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Holocene history of *Larix* in the Jeseníky Mts, Czech Republic

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Abstract: The hypothesis that *Larix* is a native species in the Czech Republic is based on archival data. However, it has not yet been confirmed by paleoecology. In this paper we present pollen evidence of the autochthonous occurrence of *Larix* in the Jeseníky Mts at four sites and systematize the study of archival records in and beyond the region. Furthermore, we provide the first detailed narrative of the Holocene history of *Larix* for the entire Czech Republic and Slovakia. In the Jeseníky Mts, larch has been recorded since the Late Glacial and Holocene boundary and persisted probably as a part of Early Holocene mixed forests until the beginning of the Middle Holocene. After that, during a critical period from around 7000 to 2700 BP, larch disappeared due to the spread in this area of mixed deciduous forests. We presume that during this mid/late Holocene bottleneck, *Larix* survived in its core refugial area around Bruntál until its recolonization of the area during and after the Iron Age. The distribution of *Larix* thus appears to have changed dynamically during the Holocene. Archival sources for the 18th century record an expansive phase in the development of *Larix* populations and illustrate how a static and sharply defined native range may not be the most suitable way to understand the history of larch. Survey maps of a total of 51 Czech and Slovakian sites illustrate a general development similar to that in the Jeseníky Mts. During the mid/late Holocene bottleneck, *Larix* was absent at many sites, except for a core area in the central Western Carpathians and two sites in the Šumava Mts and Bohemian-Moravian Highlands. In the latter two regions, *Larix* may have existed until the Modern Period, but so far there is no archival evidence to confirm this.

Keywords: bottleneck, distribution range, historical record, Holocene refugium, larch, native species, pollen

Introduction

Larix decidua Mill. (the European larch tree) is the only native larch in central Europe. At present, it has a disjunctive and, in comparison to common coniferous species, a small distribution. The native range of *Larix decidua* includes the high mountain and subalpine belts in the Alps and Carpathians, the low mountain forests in the eastern Sudetes (Jeseníky Mts.) and the lowlands of central-southern Poland (Geburek 2010, Pâques et al. 2013, Da Ronch et al. 2016). By contrast, larch occurred over a much larger area during the first and second Weichselian interstadials, including eastern France, Denmark and even the Netherlands. It reached its maximum distribution in the Late Glacial and Early

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Holocene (Wagner et al. 2015a). After the climate warming during the Early Holocene, the distribution of *Larix* started to fragment due to the increased spread of ecologically more competitive species (Lang 1994, Kalis et al. 2003, Wagner et al. 2015a).

The present disjunct range of larch is considered to be the remnant of a once more contiguous distribution. This is confirmed by genetic studies of *Larix* populations in the Alps, Carpathians, Poland and the Czech Republic. Based on 1012 trees from 21 populations (including four populations in the Czech Republic), Dostálek et al. (2018) report that the genetic structure of larch populations in the Czech Republic, Poland and Slovakia is rather homogenous and significantly distinct from genetically diversified populations in the Alps. Based on the mitochondrial genetic structure of 1026 individuals from 45 populations (of which 94 were from four populations in the Czech Republic), Wagner et al. (2015a) report that the largest genetic difference existed between the Alpine and 'Central-European' (Sudeten, lowland Polish and Carpathian) groups and that ecotypes within the Central-European group were relatively closely linked. Furthermore, based on the nuclear genetic structure, Wagner et al. (2015a) identified at least seven clusters of native European larch populations, four of them in the Alps and three or four outside the Alps: in the eastern Sudetes, the lowlands of Poland, the High Tatra Mts and possibly also the south-eastern Carpathians. By combining genetic data and fossil records, the authors consider nuclear clusters as refugial areas from which European larch spread in the Late Glacial and Early Holocene.

Such expansion seems probable for the Alpine and Carpathian larch populations, whose continuous presence throughout the Holocene is supported by copious palaeoecological evidence (reviewed in Wagner 2013, see also Brewer et al. 2017). By contrast, less is known about the Holocene history of the Czech and lowland Polish larch populations (Wacnik et al. 2004). In the Czech Republic, the presence of larch during the Last Full Glacial Period is based on pollen and macro remains (Opravil 1980, Willis & van Andel 2004, Jankovská & Pokorný 2008). In this period, *Larix* occurred in the predominantly treeless vegetation on the Bohemian Massif. In the Moravian part of the Western Carpathians, larch was a component of the local taiga vegetation together with *Pinus cembra* (Jankovská & Pokorný 2008, Kuneš et al. 2008). Pollen evidence of *Larix* from the Late Glacial is rather scarce (Jankovská 2006, Kuneš et al. 2007, Dudová et al. 2014) and that from the Holocene (except for the past few centuries) is almost absent (only Rybníčková 1974, Rybníčková & Rybníček 1988, Dudová et al. 2013, 2014, Hájková et al. 2018). There are no macrofossils of larch dated to the period after the Full Glacial. Therefore, one can only conjecture that, as in Poland (Wacnik et al. 2004) and other areas in central Europe (Wagner et al. 2015a), larch spread into the region we studied in the Late Glacial and Early Holocene. In this period, *Larix* was associated with open vegetation and heliophilous species (Jamrichová et al. 2017). According to Sádlo et al. (2005) and Pokorný et al. (2015), there was a critical period for the persistence of heliophilous species during the Middle Holocene, when mixed deciduous woodlands with high canopy cover developed. Ecological conditions in this period are regarded to have been unfavourable also for the survival of light-demanding *Larix*. The only population that is thought to have survived is the one in the easternmost part of the Sudetes (Jeseníky Mts).

Research on the autochthony of larch in the Sudetes goes back to the mid-19th century, making it an early example of its kind in Europe (Micklitz 1857). Similar studies continued throughout the 20th century (Cieslar 1904, Herrmann 1933, Kraus & Riedel

1936, Rubner 1943, Šindelář 1999) and these authors generally agree that larch was native in the Jeseníky Mts. The evidence to support this hypothesis mainly came from archival (historical) sources most of which were thoroughly compiled by Nožička (1962). However, the time-span covered by historical sources is too short to prove the continuous presence of larch between the Full Glacial and the present. Even though genetic evidence corroborates historical records, fossil evidence of the existence of *Larix* throughout the Holocene is needed to establish its autochthonous status beyond reasonable doubt. However, pollen evidence of larch in the Jeseníky Mts is so far rather inconclusive and does not include the critical period of the Middle and Late Holocene, except for the two pollen grains found at the Skřítek and Vozka sites (Dudová et al. 2013, 2014). In addition, the interpretation of archival material is not without problems. As a result, the hypothesized natural distribution of larch in the Jeseníky Mts is presented in markedly different ways in the literature (e.g. Nožička 1962, Šindelář 1999, Pâques et al. 2013).

Until recently, there was no reliable information on the existence of non-planted larch populations in the Czech Republic outside the Jeseníky Mts during the Holocene (Jankovská & Pokorný 2015). Based on his unparalleled knowledge of archival sources, Nožička (1962) even proposed that the Sudeten ecotype be renamed "Jeseníky" ecotype, as the species was autochthonous only in that mountain range. However, a number of sites with Holocene records of *Larix* (Kuneš & Abraham 2017) and a summary *Larix*-pollen diagram (Pokorný & Abraham 2021) recently revealed that the pollen record for larch for the whole Czech Republic is in fact quite continuous over the Holocene and includes locations outside the Jeseníky Mts. Therefore, the hypothesis that larch only survived in the Czech Republic throughout the entire Holocene in the Jeseníky region needs to be re-examined. In this paper we present new pollen evidence and systematize the study of the available historical sources. The main aims of this paper are (i) to test the hypothesis that *Larix* survived in the north-eastern Czech Republic throughout the Holocene, i.e. that the Sudeten ecotype is autochthonous to the Jeseníky region, (ii) to provide a novel interpretation for the native range of this species, and (iii) to examine whether and to what extent larch occurred in the Holocene outside the Jeseníky region.

