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Modelling the location of interglacial microrefugia for cold-adapted species: insights from the terrain-mediated distribution of *Rhododendron tomentosum* in a temperate region in central Europe

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Abstract: *Rhododendron tomentosum* is a vascular plant common in northern regions of Europe, Asia and North America. In central Europe, this species is considered a glacial relict. In recent years, systematic floristic mapping of the distribution of this species in the Bohemian Switzerland National Park has revealed that this rare and highly sensitive species is strongly associated with a specific type of habitat. *Rhododendron tomentosum* adapted to environmental changes throughout the Holocene: soil acidification, repeated fires and negative effect of forestry on species composition. To identify the survival mechanisms of *R. tomentosum*, suitable sites in well-preserved parts of a sandstone landscape with assumed minimal human influence were selected. Based on data from intensive field sampling and a set of environmental variables for the whole area of the National Park, habitat suitability maps for *R. tomentosum* were developed. These maps were then combined with the palaeoecological data and used to identify sources of pollen with greater precision and extend the knowledge of the potential distribution of *R. tomentosum* outside the intensively sampled areas. Palaeoecological data was particularly useful for reconstructing the past population dynamics of *R. tomentosum*. The results indicate the long-term stability of sites suitable for this species, supported by locally diversified vegetation development in sandstone areas. This research could therefore provide the first direct evidence of the persistence of *R. tomentosum* micropopulations throughout a large part of the Holocene.

Keywords: Bohemian Switzerland National Park, environmental changes, glacial relict, habitat suitability, palaeoecological data, potential distribution, sandstone areas.

Introduction

During the last glaciation, many cold-adapted species were more widely distributed than they are today (Musil 1985), which indicates that they responded to interglacial climate warming in the opposite way to species adapted to temperate climates. Once the regional climate ameliorated sufficiently to support more demanding taxa, their geographical ranges shifted to northern latitudes and simultaneously to specific sites that provided the habitat conditions necessary for their survival. We can therefore consider present-day relict

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populations of cold-adapted species at lower latitudes as being restricted to their southern interglacial refugia (Stewart & Lister 2001, Birks & Willis 2008, Stewart et al. 2010). These sites are the conceptual counterparts of so-called cryptic refugia or microrefugia for those taxa adapted to temperate conditions (Rull 2009), which hosted a large degree of biodiversity during the cold phases of the Pleistocene and played an important role in postglacial recolonization pathways (Willis et al. 2000, Stewart & Lister 2001). Conversely, many cold-adapted species were able to cope with the warming climate in environments that promote local decoupling from regional temperature and/or moisture regimes. This is especially the case in mountainous areas (Dobrowski 2011). Nevertheless, terrain-mediated factors such as topographic shading and thermal inversions can produce cool and moist microclimates that are significantly different from their surroundings and may support the persistence of cold-adapted species in low-altitude landscapes. As these species are adapted to or even dependent upon certain disturbance regimes, other ecologically relevant factors can be involved. For example, many boreal taxa exhibit adaptive traits to repeated fire events that are inherent to boreal biome dynamics (Keeley et al. 2011). Fires can result in a heterogeneous age structure and forest stand density, both of which promote the early successional stages on which many of these species depend. Therefore, habitats subject to frequent fires in low-disturbance landscapes are crucial for the long-term persistence of fire-adapted boreal taxa.

Ongoing anthropogenic climate change is of immediate concern for species that prefer cooler conditions and are therefore vulnerable to rises in global temperatures (Svenning & Skov 2006). As future climate change will affect both habitat conditions and disturbance regimes, cold-adapted species can be expected to decline in temperate Europe or even disappear. Therefore, landscapes that have a higher potential to buffer local environments from regional climate change should be of interest for biodiversity conservation (Keppel et al. 2015). The identification of areas that facilitate the long-term persistence of species has been repeatedly done on the basis of palaeoecology or phylogeography, i.e. searching for fossil evidence and phylogenetic patterns (Gavin et al. 2014). In particular, continuous time-series of pollen can document millennial-scale population dynamics and provide evidence of refugial areas (Tzedakis et al. 2002). While this approach is essential for documenting the past presence of species, the paucity of fossil records means it generally provides an incomplete record of palaeodistribution. Therefore, species distribution modelling (SDM) is increasingly used for indicating the distributions of species during the Late Pleistocene (Svenning et al. 2011, Varela et al. 2011), thus allowing the potential range of suitable habitats to be predicted.

