Pinus L. subgenus *Pinus* (subgen. *Diploxylon* (Koehne) Pilger) – **Pine**

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Present distribution in the Western Carpathians

Pinus sylvestris, on a global scale, is one of the most abundant *Pinus* species and is native to areas of Europe and Asia. The Polish flora comprises four native *Pinus* species: *P. sylvestris*, being the most numerous one, the montane *P. mugo* and *P.* × *rhaetica*, all classified within subgenus *Pinus* (previously *Diploxylon*), and *P. cembra* of subgenus *Strobus*. Pollen grains of *P. cembra* and of plants representing subgenus *Pinus* differ slightly in their morphological structure (Boratyński 1993, Moore et al. 1991).

Within the Carpathians, *Pinus sylvestris* is found in minor amounts, exclusively at small sites, some of which attain the upper forest limit in the mountains. Most frequently the species is accompanied by *Picea* and *Abies*. The Bieszczady Mountains are located beyond the range of occurrence of dense, natural stands of *Pinus* and only single, isolated sites are recorded there. *Pinus sylvestris* forms several varieties differing in their morphological traits, depending on local habitat conditions (Boratyński 1993). *Pinus mugo* is a montane shrub species growing above the upper forest limit, in the subalpine belt, e.g. in the Tatra Mountains and in the Beskid Żywiecki range (Babia Góra and Pilsko Mountains as well as small sites in the Polica, Romanka and Czyrniec Mountains). Until the 1990s, a relic site of dwarf pine was also situated in the Beskid Niski range (nature reserve "Kornuty"). The taxon is a dominant component of the association *Pinetum mugo carpaticum* Pawł. 1927. The Carpathian dwarf mountain pine scrub shows optimum development in the Tatra Mountains, the Babia Góra Mountain and at the summit of the Pilsko Mountain in the Beskid Żywiecki range (Matuszkiewicz J.M. 2002). *Pinus* × *rhaetica*, an interspecific hybrid of *P. sylvestris* and *P. mugo*, is found at a few sites in the southern areas of Poland (Staszkiewicz 1993b).

Ecology

Pinus sylvestris is a monoecious, evergreen tree which usually attains a height of 15–30 m and a trunk circumference of ca 1 m. Leaves of this species form long needles, replaced every 2–4 years under a mild climate and up to every 9 years in areas subject to a subarctic climate (Steven & Carlisle 1996, Farjon 2005). The life expectancy of pine amounts to 150–300 years, however the age of particular specimens in Sweden is estimated to exceed 700 years (Steven & Carlisle 1996, Farjon 2005).

P. sylvestris grows on various types of soils, including poor soils and peat bogs. Its root system is horizontal and grows shallowly into the ground, however individuals occupying sandy soils occasionally develop vertical roots reaching a depth of as much as 1.5–3.0 m.

It is a wind-pollinated tree producing large amounts of pollen grains provided with air sacs and showing good adaptations for air dispersal (Dyakowska 1936, Koski 1970, Niklas 1985). At a wind velocity of 5 m/s, pine pollen grains are likely to travel a distance of 47–60 km within 3 hours (DiGiovanni & Kevan 1991). *Pinus* pollen has even been recorded hundreds of kilometres from its closest sources (Koski 1970, Nichols et al. 1978, Campbell et al. 1999). In advantageous atmospheric conditions, many pollen grains are still viable after travelling such a distance (Varis et al. 2009, Williams 2010).

In nature, pine does not reproduce vegetatively (Skilling 1990). It becomes able to produce viable seeds relatively early, usually when 10–15 years old, and may perhaps continue to do so for 200 years, with periods of intensive seed production repeating every 3–6 years. Mature seeds, possess an elongate wing and fall out of opening cones in spring, ca 22–24 months after pollination, but most of them are not dispersed more than a distance of 50–100 m from the parent tree (Skilling 1990). Seedlings develop properly only if access to sufficient amount of light is available. Those growing in shade mostly do not live to be more than 7 years old, and only infrequently do single individuals live to be 50 years old under such conditions (Steijlen & Zackrisson 1987, Tarasiuk & Zwieniecki 1990). Acid soils with a low pH suit the growth of pine seedlings (Carter 1987). Young seedlings are most frequently found in forest clearings or in areas where the forest cover was destroyed by fire or disturbed by human activity.

Expansion in Europe during the Late Glacial and Holocene

The Carpathians and the Sudety Mountains were most likely the regions in which *Pinus* encountered conditions enabling its survival during the last glacial stage. From here, ca 13 000 BP, the taxon spread into the area of Poland (Latałowa et al. 2004a). The occurrence of pollen grains and macrofossil remains of *Pinus sylvestris* and other trees, recorded in Slovakia and the Czech Republic for the period of the Last Glacial Maximum, confirms previous reports of a large refugium located in the Western Carpathians (Jankovská & Pokorny 2008). Data obtained from analyses of present-day populations also indicate the Carpathians as part of the *Pinus* migration pathway, passing through Slovakia to South Poland and Germany (Androsiuk et al. 2011).

History of expansion in the Western Carpathians during the Holocene (Fig. 22)

In the area of Poland, including the Carpathians, presence of *Pinus* pollen was recorded for the Late Glacial. In the period preceding the beginning of the Holocene (ca 10 500 BP), percentage values of *Pinus* pollen constantly attained 40–60% across the entire Carpathians (Latałowa et al. 2004a), indicating the local occurrence of forests abundant in this taxon.

10 000 BP

Pinus was found over the entire area of the Carpathians. A distinct boundary, overlapping areas of the Beskid Wyspowy and Beskid Śląski ranges, separates the Carpathians into two regions marked by different proportions of pine pollen. The eastern part is characterized by values between 18.2 and 56.7%, while a large part of the Western Carpathians displays higher amounts of *Pinus* pollen, from 41.5% in the Tatra Mountains to 78.6% at the site Molkówka (site no. 264), also located within the Tatras. During this period, forests strongly dominated by pine attain their maximum Holocene distribution.

