit = Whitten, Glamorgans. (Osborne 1981)
WHS = West Heath Spa, London (Girling 1989)
Wil = Wilsford, Wilts. (Osborne 1969)
WilG = Willow Garth, E. Yorks. (Bush 1988)
Wils = Wilsden, Worcs. (Shotton & Coope 1983)
Wool = Woolpack Farm, Fenstanton, Cambs. (Gao and others 2000)
World = Worldsend, Church Stretton, Salops. (Osborne 1972)
4. **Naturalistic grazing and conservation**

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**Foreword**

K J Kirby, English Nature.

There is increasing interest in promoting nature conservation at landscape-scale, making more use of natural processes, and placing less reliance on traditional farming and forestry practices to maintain habitats and species. However how widely are we prepared to set the acceptable limits of change for a site (or landscape) in terms of habitats, species and processes, before we intervene?

In most Sites of Special Scientific Interest there are key features that we wish to maintain and often there are set prescriptions to preserve these features (Box 1a); in contrast the most naturalistic system might impose no limits at all (Box 1c). This latter is not likely to be an option in England, except perhaps with respect to some coastal and marine features. However, there may be sites and landscapes where the limits could be broadened to various degrees (Box 1b). This is sometimes referred to as ‘re-wilding’ and has been extensively discussed in recent issues of ECOS (volume 25, 2004) and in a book from Earthscan and BANC, by Peter Taylor: *Beyond Conservation - a Wildland Strategy* (May 2005).

| (a) | Narrow limits set for a specific site, eg to maintain it as a meadow, a coppice wood, or veteran tree site. |
| (b) | Broader limits set: internal site processes are allowed to determine the outcome, except where intervention is deemed necessary |
| (c) | No limits set. |

**Box 1.** Possible extents of acceptable change in (a) a cultural, (b) a naturalistic and (c) a natural system.
Small areas usually require very tight limits of acceptable change if they are to maintain their interest. In bigger sites there is the option of setting broader limits. An implicit, and very important, assumption, with having a more dynamic system, with broader limits, is that within these limits species, or habitats, or processes may fluctuate quite wildly (or even disappear).

Therefore if we apply the idea of re-wilding and more natural (naturalistic) grazing regimes on conservation areas we are accepting that we cannot also prescribe in detail what vegetation we will end up with. This is a different approach to conservation than has been traditional in both the statutory and non-statutory sectors.

In practice, naturalistic grazing by itself is unlikely to retain the current abundance and range of habitats and species, because most of England is a strongly cultural landscape. If we wish to maintain Hardy's heathland, or the coppice flora of the nineteenth century with its flowers and butterflies, we will probably have to apply models of 19th century regimes.

Nor can we mimic completely original natural conditions that occurred in pre-Neolithic times because environmental conditions and the flora and fauna we have available have all changed.

Nevertheless naturalistic grazing might be used to develop potentially new landscapes, albeit ones that may contain some analogues to both pre-agricultural conditions and those of traditional nineteenth century countryside. In addition they may contribute to a sense of wildness in the countryside.

The part of the study follows from our interest in the ideas proposed by Frans Vera and the experience of the Dutch at their Oostvaardersplassen reserve. Some have advocated that we should set up an English equivalent. Would this be feasible? We asked the consultants to approach the work with few pre-conceptions as to what might or might not be possible under current conditions. We believe it is useful to explore what we might expect under the ‘natural’ approach, even though some outcomes may not be acceptable (or legal) in practice.

To assist our thinking we have taken three ‘case study’ areas: blocks of land where the owners are considering forms of extensive grazing regimes. Applying ideas (in some cases what may be regarded as extreme ideas) as ‘thought experiments’ to real patches of land makes it easier to identify the issues, the benefits and limitations. We are not proposing that these areas should be put under naturalistic grazing. It is up to the respective owners to decide how they wish to take forward their plans. We hope however that our discussions will be helpful to both them and others who are thinking about the use of naturalistic grazing regimes for nature conservation.
4.1 **Summary**

- Naturalistic grazing does not have a formal definition; consequently the term tends to be used loosely. In this report we have attempted to clarify the issue by defining the differences between naturalistic and other forms of extensive grazing for conservation.

- The principal of linking or expanding sites in order to avert the ecological problems, which are often associated with small isolated reserves, is not in question; nor is the utility of extensive grazing for the management of large sites.

- The defining difference between naturalistic grazing and other large, extensively grazed conservation management is in the role of ‘natural processes’. In the naturalistic approach, there is no specified grazing density, instead herbivore populations are resource-limited. Rather than managing towards targets for habitat and species composition, direct management intervention is reduced to a minimum and the natural process is seen as an aim in itself.

- The principal issue raised by the naturalistic grazing concept is the unpredictability of outcomes: if the conservation of natural processes becomes the goal, it is then difficult to define targets and to evaluate development of wild areas. The lack of defined goals is incompatible with current management aims based on targets for species and habitats of conservation concern, which are guided by Biodiversity Action Plans, in order to fulfil obligations agreed in the Convention on Biological Diversity (1992).

- It is not realistic for proponents of naturalistic or wilderness grazing to assume that biodiversity benefits of naturalistic grazing can be forecast by describing the habitats and species found in the landscape that they assume will emerge. In fact there is little theoretical or empirical knowledge allowing prediction of the outcomes of any naturalistic grazing regime.

- Management within ‘acceptable limits to change’ may therefore be more realistic than complete non-intervention, but in areas with high biodiversity this may differ little, if at all, from managing to targets.

- Limits could be set by taking account of both ecological and cultural factors, as well as those imposed on site managers, such as reserve size and ‘completeness’ (ie the range of habitats available), climate change and airborne pollutants. These latter factors impose a limit to how ‘natural’ a system can be, because it will unavoidably be affected by inadvertent human actions.

- Legislative changes would be needed to allow the use of resource-limited herds, and even then, there would be important limits to their potential ‘naturalness’. There are unlikely to be adequately large and networked nature reserves to allow seasonal migration, and the absence of large predators has important consequences for grazing behaviour, and hence ecosystem development.

- It is likely to be very difficult to impose a wilderness ideology on the busy cultural landscapes of Britain, particularly lowland areas. Even in upland areas, it may be the sense of wilderness or ‘naturalness’ that is sought by the public and site managers. This goal is one of landscape management, rather than naturalistic management, because the main aim is to fulfil a deep psychological need for access to places that appear to be in a state of wilderness. Active management, such as the maintenance of unobstructed views will often be necessary to achieve this aim, and this requirement may conflict with stepping back from intervention.
Respondents to the case study questionnaires often expressed an interest in moving away from highly prescriptive target-led management for their landscape-scale projects; however, the potential loss of biodiversity or highly valued habitats was rarely seen as acceptable, and this lead to an impasse for groups and even individuals.

More progress was made when accepting that management is for multiple aims, including active conservation of biodiversity and also landscape management to maintain a sense of wilderness. Confusing these separate objectives may make it more difficult to grasp the exciting opportunities we now have for developing large interconnected nature reserves for the benefit of plants, animals and people.

4.2 Background

In recent years, there has been increasing interest in landscape scale conservation, and even in the possibility of creating ‘new wilderness’ areas. In the early 1990s, the National Parks Review Panel (Edwards 1991) recommended that:

A number of experimental schemes on a limited scale should be set up in the [upland] National Parks, where farming is withdrawn entirely and the natural succession of vegetation is allowed to take its course.

This idea was further explored by a Council for National Parks (CNP) report (Council for National Parks 1998) which considered upland, lowland and coastal areas. Instead of total abandonment, as suggested by Edwards (1991), the CNP report recognised that initial management works followed by low-key management of natural processes would be a more suitable approach for many areas.

These ideas have continued to be developed (Aykroyd 2004; Whitbread & Jenman 1995; Worrell and others 2002). In naturalistic reserves, natural processes could be allowed to operate, without the comparatively tight controls often required by conservation management. They are envisaged as sites where sharp boundaries would be replaced by ecotones, relatively species rich areas where habitats merge. Conservation objectives for these reserves, however, would be much more difficult to define than they are for the cultural landscapes that occupy the majority of the English countryside.

One approach is to use a past landscape as a sort of template. This does not suggest an attempt to recreate the past, but an agreement about standards against which site condition may be judged. In the restoration of “traditional management”, for instance, the landscape of the 19th or early 20th century is implicitly being used as a conservation template. For ‘natural’ or ‘naturalistic’ areas, an appropriate template would need to represent a ‘pristine’ landscape, unaffected by human activity. In north-west Europe, the landscape of the mid-Holocene may be the best reference point: this was just prior to any significant impact by Neolithic peoples (Peterken 1996).

Until recently, it was generally agreed that this mid-Holocene landscape was dominated by closed forest, at least in the lowlands. Recently, this view has been challenged (Vera 2000), and there has been considerable debate about the nature of post-glacial landscapes in north-west Europe (Mitchell 2005; Svenning 2002). Vera (2000) argues that the pre-Neolithic landscape in the lowlands of central and western Europe was not closed woodland but a relatively open park-like mosaic, and that large herbivores were an essential driving force
behind woodland-grassland vegetation cycles. The current state of this debate is summarised in this volume (Hodder & Bullock 2005; Buckland 2005) which concluded that there appears to be reasonable agreement that the mid-Holocene landscape may have been more open than was previously thought, but wood-pasture vegetation would not have necessarily been dominant. Instead, there may have been a mixed landscape including areas with vegetation cycles, and others with more permanent vegetation, including closed forest. Degrees of openness are likely to have varied in different edaphic, topographic, and climatic conditions, but at present there is no clear guidance on the patterns that might have existed.

Irrespective of the outcome of the debate about the nature of past landscapes, the Arcadian image of park-like landscapes and the appealing concept of stepping back from intensive conservation management and ‘allowing nature to take its course’, have generated considerable interest and support (Fenton 2004b; Taylor 1995, 2004, 2005). Vera (2000) advocates re-wilding as the optimal conservation strategy for the maintenance and restoration of biodiversity in Europe. Specifically, this includes the restoration of grazing and browsing by wild large herbivores ie ‘naturalistic’ grazing.

An essential difference between naturalistic reserves and other extensively grazed areas is in the approach to stock management. In a naturalistic approach, herds of large herbivores would be allowed to live almost independent lives, with fluctuating population levels, rather than numbers of animals being maintained at a prescribed stock density. The other major difference from current practice is that targets for species and habitat conservation would deliberately not be applied. Open areas could be allowed to scrub over and forested areas to open out. Clearly, numerous ecological, economic, cultural and welfare implications arise when considering the suitability and practicality of naturalistic grazing schemes. Even in the Netherlands, where the naturalistic grazing concept has been pioneered, there is no consensus on the utility of this approach in conservation (Bakker 2005; Olff and others 1999).

4.3 Objectives

English Nature does not currently have a have a formal policy or position on the subjects of ‘naturalistic grazing’ or ‘rewilding’. Proponents of these approaches suggest that they could yield benefits for nature conservation, but there are also potential barriers and objections to their introduction. This project was therefore set up in 2003 with the following aims:

Overall objective:

- To investigate the issues involved in potential implementation of large-scale naturalistic grazing programmes in England.

Specific objectives:

- To place naturalistic grazing in the context of conservation practices in England and the Netherlands (the latter because this where naturalistic grazing has been pioneered).
- To clarify the conservation aims of ‘naturalistic’ reserves, specifically how these might differ from other nature reserves.
- To critically consider issues that would arise, including the ecological, economic, cultural, welfare and political implications.
To focus on the suitability of specific (upland and lowland) sites. In general, and within the selected sites, to seek expert opinion to explore how the acceptable limits to change in current interest (cultural and ecological) might be determined.

4.4 Grazing and conservation

Large herbivores are of key importance in habitat management through their direct impact on plant communities, e.g., by grazing, trampling, and deposition of excreta, and also through their indirect cascading effects on ecosystem process. As such, they can be seen as keystone species and are one of the most important tools available to conservation managers (WallisDeVries 1998). In the latter part of the 20th century in Western Europe, agricultural intensification in productive areas, and the neglect of more marginal farmland, has resulted in great losses of species diversity. This was due to both over-grazing and under-grazing. Low intensity grazing land on semi-natural grassland and heathland has often been the first to be abandoned (Bakker 1998).

As a result, grazing management has increasingly been reintroduced specifically for the conservation of biodiversity, and a large body of research has developed in the ecology of grazed ecosystems (Eriksson and others 2002; Gardner and others 1997; Palmer 1997; Palmer & Hester 2000; Palmer & Truscott 2003). The science and practice of conservation grazing has been reviewed at length elsewhere. Small and others (1999) for instance, summarise the extent and success of conservation grazing in England. This review drew together the experience and expertise of land managers to identify constraints to the implementation of sustainable grazing schemes. Other valuable information is documented in habitat specific reviews of grazing for conservation management (examples in Table 1). There is also considerable current research interest in the ecology of grazing by large herbivores in the UK (Table 2).

**Table 1. Examples of conservation grazing reviews in the UK**

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Author / date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blanket Bog / Upland Wet Heath</td>
<td>Shaw and others (1996)</td>
</tr>
<tr>
<td>Fen</td>
<td>Tolhurst (1997)</td>
</tr>
<tr>
<td>Moorland</td>
<td>Palmer &amp; Hester (2000), Smallshire and others (1997)</td>
</tr>
<tr>
<td>Parkland</td>
<td>Cox &amp; Sanderson (2001)</td>
</tr>
<tr>
<td>Peatland</td>
<td>Bokdam and others (2002)</td>
</tr>
<tr>
<td>Sea Cliffs and Dunes</td>
<td>Oates and others (1998)</td>
</tr>
<tr>
<td>Wood Pasture</td>
<td>Holl &amp; Smith (2002)</td>
</tr>
<tr>
<td>Uplands</td>
<td>Thompson &amp; Kirby (1990)</td>
</tr>
<tr>
<td>General review (UK and elsewhere)</td>
<td>GAP Breed Profiles Handbook           WallisDeVries and others (1998)</td>
</tr>
<tr>
<td></td>
<td>Small and others (1999)</td>
</tr>
<tr>
<td></td>
<td>Bullock &amp; Armstrong (2000)</td>
</tr>
<tr>
<td></td>
<td>Vera (2000)</td>
</tr>
<tr>
<td></td>
<td>Redecker and others (2003)</td>
</tr>
</tbody>
</table>
Table 2. Examples of relevant academic research that is ongoing in the UK

<table>
<thead>
<tr>
<th>Title</th>
<th>Institute</th>
<th>Contact</th>
<th>Completion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbivore browsing and woodland regeneration; processes of change under different environmental conditions.</td>
<td>Macaulay Institute</td>
<td>Alison Hester</td>
<td>March 2008</td>
</tr>
<tr>
<td>The behavioural determinants of the redistribution of nutrients in grazed, semi-natural ecosystems and the influence on soil-chemistry and vegetation community structure.</td>
<td>Macaulay Institute</td>
<td>Angela Sibbald</td>
<td>March 2008</td>
</tr>
<tr>
<td>The distribution of large herbivores in the landscape: predicting the behaviour of groups from individual animal traits</td>
<td>Macaulay Institute</td>
<td>Charlie Shand</td>
<td>March 2005</td>
</tr>
<tr>
<td>Extensive grazing of semi-improved grassland to enhance faunal biodiversity</td>
<td>IGER</td>
<td>Jerry Tallowin</td>
<td>July 2005</td>
</tr>
<tr>
<td>MOORCO - Moorland Colonisation by Birch and Pine: Impacts for Biodiversity and Ecosystem Function – (includes grazing effects)</td>
<td>CEH / Macaulay Institute</td>
<td>Rob Brooker / Alison Hester</td>
<td>March 2006</td>
</tr>
<tr>
<td>Effects of grazing management on grassland and heathland vegetation and rare plants</td>
<td>CEH</td>
<td>James Bullock</td>
<td>Ongoing</td>
</tr>
<tr>
<td>Grazing management and grassland diversification</td>
<td>CEH</td>
<td>Richard Pywell</td>
<td>2005</td>
</tr>
</tbody>
</table>

In addition to academic research and reviews of management expertise, there has been a move to coordinate the practical application of grazing for conservation. In the UK, since 1997, the Grazing Animals Project (GAP)³ has worked to help grazing managers and grazing advisers deliver biodiversity targets. This project works in three main areas:

- Assisting local delivery of grazing through a ‘Local Grazing Schemes Initiative’
- Removal of constraints through development of the ‘Solutions Tool-kit’
- Assistance to advisers and graziers through its ‘Servicing and Networking Service’.