In this article, the current warm-stage microrefugia of the cold-adapted taxon *Rhododendron tomentosum* are modelled and used to assess its Holocene-scale continuity using the fossil pollen record. We focused on a specific area in eastern central Europe (the Bohemian Switzerland National Park), which hosts a relict population of *R. tomentosum* within a highly diverse sandstone landscape. The main objectives were: (i) to identify suitable habitats for species persistence throughout the Holocene; (ii) evaluate the long-term dynamics of *R. tomentosum* populations especially the critical bottleneck period in the Middle Holocene; (iii) assess the effect of fire on the persistence of *R. tomentosum* populations; (iv) analyse the possible (human) effect of changing forest composition on the number of *R. tomentosum* populations; and (v) discuss the effect of soil acidification on the distribution of *R. tomentosum* populations.

Material and methods

Habitat requirements of Rhododendron tomentosum

Rhododendron tomentosum Harmaja (syn. *Ledum palustre* L.) is a species of the *Ericaceae* family. According to information in the worldwide database Global Biodiversity Information Facility (GBIF) (2022a) and maps of Hultén & Fries (1986), *R. tomentosum* is common in Arctic and sub-Arctic types of vegetation in the Northern Hemisphere; northern Eurasia and North America (Fig. 1). It occurs mainly in habitats characterized by great variation in seasonal climate (tundra and boreal woodland); its occurrence in areas with purely oceanic climates is rare (Dampc & Luckiewicz 2013). The Czech distribution of *R. tomentosum* is concentrated in two different types of habitat: sandstone areas and large peatlands. *Rhododendron tomentosum* is more abundant in the sandstone areas in Bohemian Switzerland and the Adršpašsko-teplické Rocks, but is also present in the large areas of peatland in the Třeboňská pánev basin and the Doksy area (see Supplementary Fig. S1); it also occurs (more rarely) in the mountainous regions of the Czech borderlands, such as the Bohemian Forest and the Šumava, Krušné hory, Jizerské hory and Hrubý Jeseník mountains (Křísa 1990, Kubát et al. 2002, Hadincová et al. 2014, Kaplan et al. 2019). Czech occurrences of *R. tomentosum* are located close to the southern limits of its distribution in the Northern Hemisphere. In these areas, this species generally occupies a relatively narrow ecological niche, which enables the efficient use of habitat suitability modelling for *R. tomentosum*.

The well-preserved sandstone landscape in Bohemian Switzerland became a low-latitude Holocene refugium for *R. tomentosum*, which is a highly light-sensitive species that occurs in habitats with peaty substrates, raised bogs and heathlands with sparse coniferous stands dominated by *Pinus* species. Nevertheless, the continual presence of *R. tomentosum* in pine-dominated habitats in early stages of succession is likely to have been threatened by the formation of a closed canopy typical of later successional stages when broadleaved trees dominated in the Holocene. In Bohemian Switzerland, *R. tomentosum* is also an indicator of waterlogged acidic soil containing large amounts of poorly decomposed organic matter, which is simultaneously a characteristic feature of soils in the boreal zone. Kubát et al. (2002) classifies the growth form of *R. tomentosum* as nanophanerophytic or chamaephytic. *Rhododendron tomentosum* is also a diagnostic species of the *Pino-Ledion* association (e.g. Křísa 1990).

Environmental settings

The landscape in Bohemian Switzerland is strongly affected by Quaternary climate fluctuations. Mainly during the cold phases of Quaternary cycles, deep river valleys were formed in highly erodible sandstone bedrock as a result of large fluctuations in the erosion and sedimentation dynamics of occasional streams. This process is supported by the lithological composition of sandstone, their susceptibility to weathering and their dynamic relief (Svoboda et al. 2018). Glacigenic sediments are not present, but periglacial processes such as frost swirling, rock breaking, and tearing affected the local landscape. The area of Bohemian Switzerland was never glaciated, so *R. tomentosum* would have been able to survive there. The development of soils on slopes is often hindered by high levels of exposure; during interglacial periods, eroded material tended to accumu-