9500 BP

Most Carpathian areas are covered by the 40–50% *Pinus* isopoll. Regions with higher amounts of pine (exceeding 50%) are much smaller and located in the Beskid Śląski and Beskid Żywiecki ranges, part of the Orawa-Nowy Targ Basin and part of the Tatra Mountains. As for the eastern part of the Carpathians, high proportions of *Pinus* pollen, exceeding 50%, were recorded at the sites of Besko (232, 233) within Jasło-Sanok Depression), sites Tarnowiec (123) and Roztoki (121,122).

9000–8500 BP

The entire area of the Carpathians is covered by *Pinus* isopolls indicating similar frequency of pollen ranging from 20% to 50%. Proportions exceeding 50% were recorded exclusively at the site of Bryjarka (212), within the Beskid Sądecki range, for ca 9000 BP. According to the dot maps, the highest values within this period were recorded at ca 9000 BP at the site of Roztoki b (121) – 69%, while the lowest ones, at ca 8500 BP, in the Tatra Mountains (12.1%).

8000 BP

The isopollen map indicates a decrease in the proportion of *Pinus* pollen grains, particularly in eastern areas of the Carpathians (down to ca 10–20%). The site of Tarnowiec (123), marked by slightly higher values (22.2%), is an exception. In the western part of the Carpathians, reduced amounts were recorded only in a limited area, covering the Beskid Makowski range and part of the Orawa-Nowy Targ Basin. According to the dot map, frequency of pine pollen had decreased also at several sites within the Tatra Mountains.

7500–6000 BP

A progressive decrease in pine pollen percentages clearly indicates a fall in abundance of this tree within the forests. For the period of ca 7500 BP, most Carpathian regions are covered by the 10–20% isopolls. However, for a large area, particularly in the eastern part of the mountains, no data have been recorded, so that the relative abundance of pine could not be estimated. Locally, at the site of Szymbark (126) and in the south-eastern proximities of the Bieszczady Mountains, the frequency of pine pollen decreases below 10%. On the dot map, lower proportions of pine pollen are visible also in the western part of the Carpathians, at the sites of Bogdanówka-Beło (277) and Zlatnická Dolina (286), which do not contribute to isopollen maps before 7000 BP. Due to a decrease in the proportion of *Pinus*, lasting for ca 1000 years, regions marked by lower frequency between 5 and 10% are seen to expand and at ca 6000 BP included the Beskid Makowski and Beskid Żywiecki ranges as well as the Pogórze Ciężkowickie Foothills and the Beskid Sądecki range with their surroundings. Those small areas that had shown higher amounts of *Pinus* pollen grains (20–50%) at ca 7500 BP, notably parts of the Beskid Niski and Beskid Sądecki ranges, the Bieszczady Mountains, the Tatra Mountains, and the Orawa-Nowy Targ Basin, were strongly reduced by ca 6000 BP. For ca 6000 BP a large area of the Carpathians is covered by 10–20% isopolls, only sites in a limited area of the Tatra Mountains and the site of Jasiel (125) are shown on the dot maps with proportions of pine pollen exceeding10%. At sites located in higher parts of the Tatra Mountains, *Pinus* frequency may comprise mainly pollen grains of *P. mugo*.

5500–3500 BP

Changes in the composition of tree stands resulted in a noticeable decrease even in the area covered by the 5–10% isopoll over much of the Carpathians. Isopollen maps plotted for this period illustrate the presence of two

areas with higher amounts of pine pollen (10–20%). The first of these, located in the western part of the Carpathians is shown at ca 5500 BP covering the Beskid Wyspowy range, the Gorce Mountains, the Orawa-Nowy Targ Basin and the Tatra Mountains. However, the size of this area continuously decreased over the next 2000 years, so that by ca 3500 BP it only included the Tatra Mountains and part of the Orawa-Nowy Targ Basin. The second area marked by higher amounts of *Pinus* pollen comprised the Pogórze Dynowskie Foothills and part of its surrounding area. This area underwent some contraction but by 4000 BP had stabilized. The isopollen maps for this time period suggest that proportions of *Pinus* pollen generally did not exceed 20% across the entire Carpathians, except as a local record at one site Besko (232, 233), as indicated on the isopollen map. The lowest frequency of pine pollen are recorded in the south-eastern neighbourhoods of the Bieszczady Mountains, from ca 5500 BP, as well as in a small area of the Beskid Niski range, at ca 4500 BP. The decrease in *Pinus* pollen values in the Bieszczady Mountains is correlated with an increase in the proportion of *Fagus*, that was migrating through these mountains into the Polish part of the Carpathians (Madeja et al., Chapter: *Fagus sylvatica*, this volume).

3000–2000 BP

The two areas marked by higher proportions of *Pinus* pollen grains (10–20%), observed previously on isopollen maps, increased their ranges, fused and covered the larger part of the Carpathians. Boundary separating the western region, with lower frequency of *Pinus*, and the eastern one, typified by higher amounts, initially overlapped the area of the Beskid Wyspowy range, while from 2500 BP – of the Beskid Makowski range and the western part of the Orawa-Nowy Targ Basin. The isolated area of lower pollen values (5–10%), including the Beskid Sądecki range and its surroundings, became integrated with a region of similar number of pollen grains, located in the Bieszczady Mountains, at ca 2000 BP. The lowest amounts of *Pinus* pollen were still recorded at south-eastern proximities of the Bieszczady Mountains, dominated by i.a. *Fagus*.

