Fagus sylvatica L. – **Beech**

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Present distribution in the Western Carpathians

Fagus sylvatica is a common tree over much of Europe. However, it requires humid summers and does not tolerate harsh winters, therefore it does not occur in Eastern Europe, characterised by a continental climate. The north-eastern boundary of its range extends across the territory of Poland.

In the Carpathians, beech is a very important forest-forming component of the lower montane belt, although its coverage has been restricted as a result of widespread spruce plantations (Boratyńska & Boratyński 1990). In the Western Bieszczady Mountains, beech covers ca 50% of the forest areas. Most frequently, it extends in altitude from 550 (locally from 400) m a.s.l. to 1000–1250 m a.s.l., being the upper forest limit in this region. In the Beskid Niski range, beech is present already from an altitude of 350 m a.s.l.; however, it is most abundant in the zone at 450–850 m a.s.l. In the Beskid Sądecki range, it is found at altitudes from 300 m a.s.l. to 1170 m a.s.l, although the typical lower montane belt, including beech extends between 550 and 1120 m a.s.l. In the Beskid Wyspowy range, beech forests occur from an altitude of 500–600 m a.s.l. up to 1170 m a.s.l. In the Gorce Mountains, *Fagus* is still an important forest-forming species, growing at altitudes of 730–1170 m a.s.l, although large areas of beech forests have been replaced by planted spruce. In the Tatra Mountains, the zone dominated by beech forests extends between 900 and 1200 m a.s.l. Certain Tatra valleys differ in the location of the upper limit for beech; however the highest *Fagus* site in the Polish part of the Tatra Mountains is situated at 1300 m a.s.l. In the Beskid Żywiecki range, beech attains altitudes of 1150 m a.s.l. In areas of the Beskid Śląski range, beech forests, a great part of which was replaced by planted spruce forests, cover altitudes between 500 and 1000 m a.s.l.

In the Western Carpathians, *Fagus sylvatica* forms several associations: *Dentario glandulosae-Fagetum* Klika 1927 em. Mat. 1964, fertile Carpathian beech forest, on acidic brown soils or rendzinas, *Luzulo nemorosae-Fagetum* (Du Rietz 1923) Markgr. 1932 em. Meusel 1937, montane acidophilous beech forest, on cryptopodzols, and *Carici-Fagetum* (Moor 1952) em. Hartmann et Jahn 1967. thermophilous beech forest, associated with calcareous soils. Furthermore, beech occurs as an element in a number of other forest types, namely in fir-spruce forests, *Abieti-Piceetum montanum* Szaf., Pawł., Kulcz. 1923 (lower montane belt), in fir forests, *Galio-Abietetum* Wrab. 1959 (lower montane belt), in sycamore-beech forest, *Aceri-Fagetum* (described for the Beskid Żywiecki range), in sycamore forest, *Phyllitido-Aceretum* Moor 1945 (growing in the Pieniny Mountains and in the Beskid Niski range, on skeletal soils abundant in calcium carbonate), and in oak-hornbeam forests, *Tilio-Carpinetum* Traczyk 1962 (submontane belt).

Ecology

Beech is a monoecious tree, likely to live for ca 300 years and attain a height up to 40 meters (Ellenberg 1996). As a mature tree it casts a dense shade, which helps it outcompetes most other deciduous forest trees. It is a wind-pollinated species becoming able to produce flowers and seeds relatively late, i.e. at the age of 50–60 years, however continuing this activity throughout the rest of its life (Kramer et al. 2008). Beech produces pollen grains, that can easily be recognised and identified; however actual pollen production, compared with many other trees, is low (Andersen 1970), and this results in low percentage values in pollen diagrams which underestimate the actual abundance of the tree. Its seeds are generally produced in low or medium quantities (Kramer et al. 2008), but occasionally, in seasons affected by drought in the preceding year, they may develop in very high numbers (Piovesan & Adams 2001). Seeds of beech are transported over small distances. More than 90% of seeds are not carried further than 30 m from the parent tree. For this reason, dispersal of pollen grains is very important in the maintenance of genetic variety of beech populations (Kramer et al. 2008). Transfer of seeds over greater distances is performed by some animals (e.g. jays) (Nilsson 1985, van der Wall 2001). Seeds, germinating in spring, require relatively high humidity for optimum growth; however, seedlings are tolerant of rather low light levels (Kramer

1995). Mild frosts occurring in spring are also a limiting factor for the growth of young seedlings. Temperatures below –2°C are lethal for both seedlings and saplings of *Fagus* (Kramer et al. 2008).

Expansion in Europe during the Late Glacial and Holocene

During the Eemian Interglacial, the tree flora in northern and Central Europe consisted basically of the same taxa as that of the present day. *Fagus*, represented only sparsely, was an exception (Pott 2000). It is necessary to remember this in order to stress the influence that humans had on the expansion of beech during the Holocene. Opportunities provided for the spread of this taxon as a result of Neolithic settlement were described by Środoń (1990b). At present it is more often considered that the spread of beech was affected by a number of key factors, operating at the same time, in particular, temperature, humidity, the occurrence of fires, and human impacts (Tinner & Lotter 2006, Valsecchi et al. 2008).

Data on the distribution of beech and location of its refugia during the Last Glaciation are ambiguous. Usually it is the mountains of the Appenine and Balkan Peninsulas, which are regarded as the most probable refugia from which Holocene expansion into Central Europe took place. These beech populations were small and isolated (Huntley & Birks 1983, Lang 1994). The homogeneity of chloroplast DNA undoubtedly indicates that the Carpathians were colonised by *Fagus* from Balkan refugia (Taberlet et al. 1998).

Based on the information available at that time Lang (1994) reconstructed two pathways for the Late Glacial-Holocene migration of beech. The "eastern pathway", relevant to this study, proceeded from the southern part of the Balkan Peninsula towards the north-west, across the Dinaric and Eastern Alps into the North German Plain and the Polish Lowlands and further into southern Sweden. A branch from this pathway enabled *Fagus* to enter the Carpathians and eastern Poland. At 6000 BP, to the west of the Carpathians, the Bohemian Forest already included spruce-beech forests (Svobodová et al. 2002). *Fagus* appeared also in the Sudety Mountains, where its continuous curve, exceeding 1%, begins in the profile from the Zieleniec peat bog (Madeyska 2005). However, it is certain that the tree did not arrive in the Carpathians from the Sudety Mountains.