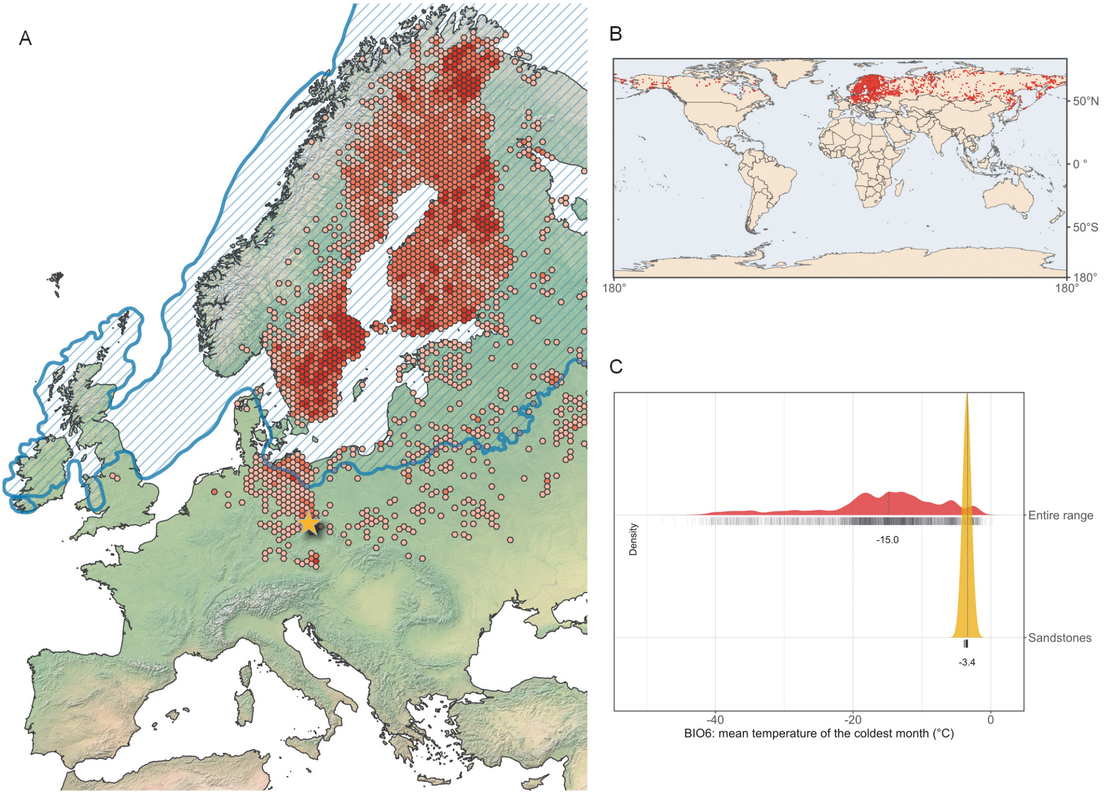

Fig. 1. Map of the current distribution of *Rhododendron tomentosum* in Europe (A) and the Northern Hemisphere (B) based on the Global Biodiversity Information Facility (2022b) and Species Occurrence Database (AOPK ČR 2018). The intensity of the red colour in a 50 km hexagon cell reflects the frequency of recorded occurrences. The asterisk indicates the area included in the SDM modelling. The maximum extent of continental glaciation (~19 ka BP) based on DATED-1 database by Hughes et al. (2016), is shown in blue. Tolerance of the species to low temperatures (C) throughout the whole geographic range (world) and study area in Bohemian Switzerland (sandstones). The density plot shows minimum temperature in the coldest month (BIO6) in °C for all occurrences. Climate data was obtained from Worldclim (Fick & Hijmans 2017) at a resolution of 2.5 minutes. Prepared by Přemysl Bobek.

late in valleys. In the Holocene, accumulations of organic material developed at protected low-lying sites affected by subsurface water. Some of these contain a valuable palaeoenvironmental record.

Although *R. tomentosum* is common in the Arctic and sub-Arctic, in Bohemian Switzerland it most often occurs at altitudes between 250 m and 400 m a.s.l., where the climate is warmer. The average annual air temperature varies between 6 °C and 8 °C, but microclimatic conditions can be very diverse (Mikuláš et al. 2007). The temperature of the air is often stratified resulting in significantly lower temperatures at the bottoms of valleys (Sklenář et al. 2007). Total average precipitation is relatively high, specifically around 800 mm per year (Vesecký et al. 1958). Climatically, Bohemian Switzerland could be classified as ‘temperate deciduous forest’ (Tolasz et al. 2007).