1500–1000 BP

Most Carpathian areas are covered by the 10–20% isopolls. Region of lower frequency (5–10%), comprising parts of the Beskid Sądecki and Beskid Niski ranges and of the Bieszczady Mountains, slightly extended to the north at ca 1000 BP. In the same period, a small area with lower amounts of *Pinus* pollen grains (5–10%), in the western proximities of the Orawa-Nowy Targ Basin, was readibly reduced. In the Beskid Żywiecki and Beskid Śląski ranges and in part of the Beskid Makowski range proportions of pine pollen grains were decreased to 5–10%. Only the site of Tarnowiec (123) is covered by isopolls of 20–50%, however dot maps indicate also the occurrence of other sites with frequency of pine pollen exceeding 20%.

500 BP

Dot map for the period of ca 500 BP confirms the record of *Pinus* pollen grains at 16 sites, while percentage values do not exceed 20%.

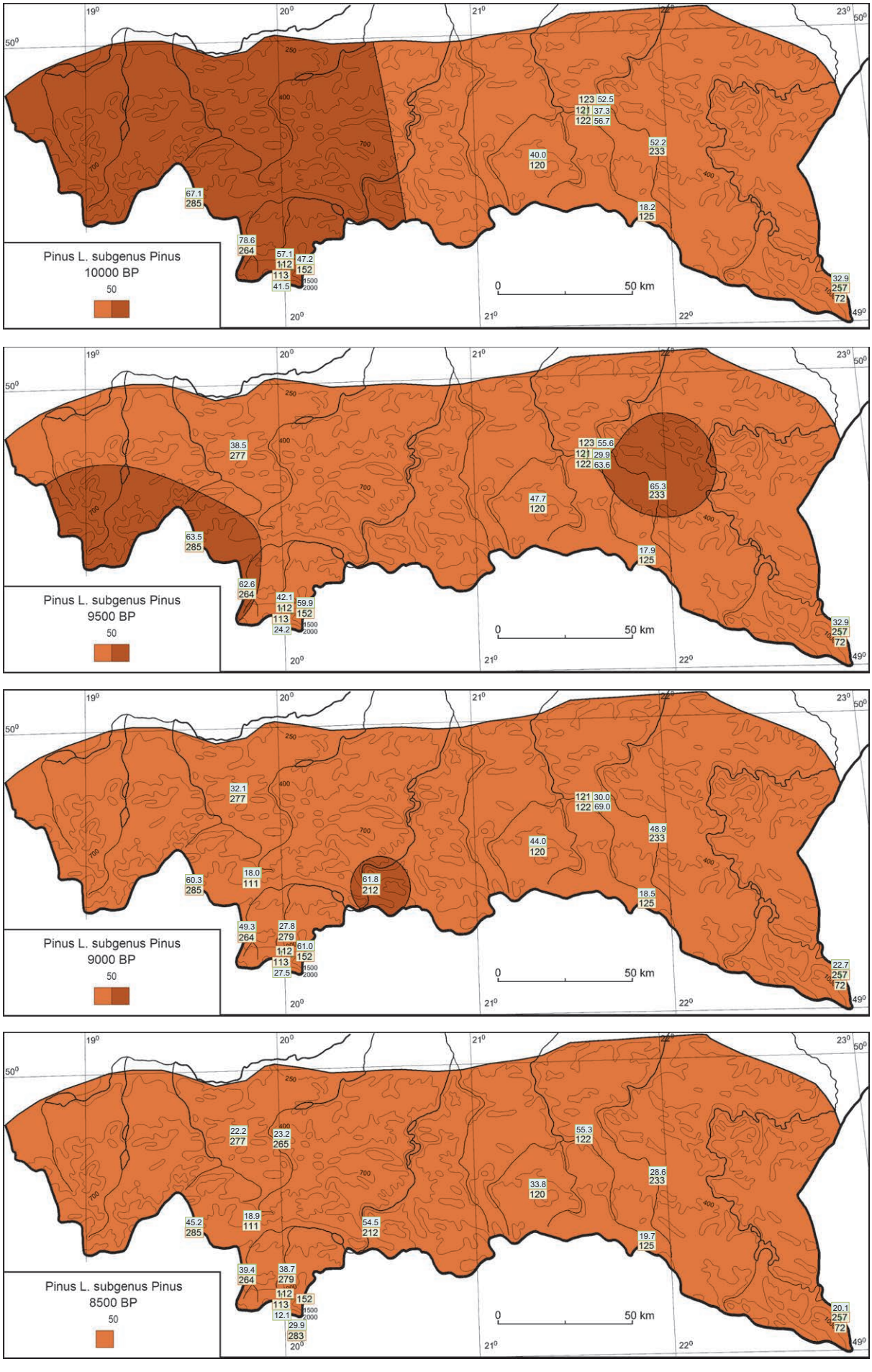
0 BP

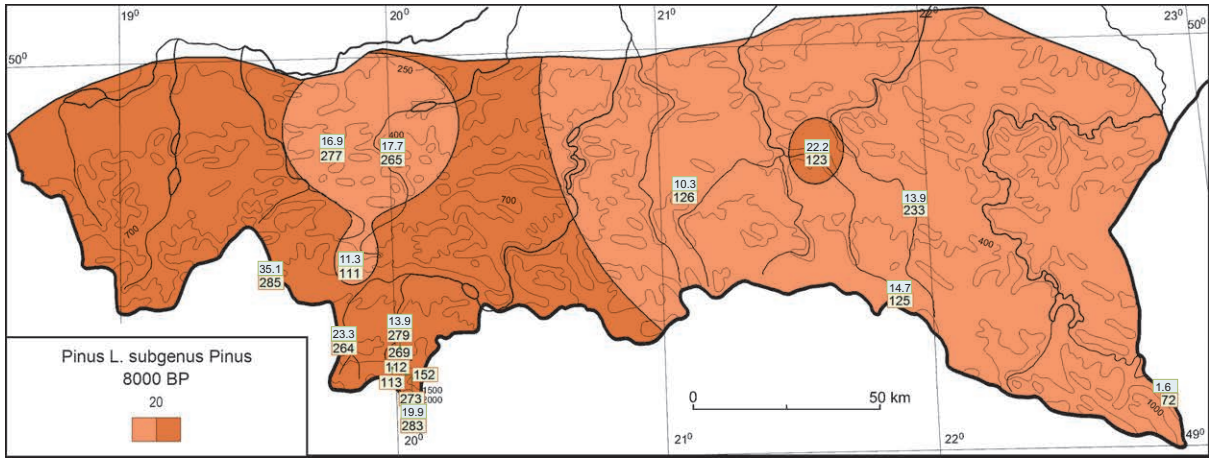
The number of sites with the occurrence of pine pollen decreases to seven. Among the sites, only one, Kružlová within Beskid Niski range (62), located beyond the southern Polish border, is characterized by high proportions of *Pinus* pollen grains (43.3%).

