



Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*)

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ABSTRACT

Aim Establishing possible relationships between the magnitudes of the glacial distribution of the European beech, *Fagus sylvatica* L., and its post-glacial spread.

Location Europe.

Methods A database of over 400 pollen records has been used to locate *Fagus* populations at the end of the last glacial and during the post-glacial in Europe and to assess the areal extent of their past distribution.

Results The rate of late-glacial and post-glacial increase in the number of pollen sites where *Fagus* was locally present conforms well to a logistic model of population growth. This suggests that the area occupied by beech populations expanded exponentially from the glacial refugia for a duration of over 10,000 years, until about 3500 yr BP. In the past three millennia beech populations increased at a slower rate, tending towards an equilibrium value.

Main conclusions The conformity of the increase in beech distribution to the classical logistic model of population growth indicates that: (1) a multiplicative biological process was the main factor shaping the pattern of the post-glacial expansion of *F. sylvatica* in Europe, (2) climate conditions, human activity and competition may have influenced its rate of spread, and (3) beech populations did not expand with a moving closed front, but with a diffuse spread from scattered nuclei. The distribution of *Fagus* in Europe at the end of the last glacial appears to have been of two orders of magnitude less extensive than at present. Pleistocene refugia were likely to have been a mosaic of sparse stands of small populations scattered in multiple regions. *Fagus* populations appear to have increased very slowly and to a moderate extent in southern Europe, where they are now declining slightly. The central European populations increased quickly and extensively, reaching northern Europe, and are now approaching their carrying capacity.

Keywords

Europe, *Fagus sylvatica*, late-glacial, logistic model, pollen data, population expansion, post-glacial.

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INTRODUCTION

Detecting the number and location of the last glacial refugia for temperate forests in Europe, and assessing directions and rates of post-glacial spread, have been the subject of a large number of palaeoecological investigations. However, the areal extent of the glacial distribution of tree populations and the order of magnitude of their post-glacial increase have yet to be

quantified satisfactorily. Filling this gap in knowledge would be especially relevant to reconstructions of past vegetation distribution and biomass changes and in contributing to wilderness conservation and ecosystem management.

The aim of this paper is to estimate the surface area covered by the glacial refugia of the European beech, *Fagus sylvatica* L., and to establish possible relationships between the magnitudes of its glacial distribution and its post-glacial spread. Among

forest trees, *F. sylvatica* is one of the most thoroughly investigated because of its wide distribution and great economic importance, so that a wealth of ecological, palaeo-ecological and genetic data are now available in the literature, and can be used to assess variations in its past abundance.

Modern distribution of *Fagus sylvatica*

Fagus sylvatica is a monoecious late-successional forest tree. It has a life span of about 300 years, and reproduces very late (40–50 years old); its seed production is characterized by irregular mast years (Ellenberg, 1996). Presently characterized by an extensive geographical distribution in Europe, it is found longitudinally from the Cantabrian Mountains in the west to the Carpathians and Balkan Mountains in the east, and latitudinally from Sicily in the south to southern Sweden and Norway in the north (Fig. 1). In central Europe, beech would be present nearly everywhere in anthropogenically undisturbed environments, as it can occupy a wide range of habitats with different soil types (Ellenberg, 1996; Peters, 1997). A long history of human impact has certainly influenced its distribution through forest clearance and, more recently, through plantations. However, there are areas in Europe where beech is absent as a native tree, such as the Po valley and the Hungarian plain. *Fagus* needs a growing season of at least 140 days, and for this reason it cannot survive too far north in Scandinavia (Peters, 1997). Moreover, due to its requirements for a humid climate during the summer period, it cannot survive in southern Spain, southern Greece and in the most arid areas of southern and central Italy. In the northern part of its range, beech occurs in low elevations down to sea level. In the southern part of its range it occurs at elevations of up to 2000 m a.s.l.

State of knowledge concerning the post-glacial history of beech in Europe

A large number of palaeoecological studies on the post-glacial history of beech in Europe have been published in the past 25 years. Two species of the genus *Fagus* are presently found in Europe (*Fagus sylvatica* L. and *Fagus orientalis* Lipsky), showing separate ranges that help to distinguish their respective histories, although their pollen morphologies are indistinguishable.

Regional reviews of the post-glacial spread of *F. sylvatica* include reconstructions by Birks (1989) for the British Isles; Björkman (1997) for south-western Sweden; Bradshaw & Lindblad (2005) for southern Scandinavia; Ralska-Jasiewiczowa (1983) and Latałowa *et al.* (2004) for Poland; Ralska-Jasiewiczowa *et al.* (2003) for the northern lowlands of central Europe; Rybníčková & Rybníček (1988) for the former Czechoslovakia; de Beaulieu *et al.* (1994) for the French Alps and the Jura; van der Knaap *et al.* (2005) for the Alps; Schneider (1978) for the southern border of the Alps; Magri (1998) for the Italian peninsula; Ramil-Rego *et al.* (2000) for the north-west Iberian peninsula; Filipova-Marinova (1995) for Bulgaria.

At the European scale, reconstructions of the location of the glacial refugia for beech and its post-glacial colonization routes have been presented by Huntley & Birks (1983), Huntley (1988), Lang (1992, 1994), Gliemerth (1995), Pott (1997, 2000), Brewer (2002) and Bradshaw (2004). Recently, three extensive papers have been published on the Holocene expansion of beech. (1) A detailed discussion on whether the main causes for the Holocene expansion of beech in central Europe were climatic change, migrational lag, delay in population increase, human disturbance or fire disturbance

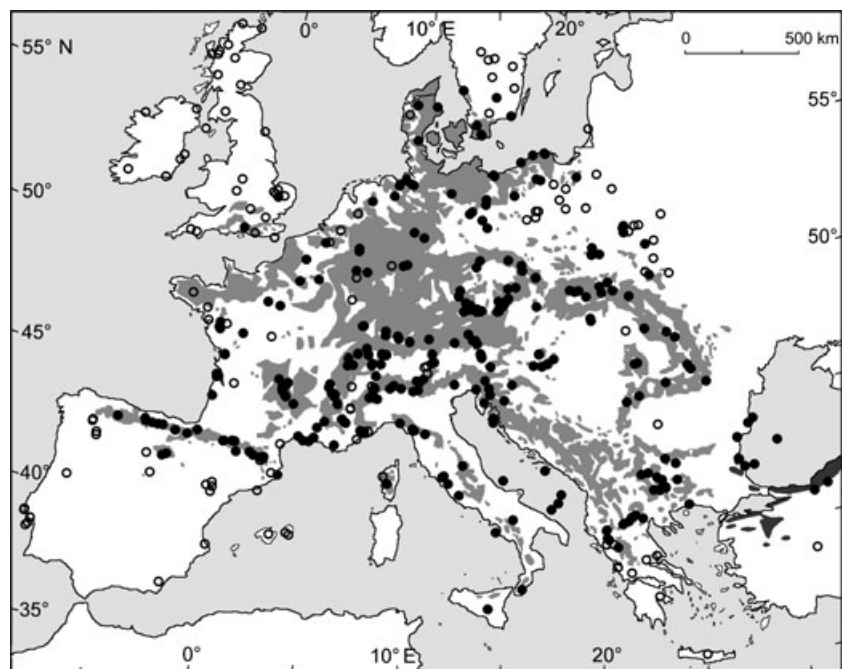


Figure 1 Modern distribution of *Fagus sylvatica* (light grey; after Pott, 1997) and *Fagus orientalis* (dark grey, redrawn from Atalay, 1994) and location of pollen sites with *Fagus* >2% (●) and <2% or absent (○) (after Magri *et al.*, 2006).

reaches the conclusion that rapid population expansions occurred as a response to climatic change (Tinner & Lotter, 2006). (2) A combination of palaeobotanical and genetic data, aimed at evaluating the genetic consequences of long-term survival in refuge areas and the post-glacial spread, indicates that the Mediterranean peninsulas were not the main source for beech in central and northern Europe (Magri *et al.*, 2006). (3) Simulations of beech distributions in relation to modelled patterns of climate parameters concluded that no single driving force can account for the distribution of beech 6000 years ago, although climatic factors are the likely major determinants of its potential range (Giesecke *et al.*, 2007).