According to other authors, the later migration of beech originated from the areas of east Slovakia and north-east Hungary (Stewart & Lister 2001). New views on the occurrence of potential beech refugia and their participation in its expansion into Central and Northern Europe have been provided by the results of multidisciplinary research. Palaeobotanical data and molecular analyses of the degree of kinship within the present-day *Fagus* populations indicate the presence of several glacial refugia of beech in Europe, the most important of which, when considering the later expansion into Central and Northern Europe, were located in the areas of present-day Slovenia and the Eastern Alps, and, most likely, in the southern parts of Moravia and the Czech Republic (Magri et al. 2006). Populations of glacial refugia in the Mediterranean region did not participate in the colonization of Central and Northern Europe. Similarly, the Balkan populations neither migrated to the north nor expanded to other European areas. Authors of the holocene history of beech in Poland (Latałowa et al. 2004b) suggest that the taxon may have arrived from regions close to the southern Polish border, i.e. from the upper Vltava river valley, for which the occurrence of *Fagus* was recorded in much earlier periods (Svobodová et al. 2001).

Considering the holocene expansion of *Fagus* in the Carpathians, the refugial area located most likely in southern Moravia appears to be of greatest importance (Magri et al. 2006, Magri 2008).

History of expansion in the Western Carpathians during the Holocene (Fig. 17)

10 000–9000 BP

At this time the Western Carpathians are still devoid of any trace of beech that might indicate its presence or even its approach.

8500 BP

The first *Fagus* pollen grains, originating from long-distance transport, are recorded in profiles from the Tatra Mountains and the Orawa-Nowy Targ Basin.

8000–7500 BP

Single occurrences of pollen grains in profiles from the Upper Orava (Rybniček & Rybničková 2002) show that a western direction of beech migration should be considered. A continuous curve for *Fagus,* though again representing only single pollen grains, nominally 0.5% of the total sum, appear also in sections from sites of the subalpine belt in the Tatra Mountains. However, because of the "high mountain effect" this observation cannot necessarily be taken as confirmation of the occurrence of beech in the Tatra Mountains. Also trace amounts of *Fagus* pollen grains in the Bieszczady Mountains suggest it probable, that the tree may have immigrated from the Eastern Carpathians.

7000–6500 BP

The range of occurrence of pollen assemblages containing beech becomes broader, both in the west and the east, from the direction of the Eastern Carpathians. In particular profiles from the Tatra Mountains and Subtatric valleys, the continuous curve for *Fagus* already attains or even exceeds 1% of the total sum, which most likely indicates the arrival of beech in this region. Similar observations are recorded in the Jasło-Sanok Depression.

6000–5000 BP

Subsequent maps showing the range of beech indicate that the initial phase of its migration into the Polish part of Carpathians occurred mainly from the west. At ca 6000 BP the western part of the Carpathians included an area with values of *Fagus* pollen exceeding 1.0% and therefore likely to suggest the local presence of beech. This is likely to reflect the spread of this taxon through the Moravian Gate and from areas of the Czech Republic and Moravia. In the later phase, *Fagus* extended its range primarily due to expansion from the Eastern Carpathians. The 5500 BP isopollen map shows the occurrence of a second area characterized by high frequencies of *Fagus* pollen grains, located in the Bieszczady Mountains, colonized by beech most likely during its migration along the southern Carpathian slopes.

At 5500 BP the species was already found in the Upper Orava and in the Beskid Wysoki range, and at 5000 BP – undoubtedly also in the Jasło-Sanok Depression. However, a vast area continued to be devoid of this tree.

4500–4000 BP

An increase in the range of beech is recorded both in the west and in the east. *Fagus* migrating from the Eastern Carpathians expanded rapidly and at 4000 BP already occupied the Pogórze Dynowskie Foothills and the Beskid Niski range and increased its amounts in the area of the Jasło-Sanok Depression.

Fagus migrating from the west was already found in the Beskid Żywiecki, the Beskid Śląski and the Beskid Mały ranges, and, undoubtedly, also in the Tatra Mountains and in a part of the Orawa-Nowy Targ Basin. The time of 4000 BP was marked by the merging of the eastern and western range of occurrence of the tree. Percentage values recorded in the study area for this period indicate that the presence of beech was unequivocal, even in sites with lower pollen values.

Therefore, already at this time the entire Western Carpathians may be described as supporting larger stands or even forests with beech. Due to the simultaneous expansion of *Abies*, fir, this is most likely when the development of fir-beech forests in the lower montane belt of the Western Carpathians was initiated (Obidowicz & Nalepka, Chapter: *Abies alba* Mill. – Fir, this volume).

3500 BP

The isopollen map for this time period shows a visible increase in the proportion of *Fagus* pollen, exceeding 2% across the entire area of the Carpathians. Areas inhabited by beech from the Eastern Carpathians locally demonstrate its very high frequencies in tree stands. The Jasło-Sanok Depression is particularly abundant in this species. A clear boundary, separating the western part of the Carpathians, with lower proportions of *Fagus*, from the eastern part, which is marked by higher values for beech, extends to the area of the Pogórze Ciężkowickie Foothills and to part of the Beskid Niski range. In a large area to the west of this boundary, amounts of *Fagus* remain at a general level of 5–10%. Only locally, in the region of the Beskid Żywiecki and Beskid Śląski ranges, in higher areas of the Orawa-Nowy Targ Basin and in the Gorce Mountains did beech forms larger stands, and there its frequency exceeds 10%.

3000–500 BP

Within subsequent centuries, *Fagus* becomes one of main forest-forming trees in the Western Carpathians. It is found as a component of various communities and associations, together with *Abies* and *Picea*, as well as forming beech-dominated stands. At that time, the lower montane belt was finally developed.

At 3000 BP, in most of the Carpathian areas amounts of *Fagus* pollen remain at the same values of 10–20%. The distinct boundary, dividing the Carpathians into a western region with lower frequency of *Fagus* pollen and an eastern region marked by high proportions of beech, shifts to the east.

