

How open were European primeval forests? Hypothesis testing using palaeoecological data

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Summary

1 The Vera hypothesis that large herbivores maintained an open landscape in the primeval landscape of lowland Europe is tested using palaeoecological data. The hypothesis suggests that the high abundance of *Quercus* and *Corylus* apparent in European pollen diagrams could not have derived from a landscape dominated by closed canopy forests. If natural forest landscapes were indeed more open, current forest conservation management policy across Europe would need to be reconsidered.

2 Relative proportions of *Quercus* and *Corylus* pollen are compared from regions which supported large herbivores with data from Ireland, where large herbivores were excluded. Similarity between the two data sets indicates that large herbivores were not required to maintain these taxa in the primeval landscape.

3 Fine spatial resolution pollen data from small hollows in Europe and eastern USA were also reviewed. Data from moss polsters show that percentage arboreal pollen is a reliable indicator of canopy openness in these sites. The palaeoecological data demonstrate that open canopy forest has only ever been maintained by human exploitation.

4 Large herbivores in Europe do not therefore appear to have maintained an open landscape in primeval times although evidence suggests that they would have influenced the species composition of the forest canopy.

5 It is proposed that data sources other than pollen should be explored as proxies for past forest structure to test this hypothesis more thoroughly.

Key-words: Primeval forest structure, Vera hypothesis, forest grazing, large herbivores, pollen analysis, forest conservation policy

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Introduction

Peterken (1996) has concluded that primeval virgin forest no longer exists in Europe. Despite this, the concept of virgin forest strongly influences nature conservation policy across Europe although, in certain circumstances, cultural exploitation such as coppicing is recognized as an important intervention to be maintained (Peterken 1993). In the absence of true virgin forest in the European temperate zone, the composition and structure of primeval forests in this region has been inferred both from studies of old stands which have received minimal human impact and from palaeoecological data. The image that emerges for lowland temperate Europe is a landscape dominated by closed canopy deciduous forest. This model is challenged by Vera (2000) who considers that large herbivores were instrumental in maintaining

a more open landscape and hence prevented the dominance of closed canopy forest.

The significance of Vera's (2000) hypothesis lies in the contention that, if it is valid, then forest conservation policy across much of Europe, and by analogy, parts of North America, is misguided where the conservation aim is to maintain the forest close to its natural condition prior to human impact. The implementation of this policy draws on very significant resources from fiscal and NGO sectors. The publication of Vera's (2000) hypothesis has already prompted a major investigation by English Nature into the future management of large-scale reserves in Britain using naturalistic grazing (Kirby *et al.* 2004), drawing on the existing experience of this approach at the 5000-ha reserve at Oostvaardersplassen in the Netherlands (Vera 2000). This paper tests the validity of Vera's hypothesis by using palaeoecological data from primeval and modified forests to explore the degree of canopy closure of the primeval forest.

Large herbivores are observed to have significant impacts on forest ecosystems today, such that the control of wild and domestic herbivores is a major conservation management issue (Mitchell & Kirby 1990; Weisberg & Bugmann 2003). In prehistoric times there was greater diversity of large herbivores in Europe; in addition to several species of deer, there were aurochs, tarpan, bison, beaver and wild boar. Vera (2000) proposes a dynamic model in which large herbivores maintained a landscape composed of a mosaic of groves of closed canopy woodland, open parkland and regenerating scrub. Large herbivores grazing and browsing in closed canopy woodland would prevent tree regeneration so that eventually the canopy would open up and ultimately form parkland. The development of browsing resistant thorny scrub (Bakker *et al.* 2004) would provide protection for regenerating trees in the parkland which would then develop into groves and so complete the cycle. An essential feature of the model is that the landscape is made up of a dynamic mosaic of the components of the cycle in which closed canopy forest exists in groves but that these are not self-perpetuating. The spatial and temporal characteristics of this model have been explored by Kirby (2003, 2005) and the basic elements of the model are illustrated in Fig. 1. Vera confines his model to the geographical region lying between 45° N and 58° N latitude and 5° W and 25° E longitude, and to altitudes below 700 m (Vera 2000, figure 1.5). These limits fall within the principal temperate zone of Europe north of the Alps. By analogy, it is also proposed that the hypothesis applies to the temperate zone of eastern North America.

Vera (2000) proposes the following null hypothesis:

‘Pedunculate and sessile oak and hazel survive in a closed forest, and regenerate in gaps in the canopy, in accordance with Watt’s ‘gap phase’ model (1947) and Leibundgut’s so-called cyclical model. The large herbivores which occurred naturally such as the aurochs, European bison, red deer elk, roedeer and

tarpan or European wild horse and the omnivorous wild boar followed the developments in the vegetation. They did not have any influence on the course of the process of the succession and regeneration of forests.’