Low species diversity is typical of acidic substrates in European landscapes. This, however, can be simply explained by historical influence. The small extent of areas characterized by acidic substrates in the past limited the total number of current species (Ewald 2003, Palmer et al. 2003, Herben et al. 2007). On the other hand, species richness increases with topographic heterogeneity, which provides greater habitat diversity and surface area and promotes the local coexistence of species (Simpson 1964, O'Brien et al. 2000). Significant differences in nutrient availability are also common, leading to the formation of a spectrum of microhabitats (Herben et al. 2007), thus increasing the possibility of *R. tomentosum* survival.

The current low species diversity is closely related to the nature-driven process of soil nutrient leaching and subsequent acidification. Studies on sedimentary archives from complex landscapes in central-European sandstone regions have identified this complex process as the most obvious and important long-term shift in environmental conditions during warm phases of Quaternary cycles (Iversen 1958, Birks 1986, Kuneš et al. 2011). In contrast to soils that developed on calcareous substrates, soil degradation is caused by changes in the geochemical cycles of nutrients within the ecosystem (Birks & Birks 2004, Kuneš et al. 2011) and is markedly modified by climatic changes, biotic influences and human activity (Bell & Walker 1992). Whereas the vegetation cover that reflects the characteristics of soils developed from calcareous substrates does not demonstrate any major changes during the Holocene (e.g. Žák et al. 2002), soils formed on acidic sandy substrates provide different information. Because of the permeability of sandstone bedrock, such soils are subject to the loss of nutrients (e.g. Pokorný & Kuneš 2005). This phenomenon is compounded by increased precipitation during the Middle Holocene (e.g. Kalis et al. 2003). The result of acidification is nutrient-poor soil with relatively species-poor vegetation (Sýkora & Hadač 1984, Kuneš et al. 2007).

The nutrient-poor substrate and the greatly diversified landscape in Bohemian Switzerland prevented permanent settlement or intensive agricultural use by humans, which has probably helped this unique landscape to persist until today. For this reason, it was declared a national park in 2000 (Kopecká & Vasilová 2003).

Floristic mapping

The National Park is known for its network of steep-sided sandstone valleys with a mixture of exposed rocks and valley bottoms (Wild et al. 2013). The rugged topography is considered to be the main underlying driver of the ecological gradients in moisture and light intensity. Considering the characteristics of the relief, 13 squares of the comprehensive floristic survey of Bohemian Switzerland (H. Härtel, unpublished data) were selected, which consisted of a network of virtual squares each measuring 350 × 350 m (Hadincová et al. 2014). Based on local knowledge of expected suitable habitats, the focus was on the squares with recently reported occurrences of *R. tomentosum*. Within the 13 selected squares, a complete and intensive mapping of the presence or absence of *R. tomentosum* was undertaken. In order to build a habitat suitability model and compare fossil pollen data from localities where *R. tomentosum* was recently reported, the occurrence data ($n = 723$) from the survey of the 13 squares in combination with all available occurrence data from recent field surveys of the National Park, were used. Because of their high uniformity throughout the area studied, geological and edaphic conditions were not included in this study; the same substrate forms similar soils. Most (macro)climatic characteristics at a landscape scale are also uniform in such an area. Microclimatic phenomena resulting from local changes in topography are more pronounced here, therefore, the possible range in topographic characteristics in the squares studied were included in the model.

Description of sites sampled, coring and core storage

The formation of the palaeoenvironmental record typically starts with sedimentation following the damming of a valley by a rock-fall or landslide upstream of the dam. The accumulation of sediments suddenly prevails over those from erosion and continues for a long period. On the basis of digital terrain model analysis and field reconnaissance verification two sites were selected for drilling. The expectation was that there would be no human-induced disruption of the sediment at these sites. Although the sites are not suitable for the occurrence of *R. tomentosum*, there were suitable sites close to the drilling sites, so the assumption was that *R. tomentosum* pollen could have accumulated in these sedimentation traps.