In this paper, a new aspect of the history of beech is considered. Special consideration is given here to the patterns and timing of increase of *Fagus* populations and to a quantitative assessment of the surface areas occupied by beech since the late-glacial in Europe.

POST-GLACIAL SPREAD OF *F. SYLVATICA* IN EUROPE

Pollen data

The present paper makes use of the data set of 408 pollen sites (Fig. 1) listed by Magri *et al.* (2006). They have partly been extracted from the European Pollen Database and checked thoroughly with respect to the chronology and some other potential sources of error (223 sites), and partly been obtained from the published literature (185 sites). The chronologies of the records are mostly based on radiocarbon dates and on interpolations between dates. Even so, the records generally lack chronological detail, so that data for European beech could not be analysed reliably at a time-resolution of less than 1000 radiocarbon years. The pollen sites are distributed over most of Europe, although in some regions (e.g. Serbia, Croatia, central Germany and central France) there is only very sparse information (Fig. 1). Based on these data, Magri *et al.* (2006) produced a set of maps, showing the distribution of sites with at least 2% pollen of beech in different time windows (Fig. 2). The choice of a 2% threshold is a subjective one, based on the observation that the geographical distribution of the sites with at least 2% beech pollen roughly corresponds, at a European scale, with the modern distribution of beech (Fig. 1). On the other hand, this minimum value does not detect sparse tree stands in an area, as shown by Björkman (1996) for *F. sylvatica* in southern Sweden and Bennett (1985) for *F. grandifolia* in North America, who interpret low but continuous frequencies in pollen records as an indication of the local presence of the species. For this reason, Birks (1989) suggested using the empirical limit, which is the point at which pollen of the taxon becomes consistently present in consecutive samples, to define the earliest local presence of a taxon. However, the accuracy of pollen analysis may significantly affect the empirical limit. Considering that no single choice (continuous

frequencies, threshold or empirical limit) is entirely satisfactory, for the purpose of the present paper the standard rule of a 2% threshold has been chosen as a conservative, but robust criterion for the presence of beech in the local vegetation, although it does not indicate the time of the beginning of its spread, which may have occurred much earlier. In several cases, macrofossils of *Fagus* are found in regions where the pollen record is lower than 2% and discontinuous, suggesting that small populations of beech were unable to increase their role in forest communities for thousands of years (Magri *et al.*, 2006).

Late-glacial and post-glacial spread of *F. sylvatica*

The late-glacial and post-glacial spread of *Fagus*, described in detail by Magri *et al.* (2006) and represented in Fig. 2, can be described as follows:

- 13–10 kyr ¹⁴C BP (15.4–11.5 cal. yr BP). Beech was present only at a few sites: a number of macrofossils have been found on the Cantabrian mountains, the Pyrenees, and in Croatia–Slovenia, a few pollen records in southern Italy and southern France.
- 10–9 kyr ¹⁴C BP (11.5–10.2 cal. yr BP). *Fagus* rapidly expanded in southern and central Italy, and in the eastern Alps–Istria–west Hungary.
- 9–8 kyr ¹⁴C BP (10.2–8.9 cal. yr BP). *Fagus* was well established in southern and central Italy. For the first time it attained the 2% value in western Bulgaria. In central Europe, beech was already present in south Moravia and south Bohemia. Fossil wood is found near Lake Constance.
- 8–7 kyr ¹⁴C BP (8.9–7.9 cal. yr BP). Beech reached 2% along the Dalmatian coast. There is clear pollen evidence for beech in the French Alps, at two sites located more than 500 km apart from the other pollen sites with beech, which is still missing in the western Italian Alps and northern Apennines.
- 7–6 kyr ¹⁴C BP (7.9–6.8 cal. yr BP). A very rapid expansion occurred in the outer alpine arch. In Romania, on the Apuseni Mountains, *Fagus* reached 2% at one site. At that time no site on the Carpathians had yet reached the 2% value, while the Bulgarian sites had only sparse records with very low values.
- 6–5 kyr ¹⁴C BP (6.8–5.7 cal. yr BP). A rapid expansion of beech occurred along the inner alpine chain in northern Italy. The northern Apennines were colonized from the central Italian populations. A second pattern of rapid expansion of beech is found from Bohemia and Moravia towards the western border of the central Bohemian basin and towards the western Carpathians, respectively. Beech diffused into the Vosges and the French Massif Central.
- 5–4 kyr ¹⁴C BP (5.7–4.5 cal. yr BP). *Fagus* expanded very rapidly in central Europe, especially in central Germany. Fossil wood in Denmark indicates that beech was moving northward very rapidly. At the same time, there was a rapid migration eastwards along the Carpathian Mountains. In the Balkan peninsula, beech has been found at many sites. However, these Balkan populations are still completely separated from those in