Vera (2000) tests this null hypothesis using evidence from a very comprehensive review of the literature on modern ecology of forest tress and large herbivores, fossil pollen data and historical information. It is impossible to reconstruct the population densities of large herbivores in prehistoric times (Bradshaw & Mitchell 1999) but Vera (2000) argues that their impact on forest structure is evident from the pollen record. Modern ecological studies suggest that oak (*Quercus petraea* (Mattuschka) Lieblein and *Q. robur* L.) and hazel (*Corylus avellana* L.) require canopy gaps for regeneration (Vera 2000). Pollen records from across Europe are dominated by these taxa in prehistoric times, and this is used as evidence to suggest that the forests must have been more open than today to maintain their regeneration. Vera rejects the null hypothesis in favour of this alternative:

‘The natural vegetation consists of a mosaic of large and small grassland, scrub, solitary trees and groups of trees, in which the indigenous fauna of large herbivores is essential for the regeneration of the characteristic trees and shrubs of Europe. The woodland pasture can be seen as the closest modern analogy for this landscape’ (Vera 2000).

The crux of the debate may be simplified thus: the traditional view implies that forest structure dictated herbivore carrying capacity, whereas the Vera hypothesis dictates that herbivore density controls forest structure. Vera’s model and hypothesis testing are based on qualitative data drawn from the literature. Kirby (2004) has taken a more quantitative approach to model the spatial and temporal aspects of the hypothesis, whilst palaeoecological data will be used here to quantitatively test Vera’s (2000) null hypothesis.

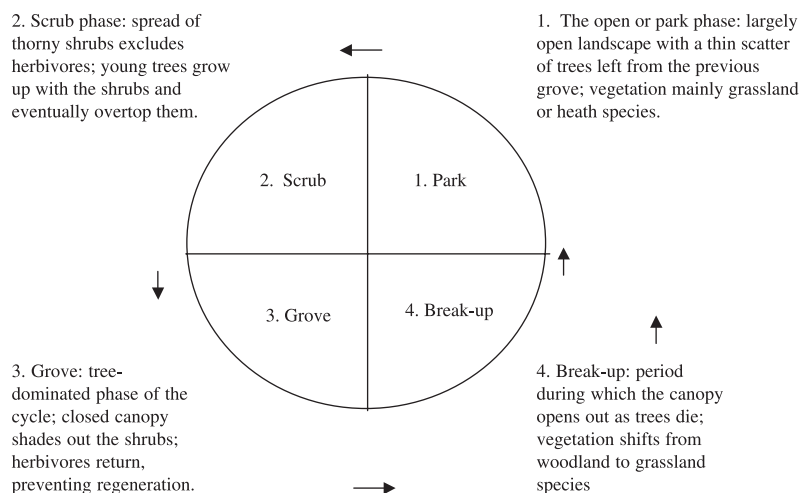


Fig. 1 Vera’s model, consisting of the three phases of Open Park, Scrub and Grove, to which a fourth Break-up has been added by Kirby (2003) to represent the transition from woodland grove back to open habitats (Park). Source: Kirby (2003) with the kind permission of English Nature.

PALAEOECOLOGICAL DATA

Fossil pollen is found in abundance in a variety of sites across the temperate ecotone (Jacobson & Bradshaw 1981). Fossil pollen data have been used to reconstruct changes in vegetation communities over time and can thus be used to infer the impact of large herbivores on temperate forest structure (Vera 2000). By contrast, fossil remains of large herbivores provide qualitative but not quantitative data because they are too rare to enable the reconstruction of population densities (Bradshaw & Mitchell 1999). However, we do have sufficient data to assess whether certain herbivore species were present in particular locations in the past. This provides us with an approach to test Vera's null hypothesis, which is analogous to the manipulation of herbivore grazing using fenced enclosures that is widely used in contemporary forest grazing experiments (Mitchell & Kirby 1990).

Grazing exclusion

Vera argues that large herbivores maintained an open forest structure or mosaic which was necessary to ensure the regeneration of *Quercus* and *Corylus*. Review of the European pollen literature confirms the universally high proportions of these taxa throughout the Holocene. It is therefore implied that without the impact of the herbivores, the forest canopy would remain closed, and thus restrict the regeneration of these taxa which would in turn be reflected in the pollen record. This latter hypothesis can be tested by examining pollen data from islands where the herbivore populations have been more restricted than in mainland Europe.

Svenning (2002) discusses the example of the island of Zealand in Denmark where Hannon *et al.* (2000) have used pollen data to demonstrate that *Quercus* and *Corylus* were abundant in the mid Holocene after aurochs and elk had been extirpated. Other deer species and wild boar remained and so the complete exclusion of large herbivores was not maintained. A more convincing case can be made for the island of Ireland. This region is outside the area of lowland temperate Europe defined by Vera (2000, figure 1.5) but shares similar topography and climates and falls within the geographical range of *Quercus petraea*, *Q. robur* and *Corylus avellana*.