Křepelčí důl (50.931874°N, 14.438233°E). This site is situated 357 m a.s.l. in a valley ~150 m long and 40 m wide and orientated north-west from head to mouth. This sedimentation trap contains a sedimentary sequence two metres deep. The age of its basal layer is at least 14,061 cal. BP (Fig. 2) and corresponds to the Late Glacial. The sedimentation process thus took place relatively slowly and continuously because erosion dynamics were limited as a result of it being a small river basin without a permanent watercourse. The pollen record therefore covers approximately the last 14,000 years (Fig. 3). The mean resolution of 1cm of peat sediment is 77 years.

Puklina (50.932394°N, 14.439768°E). In contrast to the near-by site at Křepelčí důl, situated in a valley, Puklina is located at 386 m a.s.l. in a small depression within a narrow crack on the edge of a plateau. Organic material accumulated here as a result of blocked water flow. Although Puklina is a sedimentation trap approximately 10 m long and 3 m wide, the age of the basal layer is 6,407 cal. BP. Accordingly, the edges of this narrow crack were blocked in the Middle Holocene by sandy material from the surrounding rocks. The sedimentation process was again relatively slow and continuous and terminated not long before the present. It is likely that the upper layers of the record could have been eroded. The pollen record thus covers at least 6,000 years (Fig. 4). The mean resolution of 1 cm of peat sediment was determined to be 80 years.

We used a 70 mm diameter auger to collect cores, then carefully transferred the material into plastic troughs. To prevent exchange, damage or contamination of the material during transport, the cores were marked and wrapped in plastic film. All coordinates of the coring sites are presented in Table 1. To prevent the decomposition of organic material, the cores were stored in a refrigerated room.

The final profile from Křepelčí důl (Fig. 2) was constructed using the Corel PHOTO-PAINT SE programme, version 2019, based on photographs taken in the field and a detailed description of lithological conditions. The distribution in time, was added to the final output based mainly on the age-depth model (Fig. 5).

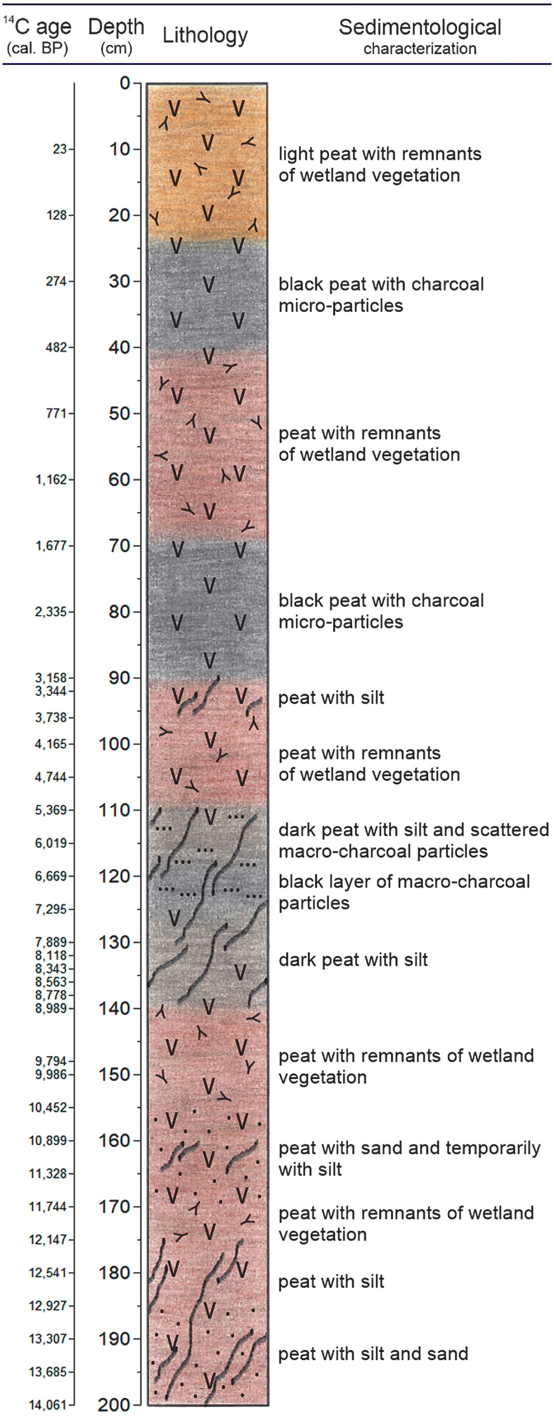

Fig. 2. Lithology of the Křepelčí důl core. Prepared by Tomáš Radoměřský.

