Alnus Mill. – **Alder**

Kazimierz Szczepanek, Andrzej Obidowicz and Dorota Nalepka

Present distribution in the Western Carpathians

Three of ca 30 species of this genus, found in Eurasia and North and South America, occur in the Western Carpathians: green alder – *Alnus viridis* (Chaix) Dc., black alder – *A. glutinosa* (L.) Gaertner, and grey alder – *A. incana* (L.) Moench.

Green alder (*Alnus viridis*) grows in the Bieszczady Mountains (Eastern Carpathians) and is commonly found on alpine meadows, in humid and rocky gullies and close to the upper forest limit, up to ca 1348 m a.s.l. Populations introduced into the Tatra Mountains and the Gorce Mountains do not show a tendency to expand. In the Eastern Carpathians, the species occurs in the *Pulmonario-Alnetum viridis* Pawł. et Wal. 1949 association, found in the Bieszczady Mountains in a diminished form (Matuszkiewicz W. 1981).

Black alder (*Alnus glutinosa*), a tree having a Euro-Siberian distribution, is, in the Carpathians, found mainly in the submontane belt and, rather infrequently, in the lower montane forest belt. In the Tatra Mountains it attains a maximum altitude of 1290 m a.s.l. (Pawłowski 1956).

Grey alder (*Alnus incana*), a tree also having a Euro-Siberian distribution, in the Carpathians grows on the banks of rivers and streams, on moist slopes and in waterlogged habitats. In the mountains of Central Europe it extends from their foothills to the upper montane forest belt, while in the Tatra Mountains to a maximum altitude of 1350 m a.s.l. (Pawłowski 1956). In the Bieszczady Mountains, it is commonly found from their base (400 m a.s.l.) to 800 m a.s.l. At the higher altitudes it occurs less frequently, however occasionally, along streams, it reaches the upper forest limit (Jasiewicz 1966). In the Beskidy Mountains, it grows in the foothills and in the lower montane forest belt, being widespread along all rivers and streams and usually forming belts of a variable width. It usually attains an altitude of ca 800 m a.s.l. *Alnus incana* is a pioneer species. It often forms secondary thickets on slopes, that have been deforested by human activity, including rocky south-facing slopes, which are well insolated (Kornaś 1957). In the Carpathians, there are also examples of its entry into abandoned fields, unmown meadows and even ruins of houses (Wojterski 1980).

The Western Carpathians include a number of associations comprising one or both of these tree species. The most typical azonal community of the Western Carpathians is the riparian alder forest, *Alnetum incanae* Lüdi 1921, associated with fluvisols and dominated by *Alnus incana*, however, it is likely to be accompanied by *Alnus glutinosa*. A less frequent association with *Alnus incana* is the submontane ash forest, *Carici remotae-Fraxinetum* Koch 1926, growing in the foothill zone. At lower locations, that also includes *Alnus glutinosa*. The most humid forest habitats of the Western Carpathians are covered by the boggy grey alder forest, *Caltho-Alnetum* (Zarzycki 1963) Stuchlik 1965, comprising mainly *Alnus incana* and, in lower amounts, *Alnus glutinosa* (Dzwonko 1986).

Ecology

Both tree alder species are naturally found in humid habitats and on fertile soils. As a consequence of their ecological requirements, the occurrence of these species is generally associated with watercourses their natural habitats include wetlands, peat bogs, and alluvial soils of river valleys and the margins of mountain streams. The distribution of black alder covers habitats with high groundwater, low-growing peat bogs, depressed areas of forest, fens, and the banks of rivers and streams. Grey alder, in the Carpathians, occupies the banks of river valleys and streams, moist slopes and boggy forest areas. The tree is resistant to harsh climatic conditions. At present, in northern Europe, it extends to the subpolar forest limit.

Alders are wind-pollinated trees. Alder pollen grains may be transported by air currents for long distances from their origin (e.g. Środoń 1960).

The morphological structure of *Alnus* pollen grains displays features, which some palynologists, believe enable them to distinguish all three of above-mentioned species, but it is not easy. Only the identification of *Alnus viridis* appears to be based on obvious morphological features. However, the history of this species is associated rather

with the Eastern Carpathians and its appearance at sites in the Western Carpathians is only occasional. As for pollen grains of black and grey alder, their differentiation using optical microscopes has only been attempted very infrequently by a few palynologists. For this reason, the following description relates to the history of expansion of both the tree *Alnus* species (*A. incana* and *A. glutinosa*) in the Western Carpathians.

Expansion in Europe during the Late Glacial

According to Huntley and Birks (1983), refugia of the genus *Alnus* were situated in Corsica, the Carpathians, south-west Russia, and in the area of the Bay of Biscay.

Comes and Kadereit suggest the Carpathians, Corsica, southern Italy, south-east Europe, southern Spain, and Turkey as the likely refugial areas of *Alnus glutinosa* (Comes & Kadereit 1998).

In answer to the question, whether *Alnus* species were likely to survive the last glaciation in the area of the Western Carpathians, Środoń (1980) considered that it cannot be excluded that *Alnus viridis* might have occurred during that time in the Tatra Mountains, which could be confirmed by records of pollen grains of green alder from interstadial sites from the Carpathians and their foreland.

Alnus incana was indeed an important component of Carpathian interstadial plant communities during the last glaciation. The broad range of requirements of this species, confirmed by the presence of its macroscopic remains in the pleniglacial Paudorf interstadial, appears to indicate that grey alder may have survived in the Western (Northern) Carpathians after the Last Glacial Maximum of the Scandinavian Ice Sheet (Środoń 1980). In contrast to this, there is no unequivocal evidence that *Alnus glutinosa* survived this period and it should rather be assumed that it occurred outside the Carpathians at that time. However, King and Ferris, on the basis of analysis of chloroplast DNA, state that most areas of Central and Northern Europe were colonized by *Alnus glutinosa* deriving from Carpathian refugia (King & Ferris 1998).