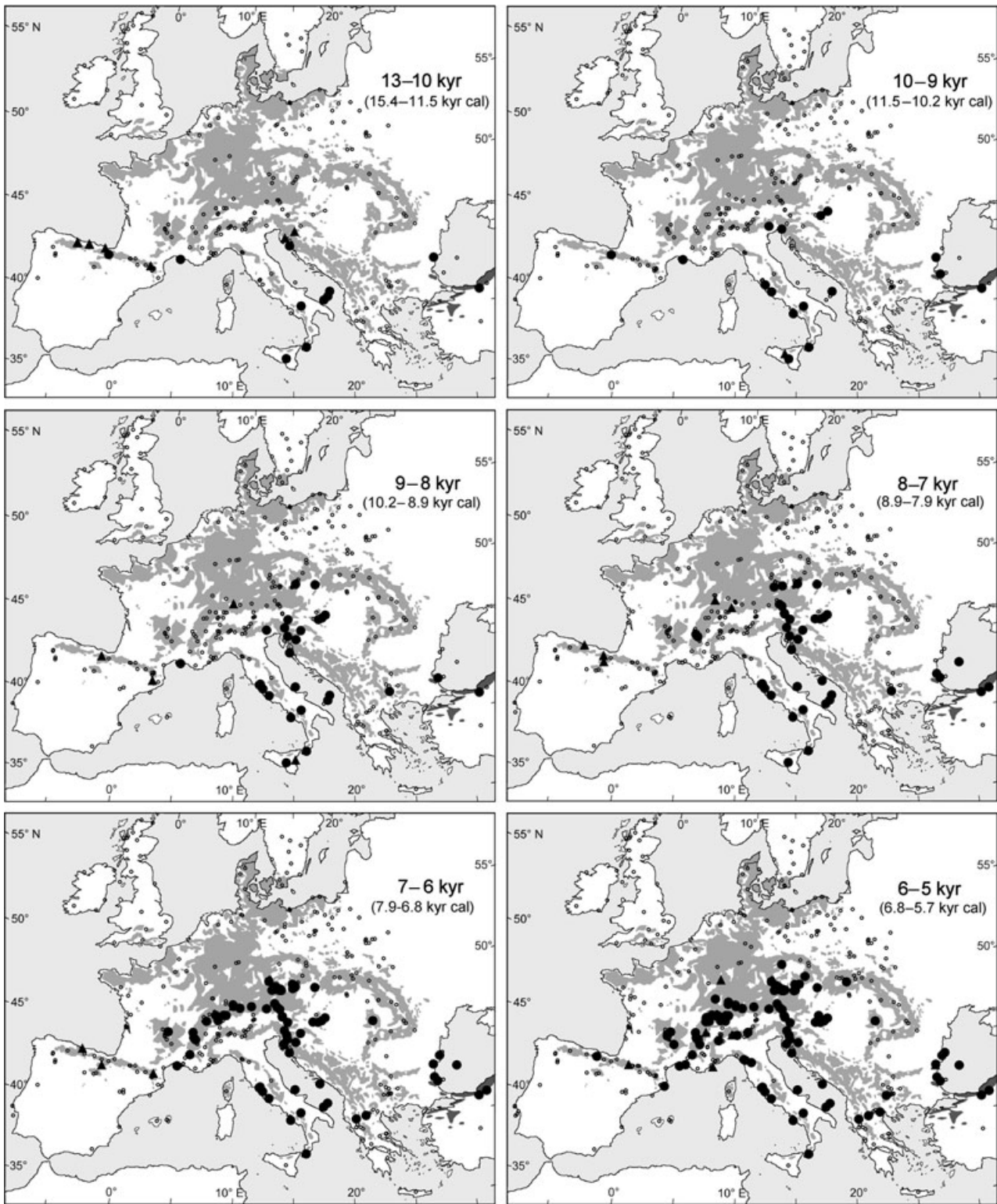


Figure 2 Geographical distribution of the late-glacial and post-glacial pollen and macrofossil records of *Fagus* in Europe: ○, *Fagus* <2% or absent; ●, *Fagus* >2%; ▲, *Fagus* macrofossil (from Magri *et al.*, 2006).

Romania. In Spain, although only two pollen sites reach 2%, many diagrams show continuous presence of beech pollen at very low percentages.

• 4–3 kyr ¹⁴C BP (4.5–3.2 cal. yr BP). *Fagus* expanded in the Cantabrian Mountains and the Pyrenees, as well as in the eastern Carpathians. In Bulgaria and Greece, the number of

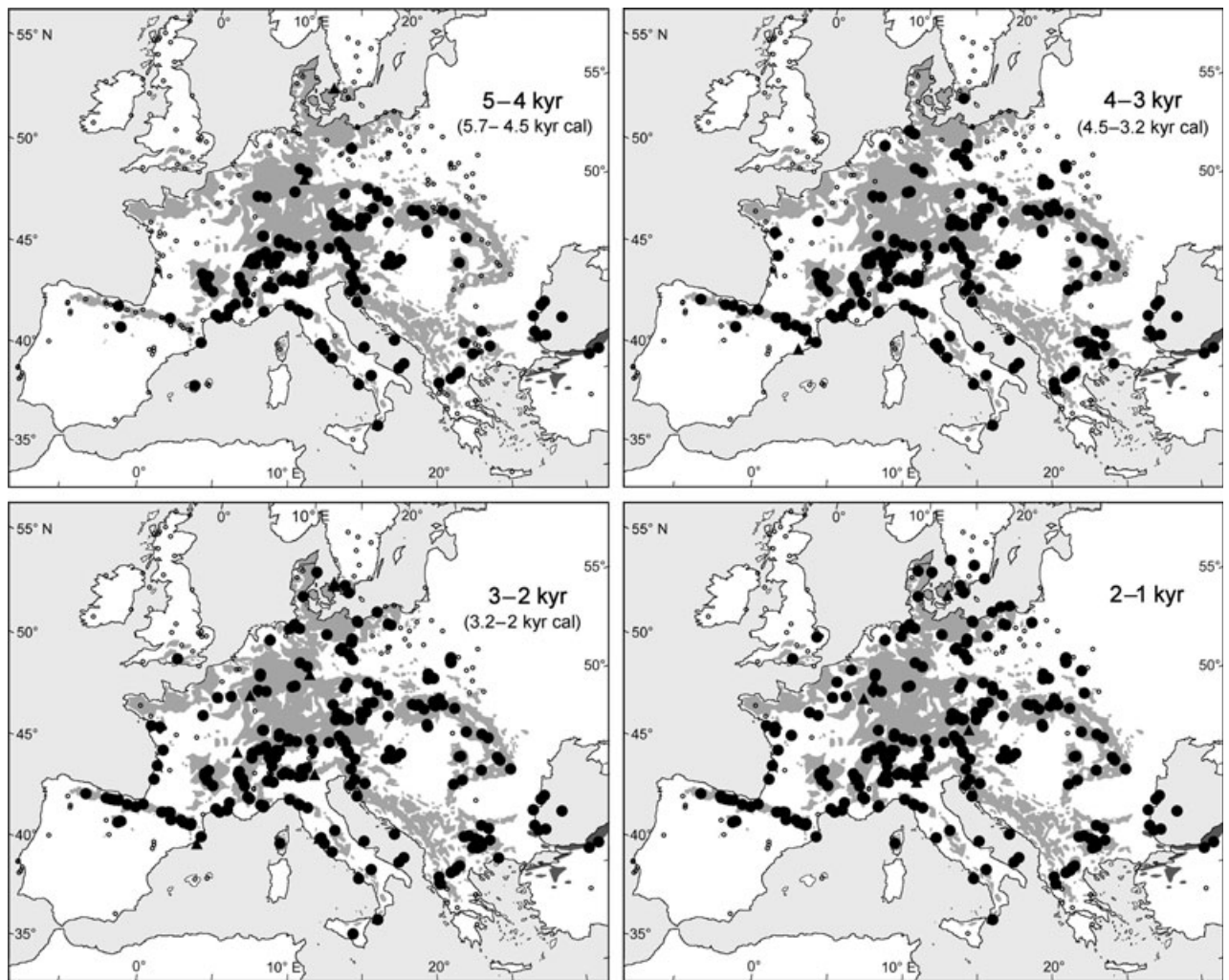


Figure 2 Continued.

sites with at least 2% beech pollen increased markedly. In northern Europe, beech migrated into southern Sweden and into the southern and eastern Poland uplands.

- 3–2 kyr ^{14}C BP (3.2–2 cal. yr BP) *Fagus* reached England and expanded in southern Scandinavia.
- 2–1 kyr BP. A further expansion towards the north (southern Sweden) and east (northern Poland) occurred. Around 1 kyr BP, *Fagus* reached a range very similar to that of today.