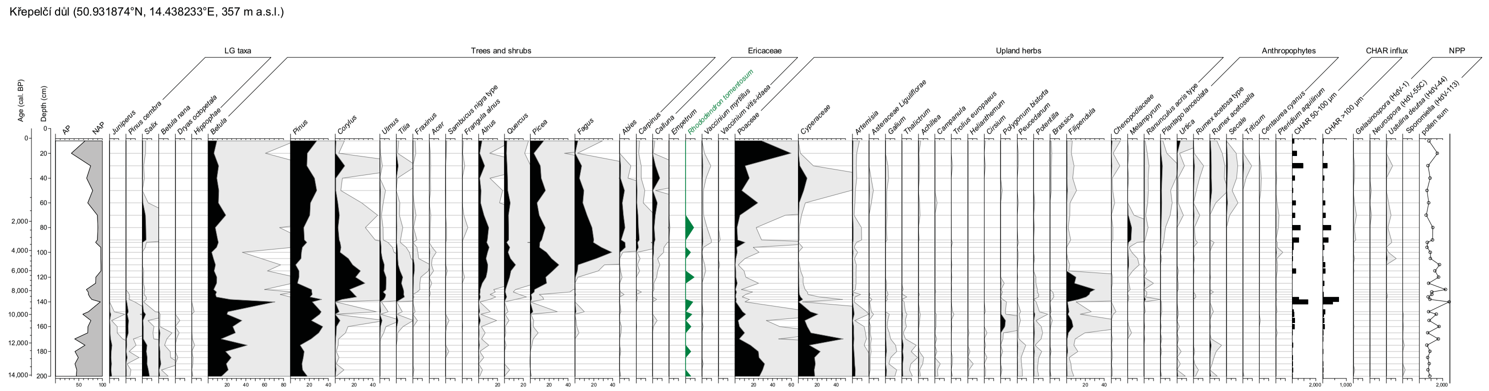

Fig. 3. Pollen percentage diagram for Křepelčí důl (50.931874°N, 14.438233°E, 357 m a.s.l.). Source: Tilia software, Version 3.0.1. (Grimm 2011). Prepared by Přemysl Bobek & Helena Svitavská Svobodová.