Other organisations are working at an international level to research, promote and coordinate aspects of grazing for conservation and also conservation of the grazing animals themselves. For instance:

- the European Forum on Nature Conservation and Pastoralism [http://www.efncp.org/](http://www.efncp.org/) which brings together ecologists, conservationists, farmers and policy makers with the aim of to increasing understanding of the high nature conservation and cultural value of certain farming systems and to promote their maintenance.

The Large Herbivore Foundation [http://www.largeherbivore.org/], an independent network organization founded by WWF International in 1998, aims to protect large herbivore species, and to restore their ecological role within their original ranges.

4.5 Naturalistic grazing

The concept of naturalistic grazing is distinct from other more general moves towards landscape-scale conservation management. The principal of linking or expanding sites in order to avert ecological problems, which are often associated with small isolated reserves (English Nature 2000), is not in question here; nor is the utility of extensive grazing for the management of such large sites (WallisDeVries and others 1998).

For the purposes of this report, the defining difference between naturalistic grazing and other large, extensively grazed conservation management is in the role of ‘natural processes’. In the naturalistic approach, there is no specified grazing density, instead herbivore populations are resource-limited (that is population numbers fluctuate according to the amount of food available, climate, pathogens and parasites, etc.). The grazing animals are key ecosystem drivers, and natural processes are allowed to act, rather than managing by intervening to achieve targets for habitat and species composition (Table 3). In naturalistic grazing, direct management intervention is reduced to a minimum, and the natural process is seen as an aim in itself.

This approach is in great contrast to conservation practice guided by Biodiversity Action Plans [http://www.ukbap.org.uk/], which are the UK government’s response to fulfil obligations agreed in the Convention on Biological Diversity (1992), and it is this contrast that is the focus of this chapter.

4.5.1 Examples of naturalistic reserves

Although a great many conservation areas in Europe, with habitats including grassland, heath or moorland, and wood–pasture, are now managed by some sort of extensive grazing; it is difficult to find examples of near-natural grazing that meet all the criteria defined in Table 3. As naturalistic (or minimum-intervention) reserves have been pioneered in the Netherlands, it is not surprising that the best known, and probably the best example, is the Oostvaardersplassen. Described as ‘new nature below sea level’ this 5,600 ha reserve began as a polder reclaimed in 1968, but was not developed for industry due to economic recession. Since the 1980s, part of the reserve has been grazed year-round by free ranging herds of Heck cattle, konik ponies and red deer (Vulink & Van Eerden 1998; Wigbels 2001). The grassy marginal area comprises 2,000 of the 5,600 ha total, this area was originally intended for agriculture, and had already been partially developed. As with many polder areas, the soil is very fertile. Rather than maintaining a prescribed stocking level, the large herbivore populations are allowed to fluctuate through births and deaths, and animals are culled only when their condition and behaviour indicates that they are near death (Tramper 1999).

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4 For instance, the ‘Beyond the Boundaries’ policy theme of the National Trust which opens the door internally to linking sites in partnership with other organisations (David Bullock pers. comm.).
Table 3. Differences between naturalistic and other forms of extensive grazing (based on wide consultation).

<table>
<thead>
<tr>
<th></th>
<th>Naturalistic</th>
<th>Other extensive systems</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Large herbivore density</strong></td>
<td>Herbivore populations are resource-limited. This may lead to population fluctuations, with the result that grazing pressure varies between years, and this may provide windows of opportunity for scrub and tree regeneration in grasslands.</td>
<td>Numbers of grazing animals are controlled to provide a predetermined grazing pressure in order to meet a specific ecological management target.</td>
</tr>
<tr>
<td><strong>Herbivore demography</strong></td>
<td>Animals allowed to breed, to form family groups etc. This may affect grazing patterns.</td>
<td>Determined by grazier – eg a single sex herd.</td>
</tr>
<tr>
<td><strong>Control of numbers (by removal or humane destruction)</strong></td>
<td>To avoid suffering, animals are removed when 'beyond hope' of recovery and it is clear that they would die anyway. This assumes that it is possible to locate stock.</td>
<td>Numbers of grazing animals are maintained at the predetermined stocking level. Usually this about 0.2-0.8 LU/ha but depends on local conditions.</td>
</tr>
<tr>
<td><strong>Seasonal or Year-round grazing</strong></td>
<td>Always year round but in a large enough reserve seasonal movements could lead to effective fluctuations in grazing pressure.</td>
<td>May be seasonal or year round.</td>
</tr>
<tr>
<td><strong>Additional management</strong></td>
<td>No</td>
<td>If necessary (eg harrowing, mowing, burning).</td>
</tr>
<tr>
<td><strong>Veterinary care</strong></td>
<td>Animals living independently may suffer from more stress from handling than a domestic animal. This should be taken into account (as well as herd dynamics) when deciding whether veterinary treatment is necessary.</td>
<td>Stock would receive the same care as domestic / farm animals. When hardy breeds are selected this may reduce the veterinary attention required.</td>
</tr>
<tr>
<td><strong>Veterinary screening/vaccinations</strong></td>
<td>As for domestic / farm stock under current UK law</td>
<td>As for domestic / farm stock</td>
</tr>
<tr>
<td><strong>Marketing of meat</strong></td>
<td>No – because of legal restrictions</td>
<td>Meat from free range animals could potentially be sold at premium prices (especially if also organic)</td>
</tr>
<tr>
<td><strong>Fallen stock</strong></td>
<td>Locating fallen stock may be more difficult in a naturalistic reserve. Implications for water contamination should be considered.</td>
<td>The law requires that these are removed</td>
</tr>
<tr>
<td><strong>Conservation targets</strong></td>
<td>Natural processes allowed to act. Open areas could be allowed to scrub over and forested areas to open out.</td>
<td>Usually involves management prescriptions for habitat type eg open grassland or dry heath.</td>
</tr>
</tbody>
</table>

The Oostvaardersplasen, however, is a special case. Starting from a polder, there was no risk of biodiversity loss, and it also has very fertile soil, and this is in contrast to the majority of conservation areas in Europe. Perhaps a more pertinent example of minimum-intervention management forms part of the Veluwezoom National Park in the Netherlands. The minimum
intervention area (4500 ha) consists of extensive heathlands, previously managed by regular burning, plantation beech and conifer, and some ex-arable fields. The reserve is grazed by Scottish Highland cattle; wild boar; red, roe, and fallow deer. The cattle graze largely on relatively high quality forage in the ex-arable fields, using the heath and woodland mainly in transit.

The Veluwezoom fulfils many of the ‘naturalistic’ criteria, but the cattle grazed in the area are not managed in the same way as in the Oostvaardersplassen; instead their density has been controlled by adjusting herd size. So the Veluwezoom reserve probably falls more into the ‘Other extensively grazed’ category (Table 3). There is very low grazing pressure, and the cattle graze mainly on ex-agricultural pastures; hence herbivore impacts are hard to detect in the heathland and forest, although the effects of wild boar are easily seen (see also section 8.2.2). In the short term, large areas of continuous heath are likely to be lost through succession to pine woodland, but in the longer term the reserve managers hope that a mosaic of smaller patches of heath and woodland will develop (Feiko Prins pers comm.). However, it has been suggested that because the current grazing regime does not affect colonisation by coniferous trees, the European bison or wisent could play an important role in determining the habitat composition of this reserve (Groot Bruinderink and others 2002).

4.6 Practical implications – case study questionnaire

A case study approach was used to explore the issues that should be considered if naturalistic grazing regimes are contemplated. Three contrasting areas were chosen to give maximum coverage of possible ecological, economic and cultural scenarios. These included an upland area, a site in lowland England largely consisting of fertile agricultural / forestry or recent ex-agricultural land, and a coastal site of varied habitats with high biodiversity and conservation value. Information about these sites was gathered using questionnaires and interview.

As many interested parties as possible were invited to participate in the questionnaire response and this included site managers, land owners, wildlife trusts, and other conservation organisations. The issues addressed concentrated on the ecological, economic, cultural and strategic implications of a ‘hands-off’ management approach. For each site, the questions aimed to establish background information about the nature of the site: area, scope for expansion, land ownership, conservation and other designations, rights of way and any other possible conflicts of interest. Our approach then aimed to determine the limits to acceptable ecological outcomes anticipated at that site (see question 2.1).

We sought to address practical issues of herbivore stocking and husbandry, what start-up works might be required and plans for ongoing management and monitoring. Lastly the site managers and advisors were asked about potential conflicts of interest such as heritage sites or rights of way, funding and effects on the local economy, animal welfare and health and safety of humans and domestic stock.

The completed questionnaires contain some information that is sensitive; therefore they are held as confidential appendices and the sites are not identified here. The case studies should be viewed as a means of exploring what might happen in different situations if site owners or managers wished to develop a naturalistic reserve. In each of the three cases, there is real interest in trying to create ‘wilder’ landscapes in which large herbivores will play a role. This does not, however, mean that the specific issues discussed in the subsequent pages will necessarily be implemented.
The sites are all situated in England, but we consider that the issues that are raised could also apply to schemes in Wales and Scotland. However, the significance of the various issues will differ across the regions because of variations in land cover, land ownership, human population density, urbanisation, transport networks and cultural attitudes.

The full text of the questionnaire now follows. Key points from the responses are given in section 4.7, with further discussion in sections 4.8 and 4.9.

4.6.1 Near natural grazing: case study questionnaire

4.6.1.1 Background

- Please provide a description of the site, including its natural features. This should include the total area and the extent of different habitat types (woodland, pasture etc). If this information is available in reports/maps etc, please may we have copies?

- What are the conservation objectives for the site? If these have been developed into a management plan please may we have a copy, in digital format if possible?

- Please give details of particular conservation interest on the site. For instance, BAP habitats/species, veteran trees, designated sites (e.g., SSSI, SNCI), archaeological sites.

- What is the management history of the site? If this has been recorded in reports/maps etc please may we have copies, in digital format if possible?

- Who owns the land on the site? Are there options for expanding the land available onto adjacent areas (by agreement of all concerned)?

- What other rights, such as common grazing or rights of way, exist on the land?

4.6.1.2 Ecological and methodological issues

- Near-natural grazing schemes have been pioneered in the Netherlands, particularly in the Oostvaardersplassen. According to Frans Vera and colleagues, the large herbivores may act as keystone species. These animals drive natural processes to produce a park-like landscape, with a cyclical turnover of vegetation types, and this leads to a shifting mosaic of open grassland, scrub and woodland groves. If this process driven approach is applied in conservation it is difficult to predict the ecological outcome. Population cycles of herbivores are essential so that scrub and woodland can develop when grazing pressure is low. This approach is very different from the prescriptive conservation more commonly applied in the UK.

- Assuming that near-natural grazing management will (to some extent) allow natural processes to function, what are the acceptable habitat and species changes in your view? At what point would some form of practical intervention become necessary? This might include control of invasive species such as bracken, Himalayan balsam or grey squirrel. It may mean fencing off areas of important woodland or controlling grazing to maintain species rich grassland in certain areas. What are the limits to acceptable outcomes in your view?
• What species/breed of herbivores will be used?

• What initial stocking density is proposed?

• What are the proposals for control of the large herbivores? For instance, this may be required if population growth resulted in overgrazing which exceeded the limits to habitat change.

• What works are planned prior to releasing animals in a minimum intervention landscape on this site? For instance, could access to water and other requirements (eg mineral supplements) be arranged to manipulate the behaviour of the grazing animals and hence their impact on the landscape (Putman 1986)? What fencing is required? Perhaps ‘transition management’ might to necessary to diversify the landscape or to eliminate unwanted species (such as invasive alien plants)?

• What are the timescales for start-up works?

• What are the plans for ongoing management?

• Do you propose to monitor ecological changes? Available methods include fixed vegetation transects, invertebrate traps, aerial photography and radio (or GPS) tracking of grazing mammals to record ranging/feeding behaviour (with important implications for nutrient transfer) and survival. These methods can record direct effects of large herbivores such as poaching and trampling, changes in vegetation structure and in plant and animal species composition. Collaboration with universities or research institutes and proposals for student projects (PhD, Masters etc) are possible vehicles for monitoring.

• Will there be opportunities to plan experimental works such as exclosure studies?

• What timescales do envisage for monitoring schemes?

• Are there any likely impacts on catchment hydrology, such as through changes in wood or scrub cover? These changes could be positive or deleterious.

4.6.1.3 Economic, cultural and welfare issues

• Are there any possible conflicts of interest on the site? What can be done to resolve these? For instance adequate protection for archaeological sites, and provision of limited access.

• What are the likely effects of this near-natural grazing scheme on the local economy? These will include both positive and negative impacts on farming and field sports, and on tourist income.

• How will the grazing scheme be funded? Are there financial incentives (such as grant schemes) available to make management of a near-natural landscape attractive to landowners/farmers and graziers?

• Are there other financial implications – such as changes to capital assets and tax relief?
• If the public will have access to the area, what measures are planned to ensure their safety? Measures could include fencing and information/education (ie how to behave in the presence of free ranging large herbivores).

• Will public information be provided to allay well-meaning, but badly informed, concerns about animal welfare? For instance, information about natural shelter and requirements of hardy breeds.