In Late Glacial sediments of the last glaciation, *Alnus* pollen grains are recorded at low percentage values and often form continuous curves. One such curve, attaining values of 1–4% for the Bölling interstadial recorded at the site of Kotoń in the Beskid Makowski range, is likely to demonstrate the presence of alder refugia in the Carpathians or in their foreland (Margielewski et al. 2003).

History of expansion in the Western Carpathians during the Holocene (Fig. 13)

10 000–9000 BP

On the 10 000 and 9500 BP isopollen maps, in the south-western area of the Polish part of Carpathians, the infrequent occurrence of alder, indicated by very low pollen values (0.5%), is recorded. However, on the 9000 BP map, two areas of expansion of this taxon are already distinguishable, i.e. a western one, with values up to 2%, and an eastern one, with rather lower values, in the central part of the Western Carpathians and in the Bieszczady Mountains. It may be considered that only *Alnus incana* participated in this first stage of expansion, as it was likely to survive in the Carpathians after the last glaciation.

8500–8000 BP

The 8500 and 8000 BP maps show that the eastern part of the Polish Carpathians was marked by a culmination of alder and spruce, recorded in forests of the San river valley in the Bieszczady Mountains and indicated by alder pollen values up to ca 50%. Spruce-alder boggy forests initiated the formation of a generation of low peat bogs in the Bieszczady Mountains (Marek & Pałczyński 1962, Marek 1965).

Undoubtedly, the second species, *Alnus glutinosa*, also participated in this process.

In the western area, i.e. to the west of the reservoirs of Rożnów and Czchów on the Dunajec river, pollen values do not exceed 5%.

7500 BP

The 7500 BP isopollen map shows three distinct regions, occupied by alder to a different extent, within the Carpathians. These were the western region (to the west of the Dunajec river), the central (to the east of the Dunajec river, up to the middle San river) and the eastern one (from the middle San river up to the Polish border). In the eastern region, the distribution of alder is uneven. Pollen values for the western region, the Bieszczady Mountains and the central region attain 10–20%, 20–50%, and 5%, respectively.

7000–6500 BP

The 7000 and 6500 BP maps are very similar. The most Western Carpathian regions are dominated by alder, indicated by pollen values, reaching 10–20%.

Areas to the east of longitude 21°E, up to the Polish border, are also characterized by similar amounts, whereas the central region yields values of only 10% of *Alnus* pollen.

6000–5500 BP

The 6000 and 5500 BP maps seem to indicate the spread of areas having only a relatively smaller proportion of alder, so that alder was local or infrequent in the vegetation: sites Jasiel (site no. 125) and Szymbark (126) in the Beskid Niski range, Jesionowa (261) in the Beskid Sądecki range, Pcim-Sucha (265) in the Beskid Makowski range, and Lubogoszcz (275) in the Beskid Wyspowy range.

This may result from greater competition and, to some extent, changes in the structure of the mixed deciduous forests (*Quercus*, *Tilia*, and also *Picea*).

5000–4000 BP

The 5000 and 4000 BP maps primarily illustrate the extending distribution and increasing role of alder in the eastern part of Carpathians within Poland. Areas to the east of longitude 21°E are marked by a higher proportion of *Alnus* in the vegetation (10–50%). The Bieszczady Mountains are covered by the 50% isopoll, being the maximum frequency of this species in the Polish Carpathians. The most south-westerly part of the Carpathians displays an increased occurrence of this taxon as well.

3500–1500 BP

The 3500 to 1500 BP isopollen maps present the proportion of *Alnus* as generally equally distributed within the vegetation of the study area and indicated by a pollen frequency of ca 10–20%. However, from the Przełęcz Dukielska Pass, a rather small area with a greater abundance of alder (50%) gradually expanded.

1000 BP

On the 1000 BP map, the greater proportion of alder in vegetation still remains in the westernmost areas (10–20%), south-eastern regions with the Bieszczady Mountains, the surroundings of the Beskid Niski range and, in part, the vicinities of the Jasło-Sanok Depression. A large part of the Polish Carpathians, bounded by the Polish border on the east and by the Skawa river to the west, excluding the area adjacent to the Beskid Niski range, is characterized by a moderate proportion of alder in the vegetation (10%).

500 BP

The 500 BP map is marked by changes in the amount of *Alnus* within the vegetation of the Western Carpathians. The frequency of this tree decreased in the south-easternmost part of the region. Pollen spectra at certain sites provide a basis for the assumption that only in the westernmost part of the Polish Carpathians and in the northern areas of the Beskid Niski range did the amounts of alder remain at the same values as recorded ca 500 years earlier.

0 BP

The 0 BP map presents a rather low frequency of alder in the vegetation across nearly the entire area of the Polish Carpathians, excluding the Beskid Żywiecki Range and their surroundings, as well as parts of the Beskid Niski range adjacent to the Przełęcz Dukielska Pass.

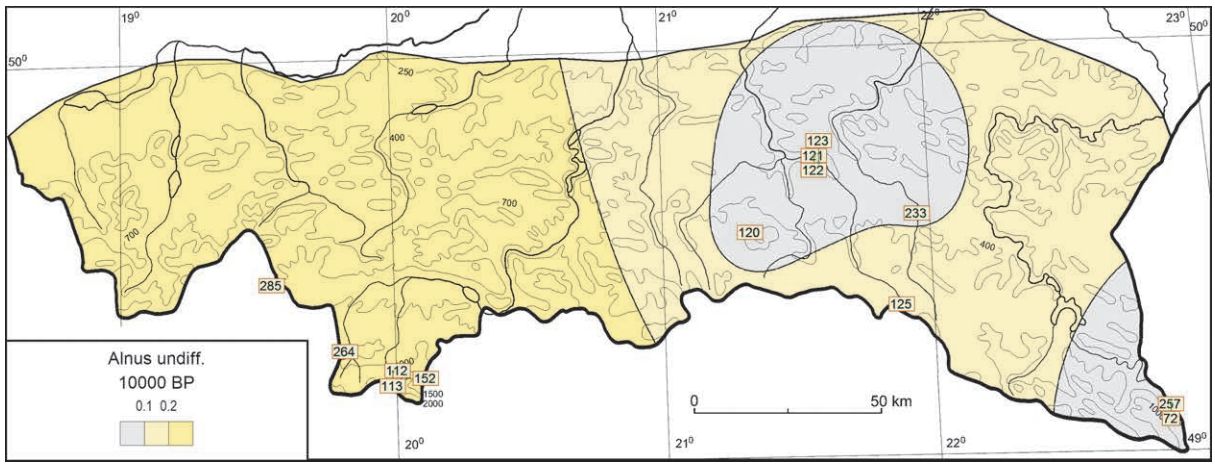
Conclusions

The history described here covers the sequence of events involving both tree alder species found in the Western Carpathians, i.e. *Alnus incana* and *A. glutinosa*. The third species of alder occurring in the Polish part of Carpathians, *Alnus viridis*, is associated with the Eastern Carpathians.