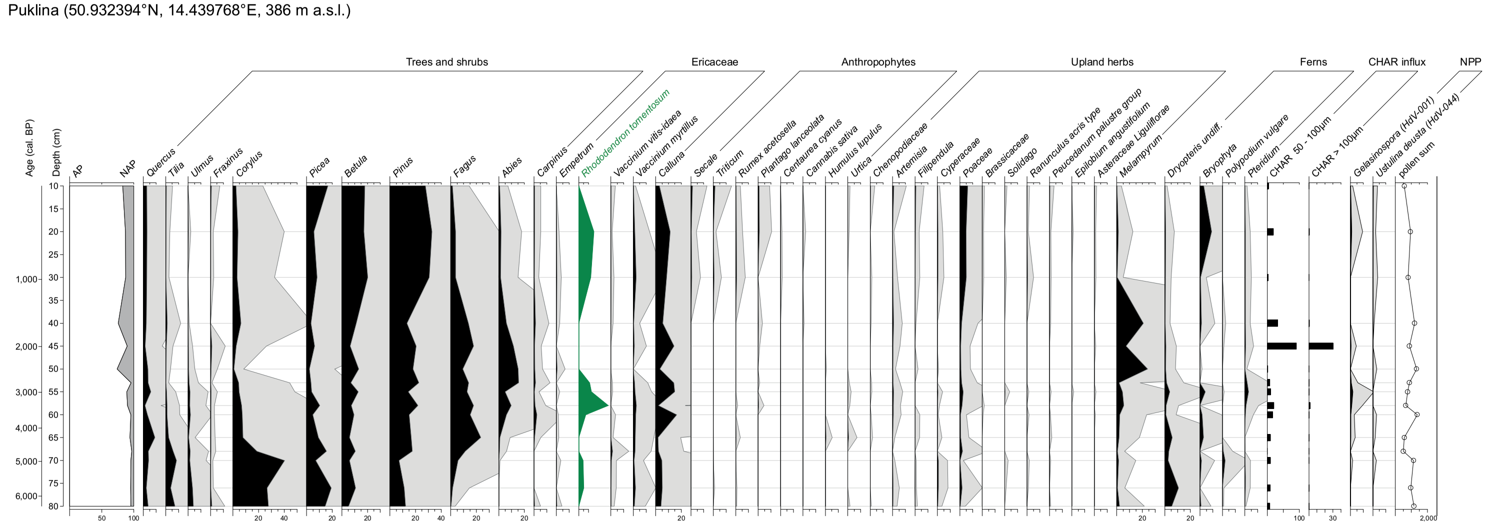

Fig. 4. Pollen percentage diagram for Puklina (50.932394°N, 14.439768°E, 386 m a.s.l.). Source: Tilia software, Version 3.0.1. (Grimm 2011). Prepared by Přemysl Bobek & Helena Svitavská Svobodová.

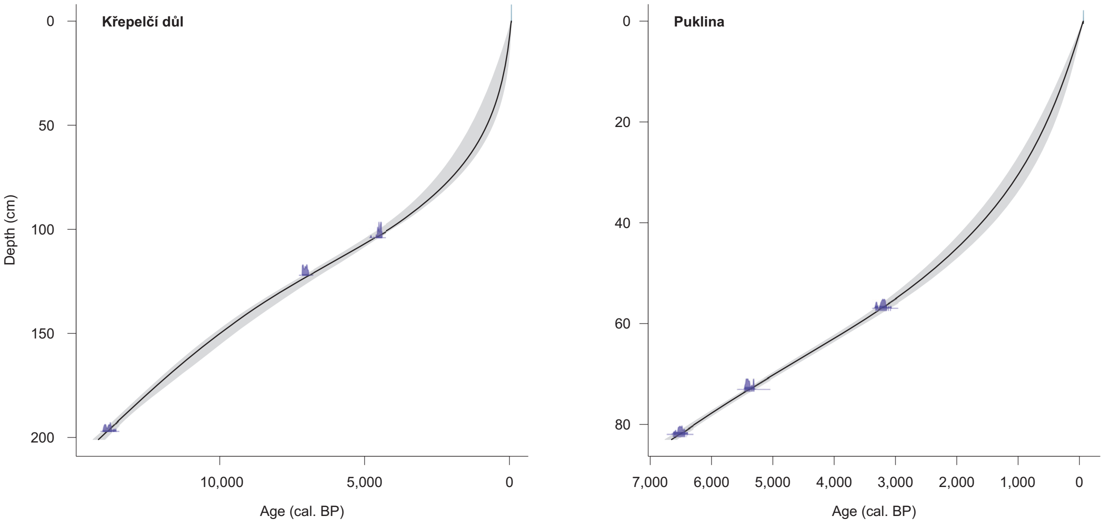

Fig. 5. Age-depth model for the Křepelčí důl and Puklina sites. Prepared by Přemysl Bobek.

Pollen sampling, laboratory preparation and processing

The samples taken for microscopic analysis were always 2 cm^3 in volume. Fifty-six such samples were collected and prepared according to standard procedures using the acetolysis method (Moore et al. 1991). First, the mineral component was removed using hydrofluoric acid. Treatment in HF is used to decompose inorganic particles (Overbeck 1958, Faegri & Iversen 1964). The contents consisting of organic substances (celluloses) were reduced by acetolysis (Berglund & Ralska-Jasiewiczowa 1986, Moore et al. 1991). Acetolysis decomposes cellulose and excess organic remains that make it difficult to see and count pollen and spores (Berglund & Ralska-Jasiewiczowa 1986).

The most important feature used for determining the pollen grains is the morphology of the cell wall of a mature pollen grain, which is a highly specialized and multilayered structure. The external walls of pollen grains are sporopollenin-based, which provides protection, while the internal walls, composed primarily of cellulose, are important for pollen germination (e.g. Jaffri & MacAlister 2021).