• What provision will be made for welfare of free ranging stock? This might include monitoring and control of disease and parasites, supplementary feeding (although this might conflict with management plans) and humane control. Plans should be in place for frequency and methodology of monitoring animal condition and veterinary support.

• What are the contingency plans if large herbivores escape from the site?

• What issues arise around the potential for free-living large herbivores to act as potential veterinary disease reservoir? If permission were given to keep cattle without vaccination requirements – how might neighbouring farms react? Is there a potential for swine fever to affect the local economy?

4.6.1.4 Strategic issues


• How do the proposals for this site link with other local conservation schemes?

• Which other local groups are likely to be involved in planning and implementation and monitoring of near-natural grazing on this site? These are likely to include government agencies, wildlife trusts, and public interest groups.

• Is there already a structure in place (eg a County Biodiversity Group) for integrating these organisations to provide a practical means for effective communication and reconciliation of potential conflicts? If not are there plans to organise such a network?

4.7 Practical implications – questionnaire responses

The responses to each of the questions are summarised in this section, bullets are used to identify specific issues or pieces of information given by the respondents from each of the three case study sites (upland, lowland agricultural and coastal). Further discussion and synthesis of the responses and their implications are given in sections 4.8 and 4.9.
4.7.1 Background

4.7.1.1 Site descriptions

- The case study sites ranged from around 3000 ha to 5500 ha (ie comparable to the Oostvaardersplassen), although inclusion of all this land in the management area had not necessarily been agreed by all parties.
- Landscapes included
  (i) relatively fertile mixed arable and pastoral farmland and woodland, plus small villages and isolated houses
  (ii) upland grazing and plantation forestry
  (iii) a complex matrix of coastal habitats: heath, acid grassland, neutral grassland, fen, reed bed, wet woodland and pine plantation

4.7.1.2 Conservation objectives

- Vision statements and concept notes for the sites made the following general statements.
  (i) Agricultural site. Establish a minimum intervention land-management experiment, which would initially run for 25 years, with aims to improve ecological diversity and consider an environmentally sustainable alternative to agriculture.
  (ii) Upland site. To allow the evolution of the site as a wild area for the benefit of people, relying more on natural processes to shape its landscape and ecology.
  (iii) Coastal site. To provide a large area where landscape and wildlife can be sustainably managed, and be adaptable to changes in the environment and land-use. To support the development of a network of habitats that are more natural in their landscape setting, less constrained by artificial barriers.
- In general, the responses suggested giving more room for ‘natural processes’ to function.
- Although there was a general feeling that a naturalistic approach was a good way to proceed, there were no firm ideas on how to approach the legal and ecological issues that may arise. Detailed plans for conservation and biodiversity objectives had not been developed at this stage.
- Specific suggestions were made about key species and habitats that should be protected or enhanced for cultural, political, and currently, for legal reasons (see 2.1 on ‘Limits to acceptable change’).
- One site had drafted suggestions for biodiversity benefits of the naturalistic approach. These were based however, on assumptions about the outcome of the minimum intervention management, in terms of habitat type and openness, which might or might not be correct.
- All sites noted that long-term thinking was important for setting objectives.
- Some respondents felt that conservation management may be made more feasible in the medium / long term by moving to extensive methods, which may be more financially viable than intensive management in small land parcels. This motivation would not necessarily require the adoption of a naturalistic approach.
4.7.1.3 Current conservation interest on the sites

- The sites had a wide range of biodiversity interest from relatively low to extremely important nationally and internationally.
  (i) The site in lowland agricultural land did not include any designated sites of international or national importance, but several small Sites of Nature Conservation Interest (SNCI) fell within the proposed ‘wilderness area’ boundary.
  (ii) The upland site included two Sites of Special Scientific Interest (SSSI) with biological designations, one candidate Special Area of Conservation (cSAC), a geological SSSI and two Regionally Important Geomorphological Sites (RIGS), as well as other species and habitats listed under the UK Biodiversity Action Plan. SSSI designations covered 40% of the total area.
  (iii) The coastal site included internationally important sites for birds and wetlands and hence had Special Protection Area (SPA) and Ramsar designation on parts of the proposed area as well as SAC candidature. It was also classified as an Area of Outstanding Natural Beauty (AONB), and had Heritage Coast, Environmentally Sensitive Area (ESA), Wildlife Heritage, and Council of Europe Diploma status.

- There were important and well documented archaeological sites on all three sites, including scheduled ancient monuments. The proposed upland site has been subject to relatively little land enclosure, allowing the survival of early archaeological remains. It includes two Scheduled Ancient Monuments and a large number of other features, many of which are of regional and national importance.

4.7.1.4 Management history

- Each site consisted of a number of habitat types and ownerships (see 4.7.1.5), and their management histories were complex. Where there were multiple landscape partners, currently or historically, they tended to have somewhat different management priorities and methodologies. However, conservation managers responsible for designated sites generally, had similar overall objectives. Where partnerships had been formed, they were actively working towards bringing management plans into alignment.

- In parts of the sites with high existing conservation interest, there were detailed and prescriptive management plans leading to highly interventionist management such as pond and ditch creation, ploughing, burning and mowing. This has lead in one example to outstanding assemblages of breeding birds and spectacular recovery of a key species.

- On one site including SSSIs or SACs, specific operations were identified that could relate to management changes in a ‘naturalistic’ approach, but that could potentially damage the special interest. In such designated areas, special permission would be required, usually from English Nature, to carry out these changes in management practice.

- The activities identified include:
a) The introduction of grazing and changes in the grazing regime (including type of stock or intensity or seasonal pattern of grazing and cessation of grazing).
b) The introduction of stock feeding, and changes in stock feeding practice.
c) Burning and changes in the pattern or frequency of burning.
d) The release into the site of any wild, feral or domestic animal, plant or seed.
e) The introduction of tree and/or woodland management and changes in tree and/or woodland management (including cessation of management).

- All sites included commercial forestry plantation, which was no longer economic. In some cases this economic change was one of the main motivators for investigating alternative landscape management scenarios.
- Where Countryside Stewardship Schemes existed, it was generally assumed that any new scheme developed for minimum-intervention management would supersede these.
- Grazing was by farmer’s or conservation organisation’s own stock, commercial graziers, and by wild deer and rabbits. Grazing by rabbits was actively encouraged in one case by creating refuges with brashings.

### 4.7.1.5 Ownership

- The sites varied in terms of both the relative complexity of ownership, and also in the type of ownership: private, commercial, public body, charitable organisation and crown land.
- In one site, 90% of land was controlled by three principal landowners, another site included between 8 and 11 partners, depending on the placement of the boundary and the third, included some large landholdings plus numerous smallholdings.
- Two of the sites had existing partnerships who were working to develop landscape scale management practices.
- In the third, agricultural, site the instigator of the wilderness proposal has made considerable effort to inform potential partners of the proposals and set up dialogue with local and national conservation organisations.

### 4.7.1.6 Other rights on the land

- There were public roads, footpaths and bridleways in all of the case study sites and two of the sites had high visitor usage. Apart from the nature conservation interest, visitors are also attracted for the cultural and scenic values of the sites. This links to tourism, which was a key part of the local economies (see 4.7.3.2).
- Some respondents were concerned that additional rights of access may become available to the public under the CRoW Act (see also 4.7.3.5). However, in the upland area, some parts of the site were subject to a ‘right to roam’ under CRoW legislation, and managers of this area have previously operated a ‘freedom to roam’ policy. Some large forestry blocks in the upland and coastal sites were being considered for dedication under the access provisions of the CRoW Act.
- All sites also included farms, and private residences, within their boundaries, and possibly also villages. These will clearly hold rights of access to property and land for
business and private purposes and have neighbourly interest in any changes on adjacent land.

4.7.2 Ecological and methodological issues

4.7.2.1 Limits to acceptable outcomes

- As the questionnaires and interviews progressed it became clear that consideration of the ‘Limits to acceptable ecological outcomes’ was the key question, and also the most difficult to answer. This is partly because all of the case study areas were at an early stage of planning and discussion, but also because it is difficult to reconcile the ideological viewpoint of re-wilding, with the day-to-day issues of practical management.

- The intention to step back from management and allow ‘natural processes’ to shape the landscape is a stated aim of some of the partners in the case study sites (see 4.7.1.2). Partners at one site explicitly state that they accept that the minimum intervention will lead to habitat and species change. They are less focussed on the outcome, what habitats develop and where they occur, and more concerned to be able to say that natural processes are principally responsible for the development of these habitats: the process is important, not the visible outcome.

- To others, the naturalistic approach presents practical difficulties in maintenance of the favourable condition of important habitats and species. They would need to be convinced that a more ‘natural’ grazing regime would deliver comparable biodiversity benefits to the active management regimes currently prescribed.

- For example on the coastal site, there was debate in general terms about the potential for removing fencing and reducing active management. However, when specific examples were discussed all partners agreed that some of the existing habitats were so valuable they would clearly not risk damage to them. Instead they would maintain current management practices.

- Likewise, individual tree protection was suggested for veterans and other specimen trees on the agricultural site.

- The sense of wildness was noted as the most important feature of the upland site, and the partners considered intervening if this feature was being significantly compromised on a ‘valley wide scale’. ‘If the whole valley was clearly reverting to dense forest and [for example] views of the mountains were being lost, then we would seek to intervene to ensure that these views remained. However we would always aim to intervene through the manipulation of natural processes eg by increasing the number of grazing animals rather than directly by clear-felling large areas of trees’.

- In the agricultural site, it was not considered acceptable to leave all the hedges unmanaged. About 25% of the hedges would continue to be trimmed for amenity purposes (landscape and hunting). Unchecked ‘natural processes’ would be likely to conflict with these other priorities (see 4.7.3.1).

- Other situations where management intervention would be considered in at least one of the sites are as follows:
  (iii) Control of invasive exotic species such as Himalayan balsam, grey squirrel and rhododendron.
(iv) Introduction of seed of native broadleaved trees to provide opportunities for expansion.
(v) Control of large herbivores by culling (in the absence of predators). The nature of this culling practice was not necessarily specified. It could just apply to wild deer, or permission might be sought to cull animals (including de-domesticated stock) in response to their condition, in a similar manner to the management used in the Oostvaardersplassen (see also section 4.5.1 and 4.7.2.4).
(vi) Control of pernicious weeds by topping, spraying or weed wiping around site boundaries, particularly near to housing and other sensitive areas.
(vii) Maintenance of woods and trees alongside roads to preserve scenic properties and as an acoustic screen.
(viii) On clay soils, excessive poaching of the ground was considered unacceptable.

- Generally respondents felt that action would be taken where proportions of specific habitat types (eg woodland or grassland) moved beyond prescribed limits. The preferred action was manipulation of grazing levels, either overall in the site by changing numbers of animals or the species mix, or otherwise by fencing.
- The need to abide by legal and statutory requirements for conservation of biodiversity was acknowledged by all sites. However, some respondents indicated that they would ‘seek to have these modified if we believe the natural process and wild nature of the [site] would be compromised by abiding with these statutory requirements’.

4.7.2.2 Species / breed of herbivore that might be used

- At one site it was considered too early in the planning stages to be able to answer this question.
- On the upland site, a native cattle breed, such as Highland is the most likely option. This is based on the breed’s suitability to the site conditions, but also on historical evidence that Highland cattle were present in the valley in the 19th century.
- On the agricultural site, there are no firm plans for species of choice but the intention is to maximise diversity of the species assemblage. Their ideal list includes species that would require legislative changes to permit release, and species thought not to have been resident in Britain in this interglacial period (Yalden 1999). The suggested assemblage includes wild roe deer (already present); red deer, fallow deer, wild boar, European beaver, European bison, ponies and Heck cattle.

4.7.2.3 Initial stocking density

- The general inclination is to start with small herds and allow these to develop and expand in response to the habitat and availability of food.
- The use of pilot areas is favoured.
- It was accepted that mowing and other management intervention may be needed while herds build up.

On one site use of store cattle (bullocks) alongside ‘de-domesticated’ animals was suggested in order to ‘keep grassland grazed’.
4.7.2.4 Proposals for regulating the numbers of large herbivores

- Ideas on how a wilderness area in the agricultural site might function are evolving, so that although the original concept note suggested a ‘pre-determined stocking rate’ this approach has now changed. One option, currently in discussion, is that there could be some possibility of the spread of woodland and scrub, and regulation of the numbers of grazing animals would be guided by the results of monitoring habitat change. Ponies might be rounded up annually and surplus animals sold.

- Respondents from the upland site suggest that a ‘phased removal of human intervention’ might be appropriate as the herd adapts and the area made available to it increases. Eventually they hope to see control ‘principally through population dynamics’.

4.7.2.5 Planned ‘start-up’ works

- Preventing escape of free ranging animals was a key concern at all of the sites. The type of boundaries needed depended on the plans for stocking the reserves.
  (i) In the lowland site, enclosing the whole area with deer fencing has been proposed to contain the free-ranging fallow deer. Additional fencing would be required along major roads, some stretches of the minor roads, some rights of way and strip developments of housing along roads. An estimate of costs for this type of fencing was provided from plans for a proposed extension to a deer park of 526 ha. This would need 27,286 m of fencing, costing £5.50 per meter, and approximately £150,000 in total. Any cattle grids and gates needed would be additional to this cost. The proposed naturalistic grazing reserve is six times the area of the planned deer park.
  (ii) Provision of new fencing, repair of existing boundaries and addition of cattle grids would also be necessary to make the upland study area stock-proof.

- Removal of internal boundaries was seen as an important goal in order to improve the appearance of the reserves, by taking away sharp and conspicuously artificial edges.
  (i) At the coastal site fencing for conservation grazing has been unpopular with members of the public (for reasons of access as well as aesthetics). Respondents felt that removal of fences between habitats should increase the area of ecotones in the reserves and hence their biodiversity. This topic was subject to unresolved debate. The general principle of removing artificial boundaries appealed to the partners, and implementing this policy was agreed to be straightforward for adjacent land parcels of similar habitat. However, where fencing was in place for specific management aims, such as maintenance of short turf, there seemed to be no easy way to remove boundaries while still safeguarding important species (see also 4.7.3.1).
  (ii) In the agricultural site, removal of all internal fencing has been proposed, apart from fencing around houses, roads, rights of way (see above), and some sensitive areas of woodland. Maintenance of some hedges (about 25% of the total) in this site, for amenity and screening purposes, is also envisaged (see 4.7.3.1). As grassland restoration was also discussed, presumably fencing would be required at least during the establishment phase.
• It was suggested that removal of internal boundaries might be an advantage for free-ranging stock, as it could allow escape opportunity for grazing animals if chased by dogs.

• The provision of water supply and mineral supplements was discussed at two of the sites, and in one case, the way in which placement of these could be manipulated to influence the grazing patterns of the stock. On one site the provision of shelter to encourage grazing by rabbits was likely to continue.