Location of glacial refugia of *Fagus sylvatica*

The analysis of the regional times and modes of beech spread, coupled with genetic data on modern populations (Magri *et al.*, 2006), indicates that *Fagus* survived in various regions of Europe during the last glacial period (Fig. 3). Slovenia and the eastern Alps, and possibly southern Moravia and southern Bohemia, should be considered as the main source areas for the colonization of central and northern Europe by beech. In France, a population in the western Alps might be responsible for the colonization of most of

southern France, while a genetically different population in the Mediterranean coastal zone expanded very slowly and locally during the late-glacial. A small population in southern Italy (Calabria) had a very limited increase, whereas a larger population in southern and central Italy colonized the northern Apennines. Three genetically different populations, separated by isozyme analysis, are found in the northern Iberian mountain ranges, and should correspond to three separate refuge areas. Similarly, at least three distinct populations may be recognized in the southern Balkan peninsula by means of both chloroplast and nuclear markers. They expanded locally but did not contribute to the colonization of the Carpathian Mountains.

PATTERNS OF POST-GLACIAL INCREASE OF *FAGUS* POPULATIONS

Fossil pollen data indicate that the post-glacial spread of *Fagus* in Europe was continuous and irreversible, or at least did not include important retreats and re-advances: beech populations

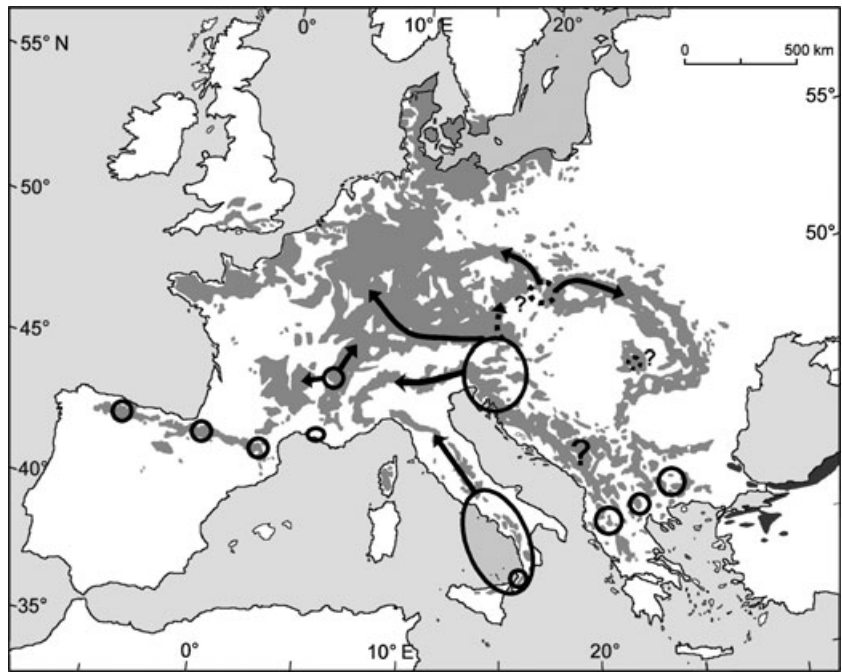


Figure 3 Tentative location of refuge areas for *Fagus sylvatica* during the last glacial maximum and main colonization routes during the post-glacial period (from Magri *et al.*, 2006).

generally persisted in the colonized territories, so that the modern distribution of beech corresponds to its maximum post-glacial extension.

This pattern clearly appears in Fig. 4(a), where the number of sites with at least 2% beech pollen ('*Fagus* sites') is plotted against time. The age of dots corresponds to the middle points of the time windows (calibrated ages) of Fig. 2. Marine cores have been excluded from this count because they contain pollen of long-distance origin. The number of *Fagus* sites appears to increase exponentially from the beginning of the late-glacial until about 3.5 cal. kyr BP, and then to diminish their rate of increase rate in the past few millennia. Fitting this

increase to the logistic function is verified by using the regression analysis of the linear transformation of the logistic equation (Fig. 4b). The correlation coefficient of the linearized logistic equation of the number of *Fagus* sites against time is 0.996, with the best-fitting asymptotic value (*K*) at 261 sites. This correlation coefficient indicates that the increase in the number of *Fagus* sites with time corresponds remarkably well with the logistic model.

In order to exclude the possibility that this pattern is due to an increase in the total number of available records in the course of the post-glacial, the number of *Fagus* sites has been divided by the total number of available sites for each time

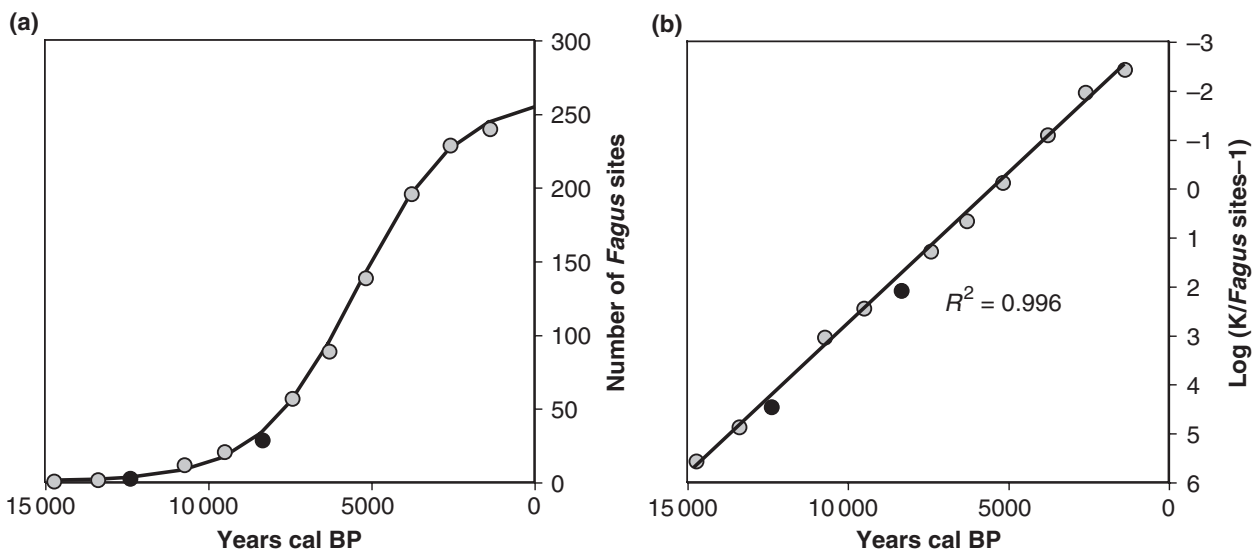


Figure 4 (a) Scatter plot of the number of *Fagus* sites against time and best fitting logistic curve; (b) linearized logistic function of the number of *Fagus* sites against time. Black dots correspond to the Younger Dryas and 8.2-kyr events, respectively.