Conclusions

Both palaeobotanical and molecular data indicate the occurrence of *Pinus* refugia in the Carpathians during the last glaciation. Most likely, these sites originated the Late Glacial migration of pine into southern areas of Poland. If the value of 50% is assumed the minimum amount of pine pollen evidencing its local dominance in communities (Huntley & Birks 1983), the greatest importance of *Pinus* in its Holocene history should be dated to ca 10 000 BP. This period is followed by a decrease in proportions of pine, recorded already on the 9500 BP map and proceeding as consequence of expansion of deciduous trees competitive to *Pinus*.

Fig. 22. *Pinus* L. subgen. *Pinus*: dot and isopollen maps for 10 000–0 BP; next to the sites number the percentage values of pollen are given


Pinus L. subgenus Pinus
10000 BP
50
Pinus L. subgenus Pinus
9500 BP
50
Pinus L. subgenus Pinus
9000 BP
50
Pinus L. subgenus Pinus
8500 BP
50
0
50 km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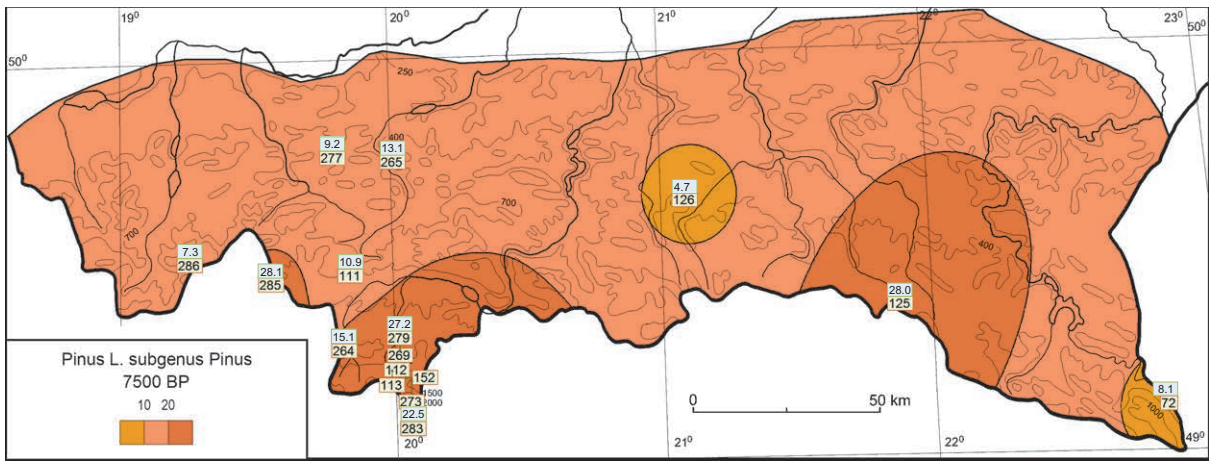
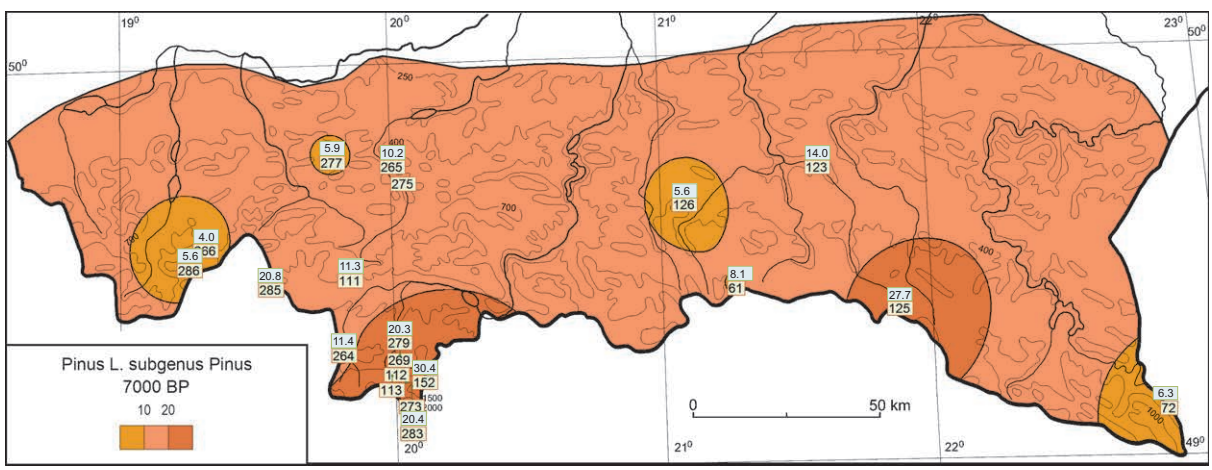
8000 BP
20
0
50 km