At 2500 BP, the progressive expansion of beech from the Eastern Carpathians leads to an increase in its proportions over a large area of the Western Carpathians. The boundary with areas of lower *Fagus* values, which remained at the same level, still overlaps the Pogórze Ciężkowickie Foothills. Subsequent maps illustrate a slight shift in this boundary to the west, up to the maximum of beech expansion at ca 500 BP. The initially small region with higher values of *Fagus* pollen, located in the Orawa-Nowy Targ Basin, is seen gradually to increase its area in subsequent maps.

Expansion of beech is most likely associated with the activity of humans living in this part of the Carpathians and burning down forests to obtain areas for pasture and, later on, also for agriculture. This is demonstrated by numerous horizons with charcoal found e.g. in the deposits of Carpathian landslide mires (Margielewski 2006). Following these widespread temporary clearances it seems that beech was the tree that was able to recolonise these areas, outcompeting many other tree species by its ability to cast a dense shade.

0 BP

A decrease in the frequency of *Fagus* pollen grains, resulting from human interference, is recorded in most of the Carpathian areas. Higher proportions of beech are still found only in the south-eastern part of the Bieszczady Mountains; they also appear in the Beskid Żywiecki range. The greatest reduction of amounts of *Fagus* occurred in the area of the Tatra Mountains and in the Orawa-Nowy Targ Basin, including a part of its surrounding areas.

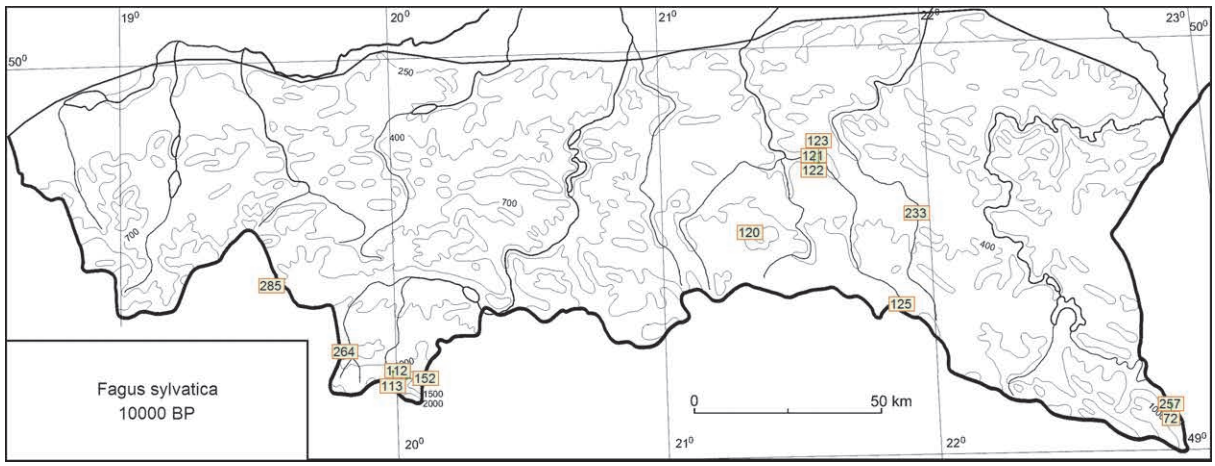
Conclusions

Different authors suggest different limiting percentage values of *Fagus* pollen as indicating the local occurrence

of this tree (Huntley & Birks 1983, Gliemeroth 1995, Björkman 1996, Magri et al. 2006). If the most commonly accepted value, over 2%, is applied, it may be stated that *Fagus* arrived in the Carpathians ca 5500 BP and entered this area through the Bieszczady Mountains. About 4000 BP beech appeared in the western part of the Carpathians.

However, authors of the presented study are rather convinced that a value of 1% should be recognized as indicating the occurrence of beech *in situ*. Following this assumption, the first indicators of *Fagus* presence, likely to occur in the area to the south of the Western Carpathians, are recorded on the maps for ca 7000 BP, when the proportion of beech pollen attains 0.5–1.0%. About 6000 BP *Fagus* is already found in the Beskid Żywiecki and Beskid Śląski ranges, as well as in the adjacent areas of the Beskid Mały range and the Orawa-Nowy Targ Basin. Between 4500 and 4000 BP the beech population may be described as covering the entire study area. The time of 3500 BP is marked by a visible differentiation into the eastern part of the Carpathians, abundant in forests including beech, and the western part, with lower amounts of this tree. The boundary separating the two areas extends close to longitude 21°E. Within subsequent centuries, *Fagus* becomes one of the main forest-forming species of the Western Carpathians. The further history of this taxon is affected by human economic activity.

Fig. 17. *Fagus sylvatica*: dot and isopollen maps for 10 000–0 BP


Fagus sylvatica
10000 BP
0
50 km
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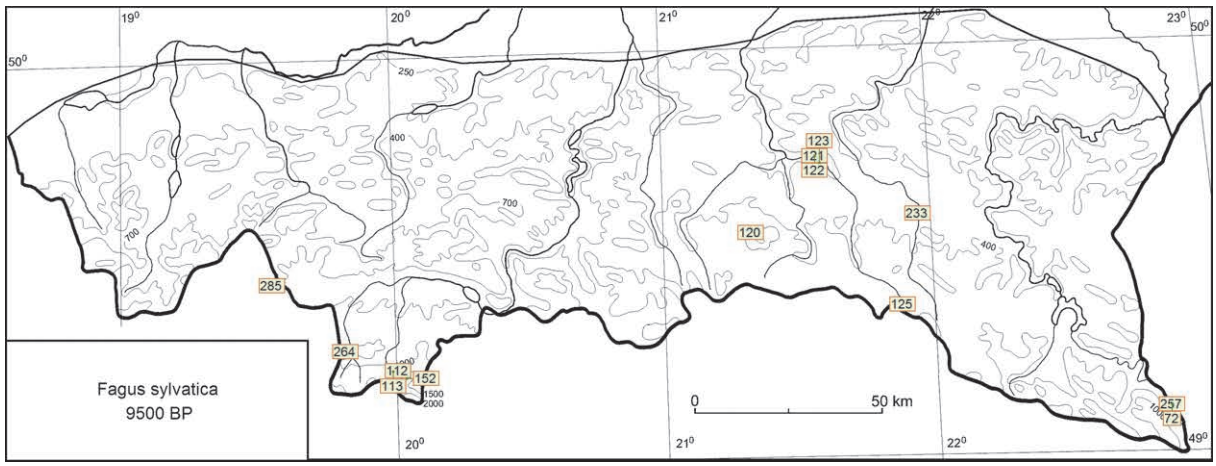
122
233
120
285
125
264
112
113
152
257
72