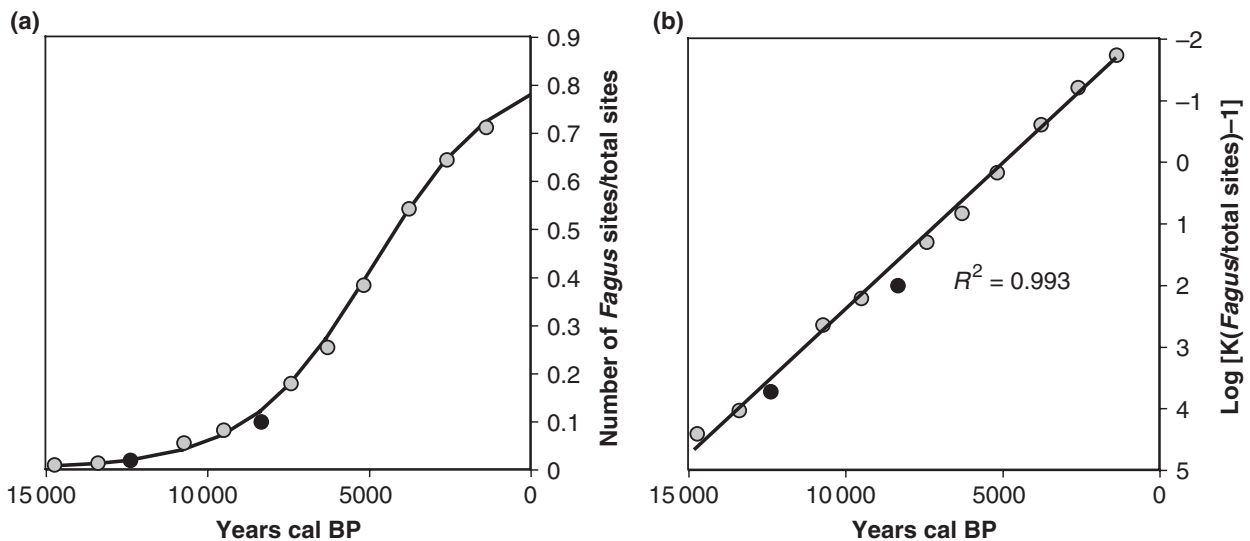


Figure 5 *Fagus* pollen sites have been divided by the total number of available sites. (a) Scatter plot of the number of normalized *Fagus* sites against time and best fitting logistic curve; (b) linearized logistic function of the number of normalized *Fagus* sites against time. The best fitting asymptotic value (K) is 0.84. Black dots correspond to the Younger Dryas and 8.2-kyr events, respectively.

window (Fig. 5). The correlation coefficient of the linearized logistic equation of the number of normalized *Fagus* sites against time (0.993) confirms a fit with the logistic model.

Considering that the pollen sites studied are scattered over most of Europe, from sea level to over 2300 m a.s.l. and from Sicily to Sweden, with no *a priori* selection, the increasing number of *Fagus* sites may reasonably be considered indicative of an increasing extent of the area where beech was locally present. This does not inform us about the abundance of beech within its range, as *Fagus* could be the dominant tree in some regions and a relatively rare species in other regions. This pattern of increase does not even mean that the overall European range of beech expanded according to a logistic model, following a moving front of beech forests. The expansion of *Fagus* was not simultaneous even in sites close to each other (Magri *et al.*, 2006), indicating that local/regional factors controlled this process and that the expansion of beech did not occur with a spatially close front. Simply, the patterns of Figs 4 and 5 indicate that the area where beech was present at a clearly detectable level, fixed subjectively at 2%, increased through time following a logistic model, presumably as a consequence of population increase.

Separating different populations of *F. sylvatica* on the basis of their modern genetic data may fine-tune this result. In particular, chloroplast markers distinguish three main groups of haplotypes: one in the Italian Peninsula; the second in the southern Balkan Peninsula; and the third in the rest of Europe, including the Iberian Peninsula (Magri *et al.*, 2006). While the European group is formed by a single haplotype, the Italian and Balkan groups include a number of small populations with different haplotypes in an area where relatively few pollen records are available. For this reason, the Italian and Balkan pollen sites are considered all together. In Fig. 6(a), the post-glacial increases of the number of Italian–Balkan sites and of

the rest of Europe ('European population') have been plotted separately. Both groups appear to follow the logistic model, although clear differences in the rate of increase are found between them: the sites corresponding to the large European populations increase at a considerable rate, while the sites corresponding to the small and diverse Mediterranean populations show a moderate, oscillating increase, and even a slight decrease in the past few millennia. The same pattern is observed in Fig 6(b), where different populations of *F. sylvatica* have been grouped on the basis of the spatial analysis of variance (SAMOVA) on nuclear markers (isozymes), distinguishing different populations not only in the Italian and Balkan Peninsulas, but also in Spain and France (Magri *et al.*, 2006). Again, all groups appear to follow the logistic model, although the large central–northern European population increased at a considerable rate, while the southern European populations (subdivided in an Italian–Balkan group and a French–Spanish group) show a moderate and oscillating increase until *c.* 3.5 cal. kyr BP, followed by a slight decrease.

In both cases, it appears that during the time interval from the late-glacial to 3.5 cal. kyr BP, the increase of the *Fagus* sites is exponential (Fig. 6). Based on chloroplast markers, the correlation coefficient for the linearized exponential function (15–3.5 cal. yr BP) is 0.970 for the European population and 0.942 for the Mediterranean ones (Fig. 6a). Based on the analysis of nuclear markers (Fig. 6b), the correlation coefficient for the linearized exponential function (15–3.5 cal. yr BP) is 0.958 for the central–northern European population, 0.969 for the French–Spanish ones, and 0.894 for the Italian and Balkan populations. The doubling times of the *Fagus* sites, calculated for the exponential increase phase as $\ln 2/r$, where r is the intrinsic rate of increase estimated from the regression analysis, are *c.* 1160, 1730 and 3470 yr for the central–northern European, French–Spanish and Italian–Balkan populations,

