

Conclusion

While this comment is not intended to be comprehensive, it introduces some of the extreme temporal and spatial variability inherent in the pollen record and draws additional forest taxa into the discussion. To attempt a synthesis of European forest dynamics using data from only one site and ignoring contributions from other taxa results in a biased interpretation of events. The contention that 'beech forest became more frequent in many landscapes' as a result of farming is unacceptable when the slow expansion and establishment time and the juvenile growth characteristics of this taxon are considered. The presence of beech in Europe during the transition to agriculture is more reliant on the rate of expansion from refugia than anthropogenic disturbance and would occur without the presence of humans, as it did in the last interglacial. Early human impacts upon beech forests have the effect of thinning the canopy, creating gaps for light-demanding taxa. Where human activity influences a non-beech forest, fast-growing light-demanding taxa (e.g., hornbeam) are again favoured until beech arrives. A mixed assemblage of beech and hornbeam then persists until large-scale landscape clearance.

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Prehistoric farming and the postglacial expansion of beech and hornbeam: a reply to Gardner and Willis

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Abstract: It is argued that the views put forward by Gardner and Willis are compatible with the opinions expressed in Küster (1997) if consideration is given to the distinctive aspects of the expansion of tree species in Central Europe and the different ecological conditions elsewhere.

Key words: Beech, *Fagus sylvatica*, hornbeam, *Carpinus betulus*, hazel, *Corylus avellana*, prehistoric agriculture, anthropogenic impacts, Slovenia, Hungary.

Competition processes between plant species, successions, spreading processes and so on are influenced by different parameters in different areas. Therefore the arguments by Gardner and Willis are not in contradiction to my opinions.

In the German palaeoecological tradition the spread of beech was often regarded as an effect of climatic deterioration, not as an effect of climatic change (whatever this might be!). This opinion was influenced by the zonation of oak and beech woodlands in German hilly landscapes: oak woodlands occur in the lower, beech woodlands in the higher (and therefore cooler) areas. This zonation does not occur in other parts of Europe such as the British Isles and Hungary; it can be shown by this example that the ecological conditions are different in different parts of Europe. In my article, I had to refer to the German scientific tradition, because I wrote on processes in this region; I had to refuse the opinion of the relation between climatic deterioration and beech expansion. Both processes cannot be linked because they cannot be observed in other parts of Europe.

I clearly wrote that the special processes of prehistoric farming favoured the spread of beech only in Central Europe. Central Europe is a poorly defined area; from Figure 2 of my paper the area can be seen in which the spread of beech was influenced by prehistoric farming. I did not write about the spread of beech in Hungary, and it is also mentioned that the spread of beech was not influenced by farming in the region of the eastern Alps which includes parts of Slovenia; in Figure 2 the shaded circles show that there is evidence from this region that the beech spread was not affected by human activity.

In all areas the relation between plant species is influenced by different autecological and synecological conditions. Certainly climatic, edaphic and other conditions were different in Hungary, in the Alps, in German hilly landscapes and on the British Isles, and in all these regions different species of trees competed against one another. For instance, such species as *Fraxinus ornus* and *Ostrya carpinifolia* invaded only areas south of the Alps. Therefore the conditions for a spread of beech were different in different areas, and it is not possible to compare these conditions without being aware that the ecological conditions differ from region to region!

It is possible that beech would have been able to invade regions between the Alps and the North and Baltic Sea coasts without human interference. However, in the pollen diagrams from this area the beech can always be seen to spread very slowly; in many cases the spread of beech took some millennia, as the example of the Görbelmoos pollen diagram demonstrates. I have not taken the view that it is necessary also to publish other pollen diagrams where the results are the same. It is also very striking that beech expansion in the region between the Alps and southern Scandinavia only took place between 6000 and 1500 BP. In this period, prehistoric settlement strategies were practised. Settlements were founded and abandoned after some decades, so that secondary successions of woodlands could take place. In the Roman period, when settlements were more permanent, secondary successions did not occur. It is very striking to observe in the pollen diagrams that beech did not expand to any part of Europe in this period. Instead of this, beech became less frequent in many areas (which, incidentally, can also be seen in the Görbelmoos diagram; Figure 1) and

expanded again at a later stage, when secondary successions of woodlands also recurred or occurred.

In an oak woodland without beech many oak seeds are available but no (or very few) beech seeds, so that an expansion of beech to an oak area is very difficult. Why does beech not expand in English oak woodlands? After clearing an oak woodland and after a settlement phase, in the course of a secondary succession of woodland, fewer oak seeds are available, but, in relation to this, the frequency of beech seeds is greater. Beech seeds might also have been introduced by wild animals to the area where the secondary succession took place. Where oaks and beech coexist, beech is often the fitter, on account of its faster growth in the juvenile phase and of the shade cast by its canopy. These points, made by Gardner and Willis, are all clear; but the precondition for all these processes is that beech seeds are available, which is hardly the case in pure oak woodlands.

It was not only the spread of beech that was favoured by the occurrence of clearings and secondary woodland successions; the spread of hornbeam and spruce in other parts of Central Europe was also affected, as mentioned in my paper. This demonstrates that the spreading processes of tree taxa in Europe were influenced by many parameters; in different regions different parameters predominated. In some areas the spread of hornbeam was favoured by the occurrences of secondary woodland successions, in other areas this species could only expand under the influence of permanent human activities. In Poland and Hungary hornbeam expanded earlier and became much more frequent than farther to the west; in the German hilly landscapes it only expanded after sustained woodland management with coppicing was in place. It was only then that the selective advantage fell to hornbeam rather than beech.

Prehistoric settlement strategies were not perhaps the only parameters which favoured the spread of beech in the region between the Alps and southern Scandinavia, but I cannot see any argument against the view that it was favoured by human activities (which in this period also included human passivities, which were the real reasons for the secondary successions of woodlands).

The comment upon my paper by Gardner and Willis emphasizes that the spread of beech was influenced by very many different parameters. In some regions the influence of climate was perhaps predominant, in other regions the development of soils. But in the region between the Alps and southern Scandinavia (which I referred to as central Europe) the occurrences of secondary woodland successions after farming phases were a very important, if not the most important, parameter which favoured the spread of beech. This can clearly be seen in the pollen diagrams (and certainly not only in the diagram from the Görbelmoos). Perhaps it would be a good idea to bring the different opinions together to write a common paper on the different processes which might have influenced the spread of beech and other tree taxa. This would improve our knowledge of woodland ecology and clearly reject monocausal explanations for species migrations as an effect of climatic change.

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