• In the coastal site there were areas of ex-arable land various stages of reversion. It was thought that intensive management work would continue in such areas for the foreseeable future. In the agricultural site, similar management for arable reversion by nutrient depletion has been proposed, with soil sampling carried out on all the fields.

• Removal of commercial conifer plantation and replacement with native woodland or other habitat types (e.g. heath) was being considered on two of the sites.

  (i) Regardless of the ecological and ideological arguments for and against removal of the exotic conifers, advisors for the upland site questioned the practicality and costs of spruce control, and noted that pragmatism was called for. Complete removal of exotic conifers was considered unlikely and a more realistic aim would be a greater balance between conifer and mixed woodland. Conifers were valued by many visitors to the upland site for shelter during inclement weather and for providing scale in the landscape. Plans were underway to remove the majority of mature conifers from one end of the site to prevent spruce regeneration dominating in future, thus reducing the sense of wildness. Native broadleaves and juniper were to be planted to provide an alternative future seed source allowing that area the opportunity to develop away from a spruce dominated landscape.

  (ii) The coastal site also included some large areas of conifer plantation. In these, the Forestry Commission has an approximate 40-year plan to replace them with broadleaves and heath. It was hoped that this would be achieved by natural regeneration during successive thinning/removal of existing pines.

• Raising public awareness, education, discussion with landowners, tenants etc, and consideration of public health risks were also seen as part of the start-up works. See section 4.7.3.

4.7.2.6 Timescales for ‘start-up’ works

• All three sites envisaged starting with small areas, and numbers of stock, and gradually expanding both area and herd size. Relatively small core areas or pilot sites (e.g. 145 ha cattle grazed) were considered at each of the sites for initial trials.

• Where arable reversion and removal of extensive commercial conifer plantation were concerned, it was noted that relatively intensive start up works would be required and that the process would be gradual and could take decades. During these years various types of intervention would be required.

It was estimated that fencing the c. 3000 ha agricultural area would be likely to take one year.
4.7.2.7 Plans for ongoing management

- The case study sites are all at an early stage of development, therefore there are currently no detailed plans for ongoing management at the case study sites.
- In the upland site, if monitoring suggested that acceptable limits to landscape change were exceeded, the intention would be to manage through the manipulation of natural processes (e.g., the number of grazing animals), rather than through direct management intervention (e.g., clear-felling) see section 4.7.2.1. Management of stock was thought likely to be through a tenant farmer.
- In the agricultural site individual landowners might manage their own land within the boundary but rangers could be employed to manage the stock and boundary fences.

4.7.2.8 Plans for monitoring ecological changes

- All sites expressed enthusiasm for monitoring of habitats and priority species but explicit plans had only been developed for the upland site.
- The need for baseline studies was noted. The upland site organisers have obtained these data using NVC habitat surveys and colour geo-referenced aerial photographs. Baseline survey work is underway at the agricultural site. Parts of the coastal site are intensively monitored already.
- A five year interval for re-survey was suggested for the upland site. This would include updated aerial photographs and coincidental fixed point photographs, and species surveys, from sample plots across the site.
- Tracking movements of the large herbivores, perhaps with one GPS tag per herd, was suggested in the upland area.
- In addition to ecological monitoring, impacts on management costs and perceptions of visitors and local people would also need to be watched closely (see 4.7.3).

4.7.2.9 Opportunities for experimental works such as exclosure studies

- Respondents at all sites were enthusiastic that there should be scope for experimental studies, but no specific plans had been made at this stage.

4.7.2.10 Timescales for monitoring ecological changes

- The importance of long term studies was noted.
- See 4.7.2.8 for proposed timescales in the upland site.

4.7.2.11 Likely impacts on catchment hydrology

- Changes resulting from a minimum intervention approach were thought likely to have a positive impact on catchment hydrology. This would be through an expected slowing of run-off, as arable land or grassland converted to scrub and relatively rough grassland.
4.7.3 Economic, cultural and welfare issues

4.7.3.1 Conflicts of interest

- Possible conflict with archaeological interest was an issue at each of the sites.
  (i) In the upland site the main threat would probably be from woodland regeneration. The organisers suggest that ‘the type and level of intervention will be decided based upon the importance of the site and the impact of the intervention upon sense of wildness and natural process.’
  (ii) The need for agreement with English Heritage and other appropriate interest groups was noted.
  (iii) In the agricultural site, elements of landscape design were important to enhance the scenic quality and to direct views. Some management limitations would be set by the need to conserve this design as well as the scheduled ancient monument in the site. This would be likely to include fencing off areas of woodland that are intrinsic to the design.

- In the coastal site, there was concern that the good local support for conservation in the region could be compromised. The public (local and visitors) may be unwilling to countenance broadening of the limits of acceptable ecological change, particularly if they perceive that the area is losing conservation value.

- Potential conflicts over public access were noted at all sites, particularly with regard to dog walkers and horse riders. For instance, family groups of horses could raise serious safety risks for riders. There were, however, differences in opinion about the level of risk posed to stock by dogs and this appeared to be based on the management experience of the respondents.

- Use of zoning was suggested as one means to limit conflicts over access, but on the agricultural site additional fencing might be needed on planned pedestrian and equestrian routes.

- Dialogue with the local communities, provision of information and education were all discussed as ways to mitigate against conflict over access.

- Potential conflict with neighbouring farms was noted at two of the sites through the possibility of crop damage by stock, or through the spread of noxious weeds. Control of such weeds in a boundary zone is the suggested solution (see 4.7.2.1).

- The importance of the visible link provided by cattle to the local community through people working the land was noted. In the upland site, if management of cattle was reduced over the longer term, it was suggested that there could be a risk of losing this important community link.

- In the agricultural site, the ability to continue hunting and shooting was a priority. This would impose certain management requirements that would limit the extent of the minimum intervention approach (maintenance of some of the hedges for jumps and cover for game birds).

- There was a perceived risk of loss of property rights and control over management decisions, should the agricultural site become a successful nature reserve.
4.7.3.2 Possible effects on the local economy

- In the agricultural site it was acknowledged that there would be some loss of agricultural income and subsidies. Cessation of commercial forestry could also lead some income loss on this site. It was also noted that loss of agricultural employment is already occurring in the area. However, this may be balanced to some extent by income from tourism if a visitor centre and guided tours were developed, but large initial investment would be required. Initial infrastructure works (fencing etc) would also provide temporary income generation, and it was hoped that meat from the large herbivores could be marketed from the proposed project on the agricultural site (but see section 4.7.3.7).

- In the upland site, a feasibility study into the potential benefits for the local economy was planned and some similar study was likely in the coastal site, where development of the (already high) tourism potential was a key aim. The potential for generation of local employment in monitoring work, specifically of livestock was suggested.

4.7.3.3 Funding

- A variety of funding sources were being explored, mostly involving some form of grant aid.

- The upland site was seeking external funding to support grazing through the Rural Payments Agency and was already registered with the Integrated Administration and Control System (IACS). In addition, a farm business tenancy might be used to support grazing by cattle.

- The potential financial benefits of scaling up from grazing in small units to a large extensively grazed area were a major motivator in the coastal site. However, several of the partners expressed concern over whether the financial savings could be made while still retaining current conservation interest.

[The questionnaires were completed before the details were known of how recent CAP changes would affect support.]

4.7.3.4 Other financial implications

- On two of the sites, there was concern about loss of capital assets and effects on owner’s income tax classification if land were to lose its agricultural classification. There may be major implications for private landowners due to possible changes in tax relief because currently farmland remains an attractive long-term capital tax shelter for individuals with significant capital gains. Taxes affected could include Capital Gains Tax Relief, Inheritance Tax, and Agricultural Property Relief. Owners could lose certain benefits, such as the ability to claim capital allowances, VAT exemption and rate relief (100% for agricultural land).

4.7.3.5 Public access and health and safety

- Access was a key consideration at all of the sites. The stated aims of the agricultural site emphasised developing the area for public information and education. Hence,
access would be important in this, as well as the other two sites, which both have an established history of access and use by the public for recreation.

- Risk of injury to the public from stock, particularly cattle and horses, was a concern at all three sites. All considered the potential benefits of using placid breeds and the possibility that horned breeds might be beneficial because they may discourage the public from approaching them.

- The potential for reducing chance of conflict between visitors and stock by careful placement of footpaths and signage was suggested at two of the sites, as well as the need for cattle grids to prevent stock straying from unenclosed areas. Fencing off footpaths in the upland site and the coastal site was not considered as an option because of the likely detrimental effect on the appearance of the area, and could conflict with access provisions under the CRoW Act.

- On the agricultural site, fenced safety zones were suggested to protect the public.

- Roads passing through the area were a particular concern in the agricultural site. In addition to fencing and cattle grids, agreement with the Highways Agency or local roads authority might be sought to set suitable speed limits, as in the New Forest.

- Respondents expressed concerns that free-ranging herds could result in greater risk to public safety and hence the risk of negligence claims. Insurance cover and costs for such claims could differ from agricultural systems. A different form of legal protection for owners/managers might be needed.

- The only other human health risk identified in the responses was the risk of increasing the incidence of Cryptosporidium spores in the watercourses and lake, and resultant potential threat to public health. In the upland site this threat would be mitigated by the proposed low stocking, the age of the animals and the permanent residence of the animals in the valley, which may allow them to build resistance. Additional protection for public water sources is provided by a treatment plant, which is fitted with a Cryptosporidium treatment facility. An advisory group is providing guidance on this issue in the upland site.

4.7.3.6 Information and education about husbandry of resource-limited animals

- All three sites considered that information and education about the cattle and/or ponies was important to help avoid conflict. On the upland site, there was a reluctance to erect additional signage because it could detract from the sense of wildness. The possibility of using temporary signs was considered until the local populace became familiar with the free ranging cattle, combined with dissemination of information as widely as possible through such channels as local tourist offices.

- All sites had considered, and in two cases already initiated, public and internal consultation. These naturally dealt with all aspects of site management, but included the issue of perception of welfare.

- Use of local and national press and internet pages to inform the public had either been considered or, in one case, was already in practice.

- Education was cited as a ‘key motivator’ for the agricultural site, where an education centre offering guided tours was envisaged.
4.7.3.7 Welfare of free ranging stock

- The need to establish links with animal welfare organisations and the veterinary service was noted, and aspects of animal welfare for free-ranging stock had been considered at all three sites. However, the approach differed from an intention to maintain low densities and provide supplemental food where necessary, to aspirations to follow the model of the Oostvaardersplassen in the Netherlands (see section 4.5) with its emphasis on self-reliance. In the latter, supplemental food would not be provided for the stock.

- On the agricultural site, it was envisaged that animal health monitoring would be carried out in a similar way to the Oostvaardersplassen, where animals would be routinely checked by a ranger with help from a veterinary surgeon. Respondents at this site suggested that the ethical guidelines developed in the Netherlands (Tramper 1999) might be a suitable model to guide development in the UK. This document can be found on: http://www.grazingnetworks.nl/userImages/File/ethical%20guidelines%20tramper.doc

- Start-up works have been identified in the agricultural site that would be necessary for the welfare of stock. These include removal of artificial hazards, such as old wire fencing, and re-profiling watercourses that have been canalised to allow access to drinking water. Design of the site must include areas, such as woodland, that would provide shelter for the animals.

- An exemption to the Defra and EU Regulations for cattle tagging was hoped for on the agricultural site, on similar grounds to the exemption obtained for the Chillingham white cattle (see section 4.9.5). These grounds for exemption would include the stock being outside of the human food chain, and a lack of handling or trading stock for any purpose. If obtained, such an exemption would conflict with the hope that meat from the cattle could be marketed to generate income (See sections 4.7.3.2 and 4.9.7).

- On the upland site, the Guide to Animal Welfare in Nature Conservation Grazing published by GAP (Tolhurst 2001) was being used as the basis for developing their animal welfare strategy. This includes the production of management plans and risk assessments as recommended by the guide. Initially, they expect that the animals will require regular checks.

4.7.3.8 Contingency plans for large herbivore escape

- Factors considered here were risk to the animals and to the public safety, and on the upland site, the consideration of escaped stock will be included in risk assessments.

- On the agricultural site it was suggested that rangers could be trained in marksmanship in order to cull escaped stock, but the aim would be that escaped ponies and cattle would be captured. The contingency for culling escaped stock in a busy area is already considered in places such as Richmond Park in London.

4.7.3.9 Veterinary health risks

- At the upland site, the usual veterinary procedures would be followed during the initial phase after introduction of cattle to the pilot site. It was hoped, however, that as the site develops, the cattle would become increasingly independent of human intervention.
The importance of close cooperation with Defra in site development was noted because of veterinary health implications of free-ranging or potentially resource-limited herds.

On the coastal site veterinary health risks were not considered to be likely to be any different from other extensively grazed areas because there were no current plans to seek permission to graze an untagged herd of animals.

The possibility of leaving dead animals in situ to provide habitat for carrion feeders was considered in the agricultural site.

4.7.4 Strategic issues

4.7.4.1 Links with national and international conservation and biodiversity objectives

It was noted that proposals for the coastal site must be complementary with national and international biodiversity objectives in order to achieve success under current nature conservation strategies. The partners also discussed how moving beyond the site-based application of these biodiversity objectives could allow more flexible site management. For instance, if conservation of a priority species were viewed at a regional level, then losses at one site (perhaps the coastal landscape project) may be balanced by gains elsewhere (or vice-versa). This however, goes beyond current legislation and guidelines.

The importance of scale was noted again in this section with relation to a possible scenario of the development of shifting mosaics of vegetation. It was thought likely that the coastal site would be too small to accommodate these processes and also that the biodiversity outcome of allowing shifting mosaics to develop could be incompatible with the conservation objectives of the site.

The way in which the upland project would link with EU and UK biodiversity objectives was fairly open and expected to evolve with the project. The need to keep in focus the initial aim of ‘allowing the [site] to develop under natural processes’ was stressed, although the importance of links to external objectives for funding opportunities was acknowledged.

Suggestions for ways in which the wilderness project in the agricultural site could aid progress towards biodiversity targets were based on the assumption that naturalistic grazing would result in the expansion of wood-pasture, parkland and riverine woodland.

4.7.5 Links with local conservation schemes

At the coastal and upland sites, partnerships were already established, including local conservation bodies, and there were aims to ensure that conservation management on land adjacent to the sites would be integrated and complimentary.

Important links for the upland site included: English Nature (management and designation of SSSIs), Environment Agency (water quality and fisheries habitat), National Park (policy to promote ‘quiet and remote places’ and ‘wild land’).

Partnership meetings have been held for the agricultural scheme, and the project is strongly supported by the local Wildlife Trust, which also runs a relatively small
reserve (156 ha of wood-pasture and reclaimed arable land) which they felt had similar aims.