Most of Ireland was covered by ice during the last glacial cold stage (Coxon 2001) and so it can be assumed that no large herbivores would have survived from earlier interstadials or interglacials. Migration into Ireland would have been hindered by the isolation of the island during the early Late-glacial and this is also reflected by the depauperate flora compared to the rest of Europe (Mitchell 2002). Early Holocene mammal faunas in Europe have been established from excavations and the data have been collated by Roberts (1998) and Svenning (2002). A subset of these data which relate to large herbivores native to north-west Europe, Britain and Ireland during the early Holocene is presented in

Table 1 Early Holocene native large herbivores. Data for north-west Europe from Svenning (2002); data for Britain and Ireland from Roberts (1998)

Species	North-west		
	Europe	Britain	Ireland
Wild boar (<i>Sus scrofa</i>)	X	X	X
Red deer (<i>Cervus elaphus</i>)	X	X	X
Roe deer (<i>Capreolus capreolus</i>)	X	X	
Elk (<i>Alces alces</i>)	X	X	
Reindeer (<i>Rangifer tarandus</i>)	X	X	
Horse (<i>Equus caballus</i> s.l.)	X	X	
Aurochs (<i>Bos primigenius</i>)	X	X	
Beaver (<i>Castor fibre</i>)	X	X	
Bison (<i>Bison</i> spp.)	X		
Fallow deer (<i>Dama dama</i>)	X		

Table 1. Ireland had only two large herbivores: wild boar and red deer. The data for red deer in Ireland are remarkable. Red deer bones are absent from early Holocene archaeological sites and no material has been dated from the early Holocene (Woodman *et al.* 1997). Some bones considered to be those of red deer have been found in early Holocene context at Belfast Lough, but the earliest Holocene radiocarbon dates for red deer in Ireland remain around 4000 BP (where BP refers to radiocarbon years before present) (Woodman *et al.* 1997). The scarcity or absence of red deer remains of early Holocene age cannot be used as proof of the absence of this herbivore but the available data suggest that, even if red deer was present in Ireland during the early Holocene, it was unlikely to have been very abundant. This is in contrast to wild boar which has been found more widely in both space and time. We can therefore consider the early Holocene forest in Ireland to be almost devoid of large herbivores compared to Britain and the European continent. Ireland can be considered as an early Holocene grazing enclosure, albeit containing wild boar and possibly some isolated red deer populations.

Some commentators have considered that the use of fire by Mesolithic hunters to open the forest canopy may confuse the assessment of the impact of large herbivores (e.g. Svenning 2002). With the absence or scarcity of game in Ireland this is unlikely to be an issue. Mesolithic people in Ireland did not have this reason to maintain open forest canopies and this contention is not disputed by the limited archaeological evidence (Woodman 1978; Woodman *et al.* 1997). Molluscan data do, however, demonstrate that some clearings were created (Preece *et al.* 1986). Bradshaw & Hannon (2004) also argue that forces like natural fire, windthrow and seasonal flooding would have created forest openness in Europe irrespective of herbivore grazing.

Fine spatial resolution pollen analysis

Traditional pollen analysis from lakes and peat deposits reconstructs vegetation on a spatial scale that is too coarse to reliably reconstruct forest stand structure

because these sites collect pollen from a radius of tens of kilometres (Jacobson & Bradshaw 1981; Sugita 1994). The pollen from numerous vegetation communities is mixed before deposition and so the ability to identify dynamics in a single community is restricted. Reconstructing the degree of forest canopy openness or the spatial mosaic of open and wooded patches in the landscape is similarly fraught with uncertainties (Koff *et al.* 2000). So, although the pollen data from these sites give an indication of the relative proportions of certain tree taxa in the landscape they cannot reveal the structure of the forest with any degree of certainty.

Modelling exercises suggest that small hollow sites in closed canopy forest collect most of their pollen from within a radius of 50–100 m (Sugita 1994) and this has been supported by empirical data from the USA (Jackson & Wong 1994; Calcote 1995). Small hollow pollen analysis from forested sites can therefore provide data on forest dynamics at the forest stand scale. If the forest canopy opens up then the pollen source area may be greater but the increased light will be registered in the pollen record by enhanced flowering of herbaceous taxa. The pollen of herbaceous taxa are normally poorly represented in traditional larger sites because of their limited pollen transport. Pollen does not travel far to small hollow sites and so forest openness can be detected. This assumption is tested below with empirical data.

