Report Number
530

What might a British forest-landscape driven by large herbivores look like?

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ISSN 0967-876X

Acknowledgements

A wide variety of colleagues inside and outside English Nature have contributed ideas and commented on drafts, including Helen Armstrong, Jim Latham, George Peterken, Neil Sanderson, Jon Webb, Tony Whitbread, John Patmore, Patrick Roper, Rob Fuller, Keith Alexander, Alison Hester, John Bacon, Jan Bokdam, Isabel Alonso, John Hopkins, Keith Duff, Fraser Mitchell, Sallie Bailey, Loek Kuiters.

Preface

Frans Vera's book *Grazing ecology and Forest History* (published in English in 2000 by CABI, Wallingford) has stimulated much debate about the nature of the former natural forest cover of western Europe. It also raises questions about the role of large herbivores in the management of nature conservation sites under current conditions.

Vera (2000) makes a convincing case that the impact of large herbivores has been underestimated. What he does not prove is that the 'natural forests' of Britain were therefore entirely or even wholly an open savannah (as some proponents of the Vera hypothesis appear to suggest), or even that large herbivores were the necessarily the dominant force in shaping our natural landscapes. There is a range of alternative possibilities.

However let us suppose that the large herbivore hypothesis is correct: what then might that landscape look like?

In this report I explore what the structure of the wildwood might have been like, using Vera's hypothesis as a starting point for a simple landscape model. The initial ideas were presented at a British Ecological Society winter meeting and at a seminar in the High Weald in September 2002. The draft report was widely circulated and I am grateful to those who provided me with ideas and comments (see acknowledgements).

The model is simple, but does illustrate that a number of different landscape outcomes are possible within the framework of the Vera hypothesis. This has implications for how data from pollen or invertebrate remains are interpreted, but also for attempts to apply Vera's ideas to modern conservation management.

The debate about the role of large herbivores in natural forests and in modern management has further to go. Any comments on this report would therefore be welcomed.

Summary

The generally accepted view of the natural forests that once covered much of Britain has been of largely closed-canopy woodland, with many mature trees; and regeneration in gaps created by the death or destruction of small groups of trees, or occasional catastrophic blow-downs.

An alternative view has recently been promoted in which large herbivores such as aurochs, grazed open areas that eventually went through scrub and woodland phases before breaking down to form open areas again. There is under this model no direct replacing of woodland by woodland such as occurs in the gap-dynamic model.

There is evidence for and against both models and the former wildwood may have contained, in different landscapes, both systems. However in areas where the herbivore model predominated what was the landscape structure?

Based on simple assumptions, possible spatial and temporal patterning were explored for an area of 5 x 5 km (2500 ha) over a 500-year cycle. Different combinations of open and closed woodland resulted, depending on the assumptions made about how long, for example, the Grove or open Park phases lasted; whether patches of a particular phase were clumped or scattered. Possible implications for different species groups are illustrated.

A predominantly wooded landscape (50% in the Grove phase, 25% in the Park phase, with the balance as scrub or break-up stands) is compatible with a herbivore-driven dynamic process and seems more likely than an open park-like one with much of the landscape as 'savannah'. Continuity of both open conditions and old trees over time and space can be achieved in this wooded landscape with an intimate mix of habitats at the scale of a few hundred metres.

This result is consistent, quantitatively and qualitatively with the main axioms of the large herbivore hypothesis and with other evidence from pollen analysis studies.

Modern conservation priorities are set against a background of 3000 years (at least) of a cultural landscape. Grazing may be part of the management regimes put in place to maintain the habitats and species deemed to be nature conservation priorities in Britain. Such grazing is however usually strictly controlled. Free-range grazing regimes cannot, *a priori*, be assumed to be better in biodiversity terms under these conditions.

There is a case for developing large areas where such naturalistic grazing regimes are trialled to determine what range of habitats and species they do support and as a way of improving our understanding of how the former natural landscape might have functioned. There are various practical issues including animal welfare and public liability that need to be resolved if such trials are to be taken forward.

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1. Introduction

“Climax vegetation of closed forest systems covered the lowlands of northern, central and western Europe…. in prehistoric times, prior to human intervention and would still be the situation had this intervention not taken place. …. Large herbivores did not affect the composition or succession in prehistoric times" Pott (2000). This represents a widely accepted view of the natural forests that once covered much of central and western Europe; that they were largely closed-canopy woodland, with many mature trees; with regeneration in gaps created by the death or destruction of small groups of trees or occasional catastrophic blow-downs. Shade-tolerant trees would have predominated where the soils and climate were suitable, at least during the later stages of a stand’s life (eg Peterken 1996; Rackham 1980). Only once humans started to become abundant did the forest become more open. Buckland (2002) comments that “in the lowlands at least 'climax’ forest appears on insect and plant macro-fossil evidence to have been lime-dominated"… but "from *c*3870 BC … closed woodland, the *Urwald*, progressively gave way to *culturstepp*e (*sensu* Hammond 1974)”.

Buckland (2002) later notes that the “the *Urwald* was perhaps more open than our pollen-inspired picture might suggest” (without specifying how open this would be) a view shared by others, eg. Tubbs (1996). Openness might be created by a variety of factors including flooding, disease, extreme storms or fire (Bradshaw personal communication; Green 1992, 2002; Whitbread 1991; Whitehouse 2000).

Vera (2000, 2002a,b) has, however, put together a case that across western Europe it was large herbivores that not only created open conditions, but drove the whole forest regeneration cycle. He argues that herds of aurochs, bison and wild horse grazed large open areas that eventually went through scrub and woodland phases before breaking down to form open areas again (Figure 1). There is, in this cycle, no direct replacement of woodland by woodland such as occurs in the former gap-dynamic model, but equally no permanent open areas either.

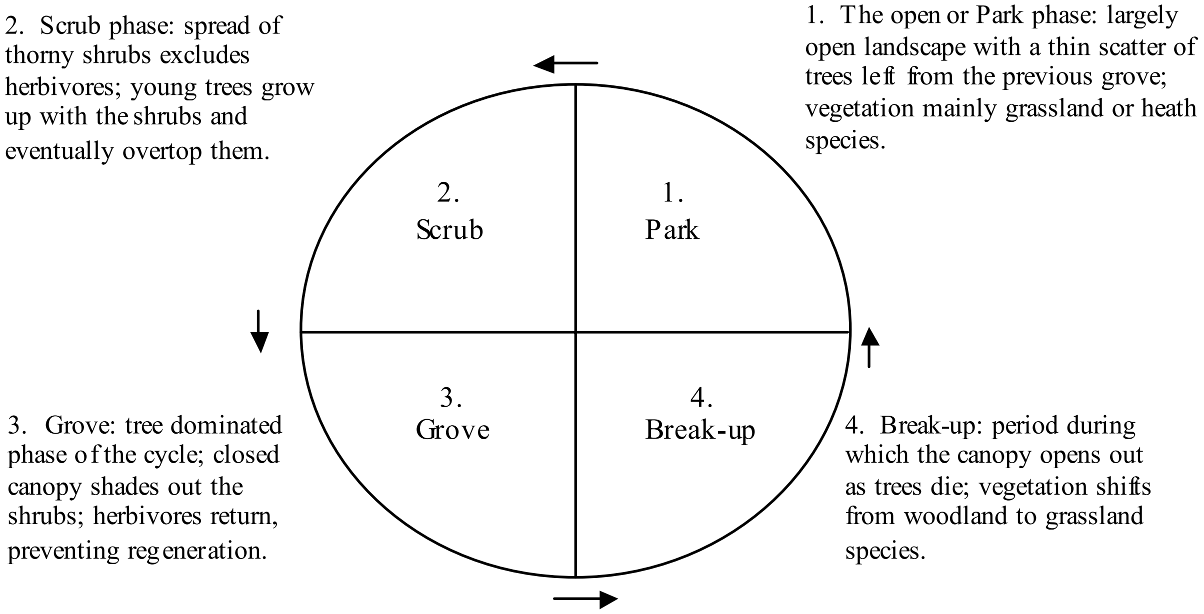


Figure 1. Vera's model, consisting of the three phases of Open Park, Scrub and Grove, to which a fourth Break-up has been added to represent the transition from woodland grove back to open habitats (Park).

The consequent debate as to the structure and functioning of the former natural forests has implications for our understanding of the origins of our flora and fauna – it may help explain the many species associated with scrub and woodland edge for example; and be relevant to how we use domestic herbivores to manage large sites such as the New Forest or parts of upland England.

There is not, however, a consensus of opinion on the use of free-ranging herbivores to promote biodiversity, even in the Netherlands where much of the pioneering work has been done (Anon. 2002). Olff *et al* (2002) comment "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 biological diversity".

The debate has been hampered by different interpretations of what a landscape driven by large herbivores according to Vera's hypothesis 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 compared to the small-gap regeneration hypothesis (Vines 2002).

Vera (2000) himself gives little quantitative spatial detail, apart from indicating that wooded groves could be several hundred hectares in extent. He also provides no indication as to the how long it would take for any patch of land to go through the cycle illustrated in Figure 1. This report therefore addresses the following question:

> *If we assume that the Vera model did apply to a significant area of Great Britain what would that forest landscape look like; what sort of spatial and temporal patterns might occur?*

Exploring these questions first makes it easier to interpret the evidence for what the natural vegetation cover was like in the Atlantic period. For example if the Vera model has to produce a landscape with extensive grassland, an explanation is needed as to why there is little pollen evidence for this (Vera 2000, *pages 88,99*); on the other hand if the Vera model can produce quite a wooded landscape then the lack of grass pollen is not an issue. If proponents of the 'small-gap dynamic' model do not allow for any open space at all then evidence for some grassland (eg Bush and Flenley 1987) immediately discredits their view; if up to (say) 20% open space is accepted as part of the gap-dynamic model then a low level of grassland species is still compatible with this argument.

While this report is primarily about what the past natural landscape was like I return in the final discussion to some of the implications of Vera's ideas for modern conservation in a British context.

1.1 The Vera hypothesis

Key features of the landscape under Vera's hypothesis (Vera 2000, 2002a,b) that are different to what might be termed the traditional closed woodland view are:

- larger areas of open space and scrub;
- more mosaics of patches of trees next to open space or scrub;

- an increased role for light demanding trees and shrubs such as oaks *Quercus* spp. and hazel *Corylus avellana* and a reduced role for shade-bearing species such as beech *Fagus sylvatica*, lime *Tilia* spp. and elm *Ulmus* spp.;
- high populations of large herbivores, particularly grazers such as aurochs *Bos primigenius*, bison *Bison bonasus* and wild horse *Equus* spp., although neither bison nor wild horse were present in Britain in the Atlantic period (Yalden 1999; 2003);
- a shifting large scale mosaic of habitats, with no direct replacement of woodland by woodland, but equally no areas of permanent grassland or heath.

Vera justifies his model in particular by the high levels of oak and hazel (both light-demanding species) found regularly in pollen deposits and the difficulty in separating closed forest landscapes from those with more of a wood-pasture structure through pollen records alone. He notes the poor regeneration of oaks in 'near-natural' reserves such as Fontainebleau (France) compared to more shade-tolerant species such as beech, in contrast to the abundance of oak in the pollen-record at these sites. He draws analogies with savannah landscapes elsewhere in the world and with the state of the woods of the eastern United States when European colonists first arrived.

Others have also used the present abundance of species that use habitat mosaics as support for Vera's ideas, although he makes relatively little use of this himself (*page 357, 378*) (Finck *et al* 2002; Tubbs 1996). However this argument seems flawed, at least as it has been put forward to me (Appendix 1).

Vera (2000) does not propose that his model would apply in all situations; for example he suggests that in places inaccessible to large ungulates closed forest would occur; here the more traditional gap-dynamic model of regeneration might be more appropriate (*pages 59, 352,378*). Therefore regions might consist of some landscapes where one model predominated, some landscapes where the other did; and some, where the balance between which model would operate could shift over time, according to factors such as disease levels in the herbivores or landslips, fire, flood and extreme weather events.

2. Developing a model-based approach

Much of the direct evidence for what the past-natural landscape was like is inconclusive with respect to how much of the landscape was open or closed, or how different types of vegetation might have been distributed. Therefore a model-based approach was adopted to explore different possibilities.

A hypothetical landscape was set up composed of one hectare cells, each of which then moved through the Vera cycle (Figure 1). The time spent in the different phases was varied, according to assumptions that were made about the time it would take for scrub to develop and be overtopped by trees, the life expectancy of trees etc. From the patterns generated by the model suggestions could be made about the likely suitability of such a landscape for different groups of organisms (including veteran trees). The model is based as far as possible on the information and statements given in Vera (2000); relevant page numbers are given in italics in brackets.

In the next two sub-sections the assumptions used as a basis for the changes in a cell over time as it moved through the Vera cycle are set out and then how these were combined at a landscape (5 x 5 kilometre) scale.

The model is a simple mechanistic one, but it highlights a range of different landscape structures that could be consistent with Vera’s basic hypothesis. Comments on the report and ideas in it would be welcomed.

2.1 Assumptions about changes over time

At a certain point in the landscape at a given time there would be grassland first, followed by thorny scrub or other unattractive (eg unpalatable) species of plant, then forest (grove) and finally back to grassland (Vera 2000, *page* 377); but at any one time some points in landscape would be at the grassland phase (hereafter referred to as Park to reflect the occasional survival of veteran trees through this open phase), some at the Scrub phase, some as Groves. These phases (Figure 1) would not be of equal duration. The Grove phase, for example, would last longer than the Scrub phase, because trees once established would grow through the scrub quickly, but might then last for centuries.

Figure 2 illustrates this, by assuming in the first instance that it would take 500 years for any patch of ground to go from open phase to open phase, this being the sum of the different lengths assigned to each phase. This 500-year cycle was then broken-down into twenty 25-year stages. (Variations in the structure and composition of a patch occurring *within* each 25-year period have been ignored for the purposes of the model).

In Figure 2 the five points in the landscape (a-e) start at different phases; over time as point ‘a’ moves from the open Park to Scrub and Grove, point ‘b’ is moving into the Park phase. Thus variations in the occurrence of the different vegetation types would occur across the landscape over time.