- In contrast a representative from another local conservation organisation considered that the wilderness scheme in the agricultural site was not a priority in the busy and historic local landscape. Much biodiversity interest in the area is a product of a long history of management; therefore immediate priorities involve securing and expending remaining biodiversity that has declined through a lack of traditional management, and this requires direct management intervention.

4.7.5.1 Links with other organisations for planning, implementing and monitoring of naturalistic grazing

- Partners at all of the sites recognised that a wide range of groups, both national and local have current or potential interest in these projects and that it would be important and beneficial to inform and involve them.

4.7.5.2 Structures for effective communication and reconciliation of potential conflicts

- The three sites had all held partnership meetings and consultations. In one case partnership organisations were already well integrated and had a history of cooperation.
- No formal procedures were in place for ensuring effective communication or for conflict resolution. It was expected that these would evolve as the projects progressed beyond the early stages.

4.8 Conclusions from the case study sites

Respondents for the upland and agricultural case study sites were generally (but not exclusively) in favour of developing naturalistic reserves, in which natural processes would be given precedence, and management intervention kept to a minimum. Responses for the coastal site were more mixed, at least in part because this site was in very early stages of discussion. Indeed, the partnership response at this site explicitly stated that there was no intention to try and graze a ‘resource-limited’ herd on the site.

There was no disagreement between respondents, at any of the sites, that scaling-up of management had potential for ecological benefit in reducing isolation, in addition to potential economic savings. However, moving to landscape-scale management was a separate issue from the prospect of managing with minimum intervention, and the move towards the use of resource-limited grazing animals, as exemplified by the cattle and ponies in the Oostvaardersplassen, was a distinct issue again.

The key factor that emerged from the questionnaire responses was uncertainty about the feasibility of managing without prescribed targets. At all sites, this raised discussion among interested parties but there was no suggestion that management intervention would be completely removed. Instead, respondents at all sites agreed that limits to acceptable change would need to be set. These limits would be determined by issues of ecology or biodiversity but also by cultural sensitivities, such as landscape preferences, and constraints imposed by the presence of archaeological heritage on sites.
At all sites ‘limits to change’ were identified that would need to be adhered to; these could be grouped into three categories.

**Category 1. Protection of special features.** This category included cultural artefacts or rare species and habitats that required absolute protection, which might include fencing them off from grazing animals.

**Category 2. Control of unwanted species.** The second category was concerned with the control of unwanted species such as invasive alien species (eg *Rhododendron ponticum*), or pernicious weeds that might cause problems on adjacent landholdings. Direct management intervention was suggested for control of these species.

**Category 3. Change in habitat extent or species population size.** The third category was more flexible and respondents suggested that change in the proportion of habitat types (eg grassland and scrub) could be monitored and action taken if the relative proportions exceeded the agreed limits. The preferred method of action was manipulation of grazing levels; however, this may not be easy for free-ranging animals that have formed social groups (see section 4.9.5). Acceptance of this approach was not unanimous, and some advisors and respondents felt that more direct intervention might be necessary, particularly in the early stages of reserve development. The flexibility of the limits to change was strongly affected by the biodiversity interest present on the site at the outset. Where important species and habitats were already present on a site, there was understandable concern that any change in management practices could potentially be detrimental. This concern would call for minimal flexibility in limits to change; hence in such cases, there could in practice be little difference from more conventional conservation management to targets.

Even on the sites where initial biodiversity interest was relatively low, there was concern to find a way of planning site management that would guide the development of the area towards greater ecological diversity and interest. At the agricultural site there is an explicit assumption that minimum intervention management in this lowland area would produce a park-like landscape. This concept derives from the suggestion that the landscape of lowland Europe in the pre-Neolithic, just prior to significant human impact, was dominated by open parkland, rather than by closed high forest (Vera 2000). However, Vera’s ideas about past landscapes have been contested (Bradshaw 2002; Mitchell 2005), and there is no guarantee that a modern naturalistic park would necessarily closely resemble the pre-Neolithic landscape (Buckland 2005, Hodder and Bullock 2005 in this volume). As the outcome of a naturalistic approach is by definition unknown, planners cannot assume that the result would resemble parkland. It is therefore not realistic to assert biodiversity benefits of a naturalistic approach based on the assumption that a parkland landscape will emerge.

Although the visions, or overall aims, of the sites were concerned with creating wilderness areas, removing unnatural boundaries and allowing room for natural processes, on closer deliberation these aspirations were not always clearly compatible with more specific objectives. This reflected not only the difficulty of applying a wilderness ideology to cultural landscapes, but also the early stage of project development. All sites were working within partnerships, or with advisory groups to further clarify how to put their ideas into practice.

The importance of managing a site to give a sense of wilderness or ‘naturalness’ was not underestimated by the respondents, and the need to provide unobstructed views, and to remove unsightly artificial boundaries was given due consideration in the questionnaire.
responses. This goal is one of landscape management rather than naturalistic management because the main aim is to fulfil a deep psychological need for access to places that appear to be in a state of wilderness.

Ideas for husbandry of stock in the reserves varied between the sites, from an intention to adhere to the welfare guidelines developed by GAP (Tolhurst 2001), to aspirations towards adopting the concept of self-reliance as applied in the Oostvaardersplassen (Tramper 1999). In the latter, population size of cattle and ponies is essentially resource-limited, and animals are humanely culled only when it is considered that they are ‘beyond hope’ and would die anyway. This would require legislative changes before it could ever be put into practice in the UK and is not considered in the current draft Animal Welfare Bill. The general approach suggested by all three sites is to start with a small herd in a limited area, and to expand the area occupied by free-range grazing as the herd grows, such as in the Oostvaardersplassen post-1993 (Vulink & Van Eerden 1998). In the long term, the aims may be for free ranging animals with access to a large site but in the shorter term the grazing animals would be managed eg by a grazier.

Development of proposals for the three sites was not sufficiently advanced for there to be any certainty about economic implications. At the coastal site, potential financial benefits of managing at a landscape scale and in sharing resources in a close partnership were cited as a major driver of the scheme, but this aspect does not require adoption of a naturalistic approach. The possibility of economic benefit from nature tourism was particularly relevant for the agricultural site, whereas the other two sites already attracted visitors. Economic concerns were also voiced, such as the loss of agricultural subsidies and also possibly loss of capital assets through land reclassification, and it was recognised that adequate funding would need to be provided, particularly for start-up works.

4.9 Discussion

4.9.1 Culture & landscapes

A key issue that arose during this review was conflict between specific reserve management goals and more general aspirations for a naturalistic approach (as defined in 4.5). Where conservation of traditional or cultural landscapes is deemed appropriate for a region (see 4.7.4), the unknown outcomes implicit in a naturalistic approach are unlikely to be compatible. This situation is likely to apply to much of lowland Britain. One questionnaire respondent for the south of England noted that ‘Much of our woodland interest has been lost through lack of traditional management [and] much of our woodland interest in the region is restricted to a few sites. The immediate need is to secure these remaining populations and expand them into neighbouring areas. This requires direct management intervention’. There is good evidence that many species and plant communities have come to depend on maintenance of semi-natural landscapes by people and cessation of management could result in losses of biotopes and biodiversity that may never be restored (Bakker 2005).

Even large reserves that are planned in lowland areas, such as the vision for expansion of wetland around Wicken Fen, will require some active management. For instance ‘re-wetting’ of ex-arable fields around the fens will require hydrological management using sluices (Colston 2004). The target for the expanded area around Wicken fen is a mosaic of specific habitat types, and maintenance of the correct density of grazing animals will be vital to prevent succession from open fen to fen woodland (Friday & Moorhouse 1999).
In the context of the conservation of large carnivores in Scandinavian boreal forests, Linnell and others (2000) advocate that conservation focuses on real philosophical and value-orientated reasons, rather than ecological justifications. However, there is no reason why biodiversity and value or people-orientated goals should always be mutually exclusive. The Draft Natural Environment and Rural Communities Bill (February 2005 - section 8.8) guides conservation towards the more holistic approach. In other words, the needs of the public can be considered alongside management for biodiversity. There are excellent examples of large scale and extensively managed initiatives in the UK where great care is being taken to disentangle the various goals in order to explicitly state them and hence effectively manage towards them. For instance the ‘Wild Ennerdale’ scheme in Cumbria cites the preservation of a ‘sense of wildness’ as a key aim (Browning & Yanik 2004).

Particularly in upland areas, the creation or preservation of a sense of remoteness or wilderness may be the most significant factor guiding reserve design and management. Visitors to Ennerdale, for example, enjoy views of spectacular craggy mountains; unimpeded regeneration of conifers could block these views, significantly detracting from the sense of wildness (Browning & Yanik 2004). Landscape management goals are therefore very important in the design and planning of such upland sites. These landscape management aims should not be confused with an intention to allow unchecked natural processes to act in an area.

The idea of rewilding, or wilding, is often discussed in tandem with the possibility of applying naturalistic grazing, but like the phrase ‘naturalistic grazing’, there is potential for confusion with these terms.Rewilding is a very appealing concept, and hence is adopted by many authors, but in different contexts and often with different meanings. For some, it means allowing areas to develop with ‘undefined outcomes’ for habitat and species composition (Fenton 2004a). This definition fits with the idea of naturalistic grazing characterised in section 4. The hope is that ‘wild nature can do better’ than interventionist management, and authors such as Fisher (2004) wish to give it a chance. In other cases the term has a quite different meaning. For instance, in the laudable work of the National Trust resulting from the ‘Save Snowdon’ appeal, ‘rewilding’ is used to describe the planned management of a 93 ha valley that will be seasonally grazed by cattle (Neale 2004).

There is a strong emotional driver for ‘rewilding’, linked to a tendency to view semi-natural habitats as in some way deficient because they result from human activity (Toogood 1997). For instance Robertson (1995) asks whether we are ‘just rearranging nature to satisfy the human ego’, and Marren (2002) laments a loss of ‘respect’ for wildlife and a disappearing sense of mystery when nature management is driven by action plans and their targets. So the appeal of a minimum intervention, target-free, nearly-natural alternative is hardly surprising. Add to this an Arcadian image of a natural parkland landscape resulting from naturalised grazing in the lowlands (Vera 2000), and the appeal of moving away from prescriptive conservation may become very strong. However, there is no evidence that parkland or wood pasture landscapes would necessarily dominate a ‘naturalistic’ landscape, so there is a need for caution: the actual landscapes that might result from naturalistic grazing regimes cannot, by definition, be predicted.
4.9.2 Ecological and methodological implications

4.9.2.1 What replaces conservation targets?

The practical difficulties of reconciling ‘naturalistic’ ideology with the day to day issues of site management was a major theme emerging from the case study questionnaires and this is discussed in sections 4.7.2.1 and 4.8. Although the intention to step back from management, and allow ‘natural processes’ to shape the landscape, was a stated general aim for two of the three sites, it was more difficult to apply this objective in detail. Many overall aims of the sites were concerned with creating wilderness areas, removing unnatural boundaries and allowing room for natural processes; but on closer deliberation these aspirations were not always compatible with more specific objectives. None of the sites expressed an intention to give natural processes entirely ‘free rein’, as suggested for upland National Parks by Edwards (1991) and advocated by Fenton (2004b). Even when a general ambition to ‘allow nature to take its course’ was expressed, managers were understandably reluctant to accept losses when pressed about individual species or valued habitats.

The most workable alternative to complete non-intervention is probably to manage within limits to acceptable change, as suggested by the Council for National Parks (1998). Limits to ecological change mainly fall within Category 3 (Change in habitat extent or species population size) defined in section 4.8. Category 1 (Protection of special features) is discussed in section 4.9.4; Category 2 (Control of unwanted species) is discussed in section 4.9.6.

At sites where loss of biodiversity could be significant, the limits to acceptable ecological change are likely to differ very little from targets already used for conservation management. In sites with less conservation interest at their starting point, relatively flexible limits may be applied that allow more scope for ‘natural processes’ to shape the landscape. Case study respondents, in some cases, hoped that shifting mosaics of vegetation would develop as a result of these ‘natural processes’, and particularly through naturalised grazing. However, the scope for shifting mosaics to operate where stock levels are manipulated to maintain proportions of habitat within certain limits must surely be low (see 4.9.2.2).

4.9.2.2 Large herbivores, biodiversity and landscape

In the early days of nature reserve development in Britain, the emphasis was on protection from harmful activities such as disturbance and collecting. However, famous examples, such as Badgeworth (a small reserve in Gloucestershire) rapidly demonstrated that merely fencing an area was not adequate, and could even be counterproductive. The vegetation within the fence soon grew rank and temporarily extirpated the plants that the reserve had been created to protect. The solution, of course, was grazing (Marren 2002). Now, collations of management experience, and the scientific literature, provide a large and growing body of evidence that document the key importance of large herbivores in conservation (section 4.4), and our understanding of the way in which herbivores impact their environment as highly integrated components of food webs, that exert strong direct and indirect influences on ecosystem dynamics, is constantly improving (Bullock & Armstrong 2000).

Indeed, most countries in western Europe have outstanding examples of reserves with management including grazing that have high levels of biological diversity: the Camargue in France, the New Forest in England, Mols Bjerge in Denmark, Oland in Sweden, the Borkener...
Paradies in Germany and the Junner Koeland in The Netherlands (WallisDeVries and others 1998). Even grazing by sheep (not a native herbivore) can be beneficial when numbers are not kept artificially high. Soay sheep, for example, in the St Kilda archipelago, whose numbers are naturally regulated by food availability (Clutton-Brock 2004), appear to have a positive effect on plant biodiversity on the island of Hirta: species richness is higher on grazed areas and falls rapidly when fences are erected to exclude sheep (Crawley and others 2004).

In addition to their key role in conservation of biodiversity, there is also no doubt that large grazing animals can create and maintain landscape openness. Deer maintain grassy glades in British upland forests (Peterken 1996), and sheep suppress tree regeneration in British uplands (Hester and others 1996). However, it would not be realistic to extrapolate directly from research on agricultural or even extensively managed conservation grazing systems, to determine what would happen on a naturalistic reserve. The way in which large herbivores distribute themselves in a landscape is driven largely by the distribution of vegetation (Palmer & Hester 2000), water and shelter; together with social or gregarious behaviour (section 4.9.2.3). This in turn has a major effect on their impact on their environment (Gordon and others 2004).

For instance, grazing by cattle in the Wolfhezerheide, a 60 ha area in the Veluwe, Netherlands, generated dynamic grass-heather dynamics by gap formation in mature heather stands, followed by grass invasion in these stands. The cattle also suppressed late and mid-seral shrubs, trees, tall herbs, and grasses to create and maintain grass lawns in woodland gaps (many created by storms) (Bokdam 2003). These cattle were grazed at 0.2 LU / ha-1 year round with supplemental feed provided in the late winter. In contrast, free ranging highland cattle in the Veluwe mostly graze in ex-agricultural pastures, using the heathland and pine woodland mainly in transit. Exclosures in heathland on this reserve show that the cattle have no measurable effect (section 4.5.1). In the more extensive grazing regime, localisation of vegetation-herbivore interactions within the landscape (see also 4.9.2.3) becomes more important as the animals select preferred areas for feeding. Such effects of former land use are likely to persist and influence the grazing behaviour of animals for a very long time; in the Swiss National Park, for instance, grazing patterns of red deer still reflect former agricultural use 80 years after the park was founded (Schütz and others 2003).