Methods

Study area

The Jeseníky Mts are the easternmost part of the Sudetes, a central European mountain range in the Czech Republic, Poland and Germany. The north-western part of the Jeseníky Mts (Fig. 1), called Hrubý Jeseník Mts (German: Hohes Gesenke, Altvatergebirge, Polish: Wysoki Jesionik), is the second highest mountain range in the Czech Republic with summits reaching up to the alpine treeless zone. In the south and east it borders on the highlands of the Nízký Jeseník Mts (German: Niederes Gesenke, Polish: Niski Jesionik). The Nízký Jeseník Mts are considered to be the main area of native occurrence of *Larix* in the Czech Republic. They are characterized by rounded ridges and plateaus on water divides. In contrast, the Hrubý Jeseník Mts have steep slopes, deeply cut valleys and numerous rocky outcrops. Except for the north-western part, the Nízký Jeseník Mts are bordered by lowland areas. The character of the Jeseníky landscape was determined by the Variscan (Hercynian) orogeny.

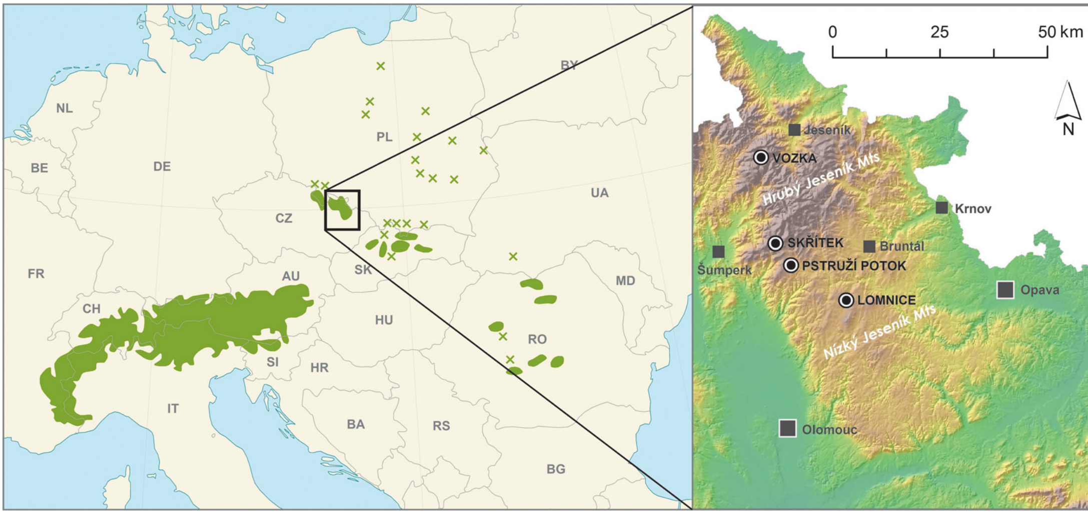

Fig. 1. European distribution of *Larix decidua* (according to G. Caudullo, https://commons.wikimedia.org/wiki/File:Larix_decidua_range.png) (left side), and the Jeseníky Mts with the four pollen sites presented in this paper (circles) and current towns (squares) (right side).

The bedrock of the Nízký Jeseník Mts is geologically uniform (in contrast to the unusually varied bedrock of the Hrubý Jeseník Mts), consisting of Palaeozoic deep-marine siliciclastic sedimentary rocks (Culm facies, Bábek et al. 2004), with remains of Tertiary volcanism around Bruntál. There are many metal deposits (gold, silver, iron ore, non-ferrous metals) in both the Hrubý and the Nízký Jeseník Mts. The prevailing soil type is cambisol, with frequent podzols at high altitudes (Hauptman et al. 2009). The climate in the Hrubý Jeseník Mts is more oceanic on the western side than on the eastern side. Because the prevailing western winds bring an abundance of rain, the mean precipitation is higher on the western windward slopes. The climate in the Nízký Jeseník Mts is milder and rather continental, lying partly in the rain shadow of the Hrubý Jeseník Mts. The Bruntál region belongs to the MT2 climatic area (Quitt 1971) with a mean annual temperature 7–8 °C and mean annual precipitation 550–700 mm (450–500 mm in the vegetation period).

The Jeseníky Mts consist mainly of cultural landscapes. Beech and fir forest would be the prevalent near-natural vegetation at middle and high altitudes, whereas oak-hornbeam forest would grow at low altitudes on the edges of the Nízký Jeseník Mts (Neuhäuslová et al. 1998). Mountain spruce forests dominate at the highest latitudes, forming a diffuse treeline at around 1,320 m a.s.l. (Treml & Migoń 2015). Alpine grasslands, heathlands, subalpine tall herbaceous plant vegetation and deciduous shrubs occur on the summits.

Sites

In the course of palaeoecological research in the Jeseníky Mts, we analysed pollen at six sites and macrofossils at three sites. Whereas no macrofossils or stomata of *Larix* were found, larch pollen occurred at four sites (Fig.1), for which two pollen records have already been published (Dudová et al. 2013, 2014). The Vozka site is a high mountain raised bog (1,350 m a.s.l.) located on the western ridge of the Hrubý Jeseník Mts. It lies below the upper tree limit and is surrounded by mountain spruce forest. The Skřítek site (850 m a.s.l.) is a former raised bog, today a complex of spruce forest growing on peat with patches of open mire. The site is partly drained and degraded by a spruce plantation. It is located in the southern foothills of the main ridge of the Hrubý Jeseník Mts. The sites Pstruží potok (690 m a.s.l.) and Lomnice (550 m a.s.l.) are located at middle altitudes in the Nízký Jeseník Mts, to the south-east of the main ridge of the Hrubý Jeseník. The Pstruží potok site is a moderately rich fen surrounded by spruce stands. Lomnice is a degraded moderately rich fen overgrown with reeds, located in the village of Lomnice.

Pollen analysis

Organic sediments were obtained either from an open excavation or by using hand corers. Each sediment was sampled and processed in the laboratory by acetolysis for standard pollen analysis (Faegri & Iversen 1989). At least 500 pollen grains of terrestrial plants (i.e. except *Alnus* and wetland or aquatic species) were determined in each sample, except samples from Pstruží potok and Lomnice, where at least 300 terrestrial pollen grains were determined, due to the high amount of *Alnus* pollen (excluded from the basic sum) and fern spores. For detailed methodology, see Dudová et al. (2013, 2014).

Tracking *Larix* in the fossil pollen record is rather difficult. Larch produces little pollen with limited dispersal abilities and poor preservation after falling from the catkin to the ground (Jankovská 2007). As a result, the larch fossil record is generally fragmented and even a single pollen grain of *Larix* is considered to be a reliable indicator of its local occurrence (Huntley & Birks 1983). In palynological taxonomy, the pollen of *Larix decidua* Mill. is morphologically identical with other species of the *Larix* genus. Together with the *Pseudotsuga* genus it belongs to the so-called "*Larix* type" (Moore et al. 1991) or "*Larix, Pseudotsuga*" pollen type (Beug 2004). The pollen grains of *Larix* are quite large (80–90 μm in diameter, Beug 2004), circular, but very often crumpled or split (Moore et al. 1991), without significant morphological features. The wall of the pollen grain has two layers and is about 2–3 μm thick. Sometimes a thinning of the wall is visible on one side of the grain and a thick hem on the opposite side. Determining larch pollen grains is not trivial, as they can be confused with non-pollen objects (various algae or eggs of aquatic organisms). Therefore, we photographed all pollen grains of *Larix* in our samples and discussed their identification with experienced palynologists: Vlasta Jankovská (Institute of Botany CAS) and Jacqueline van Leeuwen (Institute of Plant Sciences, University of Bern).