<table>
<tr><td></td><td colspan="20">500 year cycle divided into twenty stages of twenty-five years each, with the different phases in the cycle at each of five points across a landscape.</td></tr>
<tr><td>Start year</td><td>1</td><td>26</td><td>51</td><td>76</td><td>101</td><td>126</td><td>151</td><td>176</td><td>201</td><td>226</td><td>251</td><td>276</td><td>301</td><td>326</td><td>351</td><td>376</td><td>401</td><td>426</td><td>451</td><td>476</td></tr>
<tr><td>Point a</td><td colspan="2">Park</td><td colspan="3">Scrub</td><td colspan="10">Grove</td><td colspan="2">Break-up</td><td colspan="3">Park</td></tr>
<tr><td>Point b</td><td colspan="2">Break-up</td><td colspan="5">Park</td><td colspan="3">Scrub</td><td colspan="10">Grove</td></tr>
<tr><td>Point c</td><td colspan="5">Grove</td><td colspan="2">Break-up</td><td colspan="5">Park</td><td colspan="3">Scrub</td><td colspan="5">Grove</td></tr>
<tr><td>Point d</td><td colspan="10">Grove</td><td colspan="2">Break-up</td><td colspan="5">Park</td><td colspan="3">Scrub</td></tr>
<tr><td>Point e</td><td colspan="5">Park</td><td colspan="3">Scrub</td><td colspan="10">Grove</td><td colspan="2">Break-up</td></tr>
</table>

Figure 2. Representation of the changes in the Vera cycle across time at different points in a landscape.

Vera's thesis is that regeneration of scrub and trees takes place only during relatively open, grazed conditions. For the purpose of the model this regeneration window has been assumed to be during the last 50 years of the Park phase and the first twenty-five years of the scrub phase (a seventy-five year period in total, just 15% of the whole cycle).

It has been assumed that once Scrub (phase 2) starts to become a significant component of a patch of ground seventy-five years (three 25-yr stages) are needed for the young trees growing up with the scrub to overtop them sufficiently to form a Grove. The Grove (phase 3) is the longest phase, lasting for ten stages (250 years), followed by a fifty-year period when the canopy shows fairly rapid Break-up (phase 4) to return the patch to a relatively open condition with scattered trees, the initial Park phase (1), which has been assumed to last 125 years.

The justification for choosing these initial phase lengths is discussed below. In development of the model both the assumptions about the phase lengths and the assumption that all points move through the cycle at the same speed are relaxed.

2.1.1 The lengths of the different phases

The lengths of the phases are based on the following assumptions and observations.

Scrub

Once scrub started to form during the latter part of the Park phase it would spread fairly rapidly as it increasingly hindered movement of animals. If the scrub was mainly blackthorn (*Prunus spinosa*) this spread could be concentrically through root suckering: Vera notes that a blackthorn thicket can expand to form a thicket of 0.1 - 0.5 ha in ten years (*page 150*). However even where the main scrub species was hawthorn (*Crataegus* spp.) it would require only an average rate of establishment of just 1 bush every 30 metres per year over a 75 year period, to give more-or-less complete cover (Appendix 2). Establishment of new hawthorn bushes would be favoured close to existing ones because of higher seed availability and increased protection from grazing. This is consistent with observations in the Weald on the scrubbing-up of abandoned fields within woods (Patrick Roper personal communication); and the growth of scrub on abandoned commons and downland following the decline of rabbit grazing in the 1950s.

Once formed scrub would be relatively short-lived as the dominant component in that patch, because an assumption of Vera's model is that the trees establish and grow up with the bushes (*page 150*) and then overtop them. Hence the length for the Scrub phase has been set at 75 years.

Groves

Vera (*page 304,* quoting other researchers) makes the point that thousands of acorns are buried by jays (*Garrulus garrulus*) each year. Not all of these survive, but an average rate of about 3 trees per hectare per year establishing would over a 75 year period be sufficient to give more or less complete canopy closure by the time the trees are 75 years old (Appendix 2). While Vera does refer to individual trees establishing (*page 376*), elsewhere he notes that sufficient trees must establish that their canopies will touch (under my assumptions by the end of 75 years) to form a closed Grove, in which the bushes with which the trees grew up disappear as result of the shade of the canopy (*page 377*).

The young trees would thus be subject to lateral shading from first the shrubs and then their neighbours in the grove; most would grow up as tall maiden stems (unless they were at the edge of a grove). They might have resembled more the New Forest Generation B trees (Peterken and Tubbs 1965) (*page 150*), the old oaks in La Tillaie (*page 198*) or the old oaks in the Bialowieza Forest (Poland) (*page 273*) rather than the squat pollards at Windsor or Moccas Parks. (The possible occurrence of open-grown trees is considered further in the Discussion and Appendix 2).

Tall, unbranched trees certainly did exist in parts of lowland Britain because they have been dug out of the fens and bogs. Peterken (1981) describes one such, which was at least 340 years old, and more than 1m in diameter 6.5 metres from the roots. Rackham (1980) comments that many bog oaks had clearly grown up closely-spaced; lengths of 27 m to the first branch have been found. These values are consistent with those for oaks in some German reserves (25-30 m high (*page 239*)) or those given by Falinski (1986) for trees in Bialowieza Forest: maximum heights of c40m and diameters for ash of 130cm, for elm 150cm, for lime 200 cm and oak 230cm. Allen (1992) describes a young wind-blown stand dating to the mid-Flandrian period recovered from the Severn Estuary with trees that were tall, slender and comparatively unbranched, pointing to growth in dense stands, although they were probably only about 50 years old when they fell.

Keith Alexander has suggested (personal communication) that these 'high forest' type trees were the exceptions because they grew in wet areas that were less likely to be heavily grazed. However both Svenning (2002) and J. Bokdam (personal communication) consider that floodplains would be favoured by large herbivores and so more likely (not less) to be kept at least partly open. Yalden (2003) draws analogies with Bialowieza where broad river valleys provide strips of open grassland 100-500 m wide.

From the evidence of archaeological structures Goodburn (1999) suggests that old 'high forest' trees might still be found in England at least up until the Dark Ages. Fragments of Groves may have lasted through the Bronze and Iron Ages in the same way that small patches of 'old growth' survived the European settlement of the Eastern United States (Whitney 1994).

The length of about 250 years for Grove phase (3) is based on typical current life-spans for the majority of the trees of about 300 – 400 years (phases 2+3+4) and is consistent with the age of bog oaks. Some trees could go on longer than this by continuing to be present through the whole of the next Park and Scrub phases (another 200 years), before being shaded out by the next generation of trees coming through. During this period there might be some attrition of the main canopy because of increased exposure, but also re-iteration of the canopy from lower branches. This gives the potential for some trees to grow for about 600 years within the model. Some pollards in wood-pastures and parks are believed to be more than six hundred years old. However trees whose annual growth is reduced by periodic pollarding tend to grow slower and survive longer than maiden trees.

Break-up

Closed canopy stands of broadleaves of up to about 250 years appear to be reasonably stable, at least in lowland England, where the Vera model might be most appropriate (since he considers it less applicable in mountainous areas). Thereafter, particularly if dominated by beech rather than oak, they tend to break-up either through individual tree deaths or through a catastrophic event such as the 1987 storm (Spencer 2002; Whitbread 1991). Disease (Green 1992; Dobson & Crawley 1994) could contribute to stand break-up or trees might be killed through bark stripping (*page 354)*. Fire may also have been a significant factor where stands of pine survived, for example on bogs (Whitehouse 2000), although most broadleaved woodland in Britain is considered relatively non-flammable (Rackham 1980).

The initial break-up event could happen overnight if it were a severe storm, and once the canopy started to open significantly the shift in the characteristics of the stand from grazed woodland to more those of open grassland/heath could be relatively rapid. Hence the Break-up phase (3) has been set at only 50 years. However the shift to more open (Park) conditions might be delayed if there were substantial amounts of fallen branches and trunks that prevented access to the grazing animals (Green 2002).

Park

The length of the Park phase (1), called Park to emphasise that it could contain a scatter of veteran trees, has been set initially at 125 years. This open element in the landscape is a key difference in Vera's ideas compared to the traditional gap-dynamic model. Free-ranging grazing does not limit tree invasion under the Vera hypothesis (compared to agricultural seasonal grazing which does) because of the much lower intensity of grazing involved. Various free-ranging grazing examples quoted by Siebel and Piek (2002) involve levels of 1 animal per 2-15 ha, whereas seasonal grazing systems may involve pressures 10 – 30 times those of natural systems (Helmer 2002).

Bokdam and Gleichman (2000) and Olff *et al* (1999) provide examples of how large herbivores may mediate a shifting mosaic of grassland scrub and woodland through alternation of facilitation and competitive displacement of species over periods of a few decades. However it is too early to say if the mosaics they describe will be sustainable in the longer term.

It is an axiom of the Vera model that the grazed grassland/heath of the Park phase is more invadable by bushes and trees than ungrazed grassland (*page 343, 377*). All-year round grazing does not maintain the patch in a permanently open state (*page 345*) because interruptions in grazing occur locally (eg at the hectare patch scale). The animals do not cover the whole area they graze in winter during the growing season of the shrubs. Over longer periods, large-scale interruptions in the grazing occur at a landscape level following declines in the numbers of animals by starvation or disease.

In the basic model I have assumed that tree and shrub regeneration is largely limited to the final 50 years of the Park phase (and the first 25 years of the Scrub phase); ie there is 75 years of the Park phase when regeneration is not getting away: seedlings might establish and survive during this time, but not succeed in growing above browse height. Seventy-five years without woody plant establishment may be too long (even ungrazed grassland may be invaded in this sort of time period (*pages 343, 344*)), particularly as it would encompass several generations of large herbivores, given a typical lifespan of only 15-25 years (Beije 2002).

A shorter period in the Park phase would be more consistent with the idea that regeneration is rapid once open conditions have been created. It would also be closer to the timescales that have been observed for conversion of commons, grassland and heath to scrub in Britain over the last century, and for the development of woodland and scrub on the Oostvaardersplassen in the 40 years since it was formed. However, shortening the Park phase relative to Grove and Scrub phases has the effect of reducing its overall contribution to the landscape, and hence diminishes the distinctiveness of the Vera model.

2.2 Developing the pattern of spatial variation

2.2.1 Initial assumptions

Vera's cycle of vegetation change was applied to a hypothetical area of 5 by 5 kilometres. The 5 x 5 km area was broken down into 2,500 one-hectare cells. Internal variation within the cell was assumed to be insignificant over any one 25-yr stage.

Other initial assumptions were as follows.

a. The area is uniform in terms of its topographic, physical and other environmental characteristics, apart from those patterns generated by the model itself.

b. The vegetation is overall more-or-less in equilibrium with the use that the animals make of it and is not in the process of changing either to more open conditions or to more closed forest; the animals might range more widely but as long as the proportion of time spent on this area was equal to its proportion of the entire range then the model assumptions can still apply.

c. All the area is within the Vera cycle, ie there are no permanently open spaces and no areas that are permanently wooded: this is a fundamental requirement of the Vera model, his cyclical turnover of vegetation (*page 378*).

d. Large herbivores may range several kilometres in a day (Putman 1986), so the grazing animals potentially have access to all parts of the 5 x 5 km area except insofar as vegetation structure limits their movement as required by Vera's hypothesis.

e. The stage of each cell can be independent of that of its neighbours; a Grove cell can occur next to Scrub or open Park etc.

The landscape size used (2,500 ha) is about half the size of the Oostvaardersplassen Reserve (5600 ha) in the Netherlands (Kampf 2002b), which Vera uses to draw modern analogies for his model, so seems a reasonable starting point. A larger area could by adopted if necessary. It would not alter the basic approach or the main findings, but merely increase the size of the spreadsheet needed to do the calculations!

One hectare has been used as the minimum cell size because it is large enough for light-demanding thorn bushes to establish themselves (*page 378*) during the Park phase and for a significant grassland glade to be able to establish in it during the Break-up phase (*page 377*). Vera notes that a blackthorn thicket can expand to form a thicket of 0.1 - 0.5 ha in ten years (*page 150*): so changes over a hectare in 25-year time-steps seem reasonable. Appendix 2 shows that only very low rates of establishment of thorn bushes per year are required to fill up one hectare within the timescales allocated to this in the model. If a smaller cell-size were adopted the gap created would become similar in scale to that created under the traditional gap-dynamic model; there would be significant side-shading effect from adjacent trees, and open grassland and scrub species would be less able to thrive in the gaps created. A key difference with the traditional gap-dynamic model would be lost.

Putman (1986) notes that cattle in the New Forest seem unwilling to occupy areas less than 10 ha. This could be an argument for working with a larger cell size, but instead has been accommodated by scenarios in which cells that are at the same phase are clumped so that open spaces of at least 10 ha are likely outcomes.

2.2.2 Developing the model: different landscape scenarios

Each cell was assigned a unique set of coordinates in the 5 x 5 m landscape in a line on a spreadsheet. The cell was assigned a starting point at one or other of the twenty 25-yr stages in Figure 2. Each cell then moved through the Vera cycle in these 25-yr stages from its assigned starting point (for example points a-e in Figure 2). At any one time in the cycle the extent of the different phases (Park, Scrub, Grove, Break-up) was calculated according to the different cells that were in the relevant 25-year stages that contribute to each phase.

In the initial runs of the model assignment to a starting stage for each cell was at random and each 25-yr stage had 125 cells, a twentieth of the landscape, assigned to it. The rate of progress through the cycle was assumed constant for all cells. Different scenarios were then developed in which the area allocated to each stage initially was varied; the cells assigned to a particular 25-year stage might be clumped rather than scattered randomly; and the rate at which the cells moved through the cycle was varied.

Box 1. Scenario	**Possible ecological analogues for the scenarios developed**
1. Wooded landscape	Homogenous landscape; herbivores move freely across it such that all suitable patches are equally likely to be used; fine-scale mosaic of habitats.
2. Clumped mosaic	Animals tend to concentrate in patches leading to coarse grain mosaic, with grove cells next to scrub or break up, but not park etc.
3. Varying area of different age stages	Homogenous landscape, but some temporary variations in extent of different stages; storms may lead to temporary increase in openness; or lighter than usual grazing to patches closing more quickly.
4. Cycle length varying in a systematic way across landscape	Different parts of the landscape might vary in the speed at which they go through the cycle: the presence of a river along the left hand (western) edge for example might lead to a gradient of grazing pressure across the landscape; some cells therefore have a longer Park phase; but less grazed areas have a shorter Park phase (more closed landscape).
5. Patchy variation in cycle length across landscape	Different patches move through the cycle at different rates, for example one cell is more nutrient rich and grazers tend to concentrate on it, so it stays longer in the open Park phase; other cells nearby are cut off by a stream so grazed less often so tend to move to the Scrub and Grove phase quicker.
6. Dense Savannah	Under winter conditions animals might bark mature trees; this rarely kills them, but with severe barking some might be killed or other factors such as disease might lead to much earlier, but prolonged break-up of the Groves through tree death.