Fagus sylvatica
9500 BP
0
50 km
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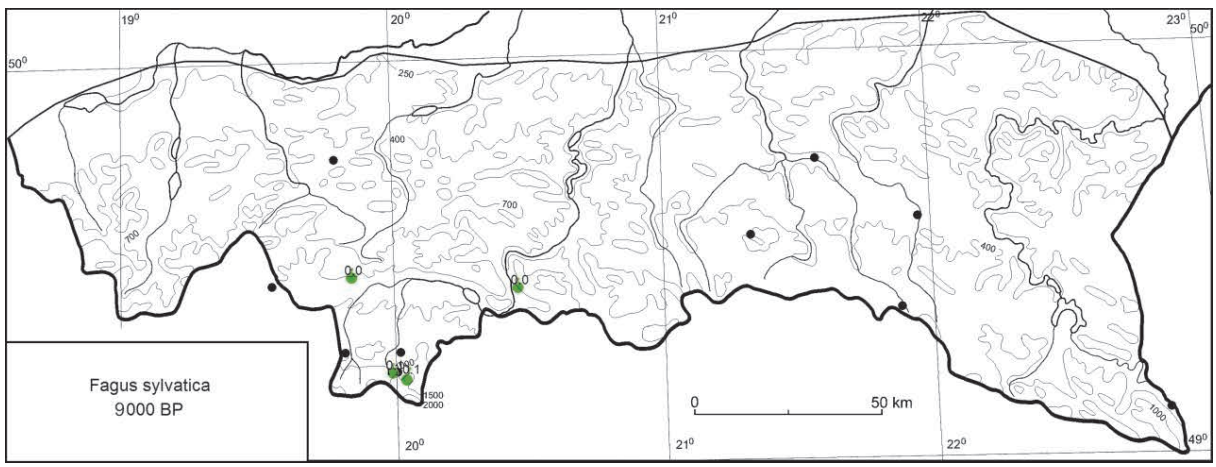
121
122
233
120
285
125
264
112
113
152
257
72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