Survey maps

In addition, we obtained all the freely available and radiocarbon dated pollen data of *Larix* from the Czech Quaternary Palynological Database (PALYCZ; Kuneš et al. 2009) and those existing in the literature. Sites with *Larix* pollen situated in the Czech Republic and Slovakia are shown on maps based on the modelled time of larch occurrence.

Radiocarbon dating

Sediments from our sites were radiocarbon dated mainly by Acceleration Mass Spectrometry (AMS). Seeds of terrestrial herbaceous plants, wood or charcoal were cautiously selected for AMS dating. Based on the radiocarbon dates obtained, the age of each sample in the sediment was modelled using the OxCal 1.2 program (Bronk Ramsey 2009), IntCal20 calibration curve (Reimer et al. 2020) and constant k0 = 1. The radiocarbon dates and depth-age models are presented in Supplementary Table S1 and Fig. S1, respectively. Inverse dates were omitted in depth-age models. All dates mentioned in the text are calibrated (calendar) years BP (Before Present = before AD 1950) or AD/BC (AD = Anno Domini = after Christ; BC = before Christ). We use stratigraphical borders according to Walker et al. (2009, 2018) and Rasmussen et al. (2014): Full Glacial/Late Glacial – 14,460 years BP, Late Glacial/Early Holocene – 11,650 years BP, Early/Middle Holocene – 8200 years BP, Middle/Late Holocene – 4200 years BP.

Archival sources

We studied historical sources for three periods of time. First, early documents (AD 16th–17th centuries) were collected partly from archival originals and partly from existing literature (Nožička 1962). We considered all possible types of documents (e.g. letters, charters, herbaria). Second, the Moravian and Silesian parts of the earliest comprehensive nationwide forest inventory were fully processed. This inventory formed part of the so-called Josephian cadaster, a complete survey of all land in the Czech Kingdom for taxation purposes in 1787–1789 (Roubík 1954). The so-called ‘Waldfassion’ of this cadaster is a detailed description of forests in each township (German ‘Katastralgemeinde’, Czech ‘katastrální území’, the lowest administrative tier in the country, essentially a village and its lands), including the name, topographic description, size, tree species composition and management of individual forests. Two even earlier cadastral surveys (the Theresian cadastre and the Carolingian cadastre for Silesia) contain much useful data (Nožička 1962), but did not record tree species composition in a consistent manner in sufficiently high resolution and were therefore not included. Third, we compiled data for the mid-19th century from two sources. The Forststatistik von Mähren und Schlesien was initiated by local forest statistician Heinrich C. Weeber. Published in the journal of Moravian and Silesian foresters (Verhandlungen der Forst-Section für Mähren und Schlesien) in the years 1853–1857, this survey was based on information gathered from local forest managers in a form compatible to cadastral surveys. We also used somewhat earlier data from the so-called Stable Cadastre (Bičík et al. 2015). Based on the principles set by the Josephian cadastre, the Stable Cadastre was a similar but even more detailed survey, which consisted of three parts: mapping, land description and tax valuation. In Moravia and Silesia, mapping was carried out in the 1820s and 1830s, and land description mostly in the 1840s. As part of the latter, detailed descriptions of forests were prepared. Data for the second and third periods of time were extracted from the LONGWOOD forest historical database (Szabó et al. 2018). All data were processed in GIS using ArcGIS 10.2. For visualization of historical data, we used the current boundaries of townships.

Results

Radiocarbon and pollen data

Based on depth-age models (Supplementary Fig. S1), we estimated the age of each pollen sample. The ages of the bottom samples are estimated as follows: Vozka 5990 BP, Skřítek 11,720 BP, Pstruží potok 10,020 BP and Lomnice 11,800 BP. Due to many inverse dates, the depth-age model of Lomnice was constructed using only three dates. The estimated age of its bottom sample is therefore rather approximate, it nevertheless corresponds well with its pollen assemblage.

Pollen grains of *Larix* at these sites are shown in absolute numbers on a timeline (Fig. 2). The oldest larch pollen grains were found at Skřítek and dated to 11,720 BP, i.e. shortly before the end of the Late Glacial and beginning of the Holocene. Furthermore, two pollen grains of *Larix* were dated to 11,640 and 11,550 BP, which is prior to the expansion of *Pinus cembra* (Dudová et al. 2014). The next oldest *Larix* pollen grains are dated to 10,940 BP and 10,780 BP, which is after the decline of *Pinus cembra* and before the expansion of *Picea*. Further occurrences of *Larix* were noted in the period after the postglacial expansion of *Picea* and deciduous trees. At Pstruží potok, larch pollen grains were dated to 9850 BP, 8310 BP and 6940 BP, and at Lomnice, to 9760 BP and 8310 BP. After these finds, records of larch pollen were absent in the Jeseníky Mts for a period of 4200 years. We call this period "the mid/late Holocene bottleneck". *Larix* pollen reappeared around 2710 BP (760 BC) on the western summits of the Hrubý Jeseník Mts at the Vozka bog, around 2470 BP and 2200 BP (520 and 250 BC, respectively) at Lomnice and around 1340 BP (AD 610) at Pstruží potok. Lastly, numerous *Larix* occurrences dated to the period from 500 BP (AD 1450) to the present were recorded at all four sites.

Larix pollen data from other sites in the Czech Republic and Slovakia are shown as presence-absence on four maps (Fig. 3) according to their modelled age. For details about sites and samples with *Larix*, see Supplementary Table S2 and Fig. S2. We set four time windows pursuant to our results from the Jeseníky Mts: (i) the Full Glacial and the Late Glacial (before 14,640 BP and before 11,650 BP, respectively), (ii) the Early and early-Middle Holocene (i.e. before the mid/late Holocene bottleneck, 11,650–6940 BP), (iii) the mid/late Holocene bottleneck (6940–2710 BP) and (iv) the youngest part of the Late Holocene (i.e. after the mid/late Holocene bottleneck, 2710–350 BP, i.e. 760 BC–AD 1600) and subrecent period (younger than 350 BP, i.e. AD 1600). For the fossil pollen record, we set the threshold of data reliability to AD 1600. This is due to the less accurate modelled age of subrecent samples, which are usually imprecisely dated by radiocarbon and therefore mostly extrapolated based on depth-age models.

During the Full and the Late Glacial periods, *Larix* pollen was recorded at sites at various altitudes in both countries. In the early Holocene, *Larix* pollen was found in the Jeseníky Mts, Krkonoše Mts, Bohemian-Moravian Highlands and South Bohemia. In Slovakia, it occurred in both the central and marginal parts of the Western Carpathians. During the absence of *Larix* in the Jeseníky Mts (the mid/late Holocene bottleneck), larch is recorded in the central Western Carpathians and at three sites in the Czech Republic, situated in South Moravia, the Bohemian-Moravian Highlands and the Šumava Mts. During the latter part of the Late Holocene, larch occurred frequently at numerous sites in both countries. *Larix* pollen dated to the last four hundred years possibly came from modern plantations.