Pinus L. subgenus Pinus
7500 BP
10 20
0
50 km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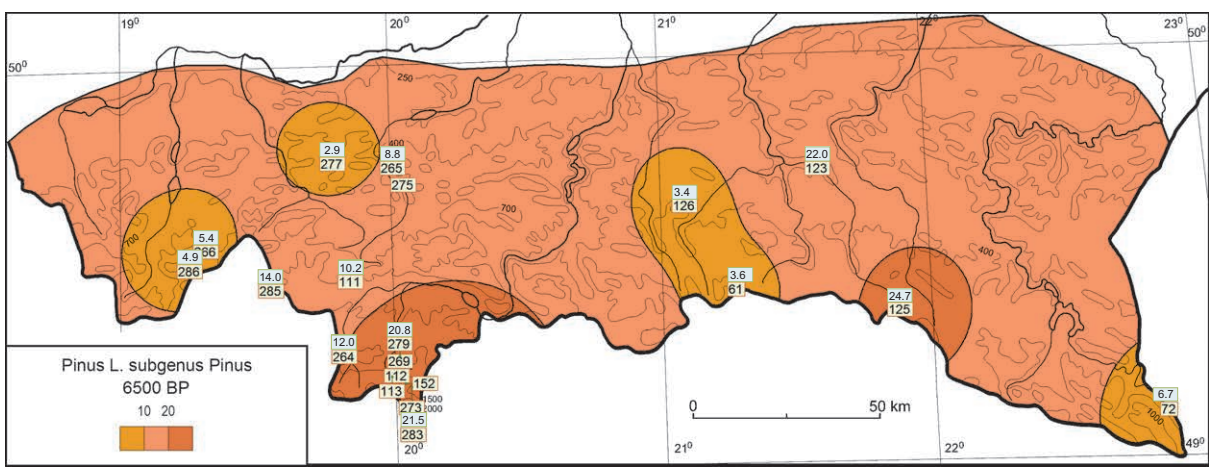
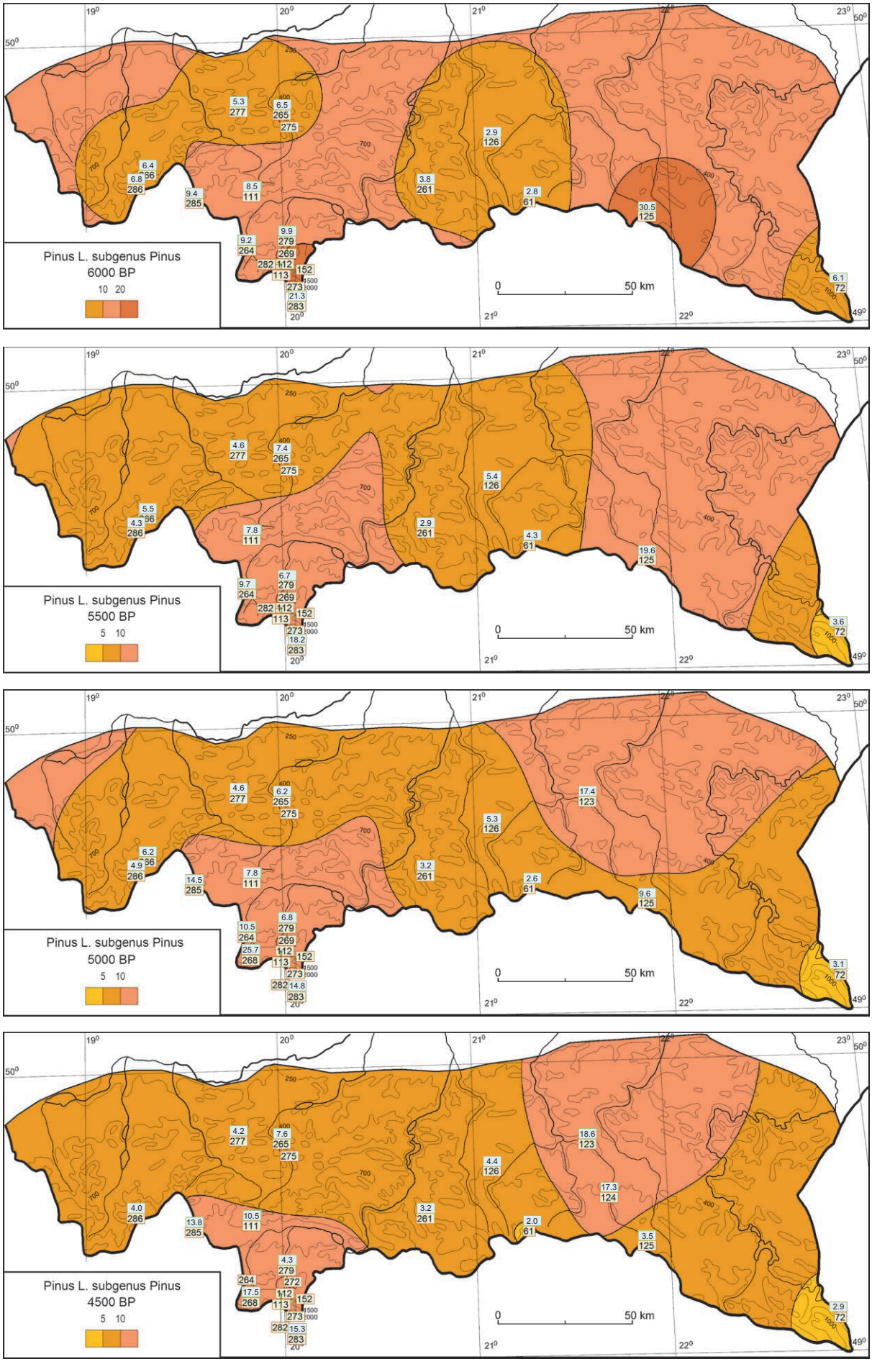