The sparse occurrence of *Alnus* at the beginning of the Holocene tends to confirm the assumption that *Alnus incana* survived the last glaciation in the area of the Western Carpathians. At 8500–8000 BP, to the east of the Dunajec river valley, alder greatly increase its area of distribution. As this was also the time of appearance of alder bogs, it may be considered that *Alnus glutinosa* participated in this expansion also.

For the following thousands of years the proportion of tree alders in stands of vegetation in the Western Carpathians was affected by local changes; however, these species constantly remained an important component of that vegetation.

Fig. 13. *Alnus*: dot and isopollen maps for 10 000–0 BP


Alnus undiff.
10000 BP
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121
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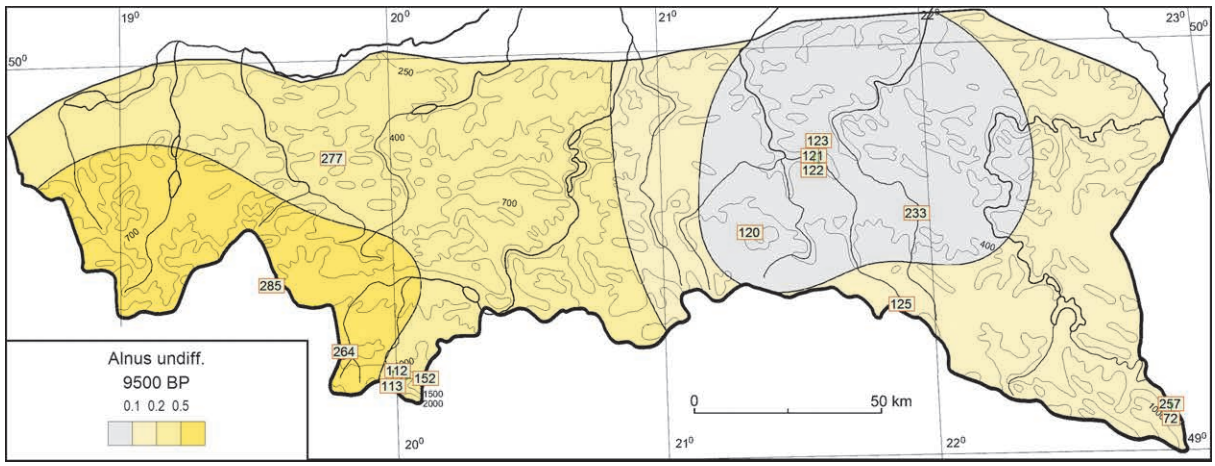
72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9500 BP
0.1 0.2 0.5
0 50 km
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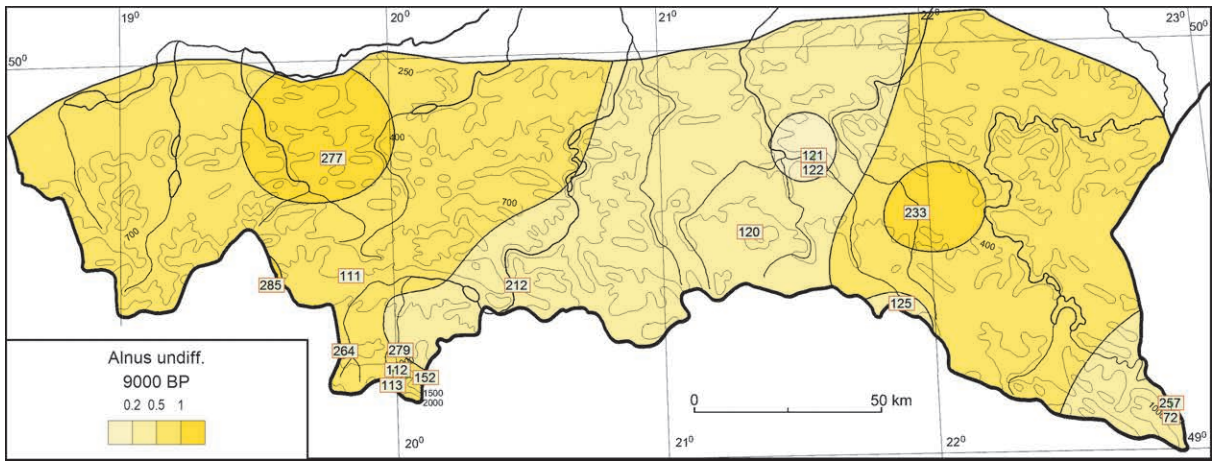
257
72