Methods

Comparison of *Quercus* (deciduous) and *Corylus* pollen abundance between Ireland and the area of Europe defined by Vera (2000, figure 1.5) provides the basis for testing the null hypothesis. The data must be temporally constrained to be late enough in the Holocene to ensure that the taxa would be present in the region but also to predate significant manipulation of the forest structure by human activity. Reference to Huntley & Birks (1983) and Brewer *et al.* (2002) indicate that the lower date should be 8500 BP. The widespread establishment of Neolithic cultures throughout western Europe after 5500 BP (Roberts 1998) provides the upper time limit for the data set.

The European Pollen Database (<http://wdc.obs-mip.fr/palaeo/epd/>) was accessed for all sites that lie within the geographical and altitudinal limits set by Vera (2000) and cover the time period from 8500 BP to 5500 BP. This search delivered 21 sites which are detailed in Table 2. The IPAL data base, which is confined to fossil pollen data from Ireland (R. Marchant, unpublished data), was also accessed and delivered 15 sites covering the desired time period and all below 700 m altitude (Table 2). The raw pollen count data for each site were converted into relative proportions based on a pollen sum of identified terrestrial taxa, including fern spores. The mean relative abundance of *Quercus* and *Corylus* pollen in contiguous 500-year time slices was then computed to capture time transgressive changes across the sites. This generated data for six time slices for each taxon at each site. The resulting data matrix for

each taxon was then subjected to principal components analysis (PCA) using the CANOCO 4.5 (Biometrics-Plant Research International, Wageningen, The Netherlands) package to illustrate the relationship between the European and Irish data (ter Braak & Šmilauer 1997–2003). Redundancy analysis (RDA), which is a form of constrained PCA, was then employed with site location (Europe or Ireland) as the single explanatory variable (Lepš & Šmilauer 2003). The data were not transformed prior to analysis. The null hypothesis that there is no difference between the data for Europe and Ireland was tested using a restricted Monte-Carlo permutation test.

The small hollow pollen record is sensitive to canopy openness so the relative proportion of arboreal pollen (AP) to nonarboreal pollen (NAP) has been chosen to represent an index of openness. Svenning (2002) has compared pollen data to other proxies of canopy openness, such as beetles, molluscs and plant macrofossils, to demonstrate that the AP : NAP ratio is a reasonable index of openness. The degree of openness represented by AP percentage in small hollows can also be evaluated using pollen data from moss polsters. Pollen extracted from the living parts of moss polsters provides an integrated pollen sample from several previous years. The pollen trapping properties of moss polsters are analogous to those of small hollows and so provide a reasonable contemporary model (Fall 1992) against which present vegetation composition and structure can be compared to pollen representation. Moss polster pollen data from both open (i.e. not forested) and closed canopy forest locations from across Europe have been accessed from the literature. The data are presented as the range of one standard deviation either side of the mean AP percentage.

Published small hollow pollen data were collated from sites which contained early Holocene records within the area of lowland Europe defined by Vera and from Ireland. The pollen data from each site were grouped into consecutive 1000-year time periods. The maximum and minimum percentage arboreal pollen values within each 1000-year time period are plotted as an AP range from 12 sites.

Results

The PCA plots illustrate that the Irish data lie within the range of the European data for both *Quercus* and *Corylus* (Fig. 2). Site location accounted for only 1% of variance in the RDA for *Quercus* and 7.6% for *Corylus*. Site location was not a statistically significant source of variation in the analysis of either taxon (F -ratio = 0.335 for *Quercus* and 2.807 for *Corylus*). This implies that there was no significant difference in the relative proportions of *Quercus* and *Corylus* in the primeval forests of Ireland and Europe despite the differences in large herbivores between the regions. Therefore Vera's null hypothesis can not be rejected, i.e. the presence or absence of large herbivores has little impact on the relative abundance of *Quercus* and *Corylus* in primeval woodland in lowland temperate Europe. If this is the