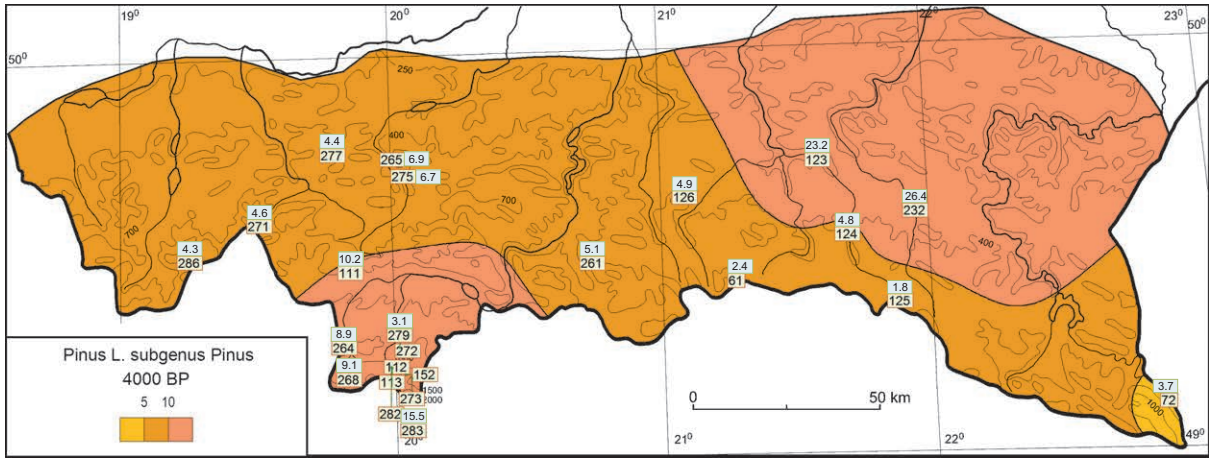
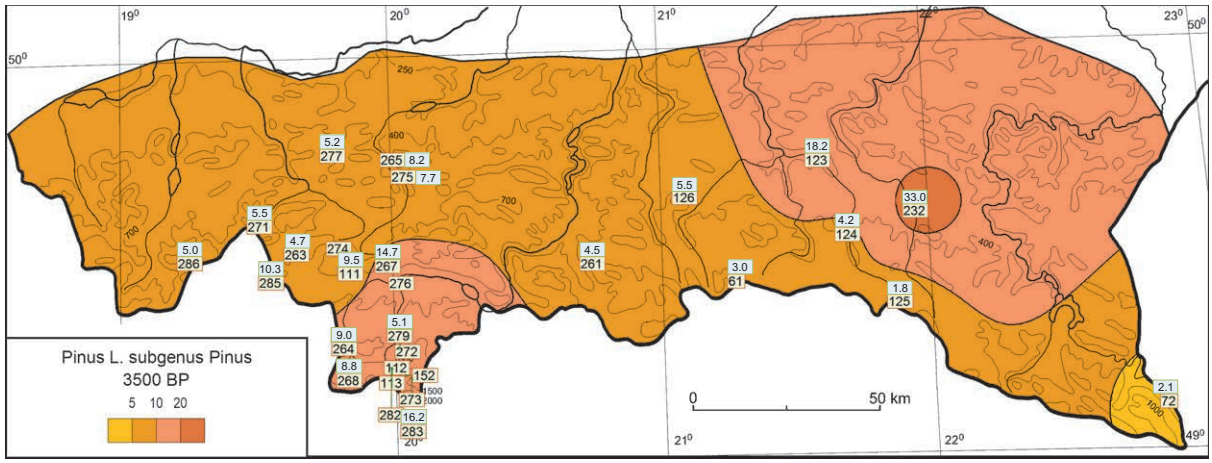
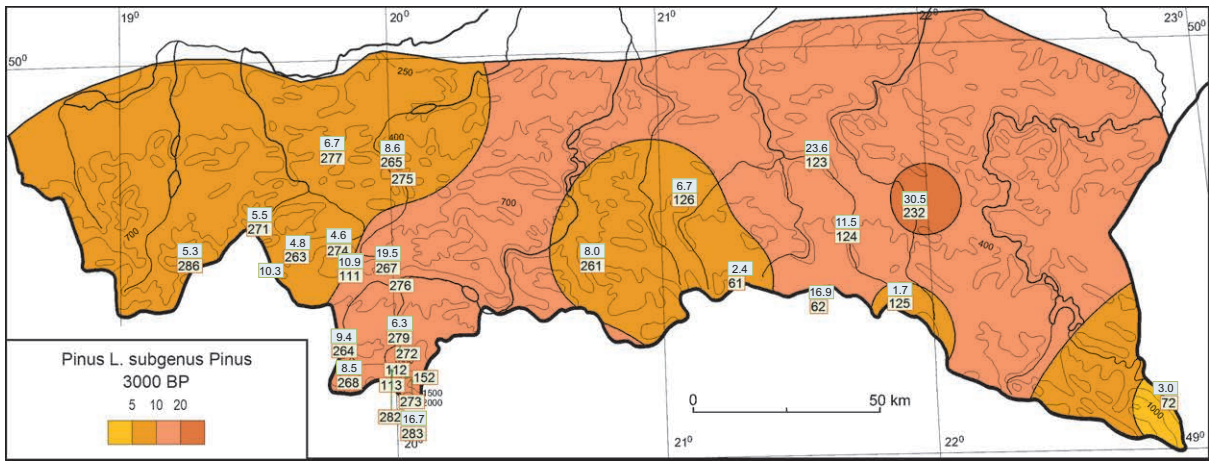
7000 BP
10 20
0
50 km