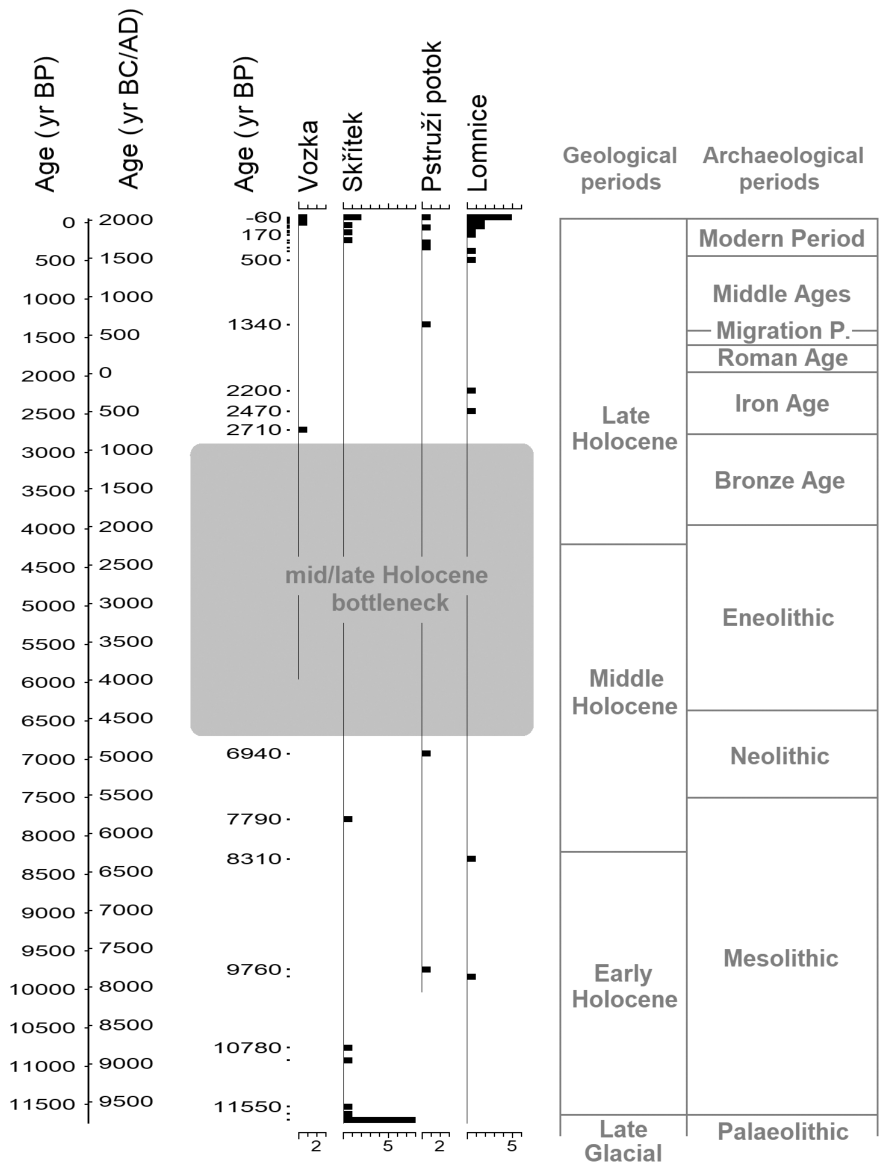

Fig. 2. Diagram of *Larix* pollen found at four sites in the Jeseníky Mts. The horizontal axis shows the number of pollen grains, the vertical axis shows the time scale in calendar years BP (before present) and BC/AD (before Christ/Anno Domini). Geological and archaeological periods are indicated on the right side.

Archival data

The three periods of time represent various possibilities. The beginnings of tree plantations (outside gardens) in this region go back to the 18th century (Nožička 1956, 1962). Some sources indicate that larch, a rare and valuable tree, may have been planted as early as the 17th century, but these can be seen as small-scale experiments (Nožička 1962: 43). Data earlier than 1700 can therefore be relatively safely interpreted as referring to autochthonous populations. This is less true for data from the 1780s, which may include

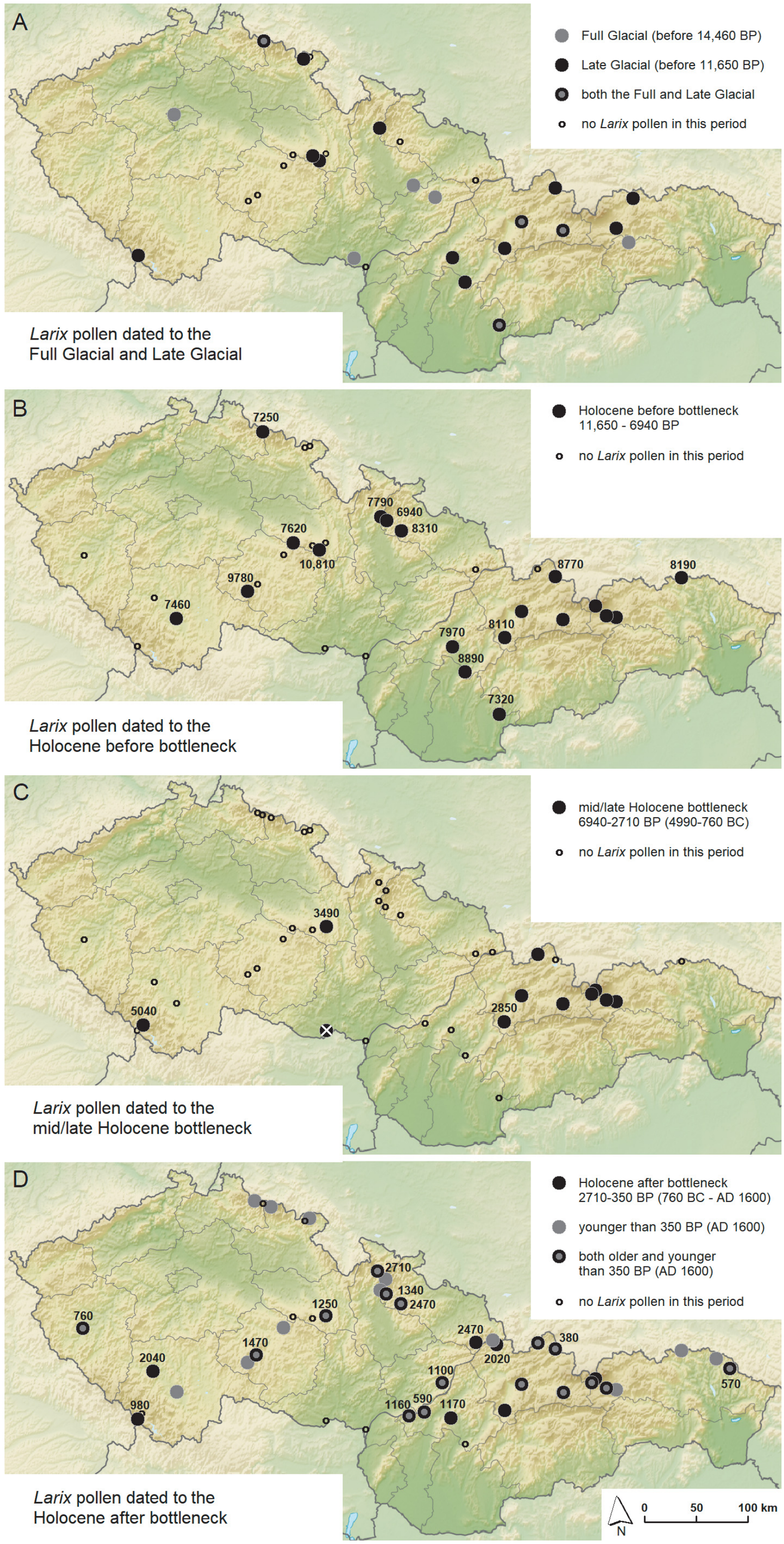

Fig. 3. Czech and Slovakian sites at which *Larix* pollen was recorded dated to (A) the Full and Late Glacial periods, (B) Holocene before bottleneck, (C) mid/late Holocene bottleneck, and (D) Holocene after bottleneck. Dates (in cal. years BP) show the last *Larix* pollen before its absence (map B) or the first *Larix* pollen after its absence (map D). On map C, the date is shown only for sites with a single find of *Larix*. The site with the white cross is an unreliable record.