Alnus undiff.
9000 BP
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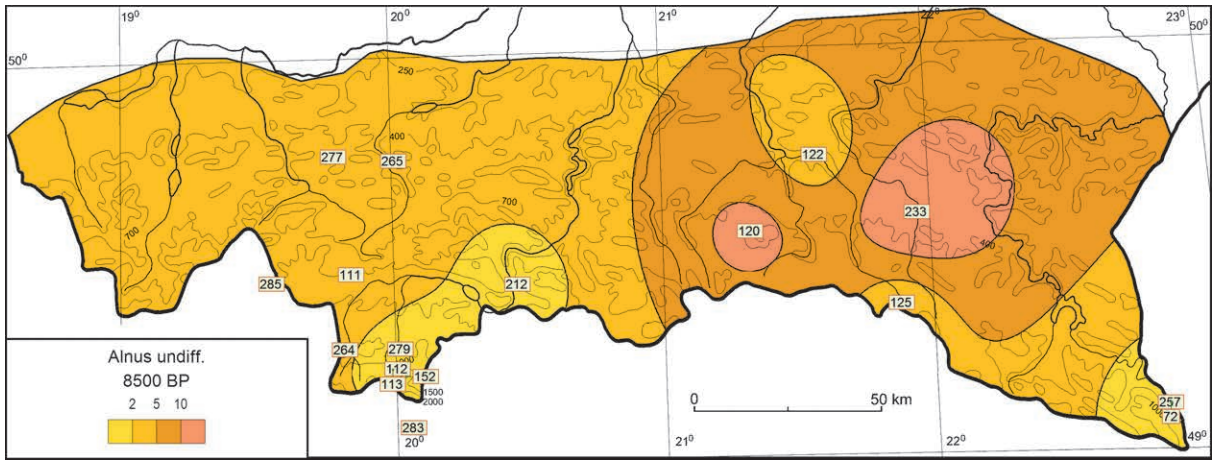
Alnus undiff.
8500 BP
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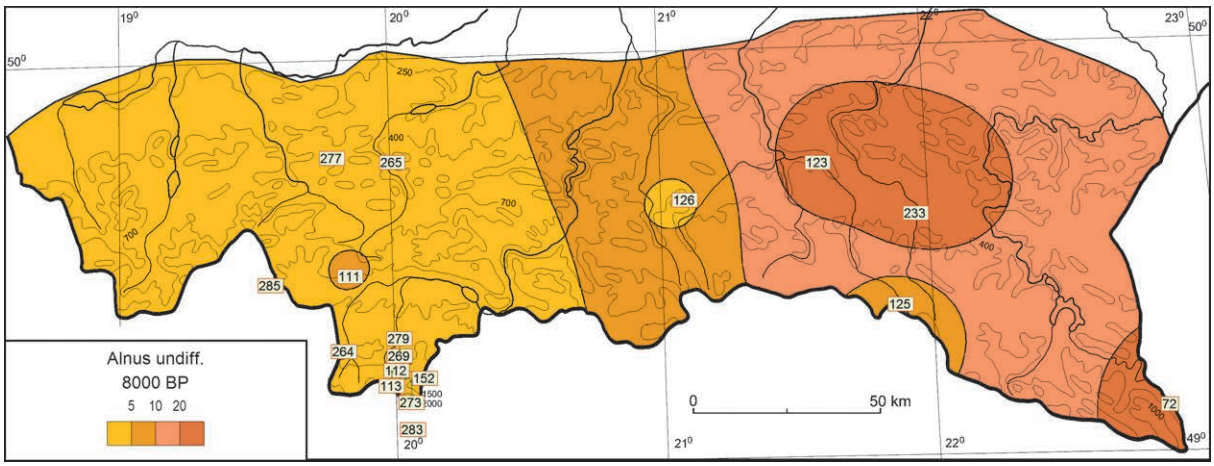