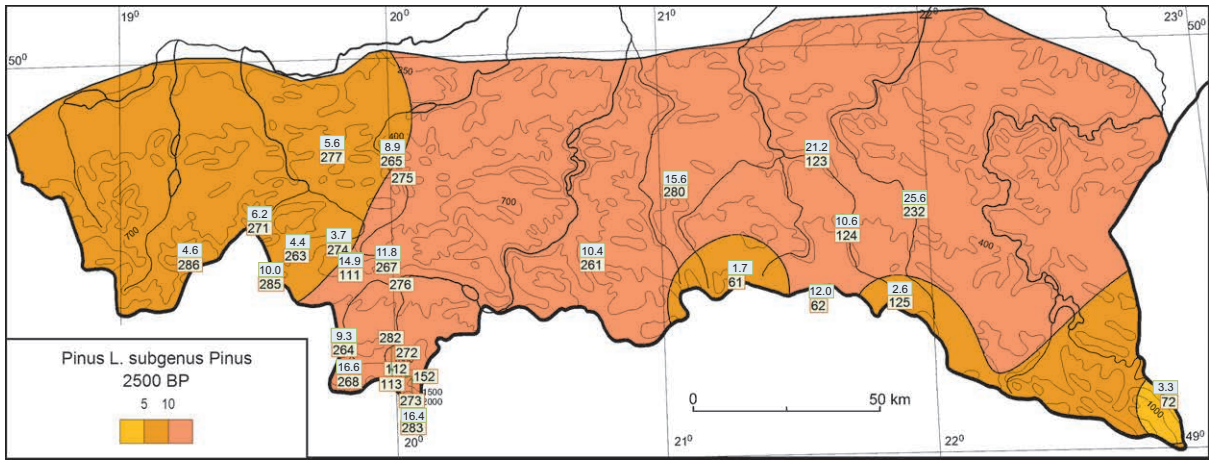

Pinus L. subgenus Pinus
6500 BP
10 20
0
50 km

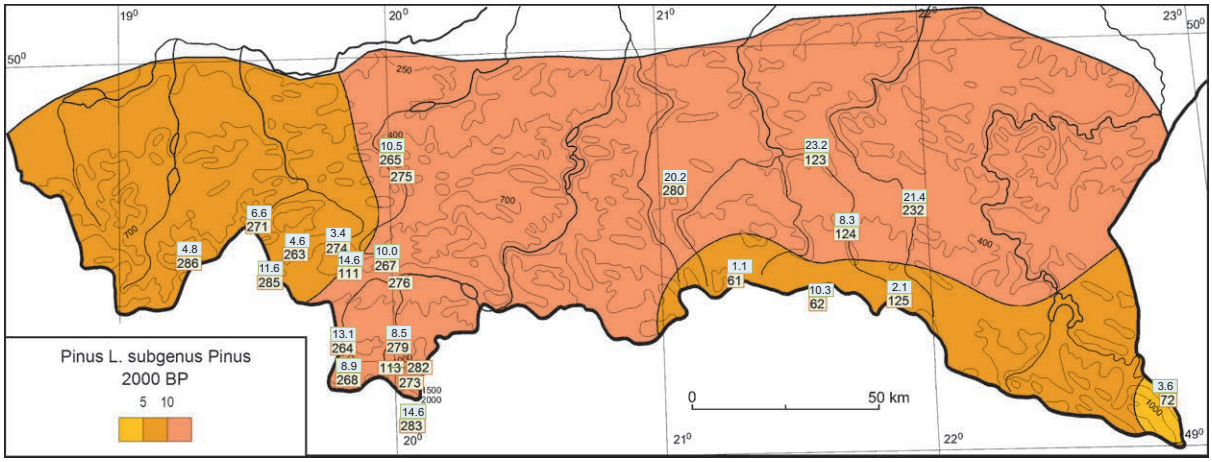

Pinus L. subgenus Pinus
6000 BP
10 20
Pinus L. subgenus Pinus
5500 BP
5 10
Pinus L. subgenus Pinus
5000 BP
5 10
Pinus L. subgenus Pinus
4500 BP
5 10
0 50 km