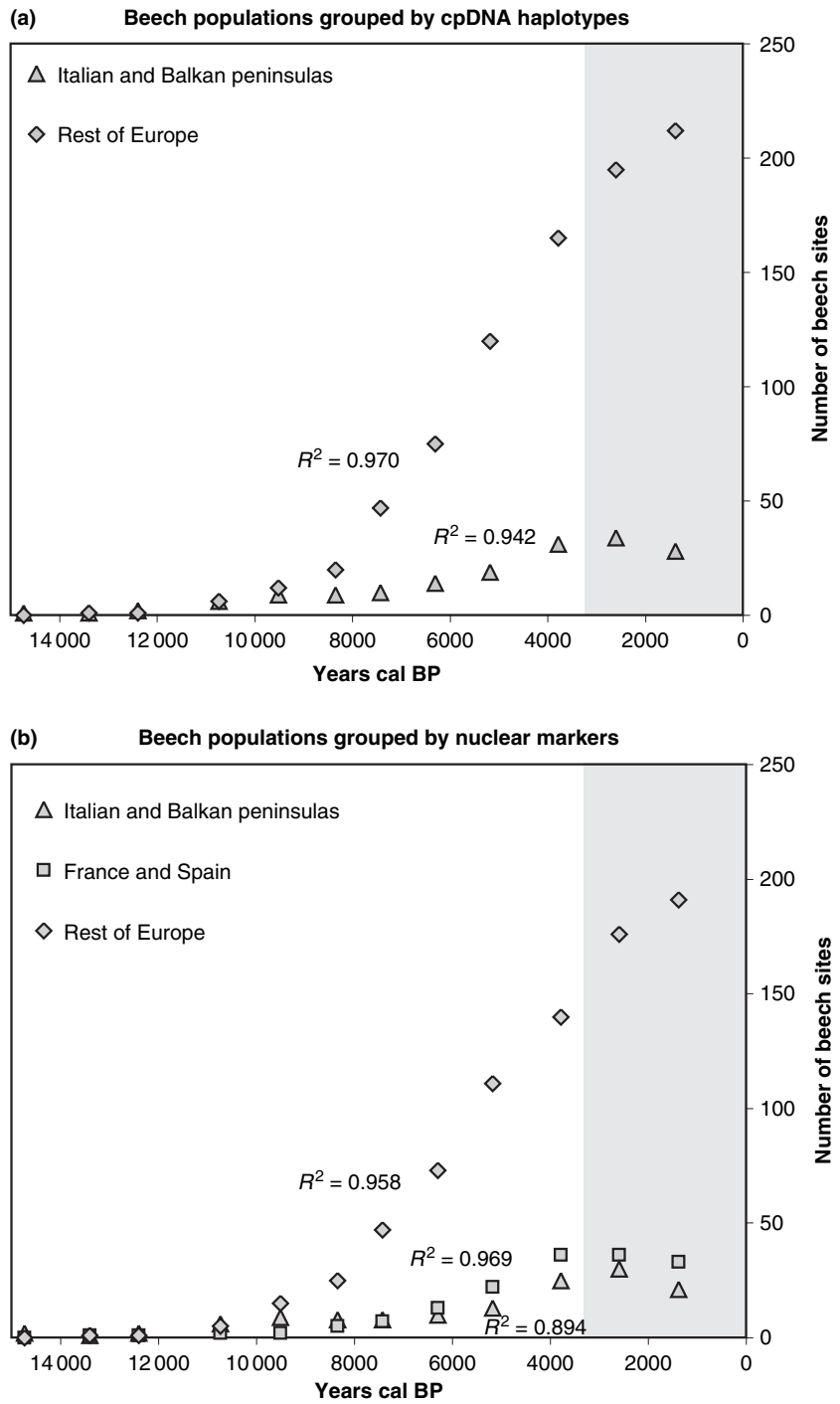


Figure 6 Scatter plot of the number of *Fagus* sites against time. Different beech populations have been grouped by (a) chloroplast DNA; (b) nuclear markers. Correlation coefficients have been calculated for the exponential part of the increase (15,000–3500 cal. yr BP) excluding the shadowed area.

respectively. These doubling times confirm that different beech populations had different rates of spread from their glacial refugia, and provide evidence that the European populations expanded three times faster than the Italian–Balkan ones, possibly because of more favourable climate conditions at higher latitudes. Estimating the doubling times for single Mediterranean populations is difficult because of the limited numbers of available pollen diagrams; however, it appears that within southern Europe, different populations had different rates of spread.

Giesecke & Bennett (2004), based on interpolations of pollen data, observed a progressively increasing trend in the cumulative area occupied by *Picea abies* during the post-glacial in Fennoscandia. However, this increase does not conform fully to a logistic model, possibly because Giesecke & Bennett (2004) considered the expansion of the whole reconstructed range: after a rapid early Holocene spread at low population density, *P. abies* shows a mid- to late-Holocene front-like spread at high population densities, although with some oscillations, due to ‘stop-and-go’ patterns, described also by Gliemeroth (1995).

DISCUSSION

Factors controlling the post-glacial patterns of beech spread

The logistic increase in the post-glacial distribution of *Fagus* adds new insights to our understanding of the primary factors controlling the spread of beech in Europe, a matter that has long been the subject of debate among palaeoecologists. Three main explanations are generally considered: (1) the spread of beech is related to changes in climatic conditions, which became cooler and wetter in the second half of the Holocene (Huntley *et al.*, 1989); (2) *Fagus* expansion is mainly a response to farming and other human activities, which may have contributed significantly to openings in the natural forest vegetation established at the beginning of the post-glacial, favouring colonization by beech (Andersen, 1984; Aaby, 1986; Latałowa, 1992; Reille & Andrieu, 1994; Björkman, 1997; Küster, 1997); or (3) the expansion of beech is an entirely natural phenomenon the timing of which, often coincident with anthropogenic interference, would be the result of slow migration and establishment rates, typical of the internal dynamics of beech forests (Gardner & Willis, 1999).

Giesecke *et al.* (2007), comparing modelled patterns of climate parameters 6000 BP with *Fagus* distribution at a European scale, have shown that climatic factors are the likely major determinants of the potential range of *F. sylvatica*. However, climatic factors are regionally moderated by competition, disturbance effects and the intrinsically slow growth rate of beech. Tinner & Lotter (2006) suggest that climatic change was the main forcing factor for the Holocene expansion of beech in central Europe. However, in the landscapes of northern–central Europe, it is likely that human activities influenced expansion dynamics, as *Fagus* populations expanded only after the beginning of the Neolithic. According to Bradshaw (2004), anthropogenic activity catalysed the spread of *F. sylvatica* through increasing the rates of forest disturbance, but it had a minimal impact on the current genetic structure and diversity of beech populations.

The conformity of the increase in beech distribution to the classical logistic model of population growth (Figs 4–6) strongly supports the hypothesis that, given non-limiting climate conditions for *Fagus*, a biological process was the main factor shaping the pattern of the post-glacial beech expansion in Europe. However, possible effects of climate fluctuations and human activity in determining the rate of change of the past distribution of *F. sylvatica* at a continental scale cannot be excluded.

The modern distribution of *F. sylvatica* is clearly limited by unfavourable climatic conditions at its southern and northern boundaries. It is therefore very likely that unfavourable climate conditions could have regionally limited the distribution of beech also during the late-glacial and post-glacial. In Figs 4 and 5, a very light departure of the number of *Fagus* sites from the logistic model is observed at 12,400 cal. yr BP (mid-point of

the time window 10,000–11,000 yr ¹⁴C BP) and 8300 cal. yr BP (mid-point of the time window 7000–8000 yr ¹⁴C BP). The hypothesis that these two gentle slow-downs in beech expansion may be correlated with the Younger Dryas and the 8.2-kyr events, respectively, is attractive and highlights the need for more detailed data to reach a conclusive assessment. A data set of high-resolution records would probably produce a curve with many more fluctuations, in relation to decadal- to centennial-scale processes, which are smoothed in Figs 4 and 5. On the other hand, the fact that the coarse procedure used in this paper was able to detect such a significant pattern of logistic increase indicates that this phenomenon is strong enough that secondary patterns do not blur it. Broad-scale interpretations are therefore needed.

The progressive decrease of summer insolation during the past 12 kyr (Berger, 1978) may have been a favouring factor for the expansion of beech, which avoids hot and dry summers. However, the insolation curve is sinusoidal, and as such it does not parallel the exponential increase of the beech sites. Numerically, the two curves refer to different functions, which are not related to each other. Therefore the insolation trend, determining increasingly cooler summer temperatures, may have favoured the expansion of beech by influencing its rate of spread, but it cannot have controlled its exponential pattern.

Exponential patterns are typically induced by multiplicative biological factors. The pattern of spread of beech populations might therefore have been induced by other biological populations, increasing or decreasing exponentially. It may be tempting to hypothesize a positive link between a possible exponential increase in Neolithic human populations and the exponential spread of beech. However, recent estimates of human population fluctuations indicate a complex history from the Mesolithic to the Neolithic in central and northern Europe, with rapid rises and crashes of enormous magnitude (Shennan & Edinborough, 2007). In particular, both Germany and Poland show a remarkable decline in population after 7000–6700 cal. yr BP, lasting until after 5500 cal. yr BP, in the course of the Neolithic. In Poland, a sudden increase in human populations at 5500 cal. yr BP is followed by a decline to very low levels until 4000 yr BP. These fluctuations are by no means perfectly in phase with the fluctuation history of the Danish and German populations. At the same time (7000–4000 cal. yr BP), a steady exponential increase in the number of beech sites is observed, corresponding to the steep part of the population growth (Figs 4 & 5). This discrepancy suggests that the exponential pattern of beech spread is not a response to the increase in human populations.