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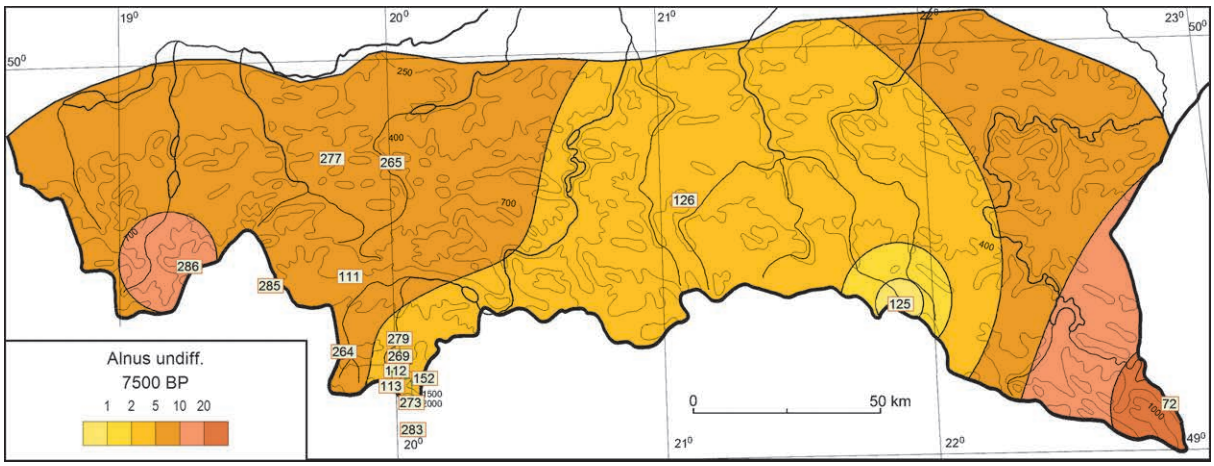
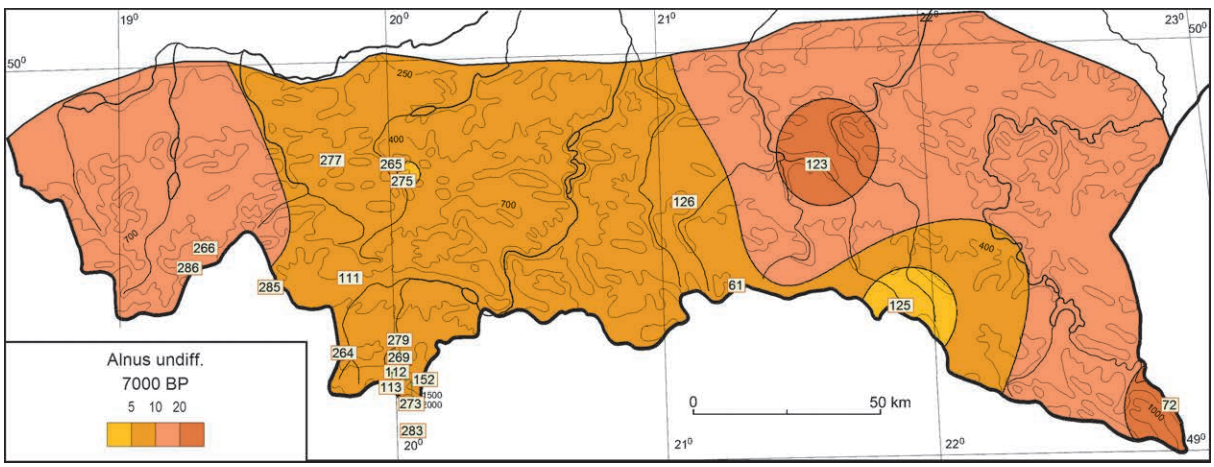
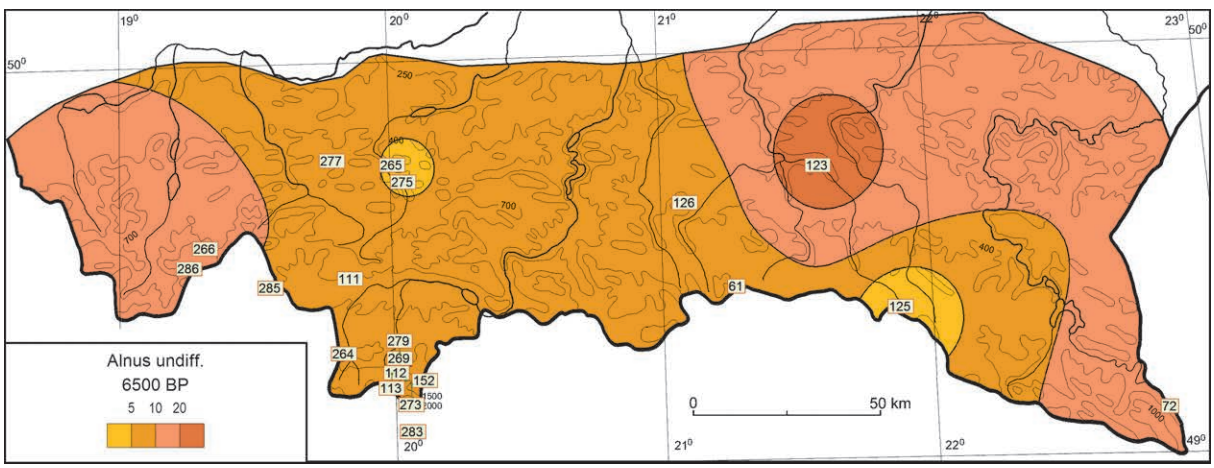
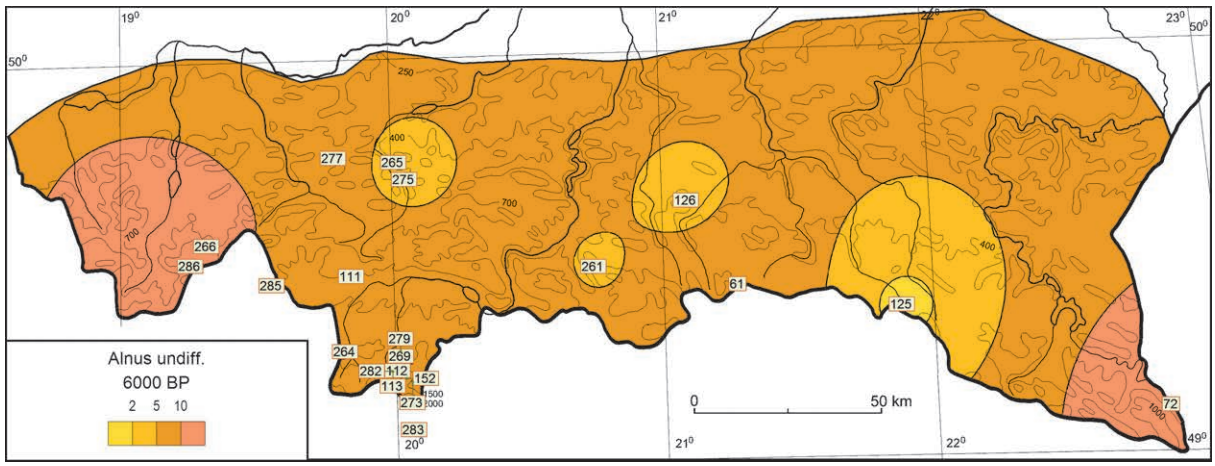
8000 BP
5 10 20
0 50 km