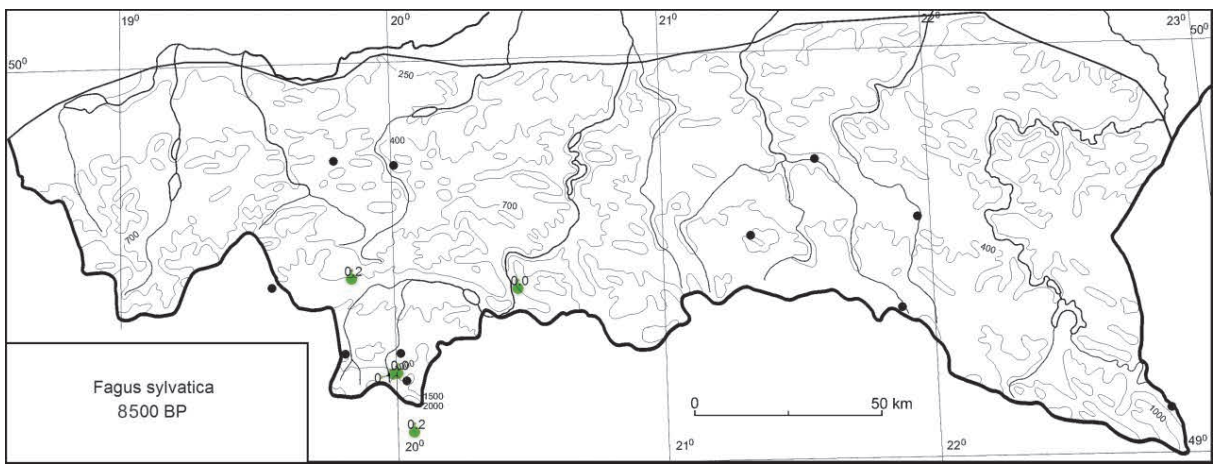
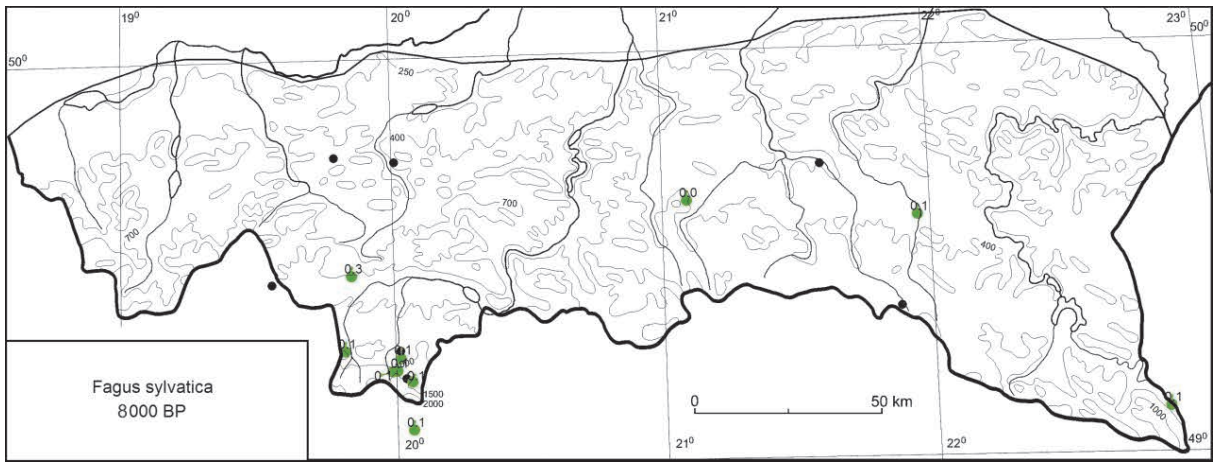
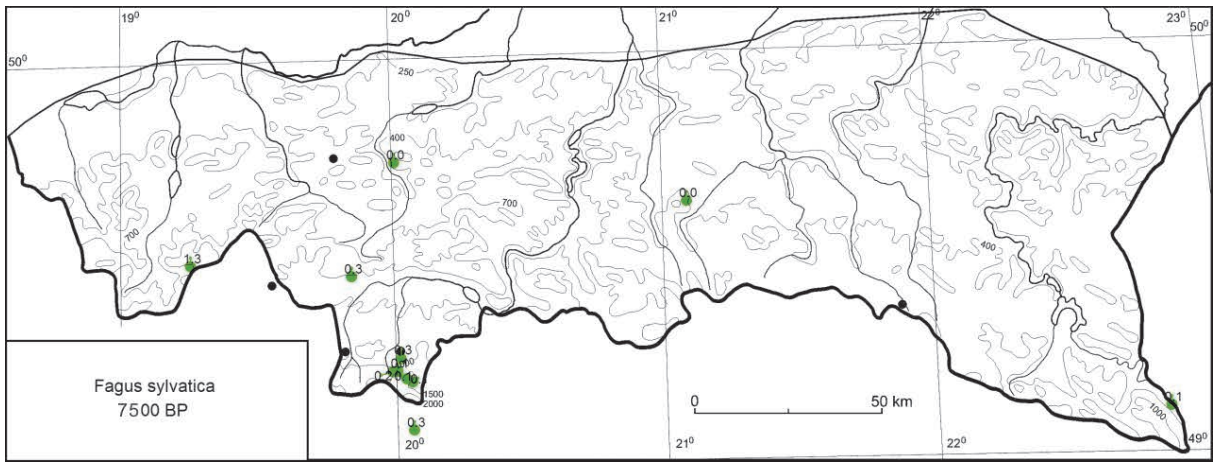
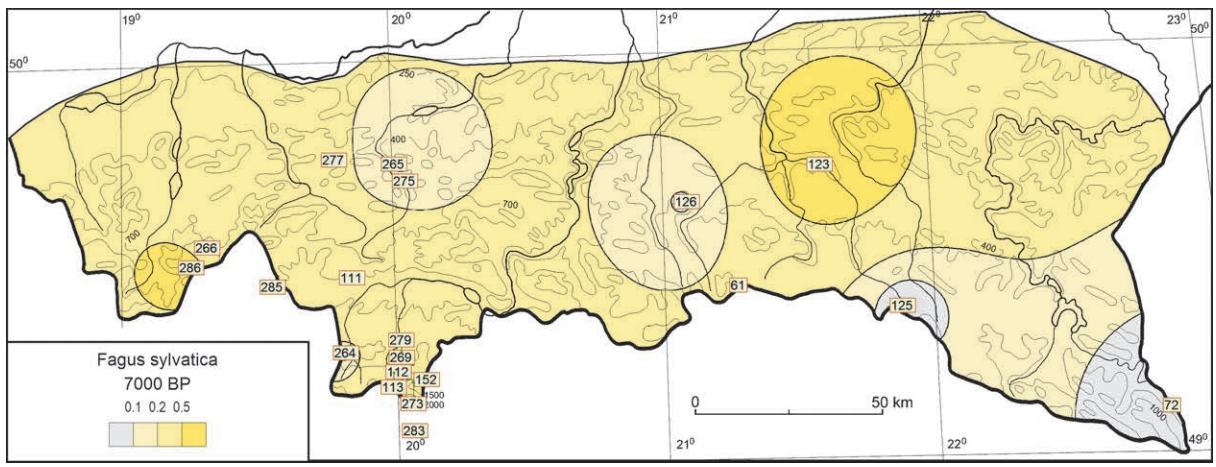
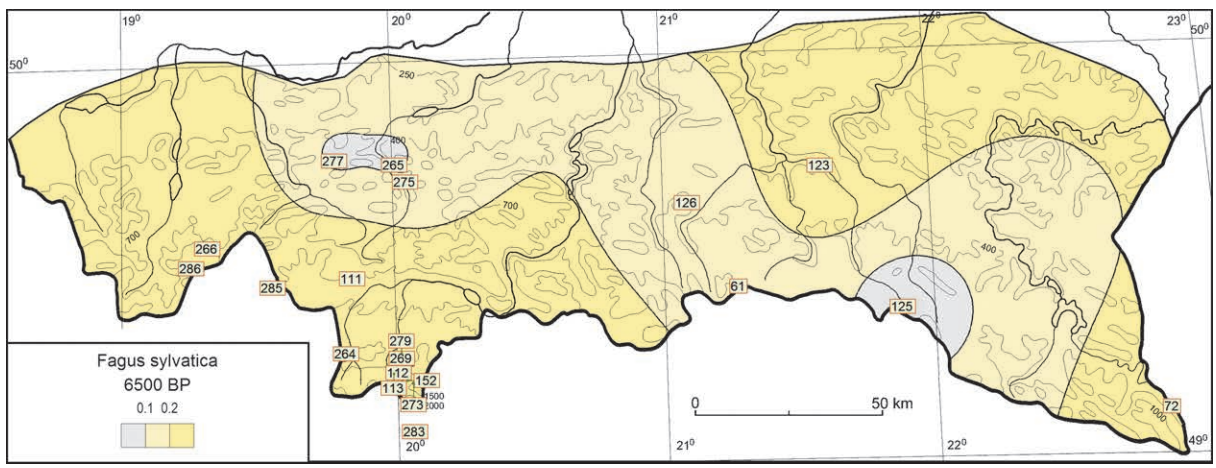
9000 BP
0
50 km