Each of the scenarios was developed in a mechanistic way, but the variations do reflect real ecologically-based processes. For example if animals concentrated their grazing in particular areas then open Park phase cells might be clumped leading, and there would also be a tendency for adjacent cells to be of the same, the succeeding or preceding phase. Soil fertility differences or proximity to water might lead to some cells moving through the cycle more rapidly than others (Box 1).

Scenario 1. All the 25-year age stages are represented by 125 one-hectare cells (one twentieth of the total area). The cells allocated to a particular stage are distributed at random across the landscape. All cells move through the cycle at the same rate taking 500 years, as in Figure 2, to get back to their starting point (125 years as Park; 75 years as Scrub; 250 years as Grove; 50 years as Break-up).

Scenario 2. The cells have been clumped in blocks of twenty-five and cells allocated at random with a bias towards cells from contiguous phases occurring in any one block; ie grove with scrub and break-up, but not park.

Scenario 3. The number of cells allocated initially to each 25-year age classes was varied between 50 and 200 ha about the mean of 125 ha (Table 1a). As a consequence the area that moves from (say) Break-up into the Park phase varies over the cycle as illustrated by Table 1b. Progress of the different age classes through the cycle subsequently is not altered.

Table 1. Variation in the extent of the different phases across the 500 yr cycle, through variations in stage extent from 50 –200 ha

(a) Extent allocated to each stage (ha)	No of stages to which this extent was allocated
50	1
75	2
100	4
125	6
150	4
175	2
200	1

(b) Area moving into the Park phase at each 25-year stage

Year	Area (ha)	Year	Area (ha)
1	150	251	50
26	100	276	100
51	125	301	200
76	150	326	125
101	75	351	150
126	125	376	175
151	100	401	125
176	175	426	125
201	125	451	100
226	75	476	150

Table 2. Phase lengths adopted in the different sections across the landscape

Sections (from west to east)	Phases	Length of phase	% landscape in that section
"Long Park" (800ha)	Park	100 years	40
	Scrub	75 years	30
	Grove	50 years	20
	Break-up	25 years	10
"Standard" (900 ha)	Park	125 years	25
	Scrub	75 years	15
	Grove	250 years	50
	Break-up	50 years	10
"Short Park" (800 ha)	Park	50 years	10
	Scrub	75 years	15
	Grove	300 years	60
	Break-up	75 years	15

Scenario 4. Different parts of the landscape might move through the cycle at different rates (N. Sanderson, G.F. Peterken personal communications): some of the scrub and young grove might go straight back to Park without the trees maturing and going through the normal Break-up phase. Other stands might stay longer in the Grove phase and have a much reduced Park and Scrub phase. The landscape was therefore divided into three portions (800 ha, 900 ha, 800 ha) from west to east. In the first block the cycle length was shortened, the importance of the Grove phase was reduced while that of the Park phase increased. The central part of the landscape had the same phase lengths as for Scenario 1. The easternmost section operated with a reduced Park phase and lengthened Grove phase (Table 2).

Scenario 5. Individual cells were moved through the cycle at different rates. At each of the 25-yr stage transitions a transition factor was introduced to determine whether the cell simply moved to the next stage in an orderly progression (as for Scenarios 1-3), stayed at the stage it was at (effectively lengthening the cycle), or jumped two or three stages forward (effectively shortening the cycle). At each stage 1000 cells were allocated the normal transition, with 500 each getting either the no-change, two-stage or three-stage transitions. The transition factors were re-randomised at each change, so the rate at which a cell moved through the cycle also varied during the cycle. This process was repeated for the twenty successive stage-transitions.

Under even progression all cells would move on twenty stages over a 500-year period. The actual number of stages that cells were moved on is shown in Figure 3: values less than 20 represent cells effectively taking longer than 500 years to move through the cycle; values more than 20 represent cells moving through the cycle in less than 500 years. There are more of the latter (ie faster cycling) because there were 1000 cells transition that could make either 2 or 3 stage jump forward, compared to only 500 where no transition occurred. A bell-shaped distribution of cycle lengths was produced ranging from 250 to 1000 years.

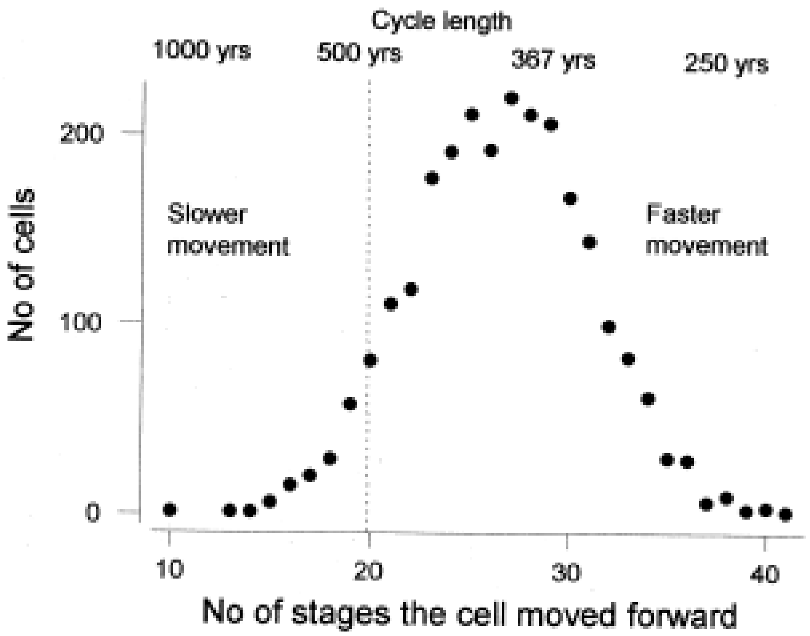


Figure 3. Frequency of cells showing different cycle lengths

Scenario 6. Scenarios 1-5 do produce significant parkland areas, areas of scrub and partially open woodland (phases 1,2,4) that would accord with suggestions by Rackham (1998) for the existence of some savannah in western Europe (including the UK) and with Vera's references to 'parkland landscapes'. In discussions on the Vera hypothesis there have been suggestions that even more of the countryside would look like an open savannah. This could happen if regeneration among the scrub was as individual trees, sufficiently isolated that they did not touch crown with any of their neighbours even when mature (*page 376*). This seems to be ruled out as the dominant pattern by Vera's reference to new glades forming within Groves and such references as there are to the size of Groves (*pages 151,161, 377*). In addition, if there is to be a continuity of age classes of open grown trees the density of trees needed per hectare may mean that they are likely to touch crowns even if they grow up individually: closed canopy conditions are almost inevitable (Appendix 2).

However the model can be changed to produce a more open landscape than in the earlier scenarios by altering the relative lengths of the Park and Grove phases.

The Park phase could be increased to 375 years, leave the other phases as in scenario 1 above (Scrub 75 yrs, Grove 250 yrs, Break-up 50 yrs) making the overall cycle length 750 years. The Park phase would then occupy 50% of the landscape with the Grove phase reduced to 33%. This would imply that grazing levels could prevent tree and shrub regeneration in the open grassland over eighteen generations of large herbivores (if a generation time of 20 yrs is assumed), but then something changes (eg a disease outbreak amongst the animals) to allow regeneration to occur. Under Vera's model grazing animals cannot prevent regeneration for very long periods of time (*page 377)*), certainly not for centuries, so this approach was not developed further.

An alternative was to keep the cycle length at 500 yrs, but reduce the length of the Grove phase to 100 years. The Grove phase could not be much less over wide areas because the Vera cycle requires that the it lasts long enough to shade out the shrubs with which the trees have grown-up, otherwise the animals cannot get back into the Grove. The Park phase was left at 125 years (to avoid the objection raised in the previous paragraph about very long open periods); the Scrub phase lengthened slightly to 100 years. The main change however was to have an earlier, but lengthened Break-up period (175 years), forming a dense savannah where the tree canopy was between 80% and 20% cover. Sufficient tree cover must be present to limit the regeneration of light-demanding thorny scrub. Early break-up might be triggered by bark-stripping of the trees (*page 354, 355*), although, as the trees would be at least 100 years old, R. Gill (personal communication) questions whether such bark stripping would be sufficient to regularly kill trees of this age and size.

Patterns generated by the above assumption were explored either with complete random distribution of cells (the equivalents of scenario 1).

2.2.3 Exploring the extent of different cover types and potential habitat for different species groups.

A criticism of the scenario modelling was that it gives the impression that there are sharply defined boundaries between the phases, whereas in reality they grade into one another. Scrub would be present in the grassland before it was sufficient to class the area as part of the Scrub phase; the tree canopies would not all suddenly emerge at once above the thorns to form Groves; the Grove patches would consist of different ages of trees.

Therefore an alternative way of exploring landscape structure and composition is presented in terms of the cover for each cell that the shrub and tree layers might have over the course of a cycle; and how these then vary across the landscape under a given scenario. For simplicity just two of the above scenarios were used: the 'wooded landscape' (scenario 1); and 'dense savannah' (scenario 6), the latter being chosen because of the particular interest from the Ancient Tree Forum in this type of landscape. From changes in the tree and shrub cover predictions were made about the likely suitability of the landscape for each of the scenarios for different groups of organisms: grassland plants, woodland flora, shrub nesting birds and veteran trees. The following assumptions were made.

Tree and shrub cover

In the Vera cycle shrub cover starts to increase during the latter part of the Park phase, peaks during the Scrub phase and then declines in the first half of the Grove phase. The canopy cover of the new generation of trees starts to be distinguishable during the latter part of the Scrub phase, peaks during the Grove phase and declines during Break-up. I have assumed that some scattered individuals survive through the next Park phase, just as scattered surviving trees still stand out in woods devastated by the 1987 storm. These survivors would however eventually be overtaken by the next generation of scrub and young growth (Figure 4).

Ground flora changes

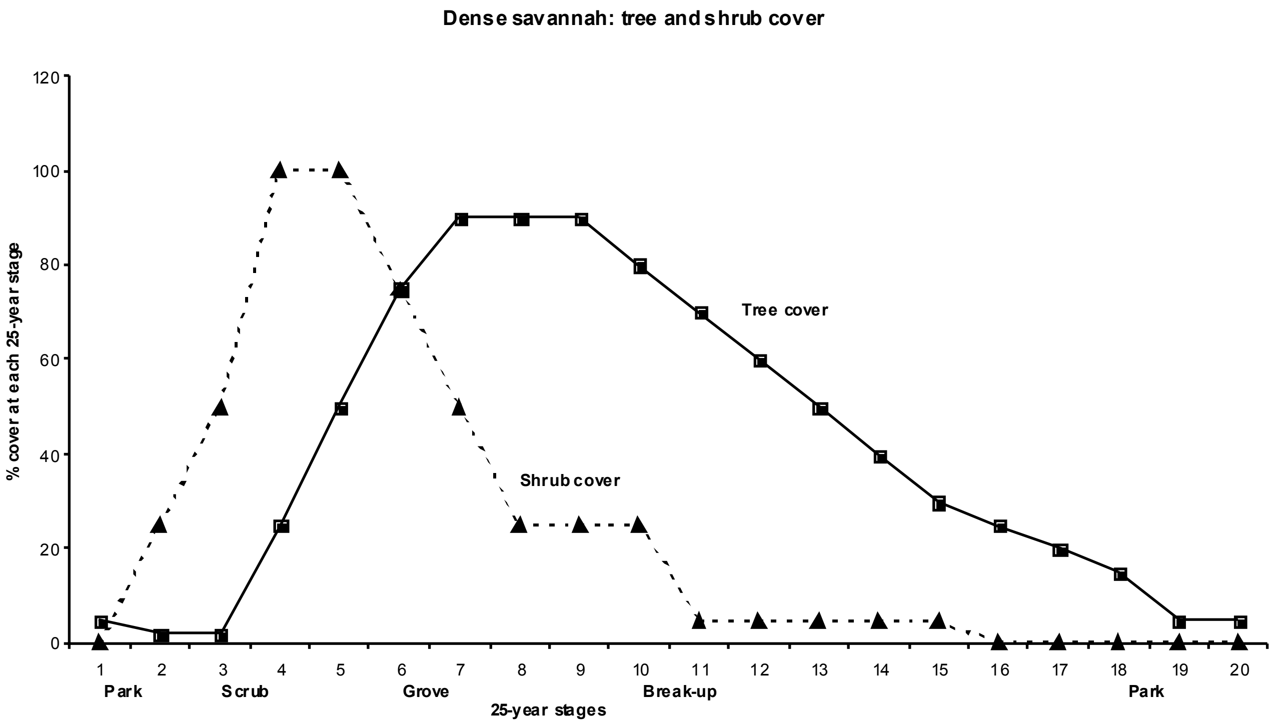
The ground flora is assumed to consist of just two types of species: those normally now associated with grassland and heathland that tend to be reasonably tolerant of high levels of grazing, but intolerant of dense shade; and those now associated with woodland that tend be less tolerant of grazing, but more tolerant of shade. The changes through the cycle of these two stress- factors are assumed to have the following patterns:

- Grazing is assumed to be highest in the Park phase, declines during the Scrub phase and is lowest in the early Grove phase. Thereafter it increases again.
- Light at ground level is high during the Park phase, declines to very low levels under the Scrub phase; gradually starts to increase during the latter part of the Grove phase (opening of tree canopy and loss of shrub layer) and increases more rapidly during the Break-up.

Total ground flora cover, and whether more like that of a woodland or grassland type, would then vary at different stages through the cycle as follows:

- In the Park phase grazing impacts are high and light levels high; so grassland species would predominate (Figure 5).
- During the Scrub phase grazing pressures start to decline, but so does the light level; the ground cover under dense scrub is typically very low, but some woodland species would start to invade/spread.
- The spread of woodland species would continue during the early Grove phase, increasing the overall cover, but as the herbivores move back in and light levels start to rise during the Break-up phase, so more competitive grassland plants start to return.

At all stages however there would be some contribution from each group of species (neither curve ever quite gets to zero).