Alnus undiff.
7500 BP
1 2 5 10 20
0 50 km


Alnus undiff.
7000 BP
5 10 20
0 50 km


Alnus undiff.
6500 BP
5 10 20
0 50 km


Alnus undiff.
6000 BP
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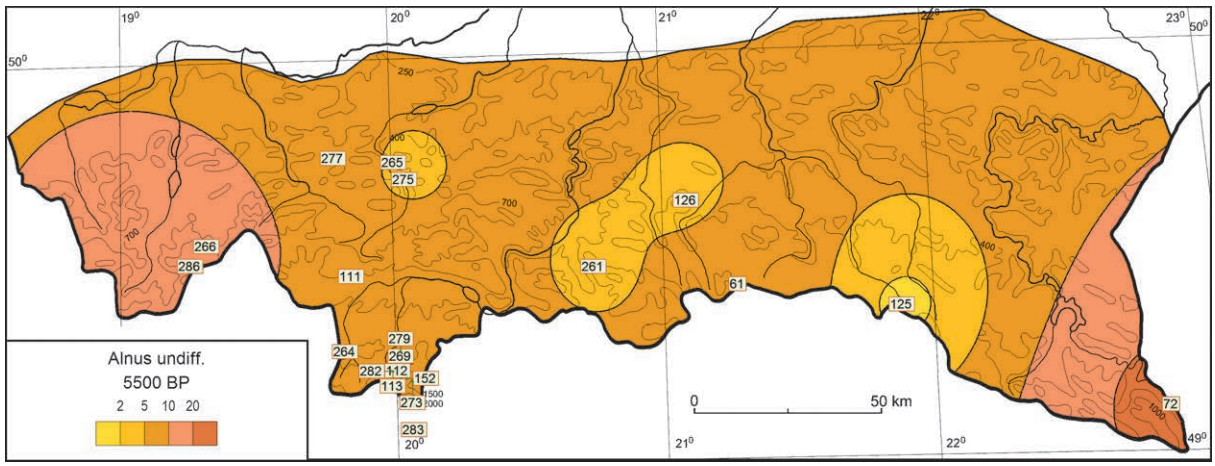
0 50 km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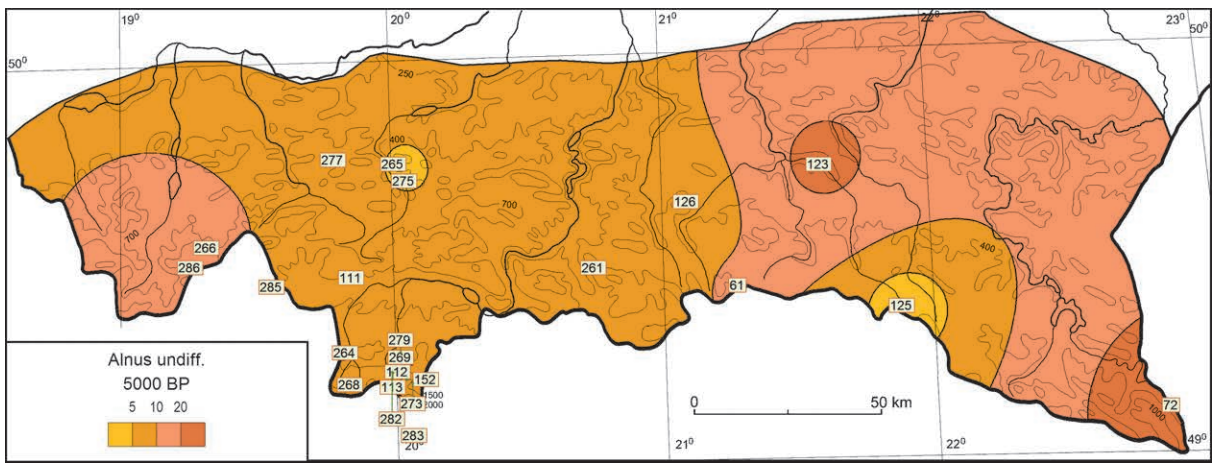