Table 2 Site details for pollen data derived from EPD and IPAL databases

Site name	Country	Grid reference	Source reference
Kamenicky	Czech Republic	49°44' N 15°58' E	Rybničková & Rybniček (1988)
Hockham Mere	England	52°30' N 00°50' E	Bennett (1983)
Pannel Bridge	England	50°54' N 00°41' E	Waller (1987)
Vallie de la Voise	France	48°25' N 01°45' E	van Zeist & van der Spoel-Walvius (1980)
Lake Balaton Centre	Hungary	46°44' N 17°24' E	Nagy-Bodor <i>et al.</i> (1995)
Zsombo-swamp	Hungary	46°21' N 19°59' E	Nagy-Bodor <i>et al.</i> (1995)
Tytuvenu tyrelis	Lithuania	55°35' N 23°18' E	Kabailienė (1990)
Błędowo Lake	Poland	52°33' N 20°40' E	Binka <i>et al.</i> (1991)
Kluki	Poland	54°42' N 17°17' E	Tobolski (1987)
Lake Lednica	Poland	52°33' N 17°23' E	Makohonienko & Walanus (1991)
Lake Skvzetuszewskie	Poland	52°33' N 17°21' E	Tobolski & Okuniewska-Nowaczyk (1989)
Puścizna Rękowońska	Poland	49°29' N 19°49' E	Obidowicz (1989)
Słopiec	Poland	50°47' N 20°47' E	Szczepanek (1961, 1982)
Szymbark	Poland	49°38' N 21°06' E	Szczepanek (1989)
Tarnowiec	Poland	49°42' N 21°37' E	Harmata (1987)
Ageröds Mosse	Sweden	55°50' N 13°25' E	Nilsson (1964)
Kansjon	Sweden	57°38' N 14°32' E	G.L. Jacobson (unpublished); Berglund <i>et al.</i> (2002)
Lake Sambösjön	Sweden	57°08' N 12°25' E	Digerfeldt (1982)
Mabo Moss	Sweden	58°01' N 16°04' E	Göransson (1991)
Lobsigensee	Switzerland	47°01' N 07°17' E	Ammann (1989)
Ivano-Frankovskoye	Ukraine	49°55' N 23°46' E	Artjushenko <i>et al.</i> (1982)
Arts Lough	Ireland	52°55' N 06°20' W	Bradshaw & McGee (1988)
Ballinloughig Lough	Ireland	52°12' N 10°18' W	Barnosky (1988)
Belle Lake	Ireland	52°11' N 07°02' W	Craig (1978)
Black Lough	Ireland	53°15' N 07°41' W	Heery (1998)
Borheen Lough	Ireland	52°24' N 08°12' W	E. Cole (unpublished)
Camlaun Lough	Ireland	52°10' N 10°24' W	Dodson (1990)
Clara Bog	Ireland	53°32' N 07°41' W	Connolly (1999)
Cornaher Lough	Ireland	53°23' N 07°28' W	Heery (1997)
Cregganmore	Ireland	54°15' N 09°36' W	McKeever (1984)
Glendalough	Ireland	53°00' N 06°20' W	J. Maldonado (unpublished)
Kellys Lough	Ireland	52°50' N 06°15' W	E. Cole (unpublished)
Ladies View	Ireland	51°58' N 09°36' W	Vokes (1966)
Lough Anaffrin	Ireland	53°55' N 09°48' W	Browne (1986)
Lough Clevala	Ireland	54°04' N 09°24' W	Browne (1986)
Sluggan Bog	Ireland	54°48' N 06°21' W	Smith & Goddard (1991)

case then we should examine the structure of this early Holocene primeval forest more closely.

Contemporary moss polster pollen data indicate that closed canopy forests maintain AP greater than 60% (Fig. 3). These data can be contrasted with data from completely open sites where AP does not exceed 50% (Fig. 4). The data from Spain are an exception because the open sites investigated included arboreal scrub genera such as *Quercus* and *Celtis* (Díaz Fernández 1994). Furthermore, Spain is outside the lowland temperate region of Europe as defined by Vera (2000). Data from the forest edge in France and the Spanish Dehesa (parkland) are also included in Fig. 4 as these are rare examples of contemporary pollen data from partially wooded habitats. Significantly, the AP percentage values do not exceed 50% in these latter cases. The contemporary pollen data from moss polsters indicate that AP percentages in excess of 60% are indicative of closed canopy forest while AP percentages less than 50% are indicative of more open habitats. These data confirm that pollen analysis from small hollows in forested catchments can be used to assess the degree of canopy closure.

The arboreal pollen remains above 60% at all small hollow sites prior to 3000 years ago (Figs 5–7). Comparison with the contemporary pollen data (Figs 3 and 4) indicates the maintenance of closed canopy forest for the primeval woodland in both Ireland and the rest of Europe. Over the last 3000 years, arboreal pollen falls below 60% at some sites and in each case this is associated with documented human impact on the forest which has resulted in the artificial opening of the canopy (see original papers for details). This independent evidence further strengthens the argument that small hollow pollen sites can be used to investigate forest canopy cover. The temporal resolution of the pollen samples across the sites is variable but there is no indication of open forest canopies at any site prior to human impact irrespective of the presence of large herbivores in the region.

Discussion

Pollen data have been used to test Vera's hypothesis on two spatial scales. Data from large lakes and bogs show similar records for *Quercus* and *Corylus* irrespective of