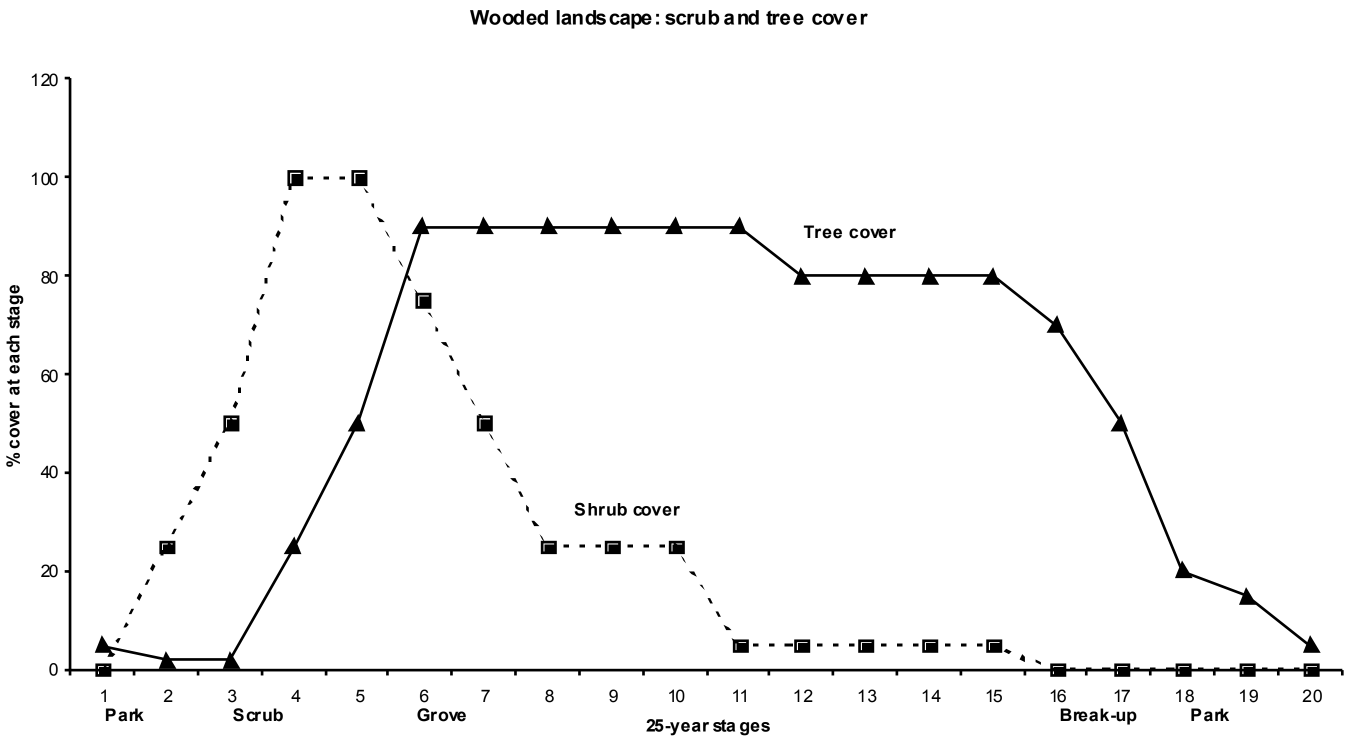
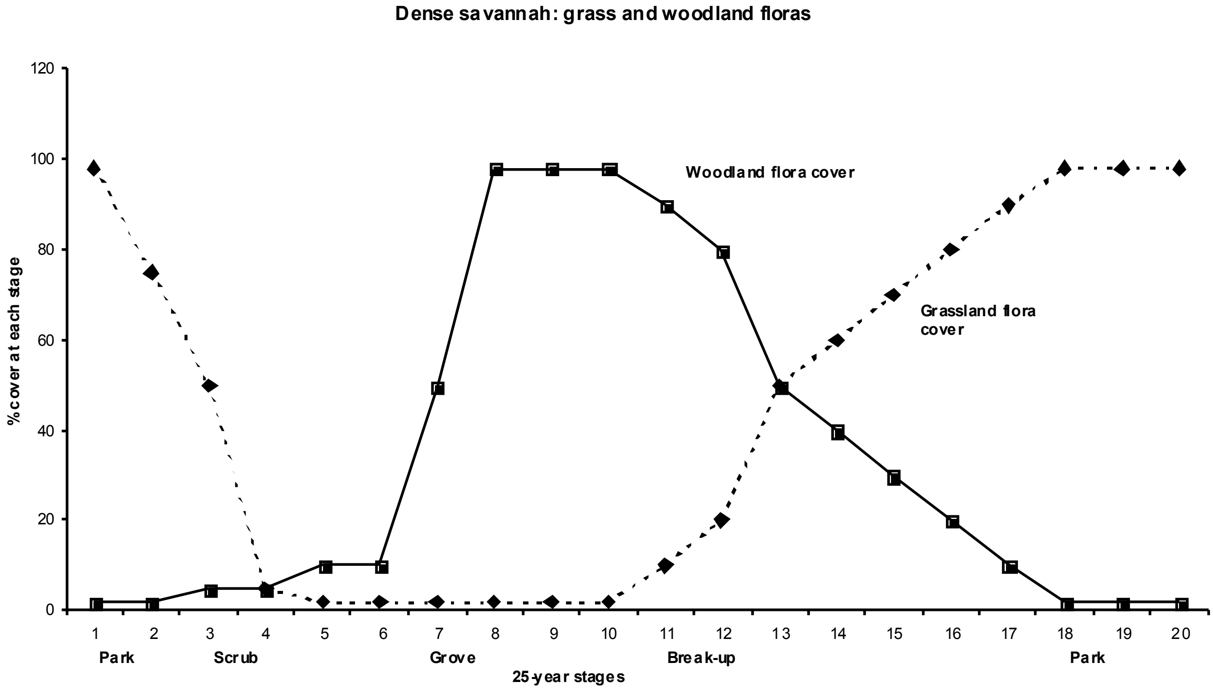


Figure 4. Changes in the tree and shrub cover by stages: upper graphs for the Dense Savannah scenario (6), lower graphs for the Wooded landscape scenario (1)



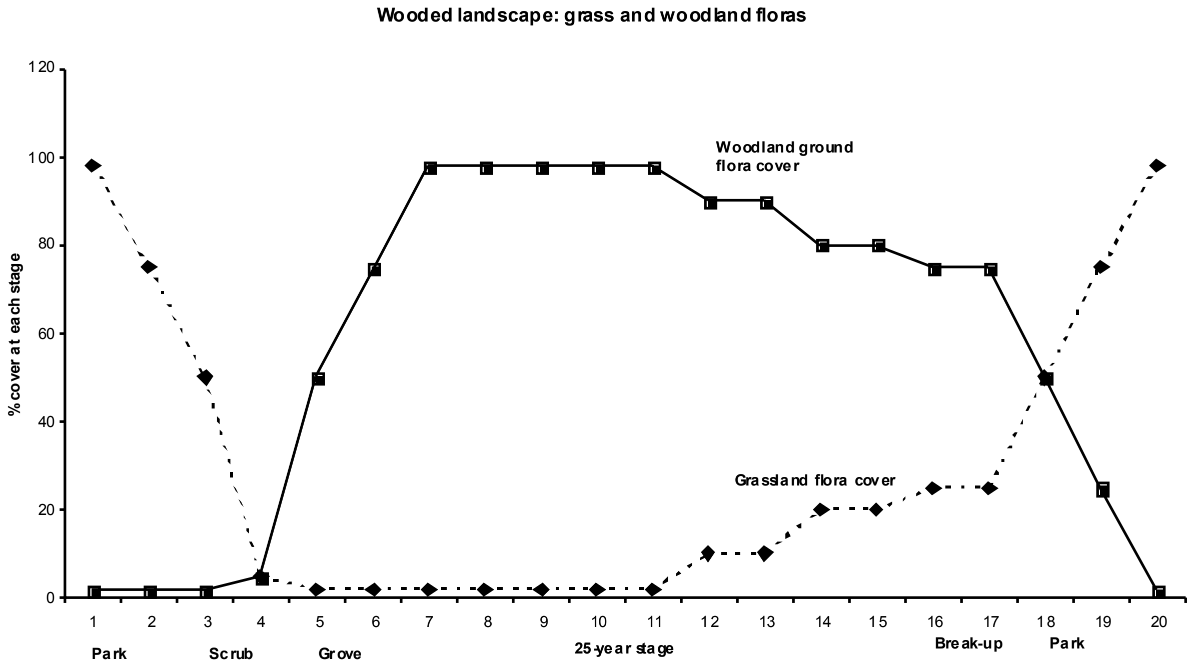


Figure 5. Woodland and grassland floras for: Dense Savannah (upper graphs) and Wooded landscape (lower graphs)

Birds of the understorey

Many of our woodland birds are associated with scrub and woodland understoreys (Fuller 1995). The distribution of birds such as warblers, often now associated with coppice, was taken to follow that of areas with more than 20% shrub cover, whether out in the open or under shade. The shrub cover under shade would normally be less suitable as habitat for these species than that in the open (R. J. Fuller personal communication). However, as the scenarios used produce a fine-scale mosaic with much intermixing of the different phases, this difference has not been incorporated in the results.

Veteran and near-veteran trees

Veteran (> 450 years-old) or near-veteran trees (taken to be those over 300 years) under the model start to appear in the latter stages of the Grove phase in the 'wooded landscape' scenario, and in the later Break-up period for the 'dense savannah' option where the Grove phase is much reduced. Some survive through the next Park phase, before declining as the scrub and young trees re-establish. They are assumed to be lost through shading out during the first 50 yrs into the next Grove phase.

Accessibility to large herbivores

The 'accessibility of the landscape' to large herbivores was assessed by assuming that cells with 50% or more shrub cover would tend to be avoided; this may be an overestimate of the degree to which scrub could limit animal movement, but on the other hand it underestimates the effect of blocks of scrub possibly 'trapping' open ground within them.

Cover types analysed for the wooded landscape and dense savannah scenarios

Differences in the cover of the different layers for the woodland landscape and dense savannah scenarios are shown in Figures 4,5. By combining these graphs with the two scenario models (1 and 6) the extent of the following were calculated and compared:

- number of hectare cells expected to have > 50% grassland species cover;
- number of hectare cells expected to have > 50% woodland species cover;
- number of hectare cells expected to have > 20% shrub cover which might be rich in breeding birds;
- number of hectare cells expected to have differing levels of tree cover;
- number of hectare cells that might contain veteran trees (> 450 years old) or near-veterans (301-450 years old);
- number of hectare cells that might be inaccessible to herbivores because the shrub cover was greater than 50%.

3. Results I: Landscape patterns

3.1 Landscape characteristics of different scenarios

The composition of the landscapes produced by the different models are summarised in Table 3.

Table 3. Summary of the composition of landscapes produced by different scenarios

	% landscape which is under different phases			
Model scenarios	Park	Scrub	Grove	Break-up
1. Wooded landscape	25	15	50	10
2. Clumped mosaic	25	15	50	10
3. Varying area of different age stages	21-31	9-19	44-56	5-13
4. Cycle length varying in a systematic way across landscape	25	16	47	12
5. Patchy variation in cycle length across landscape	24-26	14-16	49-51	9-11
6. Dense Savannah	25	20	20	35

Scenario 1 'wooded landscape'. The basic model produced a landscape such as Figure 6, based on the random allocation of cells to an initial starting phase. The fine-scaled mosaic is predominantly wooded (50% Grove, 10% Break-up stands) with more open patches (Park 25% and Scrub 15%) of variable sizes. Some contiguous patches of Park phase are several hundred metres across and at least five hectares in size in a more or less compact block. Areas of continuous Grove are larger although the cells are not all the same age (since the grove stage lasts 250 years).

The open Park patches (25% of the total) and Scrub (15%) are scattered through in a more-or-less interconnected way. (Dawson (1994) and Peterken (2002a) point out that at about 30% cover of any particular landscape element, even a random distribution of cells can often produce high connectivity for that habitat type across the landscape).

If the model was moved forward 125 years the extent of each stage and of the phases remained as before (because of the assumptions used in this scenario), but their distributions change (Figure 7). All the cells that were in Park phase at the beginning have become either Scrub or Grove, while an equal number of Grove and Break-up cells turned into Park (Figure 5). The overall pattern of the landscape is superficially the same but the detail changes in line with Vera's concept of cyclical turnover of vegetation. 50% of the landscape was, with the assumptions used, open Park at one or other of the times. This dynamic applies also to the Grove phase: 25% was Grove at both times and a further 50% was Grove at one or other time.