The open wood-pasture type landscape that has been envisioned for naturalistic lowland areas (grazed by large herbivores) depends on the development of a shifting mosaic of vegetation types. This mosaic includes open grassland and woodland glades (Olff and others 1999; Vera 2000) (Hodder and Bullock 2005, this volume). If the management aims for a reserve include large stocking herbivores at sufficient density to maintain short sward in grassland areas (as required in the agricultural case study) this would not permit the woodland regeneration phase of the shifting mosaic to occur. Herbivore population crashes would be required to provide windows of opportunity for scrub and tree regeneration. This could potentially be managed by simulating herbivore population crashes by periodically reducing stock density, but of course, this would not be ‘naturalistic grazing’ as defined in section 4.5. Timescales for this sort of simulation would need to be long, at least decades, because temperate woodland regeneration may take at least 30 years (Harmer and others 2001).

In the Oostvaardersplassen, more than twenty years after the start of grazing by cattle, ponies and deer, the fertile soil supports a high density of the herbivores on a close cropped turf. There are patches of scrub (mainly willow and elder) that colonised the marginal area prior to
its addition to the grazing reserve, but since then, bark stripping by the herbivores has killed most of these trees. There is no sign of tree or scrub regeneration, and it seems likely that a major population crash would be required to start this process. There is no way of accurately predicting the temporal or spatial patterns that might emerge.

Fluctuations in herbivore population size could be exaggerated in a fenced reserve in comparison to a truly wild situation, where animals would be free to disperse. Fenced reserves are analogous to island populations, and constraints on dispersal may amplify fluctuations in population size. For instance, this appears to occur to Soay sheep living on the island of Hirta (St Kilda), although here, the island effects are exacerbated by severe weather and possibly also by parasite load (Clutton-Brock 2004).

Large herbivores influence their environment not only through grazing, but also through nutrient cycling and transfer (Bokdam 2003; Crawley 1997), trampling to provide new germination niches, and seed dispersal (Couvreur and others 2004; Poschlod & Bonn 1998). For instance, wild boar *Sus scrofa* in forests increase decomposition of organic matter, and soil nutrient mobilisation, and hence have stimulating effects on forest growth (Van Wieren 1991). In such complex systems, with many interactions between species and feedback mechanisms between plants and grazing animals, specific effects of grazing on individual species and community composition may be difficult to predict (Vesk and others 2004; Watkinson & Ormerod 2001). Interactions between grazing species are particularly important and these include both competitive exclusion and facilitation. On the Isle of Rum, species diversity of grassland was reduced after cattle were removed, leaving red deer as the main grazer. When cattle were reintroduced not only did the grassland diversity recover, but the reproductive performance of the red deer also increased (Gordon 1988). There are also important interactions between large and small herbivores. Scrub and trees regenerated in grassland grazed by cattle at low density, but when rabbits were also present, regeneration was prevented (Bakker 2003).

Interactions between herbivores and their parasites may also affect population dynamics and hence the impact of herbivores on their environment, but the role of parasites in host dynamics has not been studied for the vast majority of ungulate species (Wilson and others 2004). The negative impact of nematode parasites on the fecundity of Svalbard reindeer living in the arctic may be sufficient to regulate population densities (Albon and others 2002). Evidence for parasite influence on population dynamics of Soay sheep on Hirta are less convincing (Wilson and others 2004) but it is likely that the population crashes are generated by a complex interaction between the sheep, their food supply, their parasites and climate (Clutton-Brock and others 2004).

4.9.2.3 Large herbivores: behaviour, breeds and ‘de-domestication’

By definition, a naturalistic system should be grazed by native herbivores, in other words those that were present in the UK during the mid-Holocene, just prior to any major environmental impact by Neolithic peoples (Hodder and Bullock 2005, this volume) The large herbivore fauna at this time included aurochs, red deer, roe deer and wild boar. It is unlikely that there are any direct descendents of British wild horse in our modern fauna, and there is no evidence for the European bison *Bison bonasus* in Britain following the last glacial maximum (Yalden 1999, 2003). Horses are, nevertheless, used very successfully in grazing for biodiversity in Britain, providing double benefits; nature conservation and also conservation of rare breeds. Hardy rare breed ponies are particularly well suited to extensive
grazing for conservation, and are often more able to defend themselves from attack by dogs than other large herbivores. However, assuming that the fossil evidence is correct, a truly naturalistic approach in England would not include this herbivore.

The importance of stock choice for conservation grazing has received considerable attention and will not be reiterated in detail here (Rook and others 2004; Tolhurst & Oates 2001; WallisDeVries 1994; Wright and others 2000). Species, breed, background, age and sex all need to be considered on a site specific basis. Some breeds are well suited to wet sites, horned breeds may have more effect on trees and scrub (WallisDeVries 1994), and docility may be a key factor for sites that receive many visitors.

In addition to the considerations necessary for any conservation grazing scheme, a naturalistic approach also aims to gradually allow horses and cattle to revert to a wild state; ‘de-domestication’ (Tramper 1999). Under current welfare legislation this would not be permitted in the UK (section 4.9.5), but if it were possible, the genetic composition and minimum size of the herd would be important factors (Overmars and others 2002). The Oostvaardersplassen (section 4.5.1) has been stocked with Heck cattle and konik ponies; breeds which are thought to resemble their extinct progenitors as closely as possible. The Heck cattle breed was created in the 20th century in Germany, with the specific goal of producing an animal with the appearance of the extinct aurochs, which were last seen in the wild in the 16th century in Poland (Bokdam 2003) and in captivity in the early 17th century (Szafer 1968). Konik, or Polish primitive ponies, are thought to be closely related to the tarpan or wild horse, which only became extinct in Poland in the 19th century (Kownacki 1992).

In a naturalistic grazing regime the large herbivores would live in social groups and these would clearly exhibit different behaviour from domestic herds. Cattle, for instance, form groups primarily composed of related females; bulls leave the group after about three years and form bachelor herds (Overmars and others 2002). Social structure is likely to affect grazing patterns, low ranking bulls in the Oostvaardersplassen tended to graze separately from the main herds on less favoured parts of the site, with poor forage. As result, a large proportion of these bulls failed to survive the severe winter in 1999 (Beije 2002). With such social groups, the manipulation of grazing pressure through changing livestock density (see section 4.7.2.1 and 4.8) would be less straightforward than when domestic herds are used. Disruption of social units is likely to cause stress to the grazing animals hence affecting their welfare (see section 4.9.5).

Natural behaviour of large herbivores also includes seasonal migration and dispersal, and this is one reason why the island effect of fenced nature reserves limits their ‘naturalness’. In nature reserves with limited habitat types, seasonal grazing may be more ‘natural’ than year-round grazing with supplemental feeding because the former should more closely mimic migration between summer and winter grazing areas (Bokdam & WallisDeVries 1992). A solution to this would be creation of very large reserves (tens of thousands of hectares) encompassing both summer and winter grazing areas, or linking reserves in large scale ecological networks (Baerselman & Vera 1995; Groot Bruinderink and others 2002, 2003).

4.9.2.4 Ecological monitoring

It may be misleading to describe naturalistic grazing and wilderness projects as experiments in their entirety, because they lack key elements such as replication and repeatability. They
could however, have the potential to provide useful observational studies providing that adequate planning and provision of resources results in sufficient baseline and monitoring data.

Well planned and long term observational studies could help to determine the mechanisms and processes which underlie the distribution, movement and foraging behaviour of large herbivores, and how the dynamics of plant species and communities, and invertebrate and vertebrate (eg small mammal and bird) populations are affected. Work in North America demonstrates the importance of long-term studies. Early predictions in the Yellowstone National Park suggested that strong density-dependent mechanisms would regulate the ungulate populations around a single equilibrium point. However, evidence collected in recent decades has indicated that the systems are more complex, stochastic events can alter the equilibrium, and multi-equilibrium or even non-equilibrium states are just as likely (Singer & Mack 1999).

4.9.3 Constraints – unintentional human impacts

Even if naturalistic reserves are managed without prescriptive targets for species and habitat composition, limits to ‘naturalness’ of these areas will inevitably be imposed, not only through limits in spatial extent and ‘completeness’ of habitats in the reserves (see 4.9.2.3) but also through unintentional impacts of human activities. Atmospheric pollution, exotic species, groundwater depletion, and the extirpation of key species, particularly, large predators and the European beaver, are all factors that may impose important constraints. The following examples are merely illustrative and not intended as an exhaustive survey.

4.9.3.1 Introduced species

In Britain, the rabbit *Oryctolagus cuniculus*, provides a classic example of a naturalised species that has a significant effect on the landscape. Grazing pressure from high densities of rabbits can prevent regeneration of scrub and woody plants (see also section 4.9.2.2). This has been demonstrated in exclosure experiments in the Baronie Cranendonck reserve on the Dutch-Belgian border (Kuiters & Slim 2002) and in the Junner Koeland, the Netherlands (Bakker 2003). Development of wooded areas in naturalistic areas could also be affected by the introduced grey squirrel *Sciurus carolinensis*; debarking of young trees by this species is recognised as an important problem in the New Forest (Mountford 2001). Attempts to eradicate these two species have failed, and in the case of the rabbit in England, eradication would often be deemed undesirable by conservation practitioners, who in some circumstances need to encourage grazing by this species in order to provide a short sward (see 4.7.1.4).

Many invasive exotic plant species (eg *Rhododendron ponticum* and *Impatiens glandulifera*) have also proved extremely difficult to control, never mind eradicate. Some form of intervention seems necessary even under a naturalistic regime in order to prevent excessive colonisation by aggressive plants. In the case studies (sections 4.7 and 4.8) all interested parties agreed that some control of exotics would be necessary. Interestingly, partners in the plan to create a ‘Wild Ennerdale’ do not plan to eradicate exotic conifers from the whole valley. In the central part of the valley, well thinned conifer is thought to add to the wild character of the area (Browning & Yanik 2004). In other words, landscape management for public use is considered in addition to managing for biodiversity, or in the case of Ennerdale, allowing space for ‘natural processes’ (see sections 4.8 and 4.9.8).
4.9.3.2 The absence of large predators

The effects of food limitation and predator pressure on prey populations are a complex and central issue in ecology. There has long been a debate about the relative importance of top-down and bottom-up forces, in other words whether little things (Wilson 1987) or big things run the world. It is likely that these ‘trophic cascades’ act in both directions simultaneously, and that the dichotomy between the two is artificial (Hunter & Price 1992). It is certain though, that the absence of large predators in England imposes a constraint on the naturalness of potential naturalistic reserves.

Assuming that large carnivores will not be reintroduced in England due to the very large tracts of land that would be required for viable populations (Wilson 2004), a pragmatic solution promoted by proponents of naturalistic grazing is to attempt to mimic natural selection by culling (or removing) any animal that appears to be beyond hope of recovery. Site managers of Dutch Track A (almost natural) reserves are described as seeing stock ‘through the eyes of the wolf’ (Tramper 1999). This may also fulfil animal welfare requirements, as suffering animals are not left to die slowly, provided that they can be located (section 4.9.5).

However, the interaction between vegetation structure, predator hunting behaviour and herbivore response to predation risk is likely to be profound, variable and complex (White and others 2003). Recolonisation by wolves in the Banff National Park, Alberta allowed Hebblewhite and others (2002) to demonstrate important differences in ungulate population dynamics in the presence and absence of wolf predation. The behavioural response of ungulates to the presence of wolves however, has more far-reaching consequences than just predation on individuals (Laundré and others 2001). Fascinating ecosystem changes have been recorded following the reintroduction of wolves in 1995-6 after almost 70 years absence in Yellowstone National Park. The study provided rare empirical evidence of a top-down trophic cascade through three trophic levels. At high predation risk sites (low visibility or escape barriers), riparian vegetation (cottonwood and willows) appeared to have been released from browsing by deer *Cervus elaphus*, whereas at low risk sites (open areas), riparian vegetation was still suppressed. Although it is too early to determine whether the trend will continue and what the spatial extent of the effect will be, it is possible that numerous ecological benefits could accrue to riparian and aquatic communities such as stream-bank stabilisation, and increased litter inputs (Ripple & Beschta 2003).

Risk sensitive foraging, in other words, leads to different grazing patterns than can be achieved by culling – even if managers seek to view stock ‘with the eyes of a wolf’.

4.9.4 Constraints – conflicts of interest

Possible conflicts of interest that could arise in a naturalistic reserve were considered in the case studies (section 4.7 and 4.8). Issues of access were particularly pertinent, and although these concerns were not all exclusive to the naturalistic approach, use of breeding groups of large herbivores has implications for access that would not affect a large reserve managed extensively with domestic stock (see section 4.9.6.1).

Fences would be required around the boundaries of any grazed site, and this could be opposed by pressure groups. The Open Spaces Society, for instance, have been remarkably
successful in opposing grazing and fencing applications – (British Wildlife, June 2004, p. 371).

Although the Countryside and Rights of Way Act 2000 provides for public access to be restricted or excluded, for an unlimited period, from access land that can be classified as ‘Protecting nature conservation’ (http://www.defra.gov.uk/wildlife-countryside/cl/factsheet.pdf), respondents from the case study sites were keen to maximise access where possible. Site managers should therefore liaise with Local Access Forums, set up under the CRoW Act, by bodies such as National Park authorities in order to advise local authorities and countryside bodies on the improvement of public access to land.

Another potential source of conflict was presented by the presence of archaeological remains on a site and the risk that unchecked ‘natural processes’ might obscure or even damage these remains. All respondents in the case studies took the pragmatic approach that protective measures (eg fencing or felling trees) would be taken to avoid such conflicts.

4.9.5 Animal welfare

The welfare of large herbivores used in conservation projects is protected by national and international legislation, as well as strong public interest. In July 2004 Defra published a draft Animal Welfare Bill that brings together all welfare legislation relating to farmed and non-farmed animals, and is expected to become law in 2005 / 2006 (http://www.defra.gov.uk/animalh/welfare/bill/index.htm).

Among other things, the bill introduces a duty on owners and keepers of all vertebrate animals, not just farmed animals, to promote the welfare of animals in their care. Those responsible for enforcement of welfare laws will be able to take action where an animal, although not currently suffering, is in a situation where its welfare is compromised. Managers should be aware of the practical implications of carrying out adequate health checks to provide a suitable level of care. On very open and flat sites, such as the Oostvaardersplassen, it may be feasible for rangers to find and check all stock on a regular basis, but where access or visibility is more limited (ie because of tree cover or steepness) finding stock is likely to be much more difficult.