planted larch. On the other hand, this period offers a comprehensive picture of the distribution of larch rather than scattered individual records. Data from the 19th century reflect the situation after the onset of large-scale plantation forestry. We emphasize that the sources we processed do not provide a complete picture of the distribution of larch in the respective periods. Especially in the mid-19th century, for which there are a huge number of potentially relevant sources, there existed many larch plantations that were not deemed significant enough by the surveyors to be included in the sources we used. As discussed below, we also know of the existence of smaller larch stands in the 18th century that were not recorded in the Josephian cadastre. The main value of our sources is not that they locate every single larch stand but rather that they provide a reasonably comprehensive picture of the distribution of larch considering the limits and sensitivity of the methodology.

We found 13 mentions of larch forests and individual trees in documents that can be dated to the preplantation period. Of these, seven can be located to individual townships and five are of a more general nature. Larch as a significant component in local woodlands is mentioned in Razová (1523, 1530) (ZA Opava, Krnov, inv. č. 1, 2; Nožička 1962: 11–13), Milotice nad Opavou (1574) (ZA Opava, Krnov, inv. č. 5), Jakartovice (1595) (ZA Opava, Urbariální komise slezská v Opavě, inv. č. 639) and Mezina (1675) (ZA Opava, Urbariální komise slezská v Opavě, inv. č. 374). Large individual larches were recorded as boundary trees in 1579 near Jelení u Bruntálu and Oborná (Weinelt 1938). The locations of these settlements are illustrated in Fig. 4. Furthermore, three 16th-century herbaria also mention larch as growing in the vicinity of its hypothesized native range: Fuchs (in 1542), Matthioli (in 1562) and Schwenckfeld (in 1600). In 1571, six hundred larch boards were ordered to be sent to Prague from the Bruntál estate (i.e. the western part of the study region). For the same estate, there are detailed forest management instructions as well as a price list (both from 1634), which contain information on larch management and average expected market prices for larch (all above quoted in Nožička 1962: 22–34). The identification of larch in early documents is not always straightforward. Especially the usage of the Czech 'dřín' (instead of the modern 'modřín'), which nowadays refers to *Cornus*, can cause some confusion. We included those cases that were deemed to have referred to *Larix* by Nožička (1962) (for etymology, see also Meduna & Prach 2021).

In 1787–1789, larch was recorded in 85 townships, all in the Jeseníky region, which are close to one another (Fig. 4). Data showed only two small outlying larch populations: in Habartice and Šumperk. Separated from the contiguous core area of larch by the Hrubý Jeseník Mts, these townships lie at approximately the same altitude as those in the core area. In the east, the distribution of larch follows the edge of deforested areas, which roughly coincides with the 300-m altitude line. The southern and south-western boundaries are demarcated by the right bank of the Moravice river. Almost every township on the border of the distribution of larch from Lesní Albrechtice in the south-east to Horní Václavov in the west lies along the Moravice river, covering some 60 km with virtually no hiatus. It is noteworthy that these townships are not on the left bank of the river, i.e. on the inside of the distribution area, but rather on the right bank. The Moravice river does not form a geological or soil-type boundary and for most of its course it does not separate larger administrative units. In the north, the distribution of larch was again delimited by altitude. It did not grow in the Hrubý Jeseník Mts above ~800 m. Larch was mostly confined to mid-range altitudes. Eighty percent of the mean average altitudes of townships

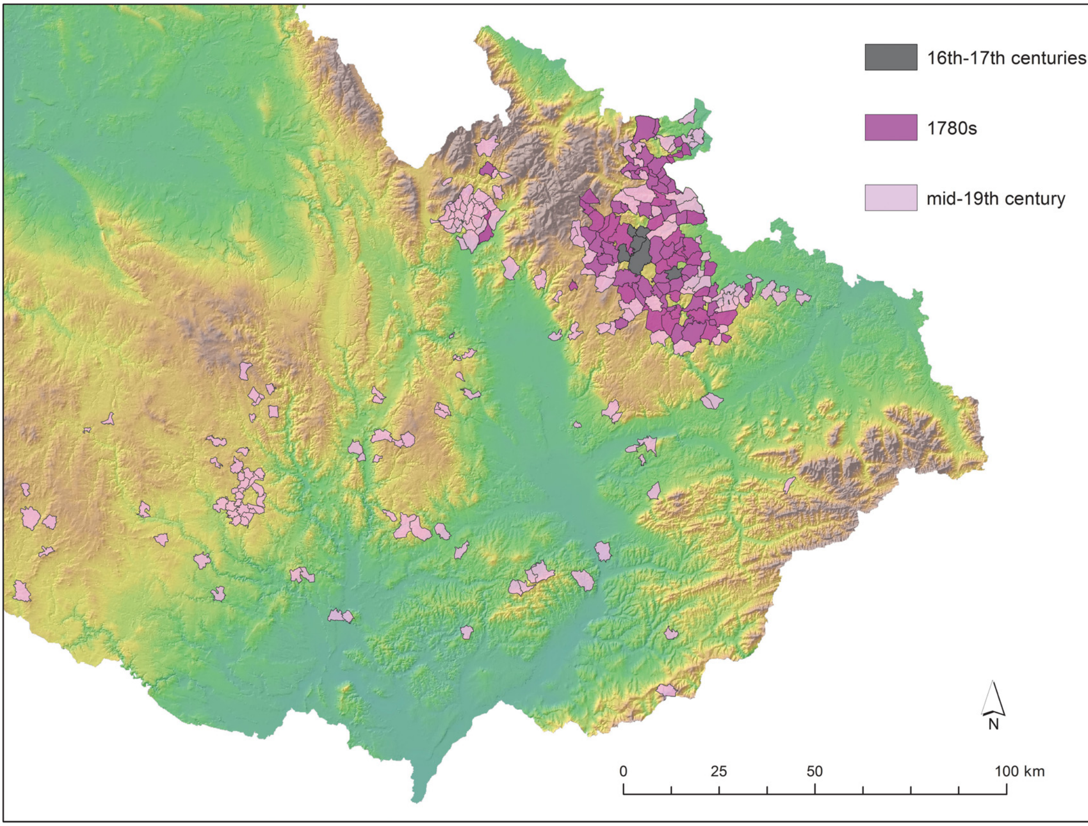

Fig. 4. Changes in the distribution of stands of *Larix* over the past 500 years in Moravia and Czech Silesia. In case of temporal overlaps, only the oldest period is shown. Note that no data are available for Bohemia (the north-western part of the map).

with larch populations were between ~360 and 635 m a.s.l., and the means approximately followed a normal distribution with most observations between 450 and 500 m (Fig. 5). There were 10,924.2 hectares of forests in which larch was significantly present in 1787–1789. Unfortunately, the Josephian cadastres only listed dominant species of trees without specifying exact percentages, but ~5% appear as a reasonable lowest estimate to be included in the list. The mean size of forests with larch in individual townships was 128.5 ha, with a median of 40.9 ha. Larch rarely formed single-species stands: only 252.42 ha of pure larch forests were recorded. Larch most commonly grew together with spruce and silver fir, less often with pine, and exceptionally also with oak, beech, birch or hazel. Pure larch stands were typically small woodlots owned by peasants rather than larger demesne forests.