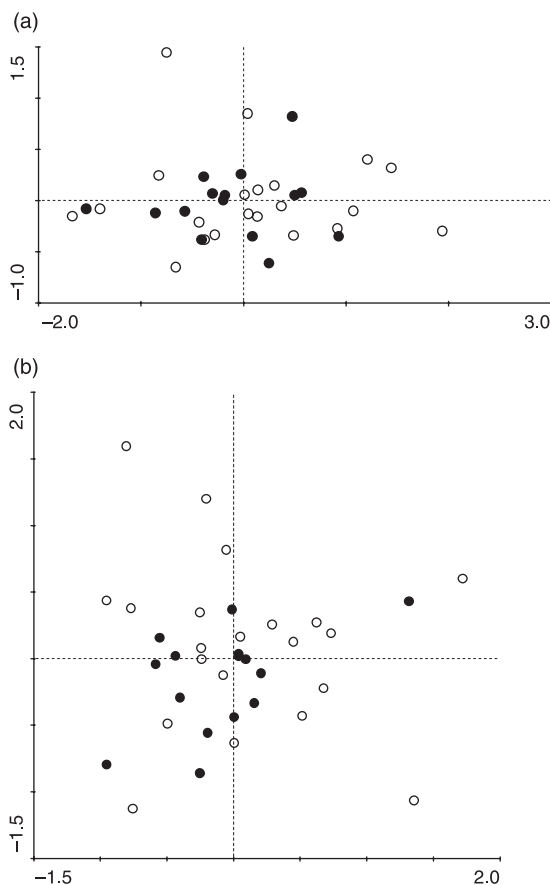


Fig. 2 PCA plots of relative proportions of (a) *Quercus* pollen and (b) *Corylus* pollen. Open circles represent sites from within the area of lowland Europe defined by Vera (2000), while closed circles represent sites in Ireland (see Table 2 for site details).

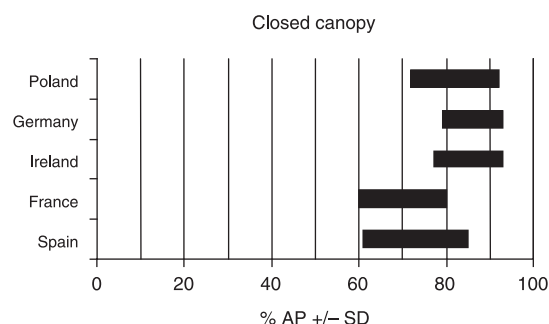


Fig. 3 Mean arboreal pollen (AP) percentage \pm 1 SD from moss polsters collected within closed canopy forests. The data sources are Poland: Dąbrowski (1975) and Makohonienko *et al.* (1998); Germany: Dambach (1998); Ireland: Mitchell (1988) and unpublished data; France: Ruffaldi (1994); Spain: Díaz Fernández (1994) and Andrade Olalla *et al.* (1994).

the presence or absence of large herbivores, thus indicating that large herbivores are not a prerequisite for the maintenance of these genera in the primeval landscape, which was a central tenet of Vera's hypothesis.

Pollen analysis at the fine spatial scale of small hollows has been demonstrated to distinguish open and closed forest canopies but there is no evidence from the available data for open canopies in the primeval forest when large herbivores were present. If large herbivores

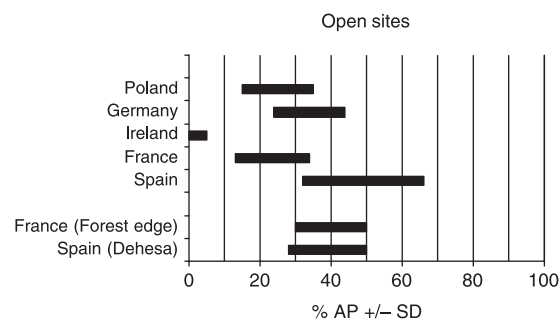


Fig. 4 Mean arboreal pollen (AP) percentage \pm 1 SD from moss polsters collected from open sites. The data sources are Poland: Makohonienko *et al.* (1998); Germany: Dambach (1998); Ireland: Hall (1989); France: Ruffaldi (1994); Spain: Díaz Fernández (1994) and Andrade Olalla *et al.* (1994); France (Forest edge): Ruffaldi (1994); Spain (Dehesa): Díaz Fernández (1994).

did not dictate the structure of primeval forests then it is reasonable to assume that the forest structure dictated herbivore carrying capacity.

A review of small hollow pollen data from eastern USA reveals AP values above 80% prior to European settlement and so prompts a similar conclusion (Foster *et al.* 1992; Schoonmaker 1992; Foster & Zebryk 1993; McLachlan *et al.* 2000; Foster *et al.* 2002; Schauflier & Jacobson 2002). The impacts of European settlement in central Massachusetts have been well documented (Foster *et al.* 1998). Widespread settlement began in the eighteenth century and by 1830 more than 70% of the forest had been converted to agricultural land. Abandonment of agricultural land from the mid nineteenth century onwards resulted in the natural regeneration of forests which cover 85% of the region today (Foster *et al.* 1998). These landscape scale changes to some extent mimic those proposed by the Vera hypothesis. The forest canopy was gradually reduced to produce a mosaic of open land with isolated copses of woodland associated with each farm. Regional pollen data from small lakes in central Massachusetts detect these changes to the landscape from the original forest with low NAP values, to the expansion of European settlement with higher NAP followed by the recovery of the forest during the twentieth century (Fuller *et al.* 1998). Similar investigations in coastal Massachusetts also reveal that closed canopy forest was maintained until European settlement (Foster & Motzkin 2003). So although the eastern USA supported a diverse suite of large herbivores, it appears that they did not maintain an open landscape in primeval times as predicted by the Vera hypothesis.