5500 BP
2 5 10 20
0 50 km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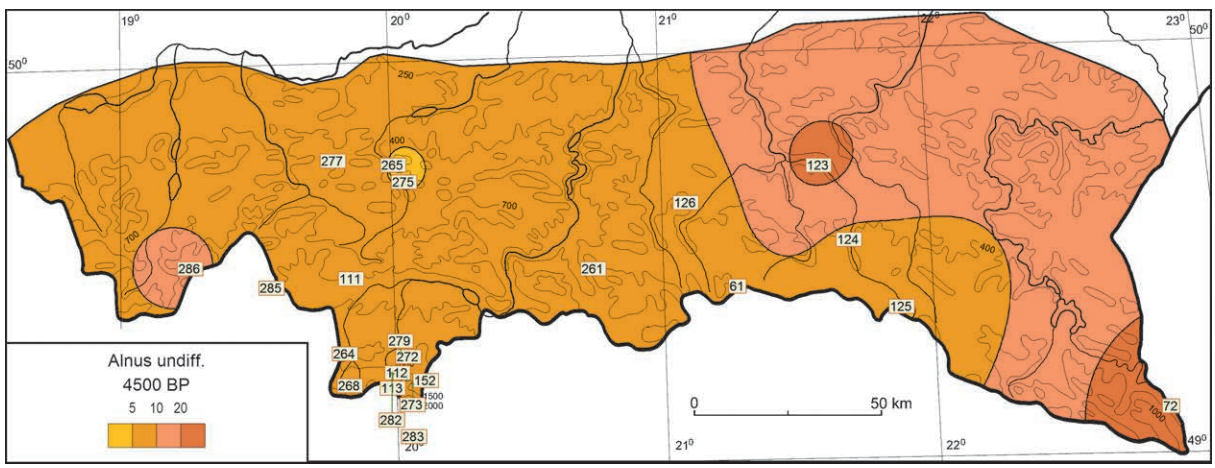
5000 BP
5 10 20
0 50 km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4500 BP
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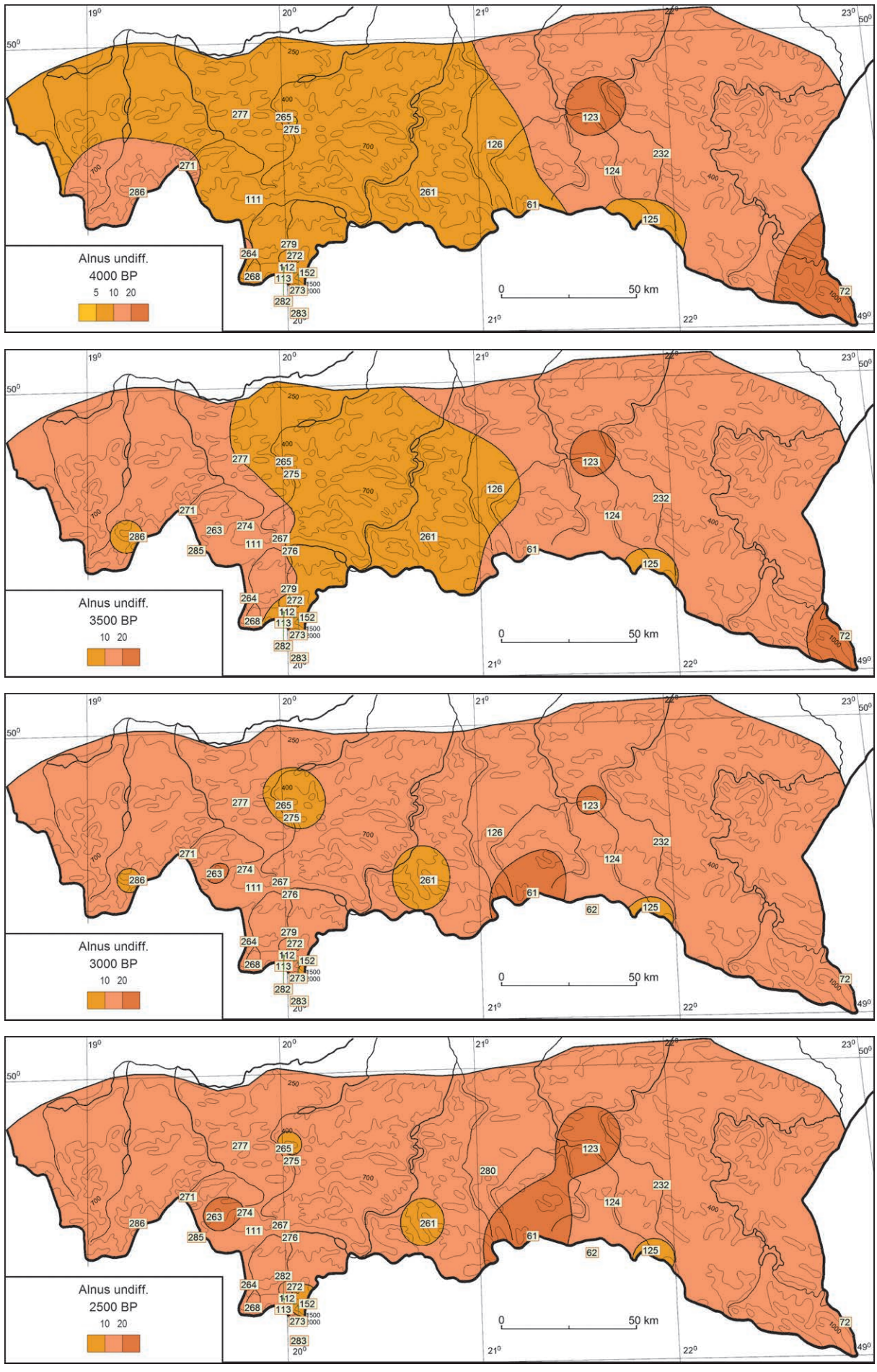
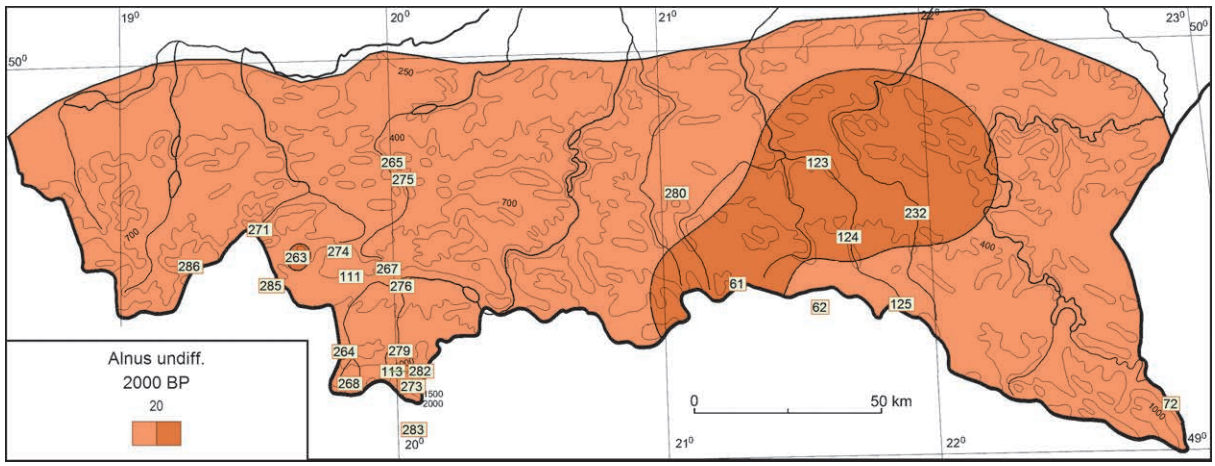
0 50 km