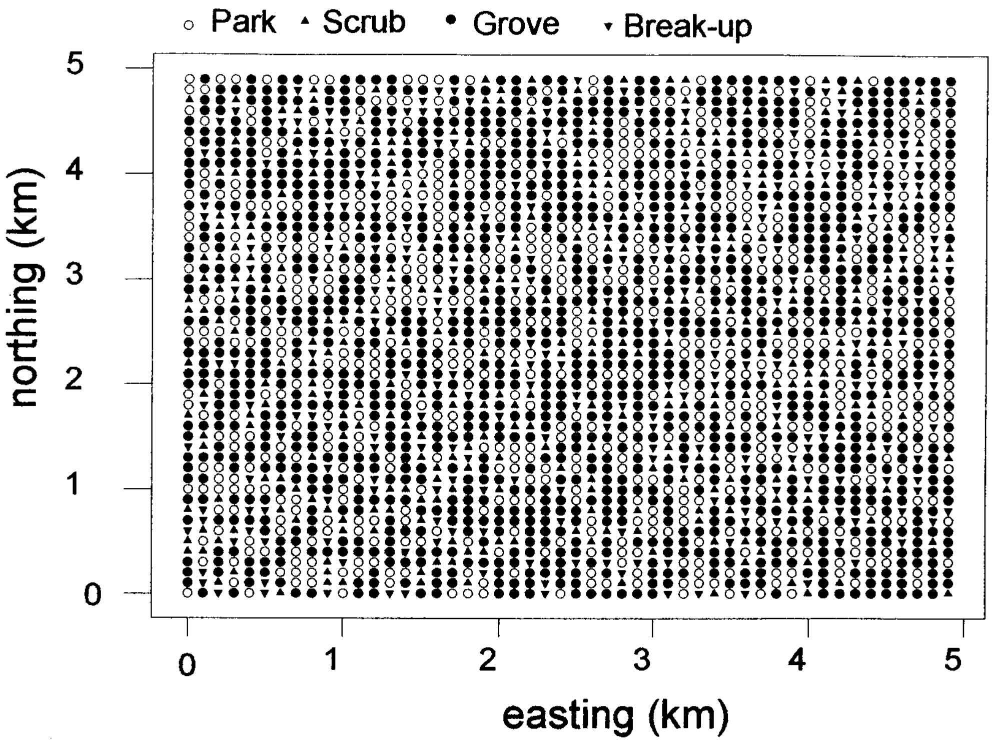


Figure 6 Distribution of all phases in year 1 using the Woodland mosaic (scenario 1)

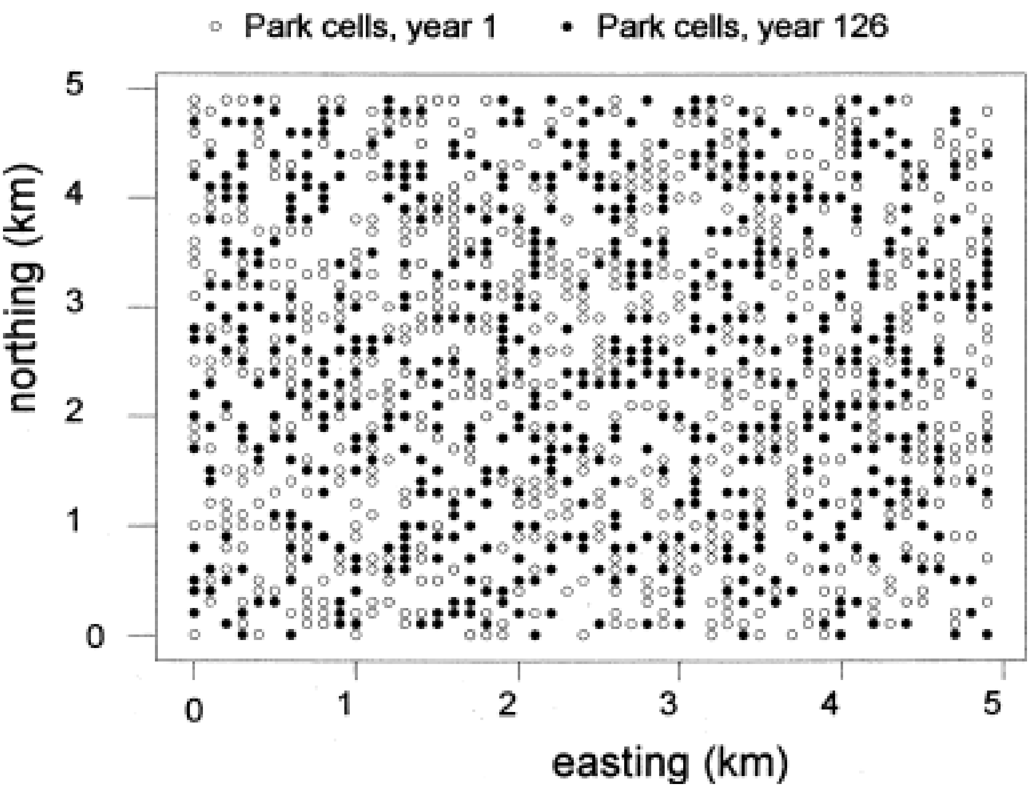


Figure 7 Distribution of Park cells in year 1 and year 126 (scenario 1)

Scenario 2 'clumped mosaic'. A coarser-grained landscape was produced with some open Park patches up to 125 ha, although the proportions of the different phases (Figure 8) stayed the same.

Clumping produced larger areas of 'core' habitat, large contiguous patches of a single phase. Species with large minimum patch-size requirements, eg a bird requiring large open spaces would probably find this a more suitable landscape than that produced in scenario 1. It might also be more attractive to aurochs, if, like New Forest cattle they preferred large areas (> 10 ha) in which to graze (Putman 1986).

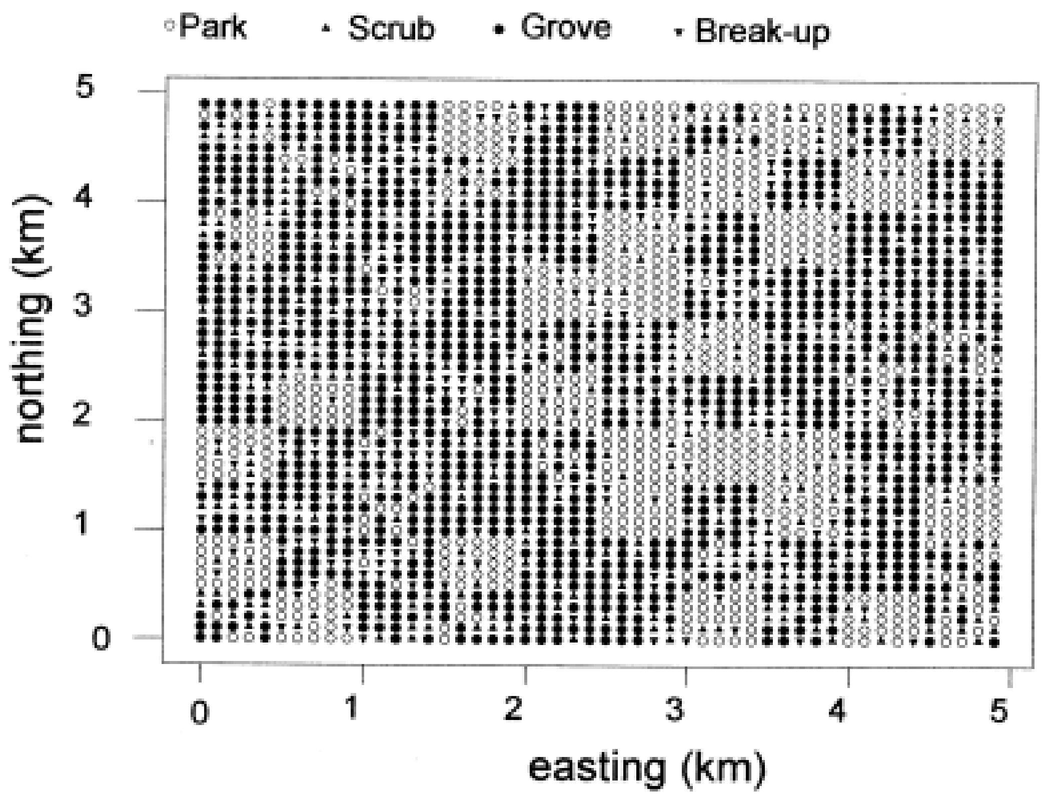


Figure 8 Distribution of phases in year 1 using a clumped mosaic (scenario 2)

Scenario 3. Variable initial starting areas. This scenario involved different extents for the various phases as a starting point; and as a consequence the area that moved from (say) break-up into the Park phase varied over the cycle, which in turn led to variations in the total area of each phase across the cycle. There were temporary shifts in the balance of the different phases but the effect was not that great overall: the Park phase for example only varied between 525 and 775 ha across the cycle, while the Grove varied between 1100 ha and 1400 ha.

Scenario 4. Variable cycles systematically across the landscape. Allowing different sections to operate on different cycles resulted in a landscape in which more open Park occurred in the west, whereas the east was more Grove-dominated (Figure 9). Overall, however, the proportions of the different phases was similar to those for earlier scenarios (Park 25%, Scrub 16%, Grove 47%, Break-up 12%).

Scenario 5. Variable cycle lengths for individual cells. Over the whole, landscape varying the cycles (Figure 10) for individual cells between about 250 and 1000 years had very little effect on the of the extent of the different phases over cycles across the 500 yr period; from 592-649 ha for the Park phase, and 1219-1280 ha for the Grove phase. The effect of varying the cycle length for individual cells occurring together as a block of nine adjacent cells is illustrated in Figure 11.

Scenario 6. Dense savannah. The landscapes generated under this set of assumptions were developed with complete random distribution of cells (the equivalent of the fine mosaic of scenario 1) (Figure 12). Significant tree cover remains over most of the landscape (the Park phase is still only 25%), but less of it is as Grove (reduced to 20% of the landscape) and more of it as the more open Break-up phase (Table 3).

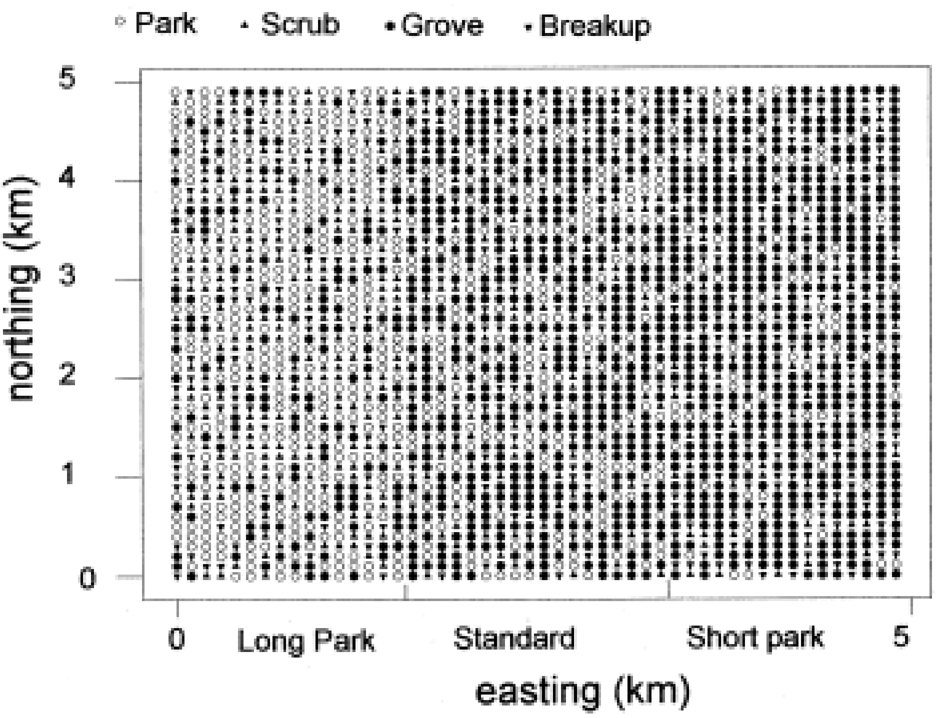


Figure 9 Phase distribution for variable cycles across the landscape (Scenario 4)

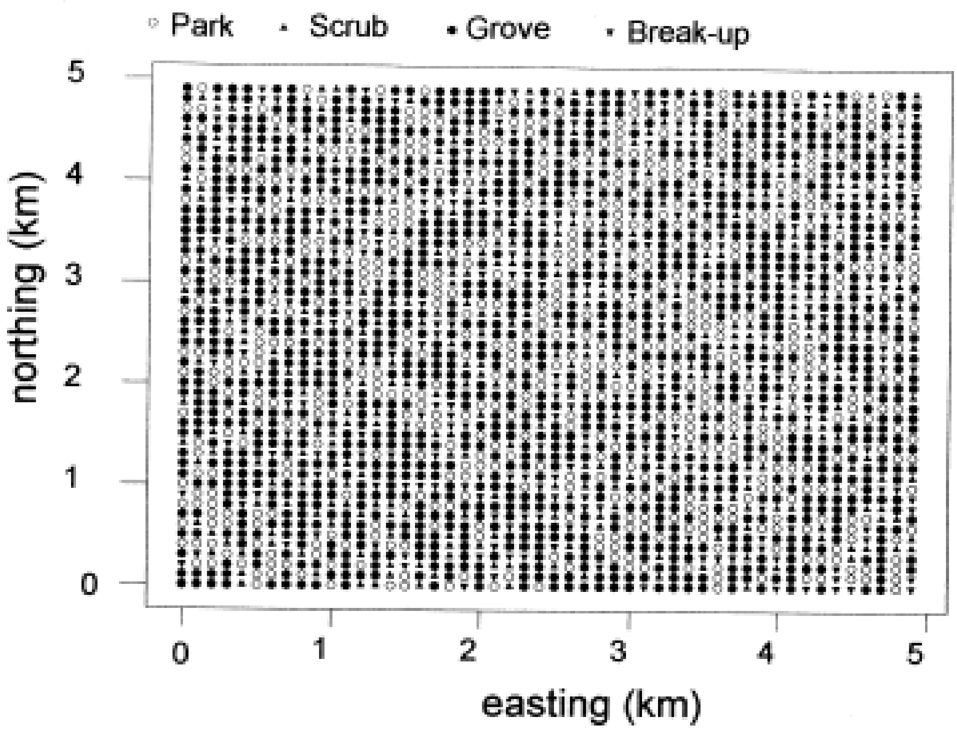


Figure 10 Phase distribution for variable cycle lengths for individual cells (Scenario 5)

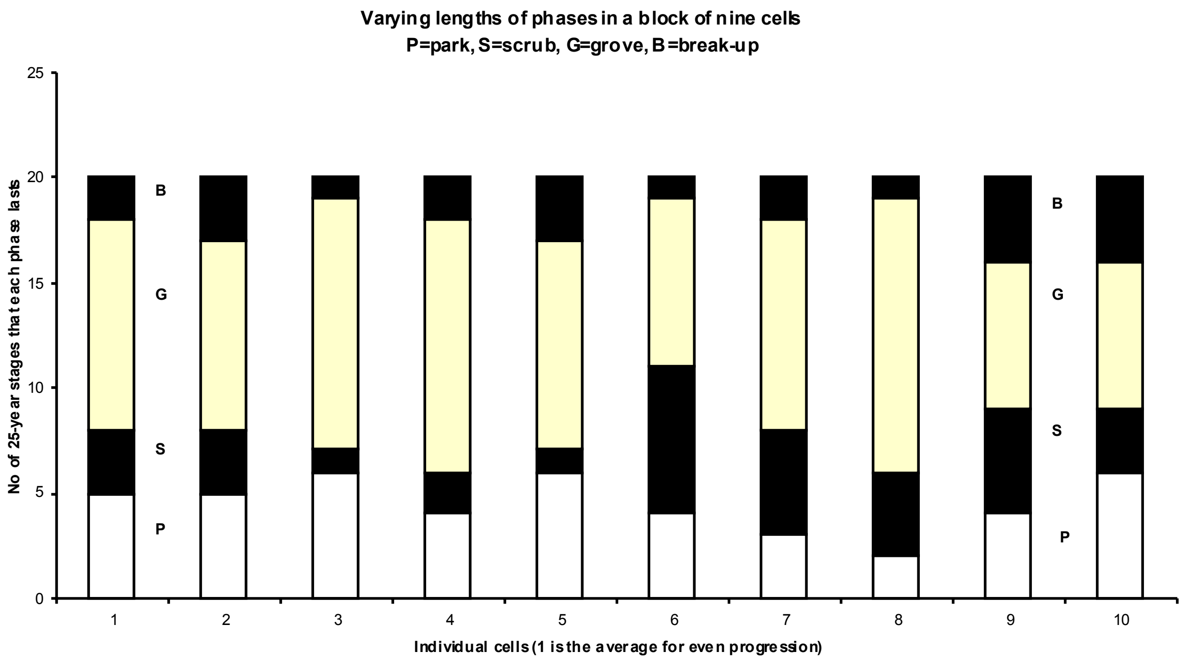


Figure 11 Differences in phase lengths for a block of nine adjacent cells, under the variable cycle scenario (5)

