Hemisphere; the impact of this shortcoming on the reconstruction has not been assessed. Only rudimentary spatial averaging was applied, considering neither the spatial representativeness of each proxy nor the difference in the quality of the records as temperature proxies. But these shortcomings do not compromise the main conclusions, and can be addressed in future work.

The results reveal substantially more variance at the century scale, and an amplitude of change equal to about 1 K (about the same as the borehole reconstructions[4], and double the estimate based principally on tree rings[5]). Moberg and colleagues' reconstruction is consistent with results published earlier this year[6] suggesting that tree-ring and other proxies produced with regression-based calibration methods commonly underestimate the amplitude of change.

What have we learned from the palaeo record of the past 2,000 years? Most tree-ring and high-resolution multi-proxy reconstructions show that Northern Hemisphere mean temperatures have varied about 0.5 K over the past millennium (temperatures were 0.5 K colder during the Little Ice Age relative to the 1961–90 mean). In contrast, reconstructions using boreholes[4], and recent modelling analyses[6], reveal a larger amplitude, close to 1.0 K. The results from Moberg *et al.* support the larger amplitude; even without the elegant mathematics, direct inspection of their compilation of low-frequency records indicates that the temperature change was about 1 K in many places.

Are the different proxies equally trustworthy and problem-free? Probably not. But the authors have taken a fruitful approach by attempting to combine information from different proxies in a way that uses the unbiased climate information found in each of them. Is it appropriate to consider change averaged over entire hemispheres? The emphasis of many palaeoclimatologists is shifting instead towards the identification of regional patterns of change. Many of the studies incorporated by Moberg *et al.* had that purpose — for example, even though the global climate system is interconnected, the tropical monsoon regions may have undergone different changes from those experienced by the high Arctic or the west Pacific.

The approach pioneered by Moberg *et al.* will serve equally well as a strategy to evaluate past climate change in each of these regions by combining information from different proxies. Indeed, the challenge for palaeoclimate researchers — and their funding agencies — is to produce multi-proxy reconstructions at the appropriate regional scale so that all of the voices can be heard. ■

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1. Moberg, A., Sonechkin, D. M., Holmgren, K., Datsenko, N. M. & Karlén, W. *Nature* **433,** 613–617 (2005).
2. Torrence, C. & Compo, G. P. *Bull. Am. Meteorol. Soc.* **79,** 61–78 (1998).
3. Cook, E. R., Briffa, K. R., Meko, D. M., Graybill, D. A. & Funkhouser, G. *Holocene* **5,** 229–237 (1995).
4. Pollack, H. N. & Smerdon, J. E. *J. Geophys. Res.* **109,** doi:10.1029/2003JD004163 (2004).
5. Mann, M. E. & Jones, P. D. *Geophys. Res. Lett.* **30,** doi:10.1029/2003GL017814 (2003).
6. Von Storch, H. *et al. Science* **306,** 679–682 (2004).

Palaeoecology

Down to the woods yesterday

Peter D. Moore

What were European forests like following the last ice age and before the advent of agriculture? The pollen record in Ireland provides a unique perspective from which to examine ideas on the question.

The past may be a foreign country, and a pretty inaccessible one at that. But it does not deter people from exploring it. One of the objects of conservation is to retain or recreate primeval habitats, but this can only be achieved with sound knowledge of the structure and composition of past ecosystems, and the factors that sustained them.

Temperate deciduous forests (Fig. 1) are an example of such a habitat, and palaeoecologists are constantly probing the mists of time to answer some difficult questions — just how dense was the canopy of forests before the advent of agriculture, and what part did large grazing animals play in maintaining clearings and open conditions? This is a controversy that is of more than academic interest, and the latest foray, published by Fraser Mitchell in the *Journal of Ecology*[1], seeks to assure us that the forests were dense and that big grazers played a limited role in woodland dynamics.

The technique of pollen analysis, developed in the early twentieth century, revealed a progressive invasion of forest over western Europe[2]. In the mid-Holocene, between 8,500 and 5,500 radiocarbon years ago (BP), trees dominated the rain of pollen that fell on the lakes and bogs, where the pollen became preserved in stratified layers. Analysts interpreted this abundance of tree pollen as indicative of closed-canopy forest that had re-established itself following the last glacial retreat and then covered most of the landscape.

There were some puzzling features, however, such as the presence of 'non-arboreal pollen', the pollen of herbaceous plants, especially grasses and sedges, that persisted through the supposed closed-forest period. These open-habitat indicators became much more abundant as agricultural activities took hold and early farmers began to clear the forests around 5,500 BP. But the bogs and lakes where the pollen accumulated had their own local vegetation that included herbaceous plants, so their presence in the pollen record of the 'closed-forest' period was not regarded as surprising.

However, there are two additional aspects

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Figure 1 **Tree story in Europe. Pollen grains preserved in ancient lake sediments show that even before the advent of agriculture there were gaps in the forest. But were large grazing mammals responsible?**

to the data that require attention: how is it that species of oak maintain their populations in closed forest when their seedlings require light? And why is so much hazel pollen present when this understorey shrub flowers abundantly only in well-lit conditions? An alternative interpretation of the data was put forward by Vera[3], who speculated that the mid-Holocene forest of western Europe was actually an open parkland, maintained in that condition by intensive grazing and browsing by large herbivorous mammals.

There is abundant archaeological evidence for the presence of many such herbivores in the European forests. Species of deer, elk (moose) and wild boar are still relatively common in many forest regions of Europe, and their impact on vegetation is often very apparent. In the mid-Holocene there were other large grazers present, such as wild horse, aurochs, species of bison, and beaver. But the experimental testing of any hypothesis relating to their role in forest dynamics is a problem, partly because we have no knowledge of their former abundance and density, and partly because their impact would probably have taken many centuries to be fully felt. Grazing experiments in the Netherlands served to encourage Vera in his views, but have not proved universally convincing. What is needed is a controlled experiment based on past conditions and operating over very long timescales. For this, one has to return to palaeoecology.

