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Research Focus

Mind the gap: how open were European primeval forests?

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There are two competing hypotheses about the structure and dynamics of primeval forests in lowland Europe: the high-forest and the wood-pasture hypotheses, both of which influence current European forest conservation policies. In a recent study using pollen-analytical data from across lowland Europe, Mitchell provides support for rejecting the wood-pasture hypothesis. His study is important for future forest management planning and for showing how hypotheses about large herbivores as biotic factors can be tested using palaeoecological data.

Introduction

The hypothesis that lowland temperate Europe was dominated by high, closed-canopy, mixed-deciduous ‘primeval’ forest before the onset of human impact ~6000 years ago was proposed by vegetation historians over 50 years ago [1–3] based on fossil pollen preserved in peat and lake deposits, and has been widely accepted by forest ecologists and conservationists. This ‘high-forest’ hypothesis [4] was recently challenged by Frans Vera [5], who proposed that, during the early post-glacial, large herbivores (e.g. deer, bison, aurochs and wild horses) had been important in maintaining an open landscape and creating a mosaic of open grassland, regenerating scrub and forested groves; the so-called ‘wood-pasture’ hypothesis [4]. Vera suggested that large herbivores determined and controlled primeval forest structure and composition, which is in contrast to the high-forest hypothesis, which assumes that forest structure influenced herbivore abundance.

There are thus two competing hypotheses about the nature and dynamics of primeval forest in lowland temperate Europe 6000–9500 years ago [4]. Vera’s ideas [5] have attracted much attention among forest conservationists [6,7] because, if his ideas are correct, then forest management policies that are designed to restore or maintain forests close to their presumed natural state of primeval high-forest might not be appropriate. In a recent article, Fraser Mitchell uses pollen-analytical data reflecting two different scales of spatial resolution to test the wood-pasture hypothesis [8]. Both data sets indicate that the hypothesis should be rejected and that open-canopy forest only developed as a result of human activity during the past 3000 years. This rejection casts doubt on the relevance of forest management policies [6,7] that assume the wood-pasture hypothesis.

The competing hypotheses

In the absence of any true virgin forest in the lowland temperate zone of Europe, defined by Vera as being below 700 m altitude and between 45°N and 58°N latitude and 5°W and 25°E longitude [5], the composition and structure of primeval forests have been inferred from existing old stands that are thought to have received minimal human impact [9,10] and from pollen-analytical studies [2,3]. The high-forest hypothesis, championed by Iversen [3], proposed that lowland Europe was dominated by closed-canopy deciduous forests of lime *Tilia cordata*, elm *Ulmus* spp. and oak *Quercus* spp., with an understorey of hazel *Corylus avellana*, ash *Fraxinus excelsior*, and a range of shrubs [11].

Vera proposed that the abundance of oak and hazel pollen in peat and lake deposits implies that the primeval forests must have been relatively open to enable oak and hazel regeneration because both require canopy gaps to regenerate [5]. This openness was, according to Vera, a result of large herbivores creating and maintaining a dynamic landscape-mosaic of closed-canopy woodland groves, open parkland, and regenerating scrub. Herbivore grazing and browsing in woodland areas would prevent tree regeneration so that, over time, the canopy opens and the stand degenerates into parkland. Scrub growth in the parkland provides ‘safe sites’ and protection for tree seedlings and saplings that would eventually develop into new forested groves.

This wood-pasture hypothesis is analogous in many ways to Watt’s classic ‘gap-phase’ model [12] for regeneration in the high-forest hypothesis. The main difference between the two hypotheses, other than spatial scale, is that, in the wood-pasture hypothesis, large herbivores create gaps and thus determine forest structure, whereas in the high-forest hypothesis, forest gaps and structure are created by wind-throw, tree death and other disturbances, rather than by large herbivores [8].

Testing the competing hypotheses

The ideal test of the wood-pasture hypothesis would be a long-term grazing exclusion experiment conducted 6500–9500 years ago so that one can compare forest composition, or at least fossil pollen assemblages, in areas with and without large herbivores. Because of its insular nature, Ireland only supported wild boar and possibly

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some red deer populations during the early post-glacial [8] and is thus a natural early post-glacial grazing exclosure [8]. Mitchell compared pollen-analytical data for oak and hazel from 21 lakes or bogs in England and the lowland European continent for the period 6500–9500 years ago with data for the same period from 15 sites in Ireland. Using multivariate data analysis with redundancy analysis and associated permutation tests [13], Mitchell showed that there are no statistical differences between oak and hazel pollen values from mainland Europe or Ireland. These results suggest that the presence or absence of large herbivores thus had little impact on the relative abundances of oak and hazel pollen during the early post-glacial in temperate lowland Europe and that large herbivores were not therefore essential for the maintenance of oak and hazel in primeval forests [8].