Codes of Practice will be developed to enable the new ‘duty of care’ to be effectively applied in a variety of circumstances. These codes will need to deal specifically with extensively grazed conservation areas, because at least some aspects of Codes of Practice developed for domestic bovines and equines would not be fully appropriate for these situations. The Grazing Animals Project has convened a working group to address these issues with the long-term aim of producing a Code of Practice for ‘extensive grazing systems’ under the new Act. The group will draw from the Guide to animal welfare in nature conservation grazing (Tolhurst 2001) and consider aspects specific to extensive systems. These include the importance of recognising the social structure of herds and awareness of how undue stresses can result from disruption of the herd. The need for veterinary treatment for extensively managed stock should be weighed up against the stress that can be caused by handling an animal, and by potentially upsetting the social structure of the herd.

Choice of breed is pertinent to this issue, as more hardy breeds adapted well to a specific habitat, should require less veterinary intervention. A comparison of breeds used on a site in Norfolk provides a good example. Although Welsh Mountain ponies are relatively easy to
handle, and are lightweight so causing minimum hoof damage to peaty soil, free ranging Konik ponies appeared to have at least three advantages over the Welsh ponies. The Konik ponies did not require anthelmintics, because their parasite burden stabilised, whereas the parasite burden of the Welsh ponies increased without treatment. Secondly the Konik ponies did not require regular hoof trimming, but the Welsh required visits from the farrier twice a year. Thirdly, unless access to ‘good grazing’ was restricted, the Welsh ponies tended to suffer from laminitis, a condition rarely reported in Konik ponies, unless their dietary choice is restricted (Sandie Tolhurst pers. comm.).

The case study interviews and the general review revealed that the Dutch Ethical Guidelines (Tramper 1999) are widely read in the UK, and that the concept of resource-limited grazing animals fits well with the aims of re-wilding. However, at present there is no indication that Defra would consider allowing owners to abrogate their responsibilities under laws relating to animal welfare (Graham Thurlow, Defra, pers com.). Even the wild white cattle at Chillingham are offered hay on a daily basis when grazing conditions are poor (Austen Widdows, Warden Chillingham, pers comm.). Neither is there full consensus in the Netherlands about the ideas presented by Tramper (1999) in the Dutch Ethical Guidelines. A response from the Royal Netherlands Veterinary Association suggested that only ‘truly wild animals’ such as deer and wild boar should be used in the naturalistic (Track A) sites (Lumeij & Oosterbaan 2000).

4.9.6 Bio-security, health and safety issues

4.9.6.1 Risks to human safety

Where there is open access to areas grazed by cattle, horses or other large herbivores, there will be a risk of injury to the public (as well as risk to the stock from dogs) and resultant liability for the owners or managers of the stock. The use of breeding groups of large herbivores may present risks additional to those found on land grazed by domestic stock. Horse riders, for instance could be vulnerable in the vicinity of stallions.

The Health and Safety Executive (HSE) reported 14 major incidents, including 5 fatalities, involving cattle in fields in the UK between 1990 and 1995. Although the risk may be minor when viewed in perspective of other risks to users of the countryside, such as risks involved in equestrian sports and infection with Lyme’s disease (Henkens & Maasland 2002), it requires due consideration. This was reflected in the concerns expressed by the case study respondents (section 6). The HSE has a clear stance on allowing cattle in fields with public access (Health and Safety Executive 2002), http://www.hse.gov.uk/pubns/ais17.pdf.

Their advisory notes indicate that Section 59 of the Wildlife and Countryside Act 1981 prohibits bulls of recognised dairy breeds being at large in fields crossed by public rights of way. Bulls of all other breeds are also banned unless accompanied by cows or heifers; this could possibly be relevant in relation to formation of bachelor herds. Perhaps more pertinent to extensive or naturalistic approaches is the requirement of Section 3 of the Health and Safety at Work etc Act 1974, that employers, so far as is reasonably practicable, do not put others at risk through their work activity. The HSE advises that keeping bulls and other cattle in fields is an activity to which this section applies.

The higher duty of care under the Occupiers’ Liability Act 1957 does not apply towards people exercising access rights under the CRoW Act 2000. However, there is still liability for
owners under the Animals Act 1971. Detailed advice on relevant legislation, and guidance on open access and public liability, is available from the Countryside Agency at: http://www.openaccess.gov.uk/wps/portal/lm/liability.

4.9.6.2 Human and domestic animal health

The naturalistic method aims for minimum intervention, and this includes the approach to stock management. Although the case studies showed that in reality, sites would begin with small extensively grazed herds, which would be subject to the same veterinary guidelines as other domestic stock, there were aspirations at two of the sites to attempt to move towards ‘re-wilding’ the large herbivores. This has health implications in two ways: the risk of disease spreading from the naturalistic reserve to humans or to domestic stock outside of the site, and secondly, health risks associated with carcasses left in the field.

Leeuwen van & van Essen (2002) suggest that scenarios should be drawn up to predict the risks of disease outbreak and spread from the Dutch nature areas, and that routine monitoring and contingency plans should be developed. Diseases to be considered include zoonotic diseases (ie those which can be transmitted to humans eg Leptospirosis, Anthrax), and diseases that could have economic impact for farmers (eg Infectious Bovine Rhinotracheitis, Bovine Virus Diarrhoea, Foot and Mouth Disease). The possibility of free-ranging stock leading to contamination of human water supplies with the protozoan parasite Cryptosporidium was a concern in the case studies. The greatest danger is to people who use private water supplies with less advanced filtration systems than public supplies. It was noted that the relatively old animals used in more naturalistic grazing should build up a resistance to this parasite, and hence may present a lower risk than farmed stock (section 4.7.3.5).

Some diseases that could occur in a naturalistic reserve are notifiable under the Animal Health Act 1981 which says that:

"any person having in their possession or under their charge an animal affected or suspected of having one of these diseases must, with all practicable speed, notify that fact to a police constable."

In practice, managers suspecting signs of any notifiable disease must immediately notify a Defra Divisional Veterinary Manager (http://www.defra.gov.uk/animalh/diseases/notifiable/index.htm).

This implies that regular checking and routine testing of stock would be required, as for domestic stock. Currently all bovines are also required to be registered and identified under Regulation (EC) No 1760/2000 of the European Parliament and Council (July 2000), referring to the European Directive 64/432.

Defra have however, granted an exemption for management of the wild white cattle at Chillingham. The Chillingham herd was determined to fall outside of all of the categories of bovines that require tagging in the Regulations (as do zoo bovines), and therefore remain untagged. The herd is also exempt from requirements for routine testing for TB. The legal argument was upheld because the Chillingham herd were felt to be a special case, not
handled, traded or moved out of the site, and not intended for the human food chain (Pers. comm. Defra’ and Austen Widdows, Warden, Chillingham).

The outbreak of Foot and Mouth Disease in 2001 inadvertently provided some insights on issues that might be relevant to ‘naturalistic’ grazing.

(i) While the reduction of stock density in upland areas is thought to have been generally beneficial in conservation terms (Robertson and others 2001), there were also some complaints about the risk of loss of treasured landscapes and the ‘spread of unsightly scrub’ (Keith Kirby Pers. comm.; see also Hudson (2005)).

(ii) Given the high cost of the epidemic to the taxpayer (National Audit Office 2005) it is unlikely that a naturalistic herd would be exempt in the event of another outbreak, especially if it was of recent origin (in contrast to the Chillingham herd).

(iii) Implementation of disease control by culling or vaccination could present problems in a naturalistic herd.

Current concerns about the possible role of deer in the spread and perpetuation of bovine tuberculosis (Defra 2005), and of wild boar in the spread of various diseases to domestic pigs are also relevant.

The possibility of leaving carcasses in the field was raised, to provide food for carrion feeders and increase the ‘naturalness’ of the system. However, rotting carcasses contain not only the pathogens that killed the animal, or caused it to require culling, but may also harbour *Clostridium botulinum* which can cause the potentially fatal disease, carrion botulism which affects many animals including humans. Hence, owners or managers are legally required to remove carcasses. An exemption to the Dutch ‘Destruction Act’, which requires removal of carcasses of cattle and ponies, was obtained by the managers of the Oostvaardersplassen. However, this exemption was soon rescinded because it was determined that it had no legal basis (Kampf 2002). This was because of the potential risks to the environment, public health and stock on nearby farms. So although, in practice, it is often difficult for nature managers to locate and remove dead bodies, they are bound, in all circumstances, to eliminate any dangers to health.

4.9.6.3 Pernicious weeds

In addition to unwanted spread of invasive exotic plants, potential impacts or conflicts could result from the presence of pernicious weeds on naturalistic sites. This was one of the factors identified in the case studies that would prompt management intervention in a site, although the overall aim was for as little active management as possible. Managers were particularly aware of the need to control pernicious weeds near the boundaries of their sites (section 4.7.2.1).

The most obvious example is common ragwort *Senecio jacobaea*, which although an important invertebrate food plant, is poisonous to horses, ponies, donkeys and other livestock, by causing liver damage, and can have fatal consequences. It is one of five injurious weeds covered by the provisions of The Weeds Act 1959, under which Secretary of State may serve an enforcement notice on the occupier of land on which injurious weeds are growing.

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5 Defra contact for cattle tagging – Lynn Newman
requiring the occupier to take action to prevent the spread of injurious weeds. There is now added protection to livestock provided by the Ragwort Control Act 2004 which amends the Weeds Act. This Act enabled the Secretary of State to make a Code of Practice to prevent the spread of ragwort; by promoting good practice and good neighbourliness the code aims to significantly reduce the risk posed by ragwort poisoning to horses and other animals. The Code provides guidance on how to develop a strategic and cost-effective approach to weed control, but does not seek to eradicate ragwort. The new Act will make it easier to prosecute those who disregard the need to control Ragwort, but it recognises that where there is no threat to animal welfare, common ragwort makes an important contribution to the biodiversity of the countryside.

4.9.7 Economic issues

It is not possible to accurately assess potential economic effects of a naturalistic approach, because by definition this approach has unknown outcomes in terms of landscape and biodiversity; assuming that ‘natural processes’ are allowed to shape the landscape, there may be potential for losses or gains, depending on the outcome.

If landscapes that attract visitors emerge in naturalistic reserves, these could potentially generate income through nature tourism. A ‘high quality natural environment’ is thought to be essential for an estimated 192,000 full time equivalent jobs in England (GHK Consulting Ltd 2004). Likewise if the public perceived a loss of landscape or biodiversity interest, economic losses could occur.

A socio-economic appraisal of the potential for developing new ‘wild land’ in Northumberland concluded that this approach would lead to negative economic and social impacts on the local economy and community; both in the medium and long term. It goes on to state that the deliberate non-management of extensive areas of former agricultural land is not a viable option, and recommends instead that policy should concentrate on enhancing existing environmental and cultural assets, rather than attempting to ‘compete’ with other countries which already include large areas of ‘truly wild land’ (Countryside Agency 2002). However, since the publication of this report there have been significant changes in the way that agricultural subsidies are organised, so it could be worthwhile repeating the appraisal to determine whether the outcome would change.

The reduction in economic viability of forestry plantations was an important motivator for investigating the potential for other forms of landscape management. Plans to remove plantations, for instance, in start-up works for a ‘naturalistic’ reserve, would however, still be subject to forestry regulations (felling licences, Environmental Impact Assessments etc.).

Marketing meat from culled livestock as suggested for the agricultural case study site (section 4.7.3.2) would clearly not be consistent with aspirations to manage for untagged ‘resource-limited’ animals. This is in contrast to managed free-range herds, which can produce meat at premium prices (Table 3).

4.9.8 Strategic issues

The case study review showed that links between naturalistic grazing and biodiversity objectives (eg BAP targets) could be problematical, depending on the degree to which
‘natural processes’ should act without management intervention, and depending on the level of conservation interest already present in the site (sections 4.5 and 4.7.2).

There are however, strategic changes in conservation approach that link with many of the aspirations of the case study partnerships. These are encapsulated in the policy statement (http://www.defra.gov.uk/rural/pdfs/ruraldelivery/bill/policy-statement-(md6460.pdf) for the Draft Natural Environment and Rural Communities Bill; published in February 2005 (http://www.defra.gov.uk/rural/ruraldelivery/bill/).

This draft bill aims to bring together and integrate responsibilities for protecting and enhancing the value and beauty of our natural environment, and will combine English Nature, parts of the Countryside Agency and the Rural Development Service into a new Integrated Agency to be called Natural England. Defra specifically refer to the potential of large-scale landscape and ecosystem restoration projects like the ‘Wicken Vision’ (Colston 2004) to illustrate the way in which the new Integrated Agency will function.

In addition to managing for biodiversity, the draft bill suggests integrating responsibilities for protecting and enhancing the value and beauty of our natural environment, alongside functions to promote access, recreation and public well-being. These objectives would not necessarily encourage the development of naturalistic type sites, with their emphasis on allowing ‘natural processes’ to act with minimum direct intervention. They would however, be compatible with setting up landscape scale reserves that seek, among other aims, to convey a ‘sense of wilderness’ that is sought by the public (see section 4.9.1). In practical terms this is likely to require specific management for landscape, as well as biodiversity objectives, such as maintenance of openness for access and to enhance the scenery.

The importance of natural areas for recreation was recently quantified in a MORI poll, commissioned by the National Trust. This revealed the pivotal role that wildlife and the countryside play in the life of the British public. The research confirmed that access to the countryside provides essential emotional, spiritual and physical wellbeing to millions – a ‘Natural Health Service’. For over 80% of adults, visiting the countryside was a vital counterbalance to the stresses of their daily life. Half those polled were in search of ‘peace and quiet,’ while ‘fresh air’ and getting ‘close to nature’ were also seen as important benefits. For one in ten people, visiting the countryside is not an optional extra but is ‘crucial to their quality of life’ (MORI poll 2004).

4.10 Conclusions

The aspirational language of ‘conservation politics’, is vital for rallying support, but can also cause confusion when vision statements are converted into practice. Site planners and managers then have to try to disentangle the various motivations and global aims to produce something that can be put into practice in the context of the landscapes they manage. Confounding factors which became increasingly evident in the course of this review included semantic issues, and more crucially, disparities between global ideologies and the practicalities of managing for biodiversity.

The term ‘naturalistic’ was used to describe a spectrum of extensive grazing practice ranging from the minimum intervention approach pioneered in the Oostvaardersplassen (section 4.4.1), to seasonal grazing by domestic stock (section 4.9.1). It is hoped that the definition
offered in section 4.5 will at least clarify the debate but doubtless, in other contexts, equally valid alternative definitions could be put forward.