Alnus undiff.
4000 BP
5 10 20
Alnus undiff.
3500 BP
10 20
Alnus undiff.
3000 BP
10 20
Alnus undiff.
2500 BP
10 20
0 50 km


Alnus undiff.
2000 BP
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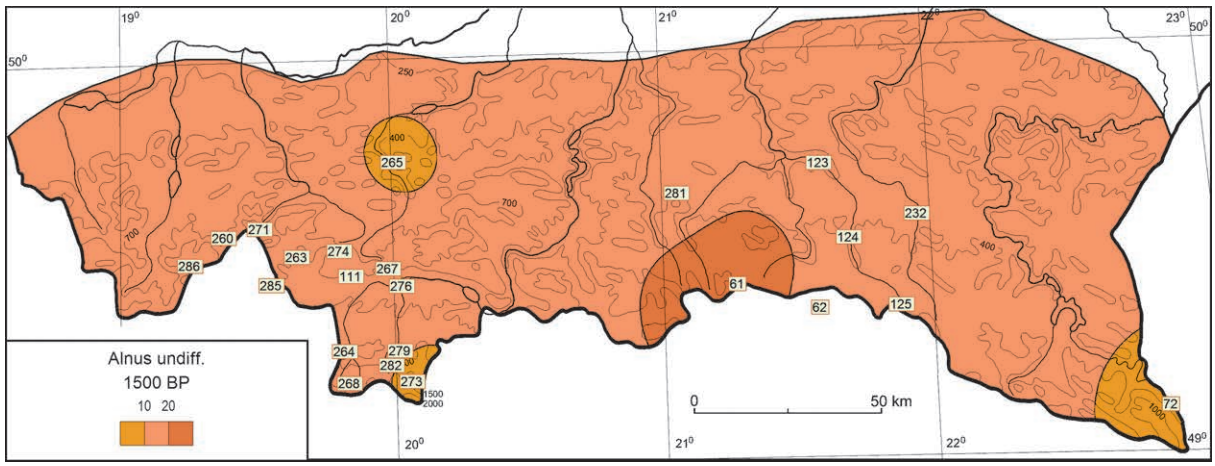
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1500 BP
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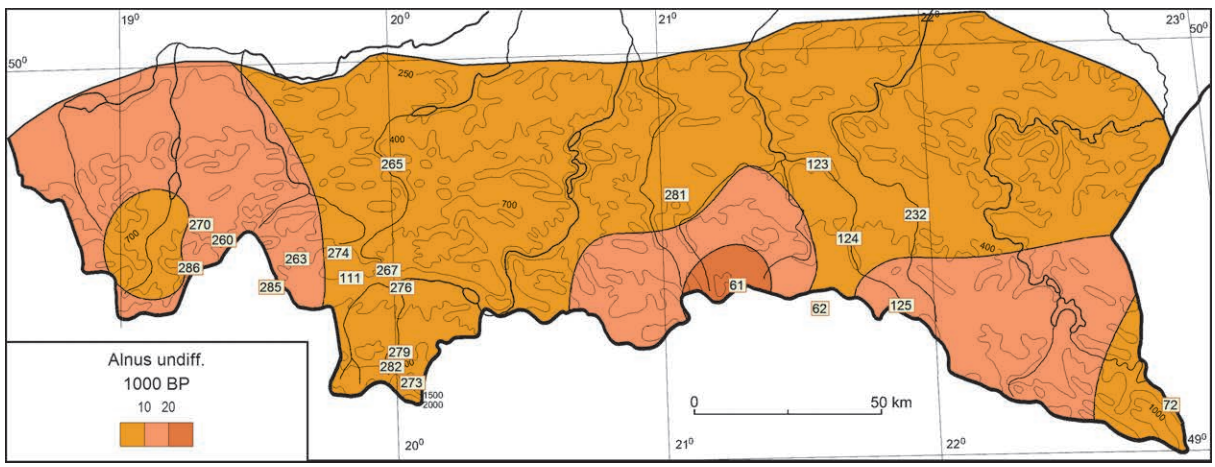
Alnus undiff.
1000 BP
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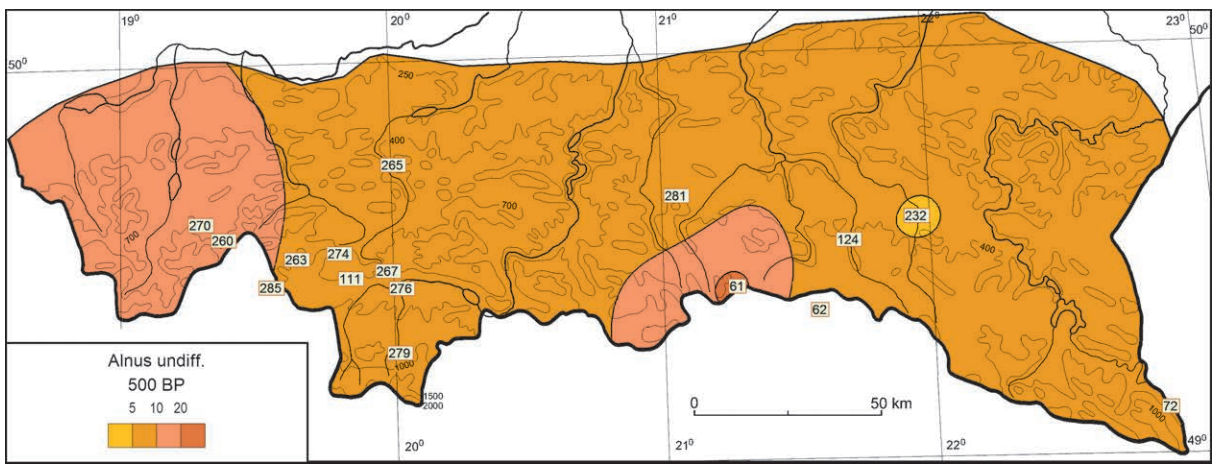
Alnus undiff.
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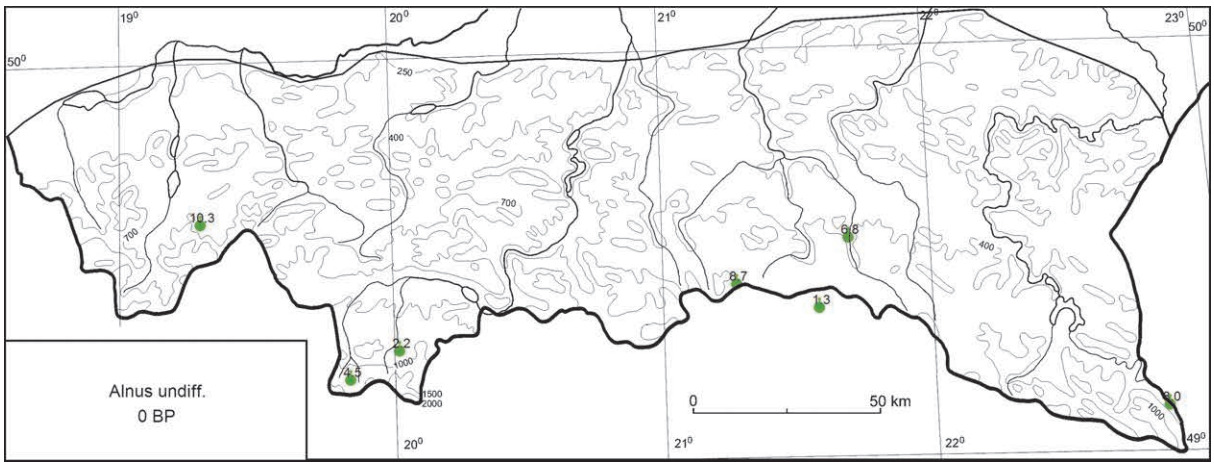
19°
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2.2
4.5
3.0
Alnus undiff.
0 BP
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50 km