However, the pollen assemblages used in this comparison are from lakes and bogs and are derived from a pollen-source area with a radius of tens of kilometres [14]. Many different vegetation types and mosaics can occur within such an area and it is therefore difficult to reconstruct the degree of landscape openness from such pollen data [15,16].

Pollen data from small (20–30 m diameter) hollows within forests derive most of their pollen from a more-restricted pollen-source area, with a radius of 50–100 m [14,16]. Such data provide a record of forest composition at the local stand scale [16]. A crucial question in interpreting such data is what percentage of tree pollen reflects local presence or absence of a closed-forest canopy around the hollow. Mitchell assembled modern pollen data from small hollows throughout lowland Europe and showed that hollows within a closed canopy always contain at least 60% tree pollen [8]. By contrast, hollows in open areas have tree pollen values of 50% or less. Mitchell thus calibrated modern tree pollen values in relation to the local presence or absence of a closed canopy [8]. He then applied this calibration to fossil pollen assemblages from six small hollows in southern Sweden, two in Denmark, and four in Ireland. At all sites, tree pollen values show the presence of closed-canopy forest throughout the early and mid post-glacial (i.e. they contained at least 60% tree pollen). Tree pollen values only drop below the critical 60% level during the past 3000 years, coincident with human impact [8]. Mitchell concludes that there is no indication of open-forest canopies at a local scale at any of these sites before human impact, irrespective of the presence or absence of large herbivores.

Pollen data reflecting two different spatial scales (regional and local) thus provide no support for the wood-pasture hypothesis in lowland temperate Europe [8]. Pollen data from northeast USA [8] similarly suggest that, in spite of a rich assemblage of large herbivores, the landscape there also supported high forest before European settlement and that there was no open mosaic as predicted from Vera's wood-pasture hypothesis [5].

Implications for forest management policies

Vera [5] stimulated much debate about the composition, structure, and dynamics of European primeval forest that resulted in management policies emphasizing parklands, wood pasture, ancient trees, and possible re-introduction of large herbivores [6,7,17]. For example, English Nature (http://www.english-nature.org.uk/ [17]) recently conducted a major study into future reserve management involving large herbivores. The absence of any crucial pollen–analytical evidence [8,18] to support the idea of open-canopy primeval forest as envisaged by Vera [5] has important implications for forest management policies that assume the wood-pasture hypothesis is appropriate and valid for natural European lowland forests. Mitchell's study [8] casts serious doubts on the relevance of the wood-pasture model in the primeval landscape of lowland temperate Europe and hence on management policies based on this model.

Future challenges

Overall, available pollen-analytical data from lowland temperate Europe and northeast USA reject the wood-pasture hypothesis [8]. There are, of course, unresolved problems and further research needs. First, palaeoecologists by necessity have to assume that 'the present is the key to the past' [19] in interpreting their data and, thus, they assume that ecological tolerances of species have not changed through time. Rackham [20] cautions that the introduction of American mildew might have resulted in oak seedlings today having a greater light demand than in earlier times. Second, lime was absent from Irish post-glacial forests but was abundant over much of lowland temperate Europe [3,11]. It is therefore likely that oak had a wider realized niche in Ireland than in central Europe. The presence or absence of lime is thus a complicating factor in interpreting the results of the 'natural' herbivore-exclusion experiment [8]. Third, pollen-analytical data inevitably give a biased picture of past forest composition because of differential pollen production and dispersal [14,16] and because most sites with preservable pollen are in damp habitats [8,18]. Fourth, other palaeoecological data (e.g. fossil beetles, dung fungal spores, oribatid mites and pollen of rare indicator taxa) might provide independent assessments of the extent of canopy cover and of animal abundance. They remain to be explored [8].

The rejection of Vera's wood-pasture hypothesis does not mean that large herbivores are not important in influencing forest composition today [21] or in the past [8]. Quaternary palaeoecologists have, however, largely ignored the potential impact of large herbivores in vegetation dynamics because of the problems of quantifying their past densities [4,8]. Increasing attention is being paid to the possible role that herbivores had as 'biotic drivers' in vegetation history and dynamics in, for example, the Great Plains of North America [22], the transition from arid steppe to moist tundra in Alaska and Siberia [23], and the maintenance of late-glacial grasslands in Ireland by giant Irish deer [24]. Ecological systems are a result of complex interactions among plants, animals and their environment and terrestrial palaeoecologists are only now beginning to consider the potential role of animals as biotic drivers. Testing of hypotheses about the roles of herbivores in past vegetation dynamics requires new conceptual and methodological approaches [22]; Mitchell's study [8] is exciting, important, and novel because it illustrates how palaeoecologists can test specific ecological hypotheses about the potential role of large herbivores as biotic drivers using palaeoecological data. It should also encourage caution among conservationists [6] about forest management policies based on the wood-pasture hypothesis as it provides convincing evidence for primeval forests having closed canopies and for rejecting the hypothesis of wood-pasture and large gaps in European primeval forests.

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