By the mid-19th century, larch considerably expanded its distribution through forestry plantations (Fig. 4, see also Nožička 1962). It was present in most Moravian and Silesian regions, except in the Beskidy Mts in the east. It is also obvious that foresters promoted the species at altitudes that were seen as those it is found at in its native range.

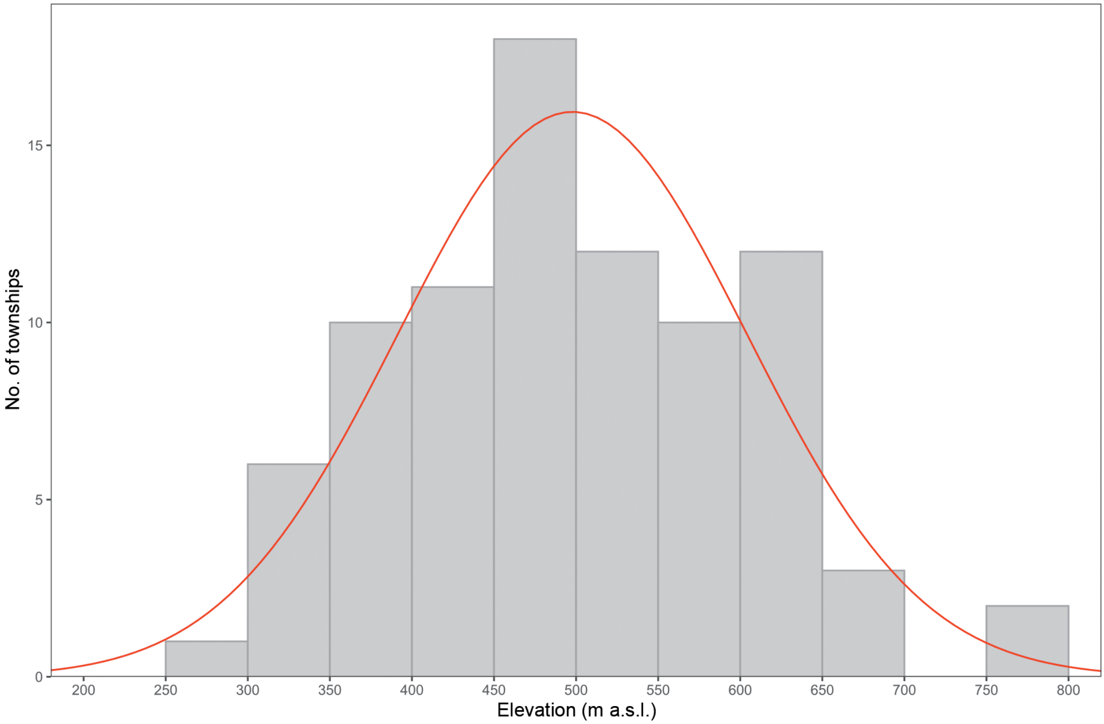

Fig. 5. Histogram of the mean altitudes of townships where *Larix* stands were recorded in the Josephian cadastre (1787–1789) with the expected normal distribution superimposed.

Discussion

Holocene history of Larix in the Jeseníky Mts

Our pollen records of *Larix* document its occurrence in the Jeseníky Mts during the Holocene. Larch was present there at least since the Late Glacial/Holocene boundary, when it colonized forest-free places and probably reached its maximum abundance. Then, it partly declined after the expansion of *Pinus cembra* and later that of temperate trees (*Picea abies* and deciduous trees *Ulmus, Tilia*, *Fraxinus* and *Acer*). Larch nevertheless survived as an admixture species in Early Holocene mixed forests until the beginning of the Middle Holocene. This pattern is in general agreement with the syntheses of palynological data from the surrounding regions. Wagner et al. (2015a) argue that thanks to rising temperatures during the Late Glacial and after the onset of the Holocene, larch as a pioneer tree spread and quickly colonized unforested areas in central Europe. Later, in the period 11,500–9500 BP, larch declined throughout most of its distribution to approximately its current distribution. Similarly in Poland, larch became widespread during the Late Glacial and Early Holocene, and after 9000 BP it gradually declined (Wacnik et al. 2004).

At the beginning of the Middle Holocene, light-demanding *Larix* was still present in this region. Based on this, we may deduce that the maximum expansion and shading by temperate trees in the Jeseníky Mts occurred after 6900 BP, i.e. more than one millennium after the onset of the Middle Holocene. This is in fact apparent in the pollen diagram for the Skřítek site (decrease in *Pinus* and *Poaceae*, increase in temperate trees after 7000 BP; Dudová et al. 2014), and is probably valid for a wider area. Similarly, *Larix* decreased to minimum values around 7050 BP in the mid-altitude refugial area in the Mátra Mts, northern Hungary (Pató et al. 2020). The following period between 6940 and 2710 BP, with no records of the occurrence of *Larix*, we consider to be a bottleneck in the postglacial survival *of Larix* in the Jeseníky Mts. After this period, *Larix* pollen again occurred during the Iron Age and later in the Migration Period.

Here, we present four possible scenarios to explain the absence of *Larix* pollen during the mid/late Holocene bottleneck: (i) The distribution of larch did not change significantly. However, due to the expansion of temperate trees with higher pollen productivity, larch pollen became too rare in the pollen fall to be recorded by standard pollen analytical methods. (ii) Larch populations decreased due to the expansion and greater shading by temperate trees during the climatic optimum in the Middle Holocene. Larch survived in a core area, from which we do not yet have a fossil record. (iii) Larch survived only in places with extreme conditions, such as on rocks and screes (in such habitats it is now also protected in reservations, Weissmannová et al. 2004). Finding larch in the pollen record is almost impossible, due to the absence of organic sediments in rocky substrates. (iv) Larch succumbed to competition and the shading of temperate trees and completely disappeared from the Jeseníky Mts. Later, in the Iron Age, it recolonized this area from the Western Carpathians or the Polish lowlands.

We consider the second or the third scenario the most probable. During the Middle Holocene, larch probably declined due to higher shading by temperate trees and survived only in its core areas. In the Jeseníky Mts, the core area, i.e. the local refugium, might have been in the vicinity of Bruntál, as is also indicated by historical records. In this area, larch could persist during the critical period. The existence of such a separate Holocene refugium for *Larix* in the Jeseníky Mts is supported by nuclear DNA research, which distinguished Sudeten larch populations (two of them from Krnov, Wagner et al. 2015b) from Carpathian and lowland Polish populations, thus contradicting the idea of recolonization from the Western Carpathians, as implied above in the fourth scenario. By contrast, lowland Polish populations, for which the differences from the Carpathian populations are less clear, could have originated in the latter area (Wagner et al. 2015b).

The hypothesis of a separate Holocene refugium of larch in the vicinity of Bruntál (and possibly Krnov) could be confirmed in the future by local pollen records of larch throughout the entire Holocene. However, none of the first three scenarios can be reliably refuted by pollen analysis, because the absence of larch in the pollen record does not indicate its absence in vegetation (Kuneš et al. 2008).