Competition with other tree taxa, which were established in Europe well before beech, does not appear to have been strongly influential on the increase of *Fagus* populations. In particular, pine and mixed oak forests were widely spread over most of Europe at the time of the exponential increase of *Fagus*, but they did not prevent its diffusion, which is still continuing at present, although at a slower rate compared to the early- and middle-Holocene.

If we exclude climate, human activity and competition as determinants of the exponential increase of *F. sylvatica* in Europe, the multiplicative biological process of population increase of beech remains the most likely explanation for the observed pattern.

It is important to note that this result is not in disagreement with the hypotheses of climate or human influence and competitive influences on *F. sylvatica*, as discussed by previous authors. Human activity and climate may well have affected the frequencies of *Fagus* in pollen diagrams, which were very variable through time, without extirpating beech populations from the landscape and therefore without causing a decrease below the 2% level.

Although considerable problems are encountered when reconstructing the spread of a plant population from the pollen record, as the initial phases of spread may have occurred at population densities too low to be detected by pollen analysis (Bennett, 1986), the increase in the number of *Fagus* sites with time is so impressive as to justify further discussion.

It is well known that a population increase conforms to an exponential function when there is a progressive multiplication of the number of individuals, depending on the dimension of the population as it increases with time. An increase of surface area occupied by a population moving with a closed front would not follow an exponential model, as the increase rate would be proportional to the linear dimension of the front. Instead, a population increase starting from scattered nuclei with a low density may produce an exponential increase, as shown in Fig. 7, where in three successive time windows the number of dots, representing small stands of a taxon, increases exponentially both within and outside the spreading front.

This model is in agreement with the distribution of pollen records, showing that after the initial colonization of a region, the density of *Fagus* sites became increasingly higher during the following millennia (Fig. 2). This pattern can be observed, for example, in the southern Balkan Peninsula and in the outer Alpine chain, where after the initial colonization, from 8000 to 3000 cal. yr BP, the number of *Fagus* sites increased progressively. This model conforms very well with the 'diffuse spread' suggested for *Picea abies* in Fennoscandia by Giesecke (2005).

The exponential diffuse spread model is also confirmed by the patterns of increase in pollen series with high temporal resolution and precision. For example, in three pollen sites located within a distance of 150 km in Switzerland (Soppensee: Lotter, 1999; Bibersee: Beckmann, 2004) and southern Germany (Schleinsee: Clark *et al.*, 1989), a synchronous exponential increase of *Fagus* is recorded, starting at 8200 cal. yr BP (Tinner & Lotter, 2006). However, the 2% threshold was reached at the three sites at 7900, 7450 and 7500 cal. yr BP, respectively, indicating that the beech stands had local differences of density. This situation may be exemplified by the difference in density of dots on the left and right sides of the diffuse spread in Fig. 7.

In the past few thousand years, the number of *Fagus* sites appears to approximate an equilibrium distribution

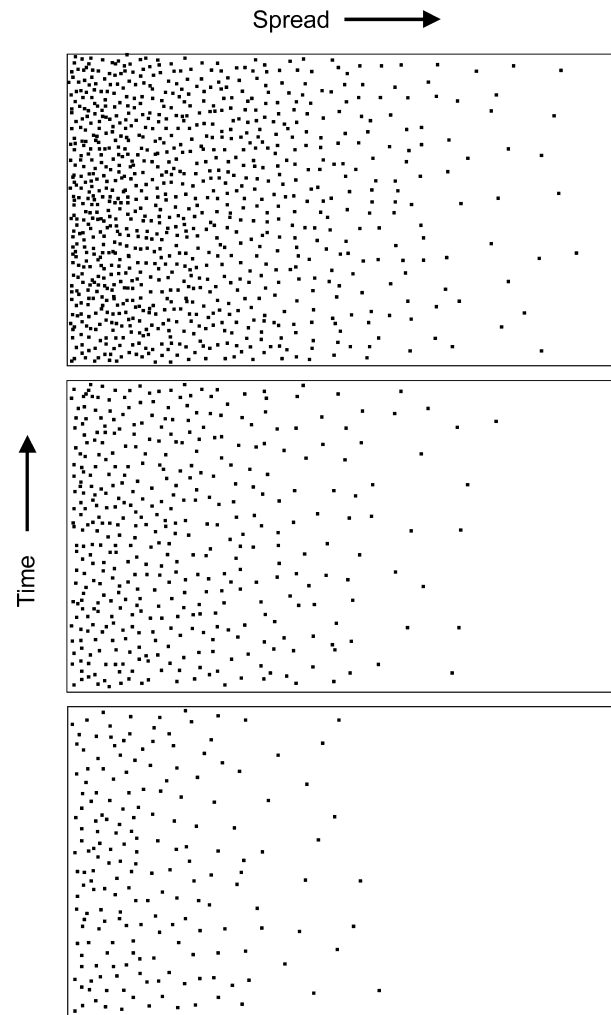


Figure 7 Schematic representation of three successive time windows of a diffuse moving front, formed by scattered nuclei of a tree population growing exponentially both within and outside the front.

(Figs 4 & 5). It is difficult to establish whether this pattern may depend on changing climate and/or increasing human impact. An alternative, but more likely hypothesis is that beech is progressively approaching its carrying capacity, due to limiting environmental conditions far north in Europe. In the Mediterranean regions, a moderate decline in beech range observed over the past two millennia may also be due to the progressive aridification of climate, documented by pollen analysis at many sites (Follieri *et al.*, 2000; Jalut *et al.*, 2000; Pérez-Obiol & Sadori, 2007).

Assessing the extent of the last glacial refugia of *Fagus sylvatica*

Based on the assumption that the post-glacial increase of beech sites corresponds to an increase of the surface area where beech was locally present, the logistic model of the past distribution of *Fagus* populations can be used to estimate the extension of

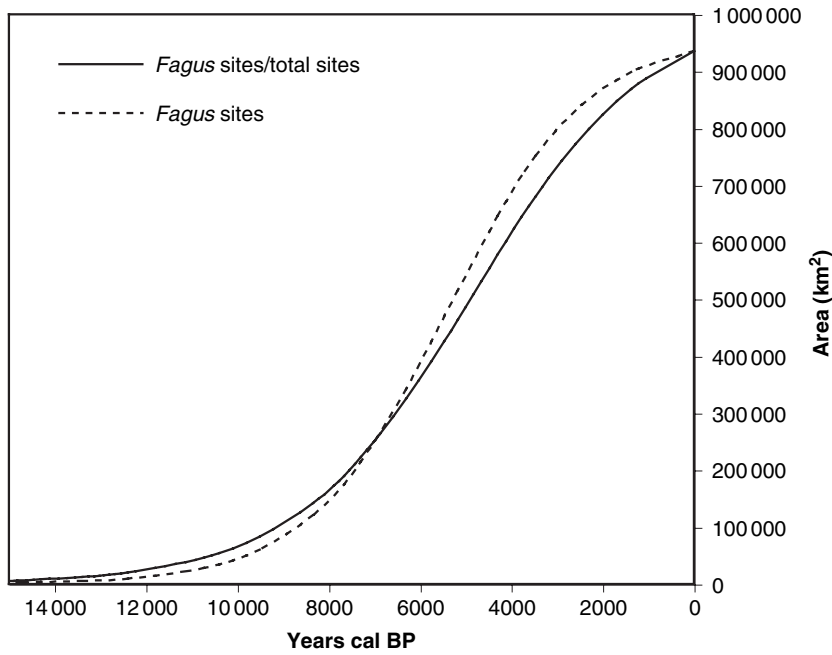


Figure 8 Modelled logistic increase of the surface area occupied by *Fagus sylvatica* during the past 15,000 years, based on the functions best fitting the increase of *Fagus* sites [dotted line, $y = 962,000 / (1 + 0.0285 \times e^{0.0006x})$, from Fig. 4] and of normalized *Fagus* sites [solid line, $y = 1,010,000 / (1 + 0.0797 \times e^{0.0005x})$, from Fig. 5].

the glacial refugia for beech, by applying the logistic function fitted to the fossil data to the value of the modern surface area covered by beech.