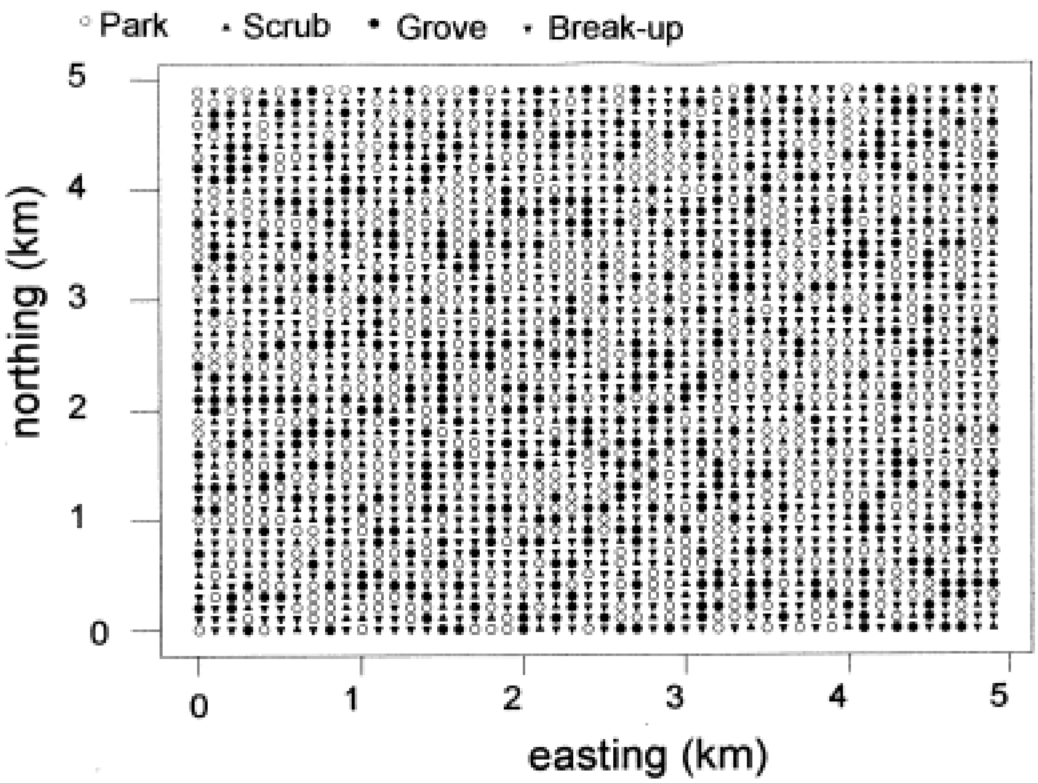


Figure 12 Phase distribution for Dense savannah (scenario 6)

3.2 The changing extent of different cover types and habitat types

Differences in the distribution of age classes and tree covers between the Wooded landscape and Dense Savannah are summarised in Table 4. The dense savannah is more open (total tree cover 41%) than the woodland landscape scenario (total tree cover 55%), but with the assumptions used, 55% of the (savannah) landscape has tree cover greater than 25%, and 35% more than 50% tree cover.

Veteran (>450 yrs) and near-veterans (301-450 yr-old trees) are found across both landscapes (thirty percent of cells for each group), but are largely absent from the Grove phase, because it was assumed that younger trees would tend to out-compete them.

Both 'wooded landscape' and 'dense savannah' scenarios could provide continuity of grassland and woodland-type vegetation over the landscape, albeit in different amounts. The interspersion of the different conditions is such that even relatively poor colonising species, eg ancient woodland indicator plants (Brunet & Oheimb 1998) would be able to adapt to the shifts in occurrence of open or closed canopy conditions across time.

Both scenarios also provide scope for species of young-growth such as warblers.

Similar extents of landscape would be open to the large herbivores; the availability of high quality summer forage from the grassland vegetation would be greater in the savannah scenario, whereas the wooded landscape scenario provides more cover and potential winter browse.

Table 4 Comparison of conditions for different species groups created under Woodland landscape and Dense Savannah scenarios.

		No of 1-ha cells in each scenario	
Species group or feature	**Measure used**	**Dense Savannah (scenario 6)**	**Wooded landscape (scenario 1)**
Woodland plants	> 50% cover of flora	1375	1750
Grassland plants	> 50% cover of flora	875	750
Shrub-nesting birds	> 20% shrub layer *	1125	1125
Herbivore Accessibility	<50% shrub cover *	1875	1875
Veteran trees present	>450 years *	750	750
Near-veterans present	301-450yrs *	750	750
Canopy closure	Tree cover 26-50%	500	250
	51-75%	375	125
	>75%	500	1250

* These do not differ between the scenarios because they are driven by the same 75 year window of regeneration.

4. Discussion

Ideally models of the wildwood (or call it what you will) would be generated from knowledge of the densities of the large herbivores, their grazing-behaviour, population cycles and how they interacted with the vegetation. However, the data to develop such models are scarce. Vera (2000) (*pages 349*) points out the difficulties of trying to derive herbivore densities directly from archaeological or other remains. Maroo and Yalden (2002) suggest population sizes for different species, but these are based on assumptions about the vegetation composition and analogies to species densities in Bialowieza Forest; these figures cannot then be used to infer past vegetation as it would be a circular argument. Experiments such as those described by Bokdam and Gleichman (2000) and observations on sites such as Oostvardersplassen may be informative about short term processes, but observations over a 20-40 year period cannot necessarily be extrapolated to what might happen over cycles lasting several hundred years. Models, even simple and mechanistic ones such as that presented here, may help to bridge the gaps between the real observations.

With the model approach, the assumptions used are explicit and can be challenged; the consequences of varying them can be explored. Even with the limited range of options considered a number of different patterns can be generated, all of which are outcomes of the Vera cycle. Therefore discussions as to 'what sort of a landscape would result from applying Vera's ideas' must start from a discussion of what assumptions the protagonists are making: there is not just one possible outcome. In particular, at least with the range of assumptions used here, the degree of tree and woodland cover is much higher than has been implied in some debates. Even the most open landscape produced - the dense savannah, scenario 6 - has overall a tree cover of 41%. It may, however be unstable, because as the tree cover starts to open out, regeneration would become possible and effectively the whole cycle would simply become shorter.

4.1 Could the necessary soil changes take place in the timescales concerned?

Buried soil profiles show that woodland soils may be converted to heathland and grassland soils. However in the short term, changes to soil properties that occur when heathland or chalk grassland becomes into scrub and woodland, particularly nutrient enrichment, has sometimes proved challenging for those trying to restore such habitats after decades or centuries as broadleaf woodland. The tendency of large herbivores to forage in the open habitats during the day and then move to woodland at night (Putman 1986) may provide a mechanism for a reversal of the enrichment process (J Bokdam unpublished paper) over time. Once a grove had opened sufficiently to be used regularly by the herbivores there would be a tendency for nutrients to be moved from the open area to night-time resting areas in the nearby groves.

4.2 Are the landscape compositions generated compatible with the forage needs and behaviour of large herbivores?

Cattle tend to concentrate on grassland over woodland for forage if the former is available (J. Bokdan unpublished paper; Hulbert 2002). In the New Forest the lawns are grazed very tightly; although the grassland occupies only 7% of the open forest extent it accounted for 50% of the animal grazing time (Putman 1986).

Woodland forage is more likely to be used in winter when the grassland resource has been exhausted and to some extent at night when the animals move into the wood for shelter. With year-round grazing winter forage quantity and quality may be the limiting factor on animal numbers. Siebel and Piek (2002) comment that one hectare of nutritious summer grazing is equal to about 10 hectares of poor winter grazing area.

Putman (1986) attempted to estimate the carrying capacity of the New Forest vegetation at different months of the year for ponies. He concluded that it was only about 200-400 animals between November and January, but between 2000 and 3,000 animals during the summer months. Even allowing for an increase in pony numbers in the summer (foals) and that the animals need to build up their body weight in summer whereas overwinter they lose condition, this difference suggests that summer production would be in excess of what could be eaten.

If available forage is in excess of the summer population needs, then marginal areas (in forage terms) will not be grazed as heavily; more regeneration of woody species will get away; and the Scrub and Grove areas will tend to increase, and the area of the preferred grassland will decline. This does happen in the New Forest (or would, if grazing were the only mechanism for keeping areas open) where the heathland has to be cut or burned to suppress tree invasion. This occurs faster than the woods open up to form new heath.

Some of the grassland in the New Forest has been improved in the past, raising its potential productivity, so that more than 7% of the landscape might need to be grassland under more natural grazing conditions to satisfy the forage requirements. Even so the model results of c25% open Park would seem to be more likely than much more extensive grassland areas.

4.3 Why would regeneration not be mainly as isolated open grown trees?

The Groves have to be large enough for them to turn into large areas of open terrain following grove break-up (*page 377*). Vera implies, by analogy with the New Forest, that groves could be up to several hundred hectares (*page 151*) and elsewhere, in making a link between groves, 'hagas' and deer parks (*page 161*), suggests that groves might often be 40-80 ha.

The model scenarios have however been criticised because no allowance is made for regeneration that leads to a scatter of isolated veteran trees such as are found in wood-pastures (Butler 2002). The argument put forward is that there must have been many such trees because of the apparent preference of many specialist species under current conditions for open grown trees (Rannius & Jannson 2000). Vera (*page 349*) reports the occurrence of a sub-fossil oak from Germany only 12 m tall with a large branch at 2.5 m high, indicating that it had been open grown. However it is possible in the model as it stands for there to be trees that are partially open-grown; trees at the edge of a cell whose neighbouring cell was much younger could develop low branches as commonly happens at the edges of woods and rides today. If the wooded landscape (scenario 1) is divided into tetrads of 4 ha (200 m x 200 m) more than 90% contain at least two phases and 45% three or more. The requirements of edge specialist species could therefore be met from the tens of edge trees per hectare.

Secondly *isolated*, open grown trees might well be rare under Vera's proposed regeneration model, although it clearly could happen (*page 376*). For a tree to be isolated when mature would require that during the period when grazing was such as to allow scrub development, no other trees of roughly similar age established within c10-15 m (otherwise their branches would start to meet and close canopy). In addition, the grazing of the intermediate ground remained high enough for several centuries to prevent the growth of younger trees which would equally lead to grove conditions, albeit with trees of differing ages within a 1 ha cell. This runs against the arguments for the facilitation of regeneration by grazing and the abundance of oak seedlings seen in grazed areas (*pages 303,304, 377*).

Moreover if there is to be continuity of veteran trees in the landscape, there must be replacement trees establishing, say every 150 years in sufficient numbers to allow for losses over the years: not every 100 year-old tree survives to become 450+ year veteran. Depending on what rate of replacement is deemed necessary and the crown diameters assumed for different ages of trees (Appendix 2), quite low numbers can give substantial tree cover. If only 45 individuals per hectare are deemed enough to provide continuity of age classes from 75 years to >450 years, with crown diameters up to 20 m for the mature trees canopy cover could be 58%. This, once an allowance is made for the scrub element (15%), leaves only 27% for open space. If tree densities are increased to 77 trees per hectare to cover the full age range then even very modest crown diameters of 13m for 300 year-old trees give a canopy cover of 40%, which with 15% scrub leaves 45% open. If the trees were spread evenly over the hectare, the mean inter-tree distance (trunk to trunk) would be 15 m (at 45 trees per hectare) and 11 m (77 trees per hectare).

In practice it seems unlikely that tree densities would be this low. Establishment of an average of three trees per hectare over a period of 75 years, which is the regeneration window used in the model, could produce *c*175 trees per ha (making some allowance for overlaps where trees grow up very close together) (Appendix 2)). This gives more or less closed canopy by the time they are 100 years old. In Mellanby's (1968) study young oaks did not grow directly under the canopy of an existing tree at Silwood Park but there were over 60 within a few metres of the edge of the canopy. Therefore using a model based on one-hectare patches of trees in which the canopy more-or-less closes would seem to represent the more likely pattern.

4.4 How do the model scenarios match Vera's descriptions?

The model uses Vera's cyclical turnover of vegetation as its base, but are the results consistent with other qualitative comments about what the landscape may have been like? The 'woodland landscape' scenario is broadly consistent with Vera's references to 'half-open park landscape', eg *page 85*, in that 40% is composed of the Park and Scrub phases. Situations matching the majority of the photographs that he uses to give an impression of his landscape vision (*pages 87, 91, 114,121,146,150, 151,152,303, 352, 353*) could occur. There is a discrepancy between the basic 'wooded landscape' model and Vera's photograph 6.27 (*page 352*). He describes this as 'an overview of how the landscape in Central and Western Europe would have looked under the influence of grazing and browsing'. Open areas such as are in this photograph could however be accommodated in the pattern generated for the western third of Figure 9, which still retains 47% Grove phase overall. Also the foreground of Vera's photograph 6.27 with only very small groups of trees is inconsistent, as an overview, with his comments elsewhere about some Groves being tens or hundreds of hectares in extent (*page 151, 161*).