In our opinion, the presence of *Larix* after the mid/late Holocene bottleneck is the most important evidence of its natural occurrence in the Jeseníky Mts. The intentional planting of *Larix* by people in the Iron Age is highly unlikely, although it cannot be absolutely excluded. The planting of trees for their fruits/nuts or for decorative purposes in the Roman Empire is well-documented, but these trees stood in gardens and orchards close to settlements or functioned as parts of agroforestry systems (Lelle & Gold 1994). Therefore, we believe that during the Iron Age, *Larix* naturally spread from its local refugium around Bruntál into the landscape of the Jeseníky Mts. As a pioneer tree, larch possibly spread into vegetation already partly opened and disturbed by humans (Pokorný et al. 2006, Kuneš et al. 2015). In this period, the highest summits of the Hrubý Jeseník Mts are thought to have been intentionally burned (Novák et al. 2010). This implies the existence of at least seasonal camps in the foothills, as well as along trade routes. Around such camps, small-scale disturbances (typically forest grazing) could lead to mineral soil exposure, which might have supported seed regeneration by *Larix*, as is recorded in the Alps (Schulze et al. 2007). The subsequent presence of *Larix* during the Migration Period and around the medieval/early modern boundary (pollen dated to AD 1450 and 1570) is probably good evidence of its natural occurrence. So far, there are no historical records of the intentional planting of *Larix* in this period in the region studied.

Native range

In agreement with earlier studies, the archival sources analysed in this paper show that larch was present in the Jeseníky region before forestry plantations became common. Several authors have attempted to define the native range of this species; Šindelář (1999) compiled a review of these efforts. Micklitz (1857) argues that the native range of larch largely coincided with the boundary of Culm facies of the Nízký Jeseník Mts. Cieslar (1904) claims that larch occurred mainly at mid-altitudes (360–860 m a.s.l..) with no recognizable preference for any type of bedrock. Herrmann (1933) and Kraus & Riedel (1936) present the first maps of the native range of larch. In his important paper, Rubner (1943) argues that the native range of larch included Polish regions around Osoblaha and Krnov, as well as areas around Opava and Zábřeh in the Czech Republic. All these authors consider the Bruntál area the core region of larch distribution. In contrast to Rubner (1943) and based on archival sources, Nožička (1962) defines a smaller native range with the Krnov area at its centre. Šindelář (1999) returns to the larger native range of Rubner (1943) including the Nízký Jeseníky Mts, the Zlatohorská Highlands, the Oderské Vrchy Mts and foothills of the Hrubý Jeseník Mts up to 800 m a.s.l. He also allows for the natural but disjunct occurrence of larch around Ruda nad Moravou and Šumperk. He describes the optimal climatic conditions for larch as transitional between oceanic and climatic: 600–970 mm of precipitation per year and 5.8–8.5 °C average temperature. He emphasizes relatively low precipitation as one of the possible reasons why other tree species did not outcompete larch.

Considering the fact that the distribution of larch was highly dynamic during the Holocene, we believe that rather than defining a static ‘native range’ for this species yet again, archival data from the end of the 18th century may be more useful in illustrating one phase in a dynamic process. The contiguous distribution of larch recorded in the Josephian cadastre, with smaller stands typically along the edges, also conveys the image of a dynamic species. Because the data record a temporal snapshot, it is difficult to say whether larch was spreading or declining in this period. However, based on the general context, the former option appears more likely. The Little Ice Age, a period that started in the 14th century, brought a colder and wetter climate (Mann et al. 2009), both of which could be favourable for larch, although also for other species of trees, especially spruce. In addition, by the 18th century, the landscape was fully cultural, leaving ample room for pioneer species, such as larch, to colonize temporarily abandoned land (also suggested by Svoboda 1947, cf. Volařík & Hédl 2013). This could happen in two major ways. First, larch could colonize abandoned land after more significant waves of settlement abandonment, for example during and after the Thirty Years' War in 1618–1648 and the War of the Austrian Succession (1740–174), which greatly adversely affected this area. The same process was observed and recorded in detail after World War II, when the German-speaking inhabitants were expelled from this region (Šindelář 1999). Second, larch could colonize smaller plots in the fashion of the infield-outfield system. As attested by the Josephian cadastre, most pure larch stands were owned by peasants and were probably in the farthest corners of agricultural plots, intended partly as pasture and partly as forest. Indeed, in a number of cases such larch stands are described as 'Feldwald' (fieldforest) or 'Feldbusch' (fieldshrub). On the other hand, as hypothesized above in connection with the mid/late Holocene bottleneck, larch could survive continuously in more extreme conditions, from where it could spread. For example, at Město Albrechtice, a larch forest of 15 hectares owned by the overlord was described as growing on poor quality, stony soil overgrown with juniper.

The late 18th century is arguably the last period when meaningful conclusions can be drawn about the distribution and spread of autochthonous larch. In the 19th century, *Larix* was planted in many places and disentangling the effects of such plantations from the dynamics of possibly autochthonous populations appears hardly possible.

Holocene history of Larix in the Czech Republic and Slovakia

In the Czech Republic and Slovakia, in addition to the well-known sites for studying the Full and Late Glacial periods (Jankovská & Pokorný 2015), there is also copious evidence of *Larix* in the Holocene. This is rather surprising, as those data were mostly not published in original papers, but only in two syntheses based on PALYCZ data (Kuneš & Abraham 2017, Pokorný & Abraham 2021). There are probably two reasons for this. First, in order to save space, pollen diagrams are usually pictured as 'simplified' with only the most important pollen taxa. Second, authors might have been unsure about their determination of *Larix* at sites outside the Jeseníky Mts. However, in the Late Glacial period, *Larix* was present also in other middle-altitude regions in the Czech Republic, for example in the Bohemian-Moravian Highlands, Šumava Mts, the Broumov region and Krkonoše Mts. Thanks to its tolerance of a continental climate, *Larix* was favoured over *Pinus cembra*, *Pinus sylvestris* and *Betula* in this period (Wacnik et al. 2004). Later, after further warming, *Pinus* and *Betula* spread and probably this partly resulted in a reduction in the distribution of larch. In the Western Carpathians, *Larix* is probably a co-dominant of taiga forest persisting since the Full Glacial period (Jankovská & Pokorný 2008, Kołaczek et al. 2017). In the Early Holocene, *Larix* still occurred in the same middle-altitude regions: the Jeseníky Mts, the Bohemian-Moravian Highlands, the foothills of the Šumava Mts and Krkonoše Mts. In Slovakia, larch persisted at the same sites and was more abundant than in the Czech Republic.

In the period of the mid/late Holocene bottleneck (6940–2710 BP), the reduction in the distribution of *Larix* was apparent in both the Czech Republic and Slovakia. In 9000–8000 BP, larch disappeared from the marginal parts of the Western Carpathians (also in Poland, Wacnik et al. 2004), and later between 8000–7000 BP also from the Jeseníky Mts and Krkonoše Mts. The central part of the Western Carpathians was the main Middle Holocene refugial area for *Larix* outside the Alps. Local sites revealed an almost continual presence of *Larix* pollen throughout the Holocene, except the westernmost site Rakša (Fig. 3C, Supplementary Table S2, Jamrichová et al. 2017), where a period without *Larix* pollen occurred between 8110 and 2850 BP. The larch pollen record of Rakša, a site situated near the core refugial area, is similar to the pattern found in the Nízký Jeseník Mts. Therefore, it supports our hypothesis of recolonization by *Larix* from close by refugia after the beginning of the Iron Age.