Fagus sylvatica
8500 BP
0
50 km


Fagus sylvatica
8000 BP
0 50 km


Fagus sylvatica
7500 BP
0 50 km


Fagus sylvatica
7000 BP
0.1 0.2 0.5
0 50 km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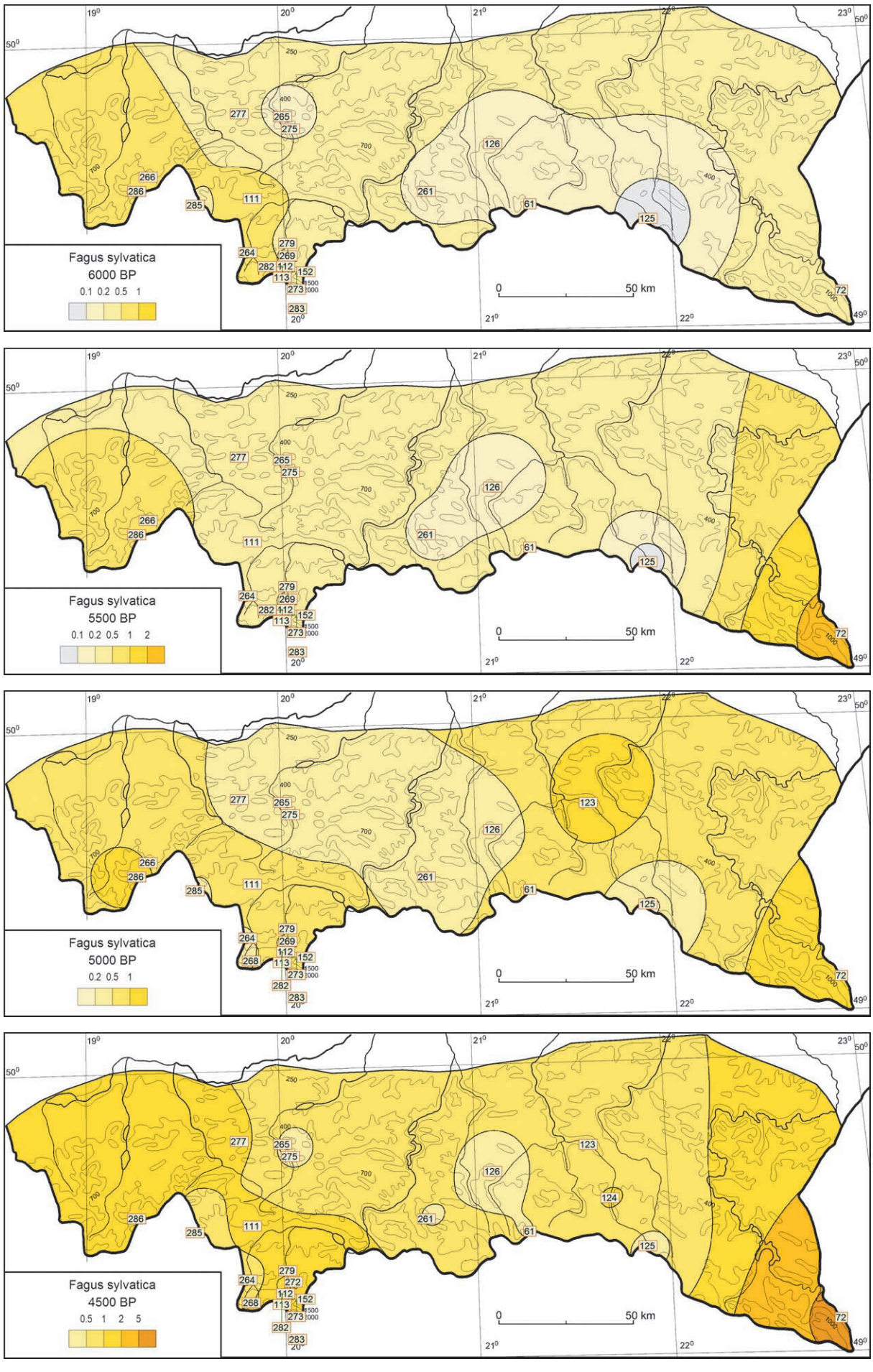