Based on the map of the natural potential vegetation of Europe by Bohn *et al.* (2000), the modern surface of beech forests is estimated as about 931,575 km² (UNEP, 2000). Setting this value at the present time in the logistic function fit for the increase of *Fagus* sites, the surface area covered by beech at the beginning of the Holocene is estimated to have been around 31,000 km² using the normalized data (Fig. 8). Pollen records, however, indicate that in southern Italy *F. sylvatica* had already started its population increase at the

beginning of the late-glacial (Huntley *et al.*, 1999), and in fact the logistic increase of *Fagus* sites is clearly observed since the late-glacial (Figs 4–6). At 15,000 cal. yr BP, when *Fagus* is found with continuity in southern Italy, the surface area covered by *F. sylvatica* would have been *c.* 5000 km². The estimates obtained from the non-normalized *Fagus* sites are somewhat lower (2000 km²), but in any case the final result is that the refuge area for beech at the end of the last glacial was likely to be of two orders of magnitude less extensive than at present (Fig. 8).

In Fig. 9, a tentative reconstruction of the distribution of *F. sylvatica* at 15,000 cal. yr BP is advanced, based on the

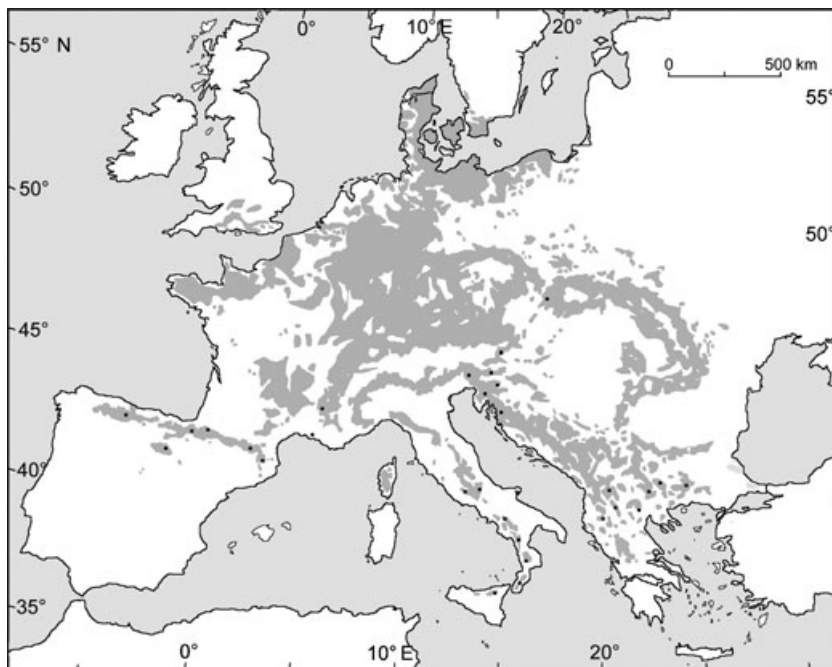


Figure 9 Black dots represent a tentative quantitative reconstruction (5000 km²) of refuge areas for *Fagus sylvatica* 15,000 cal. yr BP. Grey area corresponds to the modern distribution (*c.* 931,500 km²).

location of glacial refugia deduced from palaeobotanical and genetic data (Fig. 3), and on the quantitative assessment of the surface area occupied by beech (Fig. 8). This reconstruction suggests that the Pleistocene refugia of *F. sylvatica* were not a limited number of extensive areas with closed beech forests. Instead, they appear as very sparse stands of small populations of beech scattered in multiple regions. Starting in the late-glacial and during the Holocene, the southern European populations increased their density at a very low growth rate, without any important displacements. The populations that survived in the rest of Europe, especially those in the eastern Alps–Slovenia, and possibly Moravia, not only became increasingly dense locally, but expanded far to the north and are still expanding, but at a more moderate rate.

CONCLUSIONS

Observations on the times and modes of increase in the number of pollen sites with at least 2% *F. sylvatica* during the late-glacial and post-glacial in Europe have revealed new insights regarding the distribution of the glacial refugia and post-glacial patterns of spread.

- The spread in *F. sylvatica* from its glacial refugia started during the late-glacial and was continuous and irreversible until the present, without important retreats and re-advances, so that the modern distribution of beech in central and northern Europe corresponds to its maximum post-glacial extension.
- The increase in the number of *Fagus* sites in Europe conforms remarkably well to a logistic model. It may reasonably be considered indicative of an increasing extent of the area where beech was locally present.
- The increase of the surface occupied by beech populations was exponential from the late-glacial until about 3500 cal. yr BP, then slowed down towards an equilibrium value.
- The Italian and Balkan populations, distinguished from the rest of Europe on the basis of modern genetic data (chloroplast DNA and nuclear markers), appear to have increased very slowly and to a moderate extent in their respective peninsulas, while the central European populations have increased quickly and extensively, reaching northern Europe.
- The conformity of the increase in *Fagus* distribution to the classical logistic model of population growth strongly supports the hypothesis that a multiplicative biological process was the main factor shaping the post-glacial beech expansion in Europe, provided that climate conditions were suitable. Climate conditions, human activity and competition with other tree taxa may have affected its rate of spread.
- An exponential increase of the area occupied by beech in Europe for a time span of over 10,000 years may be explained by a diffuse spread from scattered nuclei with low density, both within and outside the spreading front. This would produce an exponential increase in population density in the areas already colonized by beech and a simultaneous colonization of new surfaces at a low density.

- A lowering of the spread rates in the last few millennia and a tendency towards an equilibrium value, according to the logistic model, might indicate that *F. sylvatica* is progressively approaching its carrying capacity.
- The logistic function representing the rate of increase of the past distribution of *Fagus* populations has been anchored to the modern potential distribution area with the aim of estimating the extent of its past distribution. The result of this calculation indicates that the refugial area of beech during the last glacial was two orders of magnitude less extensive than at present.
- The evidence provided by palaeobotanical and genetic data, the logistic model of increase of *Fagus* populations, and the quantitative assessment of the surface area occupied by beech, lead to the conclusion that the Pleistocene refugia of *F. sylvatica* were not a limited number of areas with closed beech forests, but a mosaic of sparse stands of small populations scattered in multiple regions.

The fitting of a logistic model to the number of sites, as distinct from estimates of total area, or to rising pollen values at any one site, constitutes a new methodological perspective for the study of past population expansions, which may be tested with new high-resolution and precise multiproxy data. Such data could help to disentangle the different factors that may or may not have contributed to creating the population increase of *Fagus* and possibly of other tree taxa.

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