Mitchell[1] has come up with the proposal that the island of Ireland is a ready-made continental-scale grazing 'exclosure' experiment. Isolated from the British and continental mainland by rising sea-levels early in the Holocene, its vegetation has developed in the absence of many of the large grazers found farther east in Europe. Wild boar have been present, and red deer have been recorded from 4,000 BP onwards, although their early history in Ireland is unclear and they may well have been totally absent. All of the other large mammalian grazers were absent from Ireland throughout the Holocene.

The task facing Mitchell, therefore, was to compare forest development as documented by the pollen record in Ireland with that of continental Europe. To avoid the problems of local herb communities associated with lakes and bogs, he chose to study small, hollow sites in forests for his pollen data. These have the advantage that pollen arrives at them from a very restricted radius — a maximum of around 100 m (ref. 4) — so they provide a relatively uncontaminated record of local forest history. From the European Pollen Database, Mitchell selected 21 appropriate sites from Britain and continental Europe, and a further 15 from Ireland, and analysed them by multivariate statistical methods. He found no significant difference between forest development on the continent, where large herbivores were active, and that in Ireland, where large grazers were virtually absent.

The approach is innovative in methodological terms, showing that the past is accessible for experimental analysis. But the outcome is also of great significance for forest managers and conservationists. Vera's proposals have raised questions about the appropriate target for forest management — should we be aiming for closed-canopy forest, or for open parkland (wood pasture) maintained by high densities of grazing stock? By rejecting Vera's hypothesis, Mitchell will bring those foresters deflected by the grazing proposal back to the closed-canopy model.

But not all questions have been answered. How does oak regenerate and hazel flower so abundantly in closed forest? Wind blow, fire, flood and tree death may well be sufficient to account for occasional open clearings of birch and hazel beneath which the young oak grew. After all, one surviving oak sapling per century per adult tree would be enough to ensure regeneration, and even the wild pigs are sure to miss one. ■

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1. Mitchell, F. J. G. *J. Ecol.* **93,** 168–177 (2005).
2. Godwin, H. *History of the British Flora* (Cambridge Univ. Press, 1956).
3. Vera, F. W. M. *Grazing Ecology and Forest History* (CABI, Wallingford, 2000).
4. Sugita, S. *J. Ecol.* **82,** 881–897 (1994).

Synthetic chemistry

Making a natural fuel cell

Marcetta York Darensbourg

The synthetic assembly of the active centre of hydrogen-producing enzymes adds to our understanding of their structure and function — and could produce new and useful materials that mimic these enzymes.

A host of microbes metabolize hydrogen with high efficiency by using enzymes known as hydrogenases[1]. These enzymes are exquisite miniature hydrogen fuel cells, and are based on a combination of sulphur and iron atoms, and sometimes a single nickel atom[2]. On page 610 of this issue, Tard *et al.* (Pickett and colleagues)[3] demonstrate that a close analogue of the active site of all-iron hydrogenase can be synthesized in the laboratory, and that it can produce hydrogen in an electrochemical cell, given a supply of protons and electrons.

Preparation of an artificial analogue of the enigmatic H-cluster (the hydrogen-producing active centre of all-iron hydrogenase) has been a long-standing challenge for inorganic synthetic chemists. The problem is to reproduce the unusual spectroscopic signals that emanate from the 'black box' that is the unknown arrangement of the six iron atoms in the active centre. Early approaches made use of self-assembly reactions, which typically led to 4Fe4S cube structures, but sometimes resulted in larger, cage-like clusters[4,5]. Although such expanded clusters may reasonably be expected to occur in nature, their spectroscopic signatures were not consistent with the active site of all-iron hydrogenase.

Some five years ago, protein crystallographers elucidated the structure of the functional centre of all-iron hydrogenase[6,7]. The H-cluster is actually composed of two subsites: a normal cube-shaped 4Fe4S cluster is bridged by a sulphur atom from cysteine — an amino acid forming part of a surrounding protein — to a second unit containing two iron atoms surrounded by ligands such as carbon monoxide and cyanide (Fig. 1a, overleaf). With this blueprint to hand, the challenge for chemists was to develop a synthesis method that maintains the integrity of the 4Fe4S and Fe–Fe precursors, and prevents them from rearranging into 6Fe6S expanded clusters.

The Fe–Fe organometallic portion of the H-cluster is a familiar one in chemistry. It can be modelled by a molecule that forms from iron and sulphur in the presence of carbon monoxide — $(\mu\text{-}S_2)Fe_2(CO)_6$, where μ denotes the bridging function of the sulphur atoms. This is a molecule of primordial origin, probably present in the reducing and harsh conditions of the ancient Earth, and also found today in oceanic thermal vents[8]. This compound acts as a template for condensation reactions involving small molecules, a process that possibly presaged the formation of biomolecules[9].

Pickett and colleagues[3] have developed a synthesis approach, in which an Fe–Fe organometallic unit is linked to a 4Fe4S cluster, by making use of sulphur-containing functional groups on independent subunits. These react and eliminate a small thioester molecule (Fig. 1b). As the synthetic precursor for the 4Fe4S cluster has four additional reactive sulphur-containing moieties, which are matched in nature by sulphur atoms in a protein's cysteine amino acids, it was necessary to isolate a single reaction site — hence the adoption of a large bowl-like, or cavitand, ligand[4,5]. This ligand contains three