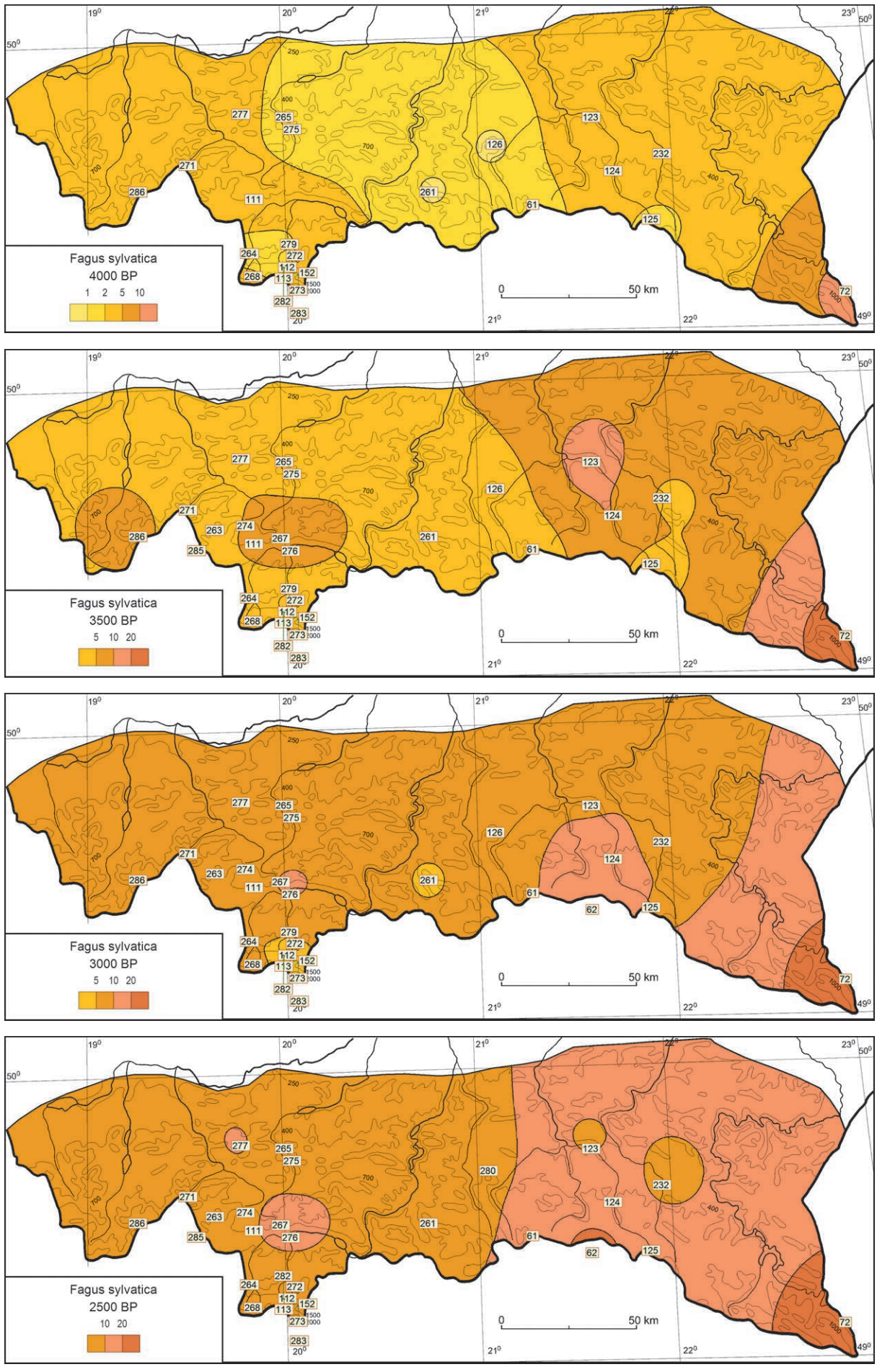
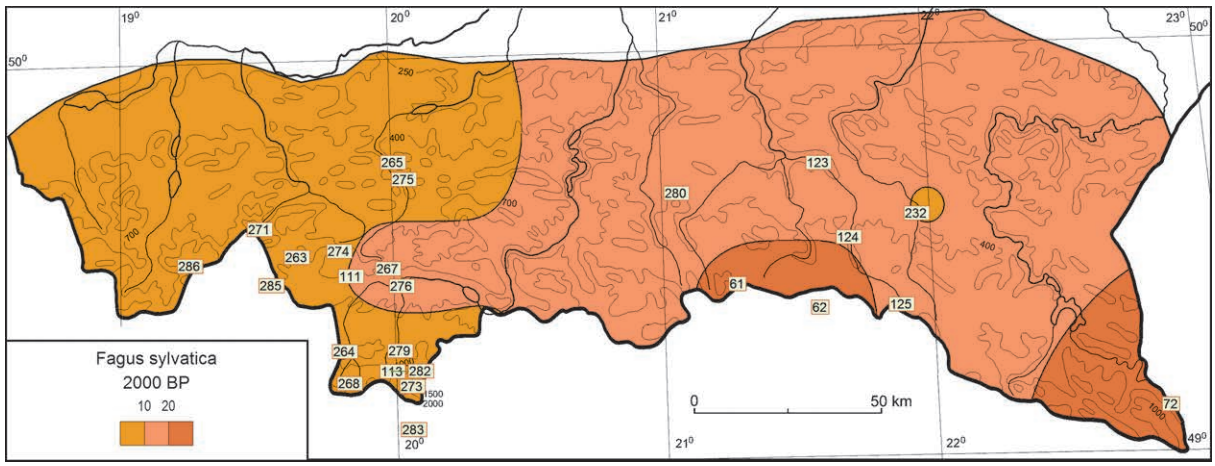
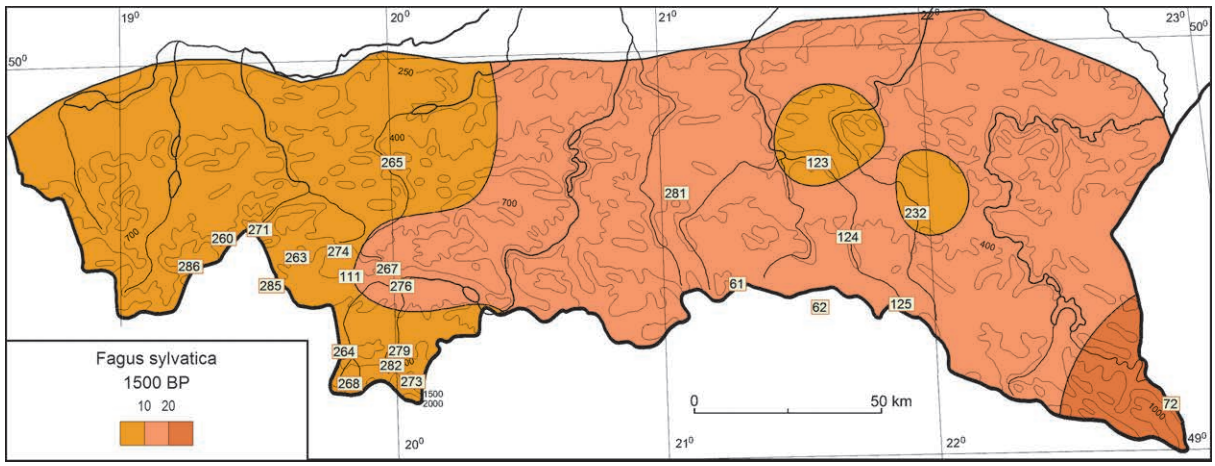
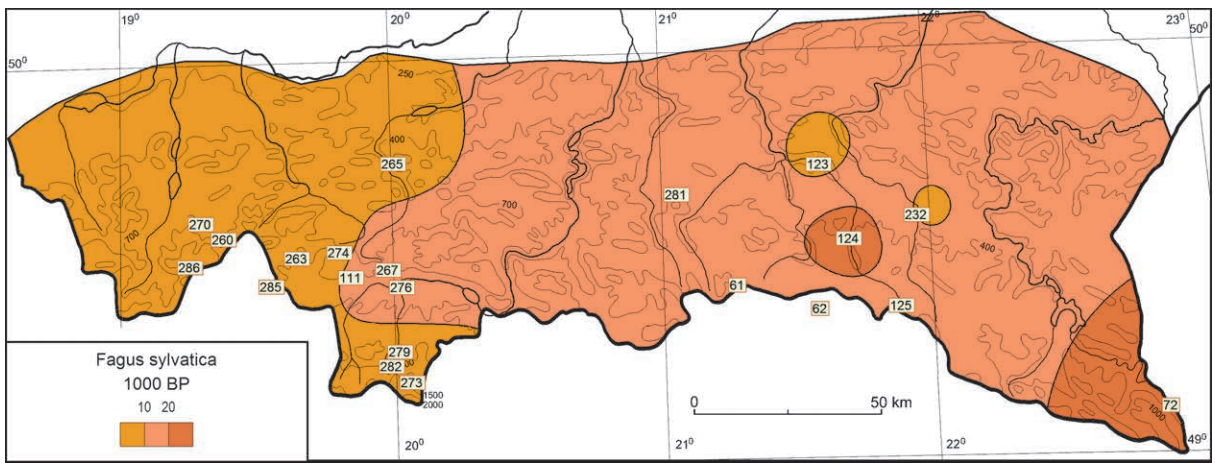
0.1 0.2
0 50 km