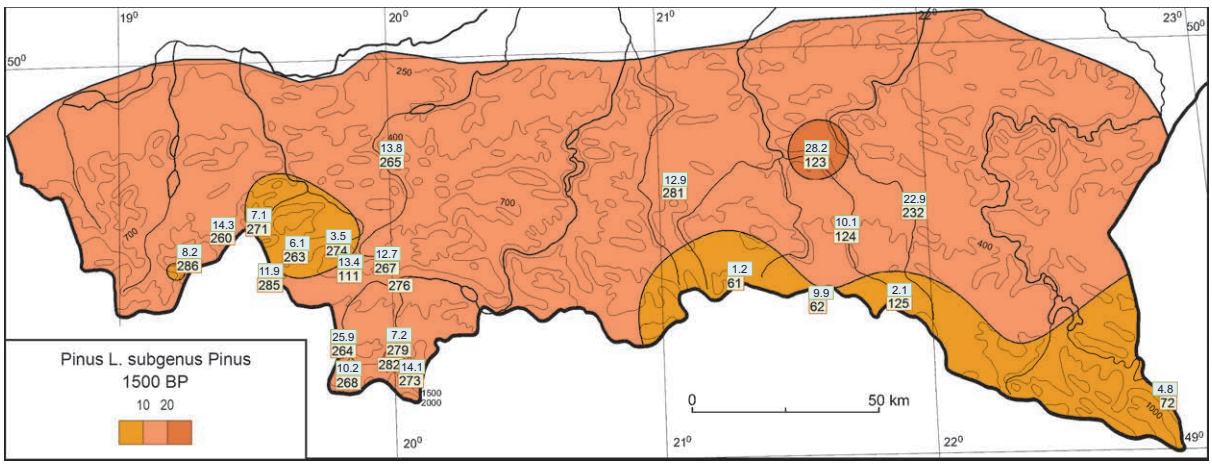

Pinus L. subgenus Pinus
4000 BP
5 10
0 50 km

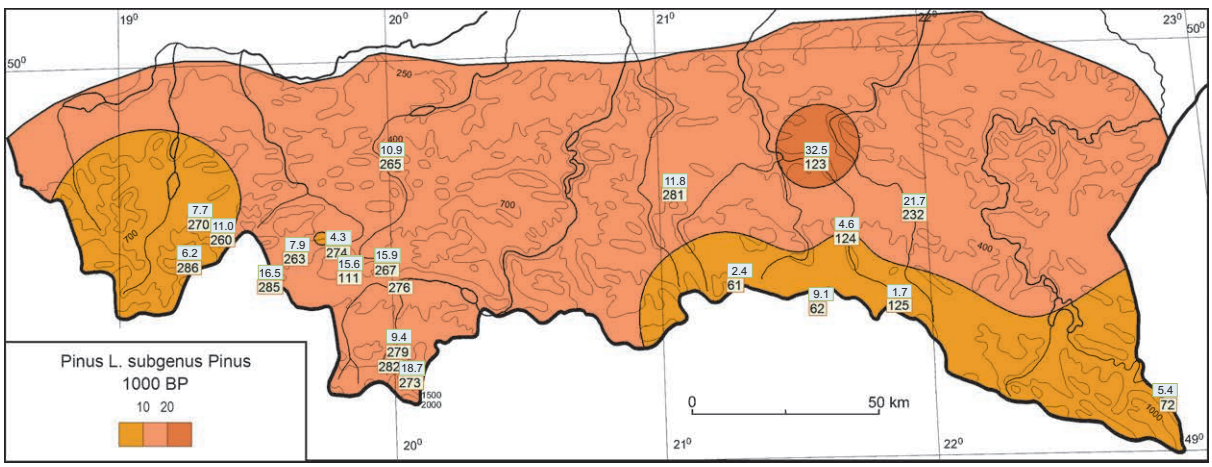

Pinus L. subgenus Pinus
3500 BP
5 10 20
0 50 km

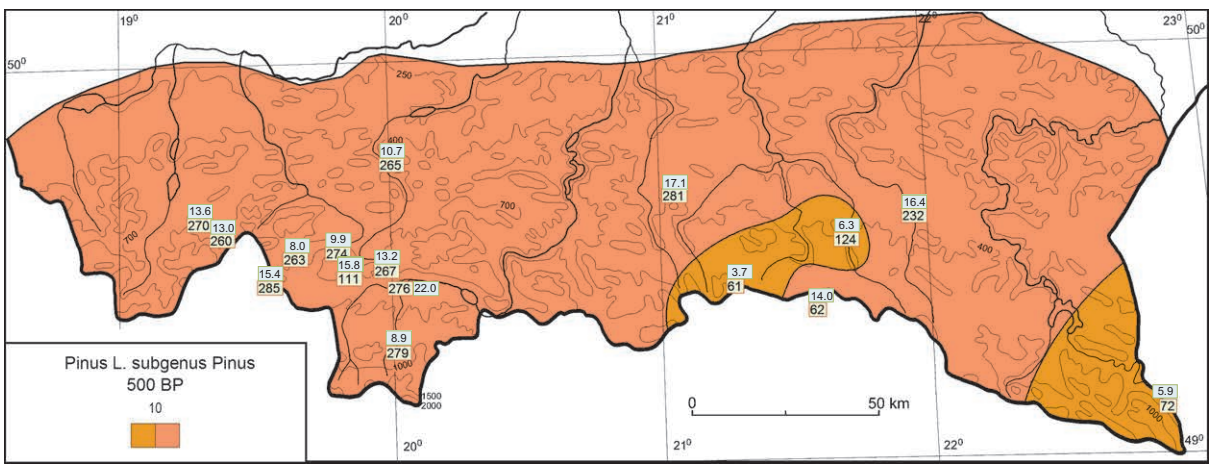

Pinus L. subgenus Pinus
3000 BP
5 10 20
0 50 km

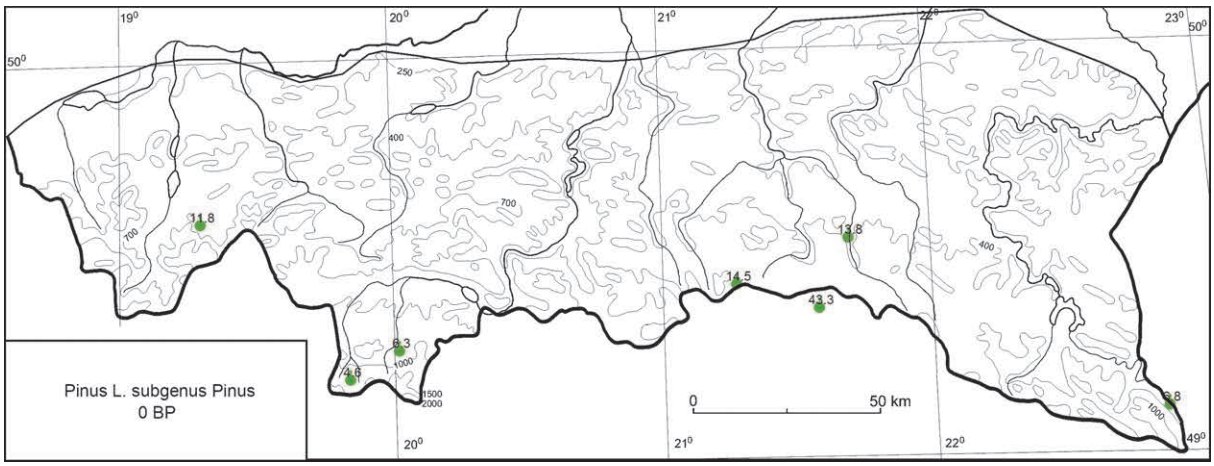

Pinus L. subgenus Pinus
2500 BP
5 10
0 50 km


Pinus L. subgenus Pinus
2000 BP
5 10
0 50 km


Pinus L. subgenus Pinus
1500 BP
10 20
0 50 km


Pinus L. subgenus Pinus
1000 BP
10 20
0 50 km


Pinus L. subgenus Pinus
500 BP
10
0 50 km


19°
20°
21°
22°
23°
50°
49°
250
400
700
1000
1500
2000
11.8
6.3
4.6
14.5
13.8
43.3
3.8
Pinus L. subgenus Pinus
0 BP
0
50 km