In the Czech Republic, there are three sites where *Larix* is recorded during the critical period: Dvůr Anšov (southern Moravia), Hradec nad Svitavou (Bohemian-Moravian Highlands) and Mrtvý luh (Šumava Mts). The record of *Larix* at the Dvůr Anšov site appears rather unreliable. This site is situated in the lowlands, not at middle altitudes and the only *Larix* pollen was identified from samples dated to the Middle Holocene. After communicating with the palynologist who identified *Larix* there, we presume that an unreliable chronology rather than erroneous determination is the most possible reason for this unusual record. Nevertheless, the other two sites are from regions where larch pollen was present before and after the mid/late Holocene bottleneck. Therefore, these sites may possibly represent other refugial areas of *Larix* during the Middle Holocene.

During the Iron Age, *Larix* was recorded in the Beskydy Mts (Hutě pod Smrkem, Kubriková) and foothills of the Šumava Mts (Řežabinec). Later on, during the first millennium AD, it was recorded in the Bohemian-Moravian Highlands (Loučky, Hradec nad Svitavou), the White Carpathians (Machová, Královec) and Šumava Mts (Plešné jezero). The recurrent occurrence of *Larix* during the Middle and Late Holocene in these regions cannot simply be ignored. Based on pollen records, we may conclude that the natural survival of *Larix* in the Bohemian-Moravian Highlands, Šumava Mts and possibly also Beskydy Mts as well as the natural recolonization of the White Carpathians (Hájková et al. 2018) prior to modern cultivation was possible. On the other hand, as it is not easy to identify *Larix* pollen, incorrect determination cannot be excluded in spite of the efforts by palynologists to correctly identify pollen.

In spite of the above considerations, thus far there is no archival evidence to support the survival of larch in the past half a millennium in regions outside the Jeseníky Mts. Attempts to prove otherwise by Salaschek (1935) and Šiman (1944) were rebuffed by Svoboda (1947). If anything, existing sources rather suggest the absence of *Larix* since AD 1500 in places where its pollen was still present in the first millennium AD (but see also Meduna & Prach 2021 for potentially new ways of identifying larch in historical sources and place-names). While it is impossible to systematically search for mentions of *Larix* in all historical sources from the 16th-17th centuries in all regions of interest, and therefore the chance discovery of descriptions of *Larix* forests outside the Sudetes is possible, it is remarkable that *Larix* was not recorded anywhere else but the Sudetes in the Josephian cadastre at the end of the 18th century. This does not mean that smaller groups or individuals of larch could not have occurred elsewhere (and therefore our results do not directly contradict the conclusion of Šindelář 1999), but rather that larch was not common enough in forests outside the Jeseníky region to be recorded among the dominant tree species. Naturally it is difficult to control for the reliability of the Josephian cadastre. It is, however, remarkable that none of the known 17th-century larch plantations (all of sizes of only a few hectares; Nožička 1962) were included in it, signifying its lower limits of sensibility. At the same time, one should note that data from the Josephian cadastre for Bohemia have so far not been processed (therefore there is no information on the Šumava Mts) and also that data on tree species in the Josephian cadastre are not complete. Two regions that lack data on tree species stand out: south-west Moravia around today's Podyjí National Park and the White Carpathians. As shown by pollen, the latter could have harboured larch populations. At the same time, the fact that larch was recorded here in only two townships in the 19th century (when data on tree species are available for practically every township) also indicates that larch did not grow in this region in significant numbers half a century earlier. That larch was not a widespread tree species in the Czech Lands is also proven by the fact that among more than 6000 dendrochronologically dated timber constructions from the entire country for the period 1450–1950, there are only 4 that contain larch wood (Kolář et al. 2022).

Conclusions

We confirmed the hypothesis that *Larix* is a native species in the Jeseníky Mts. Even though its presence in the pollen record was not continuous throughout the Holocene, we consider pollen in the Iron Age and Migration Period, corroborated by archival evidence, conclusive. Between ~7000 and 2700 years BP, during the mid/late Holocene bottleneck, there are no records of larch pollen in this region. We argue that the distribution of *Larix* was severely constrained by the spread of temperate trees in this period. *Larix* probably survived in a core area or in extreme habitats, from where it later recolonized neighbouring areas. Repeated periods of decline and recolonization may have been typical for the entire Holocene history of *Larix* in the Sudetes. Archival sources in the 18th century record an expansive phase in the dynamic development of *Larix* populations and illustrate how a static and sharply defined native range may not be the most suitable way to understand the history of larch.

In addition, we emphasize that there is growing palynological evidence that in the Czech Republic as a whole, *Larix* was very likely present throughout the entire Holocene, including the mid/late Holocene bottleneck. In this most critical period, larch definitely occurred in the Šumava Mts and Bohemian-Moravian Highlands. However, written sources so far suggest that large larch stands did not survive in these regions into the Middle Ages. In other words, while we think that the Holocene continuity of *Larix* populations in the Czech Republic is beyond reasonable doubt, at present there is no locality for which there is an unbroken sequence of palynological and archival sources from the Late Glacial to the Modern Period. Further research both in palynology and history (especially in regions with *Larix* pollen finds after the Holocene bottleneck) will hopefully refine our current conclusions. Such research should also be supplemented by genetic studies and other palaeoecological proxies (plant macrofossils, fossil stomata).

Supplementary materials

Fig. S1. – Depth-age models of four profiles from the Jeseníky Mts.
Fig. S2. – Map of Czech and Slovakian sites with *Larix* pollen.
Table S1. – Radiocarbon dates of four profiles from the Jeseníky Mts.
Table S2. – *Larix* pollen data from the Czech Quaternary Palynological Database

Supplementary Materials are available at www.preslia.cz

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Holocénní historie modřínu v Jeseníkách (Česká republika)

Modřín je považován za původní druh české flóry na základě historických údajů. Jeho původnost však dosud nebyla dostatečně potvrzena paleoekologickými metodami. V tomto článku přinášíme pylový záznam výskytu modřínu na čtyřech lokalitách v Jeseníkách a přehled historických údajů v širším území. Navíc nabízíme první podrobný scénář holocénní historie modřínu v celé České republice a na Slovensku. V Jeseníkách je výskyt modřínu zaznamenán od přelomu glaciál/holocén, a dále během raného holocénu až do počátku holocénu středního. V tomto období byl modřín pravděpodobně součástí světlých smíšených lesů. V období před 7000 až 2700 lety modřín vymizel z většiny území vlivem maximálního rozšíření stinných smíšených listnatých lesů. Předpokládáme, že v tomto kritickém období, které jsme nazvali “mid/late Holocene bottleneck”, se modřín stáhl do jádrového území svého areálu okolo Bruntálu (tzn. do svého holocenního refugia), kde přežil do doby železné, kdy se opět začal šířit. Areál modřínu se tedy během holocénu dynamicky měnil. Historické údaje z 18. století, zachycující expanzivní fázi vývoje populace modřínu, ukazují, že hledání statického a přesně vymezeného areálu není vhodné pro porozumění historii této dřeviny. Přehledové mapy s celkem 51 českými a slovenskými lokalitami dokládají, že změny rozšíření modřínu byly v širším území podobné jako v Jeseníkách. V kritickém období modřín vymizel z mnoha regionů kromě jádrového území centrálních Západních Karpat a dvou lokalit na Šumavě a Českomoravské vrchovině. V posledně jmenovaných dvou regionech mohl modřín přežívat až do novověku, avšak historické údaje, které by toto potvrzovaly, dosud chybí.

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