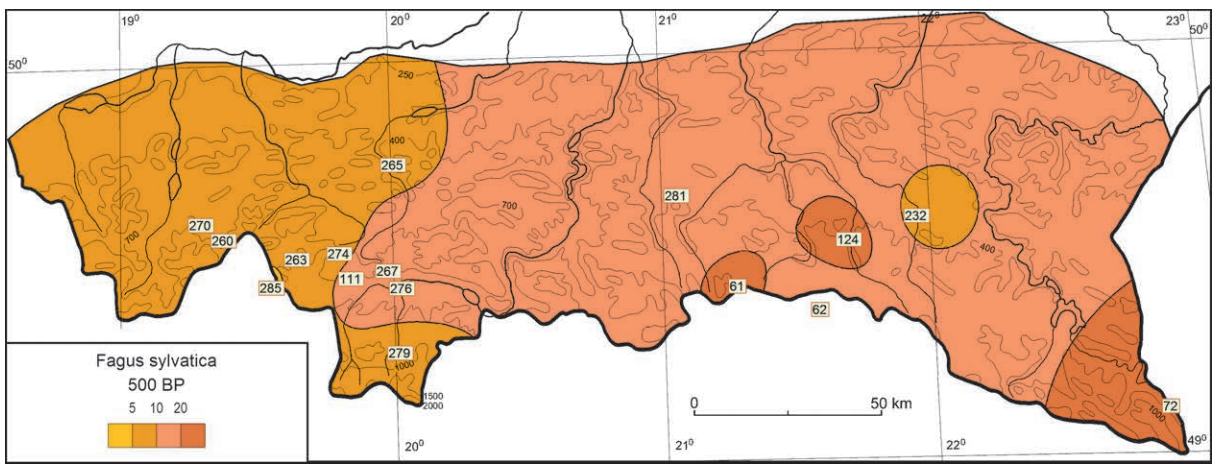

Fagus sylvatica
6000 BP
0.1 0.2 0.5 1
Fagus sylvatica
5500 BP
0.1 0.2 0.5 1 2
Fagus sylvatica
5000 BP
0.2 0.5 1
Fagus sylvatica
4500 BP
0.5 1 2 5
0 50 km

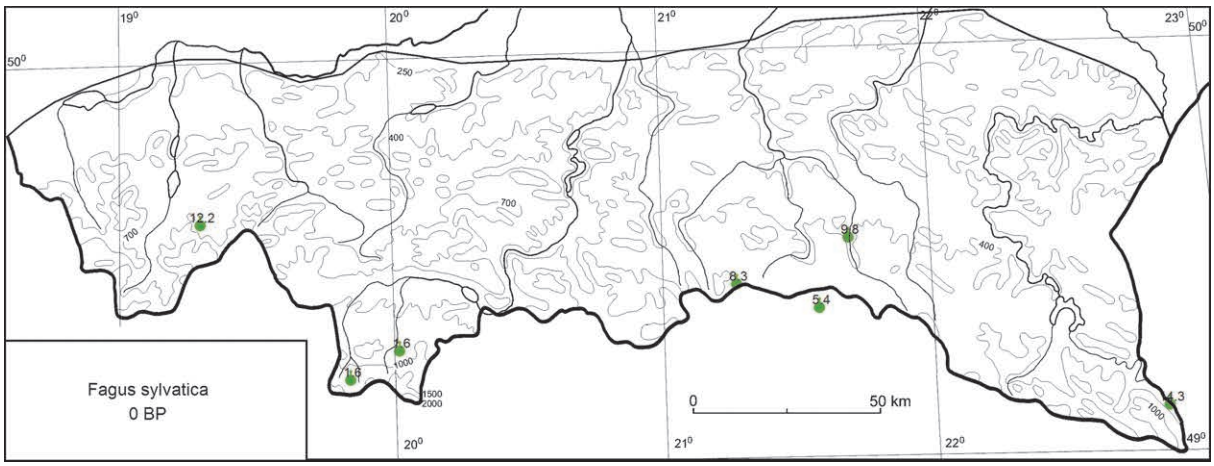

Fagus sylvatica
4000 BP
1 2 5 10
Fagus sylvatica
3500 BP
5 10 20
Fagus sylvatica
3000 BP
5 10 20
Fagus sylvatica
2500 BP
10 20
0 50 km
19°
20°
21°
22°
23°
50°
49°


Fagus sylvatica
2000 BP
10 20
0 50 km


Fagus sylvatica
1500 BP
10 20
0 50 km


Fagus sylvatica
1000 BP
10 20
0 50 km


Fagus sylvatica
500 BP
5 10 20
0 50 km


19°
20°
21°
22°
23°
50°
49°
250
400
700
1000
1500
2000
12.2
9.8
8.3
5.4
1.6
1.0
4.3
Fagus sylvatica
0 BP
0
50 km