Proponents of naturalistic grazing may in some cases seek reduction in management intervention because the ‘natural process’ is an aim in itself. More often, when actual landscapes, habitats and species are discussed, it becomes evident that the real aim is for extensification of management, and a change to practices that are less conspicuously artificial. Although an abstract desire to move away from highly prescriptive target-lead management was often mooted, the potential loss of biodiversity or highly valued habitats was rarely seen as acceptable. Thus this extensive management is not the same thing as the naturalistic approach used in the Netherlands.

Enlarging and linking nature and planning on a landscape scale has numerous advantages over conservation in small fragmented reserves, and if we are to conserve and enhance biodiversity in Europe then this approach is likely to be essential. Extensively managed herds of large herbivores would play a key role in this approach, but these networks and large reserves do not necessarily require the application of naturalistic grazing. Despite copious evidence detailing the benefits of grazing for conservation, the impacts of naturalistic grazing cannot be extrapolated from results obtained in more controlled systems.

Where there is little to lose in biodiversity interest, there may be the greatest scope for trialling naturalistic regimes, but in areas currently of high conservation interest, more management intervention will be required. In practice, managers may opt for allowing natural change to occur up to predefined limits in landscape and biodiversity, and close monitoring of naturalistic systems could enable adaptive management intervention when required. If such trials were attempted, managers should be aware that the practical implications of either stepping back from active management or aiming for a site that appears to be in a state of wilderness, often conflict. Confusing these separate objectives may make it more difficult to grasp the exciting opportunities we now have for developing large interconnected nature reserves for the benefit of plants, animals and people.

4.11 Acknowledgments

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5. **Was the wildwood closed forest or savannah and does it matter for modern conservation – some conclusions**

Keith Kirby, English Nature

5.1 **Summary**

- Large herbivores could have been a significant factor in shifting the balance towards oak and away from more shade-tolerant species.
- The Atlantic period landscape did contain open areas, but trees and woodland appear to predominate. There is no direct evidence for a half-open landscape; nor is this high level of openness a requirement for oak regeneration and cyclical vegetation turnover.
- Cyclical vegetation turnover, driven by grazing, seems less likely than more chaotic patterns. There is evidence that other disturbance factors were at least locally important. Most parts of the landscape were probably driven by more than one disturbance agent and the relative importance of these would vary over time.
- Parts of the Atlantic forest may have looked like a modern wood-pasture and there might have been some permanently open areas; but the majority seems likely to have been relatively closed high forest, but with a component of temporary and permanent glades.
- This research has emphasised the need for clear objectives as to what naturalistic grazing is intended to achieve in modern landscapes. Even if we wished we cannot re-create the Atlantic period landscape and the grazing regime that operated then.
- We can use the ‘ideal, but impossible to achieve’ naturalistic grazing model as a guide to how we approach the management of real systems. Where a choice exists we can look for the option that, within the particular constraints, is closest to our understanding of the natural situation, the option that involves the least direct human intervention.
- Encouraging a naturalistic approach to grazing has the potential to change the way that we practise large-scale conservation, but it must be based on sound ecological and animal management principles.

5.2 **Introduction**

English Nature is interested in the most recent post-glacial landscapes because these may represent almost ‘natural communities’ in Britain, i.e. before significant impacts of Neolithic agriculture. Knowledge of past distributions and function of species assemblages can help us to identify how they have subsequently changed and whether it is desirable or even feasible to recreate them. Do we need to change our vision of what those landscapes were like as a consequence of Vera’s ideas and the subsequent debate?

In addition, English Nature has been developing an interest in the concept of re-wilding and the potential for developing and maintaining wildlife-rich landscapes through low-intervention regimes such as naturalistic grazing. What can we can we learn from the past and from places such as Oostvaardersplassen about the likely outcome of naturalistic grazing in re-wilding schemes?
The aim of this final chapter is to draw some of the threads together, to indicate the conclusions English Nature currently draws from the research. The debate is likely to continue and our position may change over the coming years in the light of fresh research.

5.3 The role of large herbivores in landscapes of the Atlantic period

Vera commented at a conference in Sheffield in April 2005 that critics have focussed too much on the degree of openness in the Atlantic landscape and not enough on the role of large herbivores as a way of explaining the persistence of oak through the pollen record. However this was and is inevitable. A greater role for herbivores as a disturbance factor is not in itself too controversial; it is the proposed associated outcome of a ‘half-open park-like landscape’, compared to the closed forest view of the wildwood, that has both attracted both strong support from some quarters (eg Alexander 2002; Rose 2002) and criticism from others (eg Bradshaw 2002; Mitchell 2001, 2005; Rackham 2003). The role for herbivores is also difficult to substantiate directly – it is impossible to estimate the population sizes for aurochs etc independently of their proposed effect on the vegetation. The openness evidence can however be explored. Therefore it is worth revisiting the link between these two parts of the Vera hypothesis.

5.3.1 The oak pollen record discrepancy and minimum intervention forest reserves

Vera (2000) seeks to explain the discrepancy between the continuity of oak pollen in many records throughout the Atlantic period and its failure to regenerate in modern minimum intervention forests that lack large herbivores. He notes that regeneration occurred historically in many of these sites when they were grazed, and in modern wood-pastures. Good evidence is presented for the failure of oak to survive in ungrazed closed-canopy woodland in competition with shade-bearers such as beech or small-leaved lime (Hodder and Bullock 2005a, this volume). A similar case is made (but in less detail) for hazel.

In Britain the ‘discrepancy’ may be less of an issue because the potential competitiveness of some shade-tolerant species compared to oak is much reduced compared to the Continent.

- Beech and hornbeam were late arrivals in this inter-glacial and hardly spread beyond south-east England.
- Lime is not such a regular seed-producer because of cooler summer conditions (although it would have been more prolific in the mid-Holocene at times when the climate was more continental);
- Ash and elm would be ruled out on the more acid soils and beech on the wetter clays.
- The ability of oak to survive drought and strong winds better than beech would also tend to favour oak’s survival.

Nevertheless the tendency for other species to predominate in some minimum intervention forests does still need an explanation. However modern minimum intervention reserves clearly are not direct analogues of the former natural landscape – they lack some key elements and processes (including some large herbivores and predators) and they are subject to other factors that were not important in the Atlantic period (introduced species, raised levels of atmospheric nitrogen input; changed climate). Given that many minimum intervention woods in England are small Peterken (2000) suggested that in future there is a
case for considering two sets of sites, namely those with and without large herbivores, to at least try to correct for one element of the difference.

5.3.2 Is a half-open landscape necessary for oak regeneration?

Vera (2000) concludes that the key missing-ingredients in modern minimum-intervention reserves are large herbivores; then, using the established concepts of a cyclical turn-over of vegetation, suggests that an open, park-like landscape would result from the return of the missing landscape driver. The wood-pasture is suggested as the closest modern analogy for the former natural vegetation. However at no point in Vera’s book or subsequent debates has an argument been presented as to why the landscape had to be 50% open rather than some other level eg 10%, 20% or even 80%. Nor is any evidence put forward that a high level of openness is essential for his hypothesis.

The evidence that we have reviewed suggests that:

- from basic landscape modelling even 25% (or actually less) openness can be consistent with cyclical turn-over of vegetation (Kirby 2004);
- the pollen and fossil insect records, as well as other evidence, suggest there was some openness but it was not necessarily extensive;
- the openness of many modern wood-pastures is maintained by management other than grazing (e.g. burning and cutting);
- modern wood-pastures also do not necessarily provide a good modern match for the past pollen records, where these are available.
  - Epping Forest, the New Forest and Moccas Park all show that prior to the Neolithic period lime and hazel were more abundant and have declined since (Tubbs 2001; Baker and others 1978; Grant 2002; Dumayne-Peaty 2000). In the case of Epping Forest the lime decline is considered to have occurred about a thousand years ago and to be related to the development of the wood-pasture system on the site.
  - Struik (2001) found 10% non-arboreal pollen in modern grazed New Forest pollen samples which he notes are higher than the values of about 1% often reported for pre-Neolithic samples; there was flowering (hence pollen production) in the adjacent ground vegetation. He concluded that an open park-like landscape was not an appropriate reference point for the Atlantic period landscape.
  - The records for both Epping and the New Forest show increases in beech during the historical period when the sites were actively managed as wood-pastures, i.e the relative abundance of oak versus shade-tolerant species is not constant in grazed woodland.
  - Most wood-pastures do not show a regular succession of generations of oak (or other trees) but rather an abundance of veteran trees (> 300 years old) and little under 150 years: where younger trees are abundant it is usually a consequence of lack of grazing during the last century. Both lack of continuity in the age-structure of oaks and over-abundance of young growth at other sites have been identified as problems in the Wood-pasture Habitat Action Plan (English Nature 1998).

- Oak can regenerate, and maintain itself in open woodland, not just in grassland. For example it invades pine stands in central and eastern Europe (Mosandl & Kleinert
1998; Paluch & Bartkowicz 2004) as long as the canopy is not too dense. Vera notes (p365) that if oak and beech are growing side by side in gaps in the canopy of a closed forest the oak initially has the head start. Thus it is the subsequent competition of saplings and young trees, not necessarily the initial conditions, that may determine whether oak survives to the canopy or not. Herbivores might therefore influence the stand composition in forest gaps by causing more serious bark damage on young beech than on oak. The reduction in growth or subsequent increased risk of disease or stem breakage could tip the balance of competition in favour of oak. A modern analogy would be with damage by grey squirrels, which at low squirrel density is much heavier on beech and sycamore than on oak (Mountford & Peterken 1999; Rayden & Savill 2004).

5.3.3 Would vegetation turn-over be cyclical in herbivore-driven landscapes?

Would a cyclical vegetation turnover be the most likely outcome in a landscape where large herbivores are the main driver of landscape change? The cyclical process relies on quite finely balanced numbers of large herbivores to operate: too few, or the wrong mix of herbivores, and the area goes towards closed woodland as happens in current minimum intervention reserves; too high a level and even regeneration of thorns is prevented, as seems to be the current position at Oostvaardersplassen. Therefore it might be that cyclical turn-over would only occur at some places and at some times.

5.3.4 Interaction between grazing and other disturbance factors

Various evidence (Hodder and Bullock 2005a; Buckland 2005) suggests that in different types of woodland, even in the lowlands, different disturbance factors could be important (Peterken 1996): there is direct evidence for the impact of wind on Atlantic coastal forests (Allen 1992), for fire on pine stands on bogs and perhaps on acid free-draining soils (Chambers and others 1997); while flooding, with or without help from beavers, would have disrupted many stands in river valleys (Coles and others 2003). The contribution of wild boar to soil and ground vegetation disturbance and possible stimulation of regeneration is unknown, but likely to have been significant.

It is simplistic to regard the lowland landscape as being dominated by one type of disturbance regime. A better model may be to consider that across the landscape variations in topography, soils and past stand history would interact with different combinations of disturbance regime (e.g Peterken 1996). In limited areas, at a given time, a single factor (which could be grazing) might determine the composition and structure of the wood, but elsewhere it might be the interaction of two or more factors. This is represented schematically in Figure 1. The areas influenced by the different factors could change over time.
Figure 1. A representation of how disturbance in the Atlantic-period landscape might be viewed. Any one place might fall within different zones of overlap of the various natural disturbance factors represented by the circles (other circles such as disease or drought might be added). The circle for human disturbance has been deliberately left to one side – it could be made bigger or smaller and be placed to overlap with all of the others to varying degrees depending on views as to how significant people were in different landscapes.

5.3.5 The nature of the Atlantic forest

From the various reviews and discussions I conclude the following:

- Large herbivores could have been a significant factor in shifting the balance towards oak and away from more shade-tolerant species.
- Their influence could have been at the young tree stage in forest gaps rather than at the seedling stage.
- The Atlantic period landscape did contain open areas, but trees and woodland appear to predominate.
- There is no direct evidence for a half-open landscape; nor is this high level of openness a requirement for oak regeneration and cyclical vegetation turnover.
- Cyclical vegetation turnover seems less likely than more chaotic patterns.
- There is evidence that other disturbance factors were at least locally important.
• Most parts of the landscape were probably driven by more than one disturbance agent; the relative importance of these would vary over time. In places Mesolithic human impact would have been significant.

Parts of the Atlantic forest may have looked like a modern wood-pasture and there might have been some large permanently open areas; but the majority of, at least the lowlands, does still seem likely to have been relatively closed high forest with a component of temporary and permanent glades.

5.4 The role of large herbivores in modern re-wilded landscapes

English Nature is committed to promoting conservation at a landscape scale and we expect that similar approaches will be carried over to our successor organisation (Natural England). Separate discussions are starting on how far English Nature and its successor wish to develop the ideas being discussed on re-wilding. It is too soon to say whether or not we will have a formal policy on ‘re-wilding and wild lands’. Whatever the outcomes, grazing by large herbivores is likely to be one of the regimes we will use to deliver our various objectives for both upland and lowland landscapes.

This research has emphasised the need for clarity about what such grazing is intended to achieve (Hodder & Bullock 2005b). Even if we wished we cannot re-create the Atlantic period landscape and the grazing regime that operated then (Hodder & Bullock 2005a; Buckland 2005).

• The climate and many soils have changed.
• There is still some debate as to the grazing assemblage that was present in England.
• Aurochsen are extinct; Heck cattle are not a direct model for them.
• It is unlikely that introduced species such as rabbits, grey squirrel, fallow and muntjac deer could be eliminated from any trial area.
• Trial areas would need to be large and to incorporate a diversity of conditions such that animals could migrate from, say, floodplains to the hills, if conditions required it.
• At least in the foreseeable future extinct predators will not be re-introduced. Some other mechanism for mimicking their effect would be required.
• There are uncertainties as to whether a re-wilded area would deliver the conservation targets that we want (given that these are largely based on cultural landscapes).
• Animal welfare legislation and public opinion would not allow us to leave stock to suffer or die on site through food limitation.

This does not mean that it is a waste of time exploring what a landscape with a near-natural grazing regime would look like: it is valuable as a potential reference point. We just need to be honest and realistic in recognising how far what we actually set up is from a mimic of the past.

Having freed ourselves from the impossible strait-jacket of pretending that we can create a truly wild system, or some sort of Holocene Park, in England the scope for what we may be able to do with naturalistic grazing regimes is exciting. We can use the ‘ideal, but impossible to achieve’ model as a guide to how we approach the management of grazing in large-scale
systems. Where a choice exists we can look for the option that, within our particular constraints, is closest to an understanding of the natural situation, the option that involves the least direct human intervention.

The constraints will vary from site to site, reflecting the legal requirements to look after animals, but also conservation objectives for habitats and species and the local significance of a ‘wild-looking’ landscape. English Nature will be exploring these ideas further in the three areas that were used as the case studies in this phase of the research over the next year.

Encouraging a naturalistic approach to grazing has the potential to change the way that we practise large-scale conservation, but it must be based on sound ecological and animal management principles. The romance should come from the landscapes we create, not in the methods we adopt.

5.5 References


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