The pollen data from temperate America and Europe indicate that human intervention was the only force that has maintained open canopies in forests over the last 10 000 years. Bradshaw *et al.* (2003) argue that fire, rather than herbivores, has been a significant factor in opening forest canopies and while human intervention is often associated with fire, it is not always possible to make this connection.

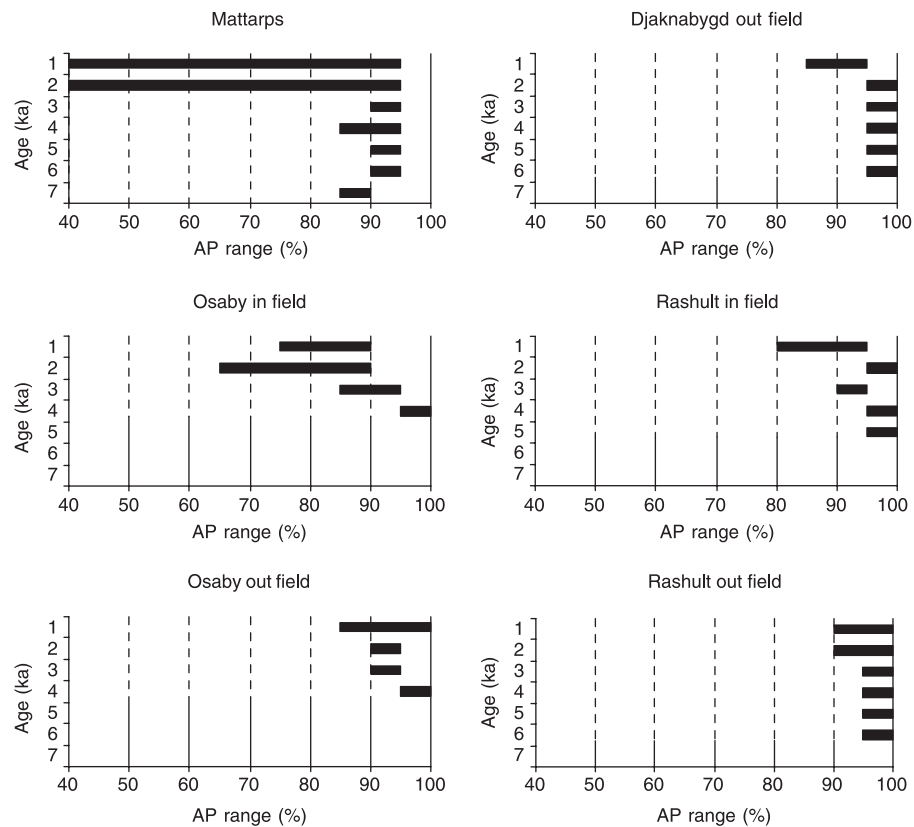


Fig. 5 Arboreal pollen (AP) percentage range over 1000-year intervals from small hollow sites in Southern Sweden. The data sources are Mattarps: Björkman (1996); Djaknabygd, Osaby in field, Rashult in field, Osaby out field, Rashult out field: Lindbladh & Bradshaw (1995).

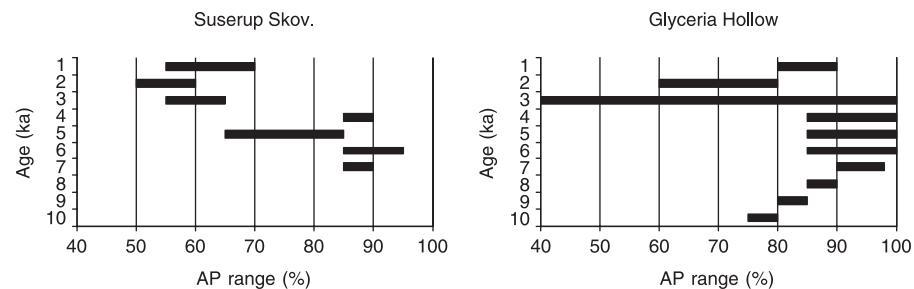


Fig. 6 Mean arboreal pollen (AP) percentage range over 1000-year intervals from small hollow sites in Denmark. The data sources are Glyceria hollow: Andersen (1984); Suserup Skov: Hannon *et al.* (2000).