4.5 Mixed landscape models

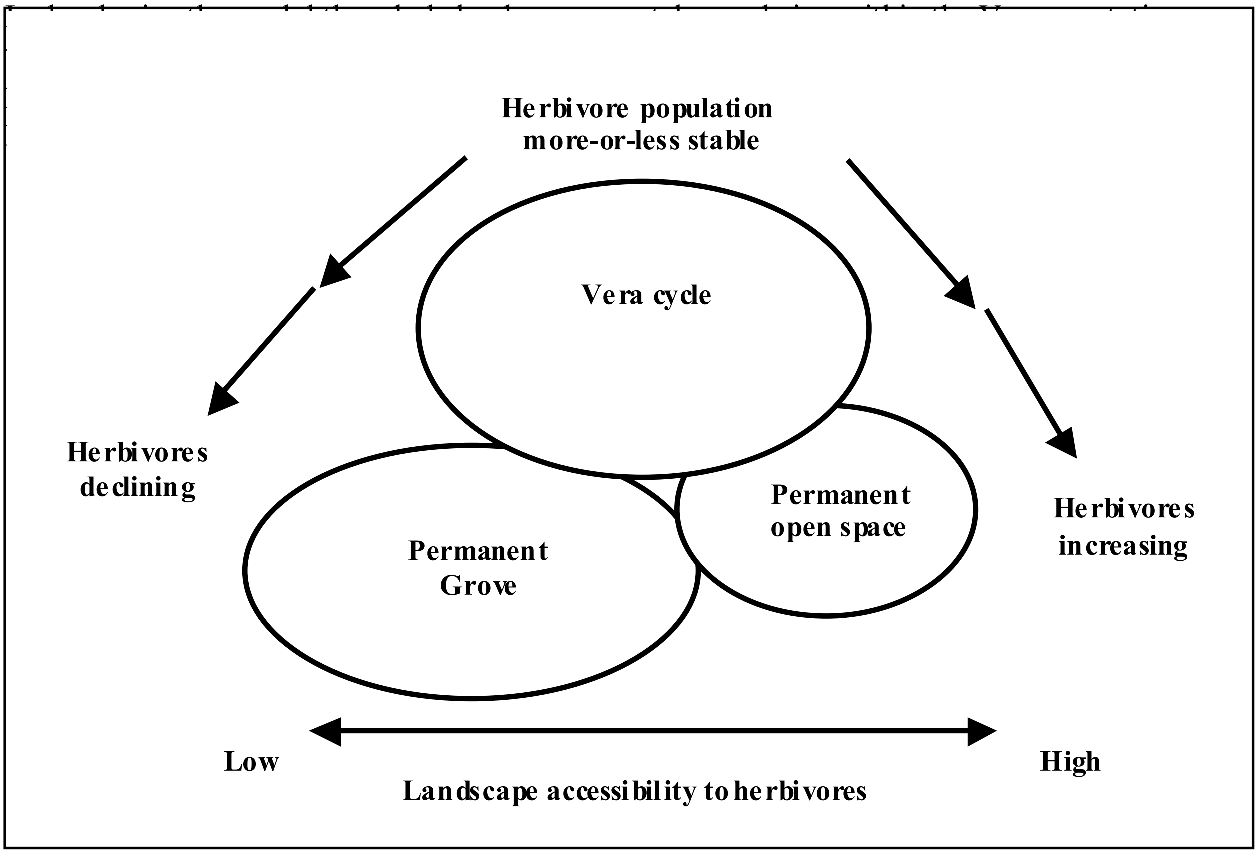


Figure 13 How differences in space (accessibility to herbivores) or over time (in terms of herbivore population dynamics) might shift the balance between the basic Vera cycle, permanent open space & permanent groves over long time-scales & large spatial scales

In developing the model the whole landscape was assumed to be within the Vera cycle, every cell went through all the phases of Figure 1 (although Vera acknowledges that not all areas would be subject to his cycle (*page 378*)). There could be no permanent open space, no permanent grove, no short-circuiting of the cycle. In practice the processes operating are likely to be more complicated. Figure 13 uses a concept proposed by G .F. Peterken and N. Sanderson separately (personal communications) that there could be at least three different cycles - permanent open space, permanent woodland, and Vera cyclical vegetation turnover - that themselves could be in flux over longer periods and larger spatial scales. This is closely related to the shifting vegetation mosaics driven by alternation of plant facilitation and competition proposed by Olff *et al.* (1999).

Geographic or topographic features (including differences in soil fertility, access to water, etc.) could mean that at a given time grazing would be overly concentrated on some areas, leaving others less grazed, so that both regions would move out of the cycle, but in opposite directions (one to permanent open space, one to permanent grove). Equally, over time, catastrophic declines or population explosions in the large herbivore population could lead to some regions moving out of the Vera cycle temporarily in one direction or another.

One final scenario is therefore presented (Figure 14). The central part of the figure is a wooded landscape operating on Vera principles as in Figure 9, but to it has been added 250 ha of permanent open space to the west and 250 ha to the east that is permanently forest, in which shade-bearing trees might predominate. The overall composition is 8% permanent open space, plus 21% as Park; 14% as Scrub; 8% as permanent forest plus 39% as shifting Groves; and 10% as the Break-up phase.

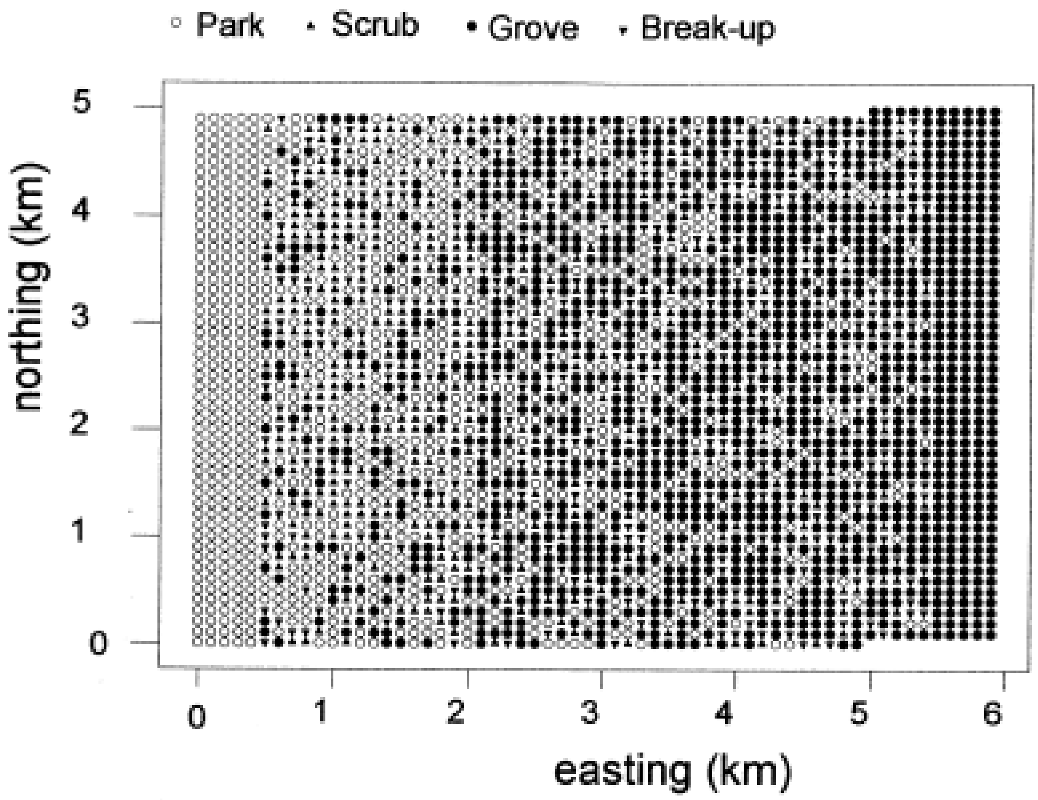


Figure 14 A mixed landscape with permanent open space to the west, permanent grove to the east and cycle vegetation turnover in the middle

4.6 Evidence for woodland as the matrix rather than open landscapes

The modelling work suggests that under most scenarios Grove (40 - 60%) rather than open Park (25-30%) would be the commonest landscape type. This would be consistent with high levels of tree pollen in profiles covering the Atlantic forest maximum.

Vera (2000) argues that the contribution of non-arboreal pollen (ie other than trees and shrubs) has been under-emphasised (*pages 88,99*) and that high levels of tree pollen may not necessarily imply closed woodland. However in modern landscapes such as southern Sweden, where high rates of tree pollen occur (>85%) they usually do represent heavily wooded landscapes (>70% wooded cover) (Brostrom *et al* 1998). Similarly F J Mitchell (personal communication) considers that small hollow pollen studies do not show evidence for an extensive open ground phase as part of prehistoric stand dynamics; and, in a study of about a dozen modern pollen profiles, those from closed forest all showed arboreal pollen values above 60%, while those from open habitats were less than 50% arboreal pollen.

Svenning (2002) compared the landscape interpretations for sites where the pollen record could be set alongside other evidence such as beetle and mollusc remains. The non-arboreal pollen percentages correlated well with independent estimates of vegetation openness as estimated from beetle, mollusc or plant macro-fossils. The traditional interpretation of non-arboreal pollen values less than 10% as evidence for closed forest with little open vegetation may not need to be discarded. Svenning concludes that the vegetation for most areas would be closed forest with localised longer-lasting openings around ponds and some grassy glades. Open vegetation would be present mainly on floodplains, on calcareous or poor sandy soils (eg Bush & Flenley 1987). The most widespread natural vegetation type would however be closed, old-growth forest.

Dirkx (2002) comments that dung beetles had been common before the Atlantic period, then declined during the presumed forest maximum, before increasing again in the Neolithic period as farming led to increases in the numbers of stock (and hence dung). Over the same period pollen diagrams show first increasing levels of tree pollen and reductions in pollen of light-dependent herbs and grasses. While Dirkx does not give specific data, his comments mirror Svenning's comparisons across sites. M. Robinson (personal communication) notes that dung beetles are scarce in prehistoric records prior to the Neolithic and the introduction of domestic animals. In a series of archaeological records there is a tendency for wood- and tree-dependent Coleoptera to be relatively more common in Mesolithic remains, whereas pasture/dung beetles were relatively more abundant in Neolithic sites (Robinson 2000).

4.7 The relevance of our understanding of natural landscapes for cultural landscape conservation

This report is primarily about the implications of Vera's ideas for our understanding of how the landscape in the Atlantic period may have looked and functioned. That landscape has however gone and cannot be re-created in Britain. What we are normally seeking to conserve are the remnants of the last 3,000 years of cultural landscapes, with their associated species.

If Vera's hypothesis is correct about the nature of the former natural landscape this alters our appreciation of how our habitats have arisen, but does not necessarily change the way we conserve them today. The conservation of chalk grassland in the form in which it has existed for much of the last 1000 years will usually involve agricultural-type grazing regimes (or no grazing at all in the case of parts of Salisbury Plain) not a reversion to free-range extensive 'more natural' grazing systems which might lead to increased scrub invasion. Bokdam and Gleichman (2000) and Bokdam (2002 a, b) found that free-range grazing did not by itself prevent invasion of heathland by pine and birch. They concluded that at their site (initially 33% woodland, 67% open) existing heathland would change into woodland before new heathland had developed within the existing woodland.

The flora and fauna of coppice woods may be partly analogous to those of the Scrub phase in the Vera cycle, but most coppice woods are too small and isolated to maintain these elements through a free-range grazing system. Direct effects of increasing deer numbers (particularly the effects of fallow which are more grazers than browsers) on the composition and nature conservation values of lowland woods are well-documented, eg Kirby (2001), Fuller and Gill (2001).

At one level, therefore, Vera's hypothesis is irrelevant to much conservation practice, where there are clear habitat and species priorities and we are also clear on what is the best management approach to achieving those priorities. The smaller the site and the more precisely the interest can be defined, the less likely it is that there will be any opportunity for applying free-ranging naturalistic grazing regimes.

Where Vera's ideas do become relevant are in the development of low-intensity ways of managing large-scale landscapes, provided certain *caveats* are recognised.

- We cannot predict the outcome of such management with any certainty.
- Some combinations of conditions may mean that the Vera cycle will not function: the landscape may move towards permanent woodland or permanent open habitat, even under free-range grazing.
- The landscape will not necessarily be predominantly open; different combinations of open and closed habitats can be consistent with Vera's hypothesis, as this report shows.
- Permanent open areas may not exist even if some open space is always present. Current areas of high value grassland and heathland areas may be lost to scrub and then woodland if free-range grazing alone is used.
- Some species may be lost permanently under free-range grazing if the micro-habitats they depend on occur at too low a density or at too infrequent intervals under free-range grazing. The potential loss of species, features or habitats under more natural regimes has been recognised as an issue in discussions on minimum intervention sites in woodland, but also with respect to some aspects of natural change on coastal sites (Box 2).
- There are a wide range of issues relating to public acceptablility, public safety and animal welfare that need to considered before any proposal can be adopted (eg Josten (2002); Korthals *et al* 2002; Klashorst & Kreetz 2002; Kampf 2002a,b; Lenwen & Essen (2002); Limpens *et al* 2002).

Despite the challenges presented by the above, English Nature does see scope for exploring more naturalistic grazing regimes in some areas, even if at present we are not in a position to develop the equivalent of Oostvardersplassen.

In the uplands there is interest in the concept of 're-wilding' in conjunction with possible moves towards more extensification of agriculture. Possible benefits and problems with such moves have been discussed in the context of developing new 'wild woods' (Worrell *et al* 2002; *www.lupg.org.uk/pubs*). In the lowlands there are projects to link up various fenland sites through conversion back from farmland, which may involve extensive grazing as part of future management regimes. The Sussex Wildlife Trust have ambitious long-term plans to try to link two of their reserves through a combination of open and wooded habitats managed with grazing (Whitbread and Jenman 1995).

Box 2. Management issues related to establishment of extensive reserves managed by naturalistic grazing regimes (based on Peterken 2000b)

- What set-up treatments are to be considered, for example:
  - elimination of unwanted species (eg rhododendron);
  - re-introduction of species lost from the site (other than the herbivores);
  - diversification of the existing habitat before introducing the herbivores?
- What species and what levels of herbivores should be introduced?
  - Bison and wild horse for example would not be appropriate in a British trial if we seek to mimic past natural conditions.
- To what extent are losses of cultural landscape features (coppice stools, banks etc) acceptable?
  - what attitude will be taken to invasion of the trial area by introduced species or the rampant spread of a native species such as holly or bracken, should this occur?