The role of herbivores in maintaining open landscapes cannot be dismissed before considering two critical issues. The first relates to the ecology of oak and hazel and the second to the adequacy of pollen data in developing and testing this hypothesis. The autecology of *Quercus* and *Corylus* suggests that they can not regenerate under a closed canopy (Vera 2000), which implies that their maintenance must rely on the more traditional models of gap dynamics (e.g. Watt 1947). Nevertheless, more thorough experimental investigations of the ecology and ecophysiology of these taxa are required to test whether light conditions under closed canopy woodland is actually the principal factor restricting their regeneration in woodland today. Rackham (2003) argues that the introduction of American oak mildew may have made contemporary oak seedlings more light-demanding than their primeval ancestors. Both beech (*Fagus*

sylvatica) and lime (*Tilia* spp.) were absent from Irish forests in primeval times and so oak would have filled a wider ecological niche than in lowland central Europe. This may account for some enhancement of the pollen values for Ireland but as Vera's hypothesis considers that oak can not regenerate under its own shade, this difference can not explain the strong overlap of the Irish and European pollen data.

Secondly, this review has focused on pollen data because of their central role in the development of Vera's hypothesis. Contemporary data have been used to validate the implications drawn from fossil pollen data although the data are limited, especially for the open and semi-open habitats which the hypothesis proposes (Gaillard *et al.* 2000). Additional data from these habitats are required for more thorough validation. The availability of small hollow pollen data from the early

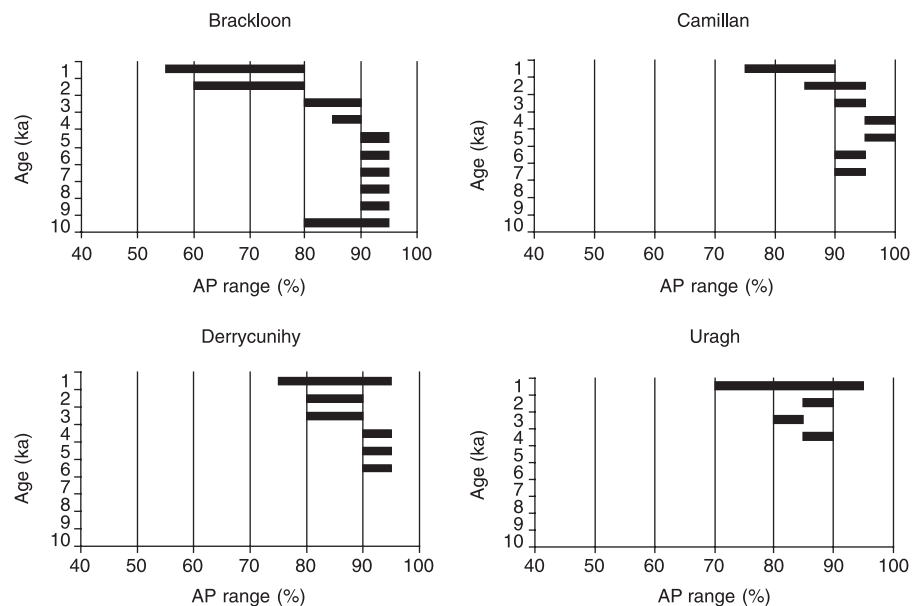


Fig. 7 Mean arboreal pollen (AP) percentage range over 1000-year intervals from small hollow sites in Ireland. The data sources are Brackloon: Little *et al.* (2001); Camillan, Derrycunihy: Mitchell (1988); Uragh: Little *et al.* (1996).

Holocene is also very limited. Bradshaw & Hannon (2004) stress that these sites bias data towards wetter habitats which may have some influence on the conclusions drawn from them. So the consideration of other independent data sources would be very valuable. To this end, the use of habitat specific coleopteran (beetle) remains preserved in small hollow deposits will provide an additional level of validation due to their ability to infer open and closed forest canopy conditions (Whitehouse & Smith 2004). Results of ongoing research in UK and Ireland are awaited. The same is true for molluscan data (Preece *et al.* 1986).

The available pollen data reported here forces the rejection of Vera's hypothesis; despite this, large herbivores (natural and domestic) can have a significant impact on contemporary forest structure and composition (Mitchell & Kirby 1990; Humphrey *et al.* 1998; Vera 2000). The difficulty of quantifying herbivore density has led palaeoecologists to ignore their potential impact in the past, although this is beginning to be redressed (Bradshaw & Mitchell 1999; Bradshaw *et al.* 2003). Two investigations where details on past herbivore densities are available demonstrate that substantial increases in herbivore grazing influenced tree species composition, but the forest canopies were maintained (Mitchell 1990; Mitchell & Cole 1998). Bradshaw & Hannon (2004) argue that natural fires were probably the principal driver of forest canopy openness during the early Holocene. Their review of pollen and macrofossils implies that factors like fire and windthrow created gaps that herbivores maintained but which they could not create.

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