5. Conclusions

What started as a relatively straightforward modelling exercise developed into a broader exploration of the nature of natural landscapes, but also future conservation policies. There is scope for further work and much more discussion on these aspects. The following are, however, current conclusions on the state of the evidence and what it means.

(a) There is broad agreement that the impact of large herbivores in the former natural landscape has been underestimated.

(b) There is broad agreement that the former natural landscape was in places more open and more variable than the traditional model, but more openness could mean 30% or 80%; it needs to be specified in any discussions what level of openness is being considered.

(c) The degree to which large herbivores were the main driver of landscape structure is still debateable; they would have been significant in some areas, but not in others. Areas with very different large herbivore populations appear to have similar vegetation histories (R Bradshaw personal communication). The different make-up of our large mammal fauna (no bison or wild horse) and the lesser role for beech compared to continental woods may lessen the arguments for herbivore-driven systems in Britain.

(d) In areas where large herbivores were the main drivers of the forest dynamics the modelling suggests that a range of different combinations of open habitats (Park) and closed woodland (Grove) could occur. It is unlikely that a savannah landscape with a very low density of trees would have been widespread; the modelling results point more towards wooded landscapes (40-60% closed canopy groves, 25-30% open park, with the balance as scrub and stands that are breaking up). This seems to be consistent with recent work on pollen analysis and invertebrate records.

(e) The current abundance of habitats and species reflect the cultural landscape practices of the last 3000 years (at least). They cannot be used to deduce the composition of the former natural landscape.

(f) Our nature conservation priorities are largely based on the composition of these cultural landscapes. The management regimes needed to maintain these priorities may consequently be quite specific and not necessarily related to the former natural regimes and processes (whether based on Vera's hypothesis or the more traditional gap-dynamic approach to woodland regeneration). We cannot make *a priori* assumptions that adopting free-range naturalistic grazing regimes will always deliver the best nature conservation outcome.

(g) There is a case for trialling the use of naturalistic grazing regimes as an alternative to 'traditional' management, to create and maintain large-scale landscapes with a high biodiversity value, provided that the *caveats* to their use, detailed in the previous section, are taken into consideration.

(h) Such trials should be designed to allow for testing of some of the processes and outcomes predicted under the Vera hypothesis as against alternative views of natural forest landscapes. Realistically, however, such trials, nor the cannot provide definitive proof of either position because they would need to run for many centuries to demonstrate that the turnover of vegetation was part of a sustainable cycle.

Frans Vera's work has generated one of the most exciting debates in woodland ecology since the 1970s 'discovery' of ancient woodland: it has made us think again at the value and origins of mosaic sites and edges, about the dynamics of sites. These ideas are to properly inform conservation practice they have to be taken forward based on scientific discourse. I expect that my conclusions will be challenged, and some changes may be needed as a consequence. I look forward therefore to seeing the evidence and assumptions for alternatives views set down, so that these too can be debated.

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Appendix 1. How useful is analysis of current species preferences in assessing past habitat distributions?

(My thanks to Jan Bokdam for contributing ideas to this question.)

A common assertion is that the abundance and frequency of species associated with habitat mosaic conditions, with open habitats or with scrub, compared to those of closed woodland suggests (even proves) that the natural vegetation of Britain was predominantly an open mosaic.

The argument that has been put to me is as follows.

a) Open habitats and mosaics must have been abundant in Britain for this diversity of species associated with mosaics to evolve.

b) Many species, if not the majority of our wildlife are associated with open habitats, with mosaics, with mixtures. Even amongst 'woodland' species a high proportion are associated with woodland edge. Therefore these habitats must have been, and remained, dominant in the natural post-glacial and Atlantic period landscape.

c) There is a high proportion of stenotypic (narrow niche) species found amongst open ground and mosaic species, whereas many of our closed woodland species are relatively wide-ranging; this suggests that open ground was abundant and woodland scarce in the Atlantic period.

d) These stenotypic species could not have been expected to be abundant now if they had had to invade or spread out from refugia in the last few thousand years during which we have had a predominantly cultural landscape.

e) The species associated with old trees, particularly saproxylics, tend to be more common in parkland and wood-pasture conditions than where these trees occur in closed woodland.

f) Remains of species that depend on open conditions can be found in archaeological and palyoecological deposits.

The above are all in my opinion potentially flawed, with respect to most of Britain.

(a) *The evolutionary aspect*

Many of the species found in mosaics today presumably did evolve in mosaic conditions, although it might be argued these conditions were rare and isolated - hence favouring high evolutionary rates. However, regardless of whether the habitats were common or rare during the evolutionary stage, most of the species probably evolved long before the current post-glacial and quite possibly elsewhere in Europe. They virtually all had to re-invade after the last glaciation. The conditions under which they evolved cannot therefore be presented as support for the occurrence of habitats present in Britain during the Atlantic period.

(b) and (c) The abundance and niche range of woodland versus non-woodland species

The frequency and abundance *now* of open/mosaic habitat species are to be expected, whatever the nature of the previous natural vegetation. Even if the natural landscape were predominantly closed woodland (say > 80% cover) in the Atlantic period we could not expect obligate closed woodland species to have survived very well to the present given the following:

- woodland cover (all types) has been below 20 % cover in England for at least the last 1000 years and went down to 4% cover at the turn of the century (data for Scotland and Wales are less good but increasingly suggest similar early clearances);
- no more than about 3% of the land area has had any sort of continuity as woodland for more than about 400 years (ie the ancient woodland sites);
- 80% of these are less than 20 ha in extent;
- most have been managed to favour scrub and open space species (ie through the coppice system) for the last five hundred to a thousand years; closed woodland conditions such as predominate in neglected coppice and plantations have become widespread again only recently;
- an increasing number of ancient woods are being shown to have gone through periods of clearance pre 1600, ie are ancient secondary.

Given the above, we should predict - *whatever the previous natural landscape* - a tendency for the majority of surviving 'woodland species' to favour the open stages, scrub and edges; and to be generally relatively good dispersers. Species which depended on long-continuity of closed, humid woodland conditions and had poor dispersal powers would have had to survive more than three thousand years in which the vast majority (>99%) of their potential habitat was likely to have been destroyed.

By contrast, for the last three thousand years, conditions for stenotypic species of open ground, scrub and mosaics have been steadily improving as agriculture came to dominate the landscape (at least up to the mid-nineteenth century).

(d) *Stenotypic species of open ground could not have colonised and spread through Britain in the post Atlantic period.*

There is no dispute that the landscape was open in the immediate post-glacial period; many of the open/mosaic species may have colonised Britain at that stage. Even if the landscape were predominantly closed woodland in the Atlantic period this would not be wall-to-wall trees. A proportion of open/mosaic habitat species could therefore then have survived as transients in temporary open space, or in beaver meadows, around cliffs, coastal strips etc. They would then have spread gradually as the conditions improved.

In the period from c13,000 BP to 7,000 BP, species had to spread up from southern European refuges to reach Britain; it does not seem too impossible that they could then spread out from refuges to occupy suitable habitat across Britain in the period say 5000 to 2000 BP. We may badly underestimate the potential dispersal ability of species over periods of 100 years or more and in situations where habitat conditions for these species are improving.

In addition many of the species that we associate with open conditions and mosaics may have been helped to colonise (inadvertently) by human agents. There was interchange across the channel from at least the Neolithic age onward; straw, hay, grain, wood and sticks would all have been common on boats etc. There was movement within Britain, which could have helped their spread.

(e) *Saproxylic species do better when old trees are open grown.*

There is research to support this idea and for the decline in the richness of the saproxylic fauna over the last 7,000 years. However most sites where really old trees occur now (both in Britain and abroad) are present or former wood-pastures - ie the trees are or have been for much of their life growing in relatively open conditions. Therefore we should expect that the majority of saproxylic species and assemblages that do survive would do best in open grown trees. Further, there is in Rannius and Jannson's (2000) study a correlation between tree diameter and whether the trees had grown in open conditions; there is therefore a possible confounding of factors. The species may 'prefer' open grown trees simply because they are the biggest currently available.

As in (c) we are looking at the fauna of a cultural landscape. We might have a very different view as to what a typical saproxylic assemblage would be in western Europe if there were large stands with thousands of three - four hundred year old plus trees that have grown up as a closed forest without human interference - but they do not now exist.

(f*) Invertebrates of open conditions turn up in remains from the Atlantic period*

This is a potentially useful field of study, but deals with the abundance of species in the past, not the present. The fossil and sub-fossil remains of relevant invertebrates (and vertebrates) are good evidence that there were some open habitats present in the natural landscape - just as the presence of closed, humid woodland species is evidence for that habitat being around as well. However the question is not whether open conditions existed but their extent: were they 80%, 60%, or only 20% of the landscape? If the evidence cannot be used to make these distinctions then it is of little help in the debate.

Svenning (2002) attempts to link abundance of different groups indicating open conditions with accompanying pollen records and concludes that the pollen record is not such a bad measure of closed canopy conditions as Vera suggests. This study is said to be flawed (Keith Alexander personal communication) but as yet I have not come across alternative studies that show positive quantitative evidence of high landscape openness, except in very specialised conditions.

Conclusion

Therefore I do not think that the arguments (a-e above), singly or in combination, can be used as evidence for Vera's model. The patterns we have now reflect cultural landscape conditions; they might be derived from similar patterns generated under a Vera landscape or could have substituted for different patterns that existed under a predominantly closed woodland landscape. The two options or some combination of them cannot be distinguished from current day assemblages.

Appendix 2. Would isolated trees be common?

Would regeneration have taken place predominantly as individual trees to give isolated veterans such as are seen in parks and wood-pastures?

For the veterans and their associated species assemblages to be sustainable there must be, over the landscape as a whole, cohorts of younger trees to ensure a continuity of the veterans. Two approaches are explored below. The first works back from a final veteran tree density, the possible cohort structure to support these, and hence a derived overall tree density. The second works forward from possible frequencies of successful regeneration events to create a tree population density at c150 years.

What sort of cohort structure would give the necessary density of veterans?

An average density of three veterans (>450 years) per ha was assumed as the sort of minimum figure that might be needed to ensure long-term survival of the associated flora and fauna (Jon Webb, personal communication). The cohort structure (columns 1,2) was assumed to ensure the continuity of the veterans, allowing that about half the trees die in each cohort before making the transition to the next age band. This density of trees is very low compared to a standard high forest plantation of oak that might be expected to have 100 trees per ha at 100 years old, and is probably conservative. For example it assumes that the death rate of the 24 trees per ha present at age 150 years is only about one tree every 15 years.

1. Age of cohort	2. Mean no of trees/ha in cohort	3. Mean crown diameter (m)	4. Total crown area per cohort (m^2)	5. % canopy cover (col. 4 minus10%)
> 450 yrs	3	15	530	4.8
301 -450 yrs	6	20	1885	17.0
151 - 300 yrs	12	15	2120	19.1
75 - 150 yrs	24	10	1885	17.0

If crown diameters for open grown trees are used, eg up to 20 m (personal observation), tree cover rises to 58% even with only 45 trees per hectare (excluding those below 75 years). (A ten percent overlap allowance has been included.) If scrub and young trees less than 75 years old (there have to be some to ensure continuity) are assumed to cover 15%, based on the various scenarios in the main text, then the amount of the landscape that would be open would be just 27%.

A higher stem density (total tree number 77 per hectare to allow for more tree deaths) and lower crown diameters might be used. For example diameter at breast height based on yield class for oak of 8 for the 75-150 trees can be obtained from yield tables. Mean crown diameters were then calculated using a regression of crown diameter on stem diameter from Koop (1989), specifically that for Otterkoi (page 154, Crown diameter = 0.08 dbh + 1.11); but with the crown diameter for the veteran trees assumed to have been reduced through retrenchment.

1. Age of cohort	2. Mean no of trees/ha in cohort	3. Dbh (cm)	4. Mean crown diameter (m)	5. Total crown area per cohort (m^2)	6. % canopy cover (col. 5 minus 10%)
> 450 yrs	3	170	10.0	235	2.3
301 -450 yrs	12	150	13.1	1617	14.5
151 - 300 yrs	24	100	9.1	1561	14.0
75 - 150 yrs	48	50	5.1	980	8.8

The canopy cover is 40%, which with scrub cover of 15% leaves 45% open. However this is again a very conservative figure for total canopy cover (ie an over estimate of openness) because these small crown diameters are based on equations for trees grown in high forest rather than as open grown specimens.

In addition, as the next section suggests the number of trees establishing would probably be greater than in the above examples.

What frequency of regeneration might occur?

Consider a hectare square where the grazing pressures are such that regeneration as scrub and trees can occur. Assume it is broken down into 2x2 m squares (ie 2500 per hectare) and that each year just 10 thorn bushes establish at random, which is equivalent to about one every 32m. Each year another set of bushes establish in the same or different squares, but if the 2 x 2 m square is already occupied only one bush is deemed to survive.

By the end of 25 years 239 2x2m squares contained a bush; by the end of 75 years (the period allowed for scrub establishment within the scenarios) 657 2 x 2 m squares contained bushes. If the bushes are grouped by 10 x 10 m blocks then after 50 yrs 70% of the 10 x 10 m blocks contained at least 4 established bushes and after 75 yrs 94% had at least 4 bushes. The mean distance between thorn stems at this density would be 5 m or less; their crowns would be almost certain to overlap. Therefore it only requires establishment rates of c10 bushes per hectare per year to form more or less complete scrub cover over a 75-year period.

Using the same set of data regeneration of oaks with the thorns was considered. If the rate of oak establishment was one oak for every four thorns throughout the 75 year period (still less than three oaks establishing per hectare per year) then 87% of 10 x 10 m squares could contain at least one tree and 55% two or more (total of 175 trees per ha).

Very low rates of successful recruitment (2.5 trees per ha per year) therefore have the potential to form closed canopy over the hectare cell under the timescales allowed for regeneration in the main model. They could also fill not just the 15% allocated to scrub but all the open space as well in the single-tree recruitment tables above.

ENGLISH NATURE

English Nature is the Government agency that champions the conservation of wildlife and geology throughout England.

This is one of a range of publications published by:
External Relations Team
English Nature
Northminster House
Peterborough PE1 1UA

www.english-nature.org.uk

Cover printed on Character Express, post consumer waste paper, ECF.

ISSN 0967-876X

Cover designed and printed by Status Design & Advertising, 2M, 5M, 5M.

Front cover photographs:
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