The samples were observed under an optical light microscope at magnifications of 400–1,000× and standard keys used to identify the pollen grains (Faegri & Iversen 1989, Moore et al. 1991, Beug 2004). The aim was to identify the pollen grains and spores in each sample and in particular to find pollen grains of *R. tomentosum*. Pollen production by *R. tomentosum* is very low. The standard pollen analysis procedure is usually based on at least 500 pollen grains. In a previous study the effect of a production bias is discussed (Radoměřský et al. 2017) as in several cases *R. tomentosum* pollen was not found even inside the living moss cover directly under flowering plants. The calibration and analysis, therefore, was based on the determination at least 3,000 pollen grains and spores in each sample in order to increase the probability of finding *R. tomentosum* pollen grains. The relative concentration of pollen grains increases in samples from the deeper parts of the

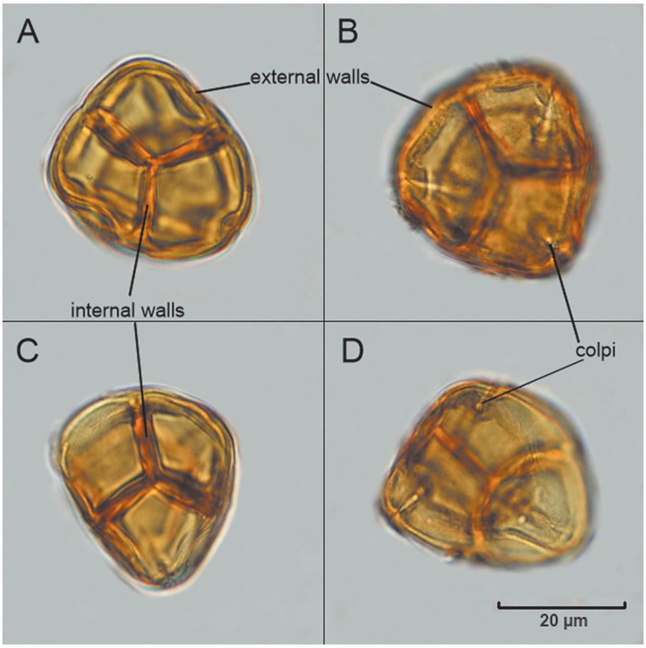

Fig. 6. Pollen grains of *Rhododendron tomentosum* from Křepelčí důl and Puklina; 1,000× magnification. Photographed by Tomáš Radoměřský.

profile as a result of material compression and more decomposition of organic matter that occur over a longer period.

The percentage values for pollen were calculated using the total sum of pollen grains (TS) of arboreal pollen (AP) and non-arboreal pollen (NAP) taxa. Pollen from (semi-) aquatic plants, spores, and non-pollen palynomorphs were omitted from the calculation of TS. Pollen percentage diagrams were compiled using Tilia software, Version 3.0.1. (Grimm 2011). To enhance the clarity of the diagrams, the majority of individual plant species was sorted into several groups (e.g. trees and shrubs, *Ericaceae*, herbaceous plants, anthropogenic indicators, finally LG taxa and ferns). Most attention was paid to the *Ericaceae* group, including *R. tomentosum*.

Here a description of the tetrads of the *Ericaceae* family is presented, which are quite similar in some parameters, based on Beug (2004): (i) *Empetrum nigrum / Rhododendron tomentosum*. Each *R. tomentosum* pollen grain is triangular in shape, whereas the similar pollen grains of *E. nigrum* are smaller and more circular. Because of the presence of an additional cellulose layer around the colpi, the thickness of the internal walls of *E. nigrum* and *R. tomentosum* pollen is in the range 2.0–3.5 µm and, therefore, thicker than the external walls and thus a typical feature of *R. tomentosum* (Fig. 6A–D) and *E. nigrum*. Both *R. tomentosum* and *E. nigrum* pollen grains contain three colpi. Morphology is the main feature for distinguishing *R. tomentosum* from *E. nigrum*: specifically, the colpi of *R. tomentosum* are longer (Fig. 6B, D) than those of *E. nigrum*. The surface of *R. tomentosum* and *E. nigrum* pollen grains is scabrate and their diameters are in the range 32.0–42.0 µm. (ii) *Calluna vulgaris* always produces irregular rhombic or linear pollen tetrads with a coarsely verrucate surface and thick walls (Fig. 7A–D). Unlike *R. tomentosum* and *E. nigrum*, the

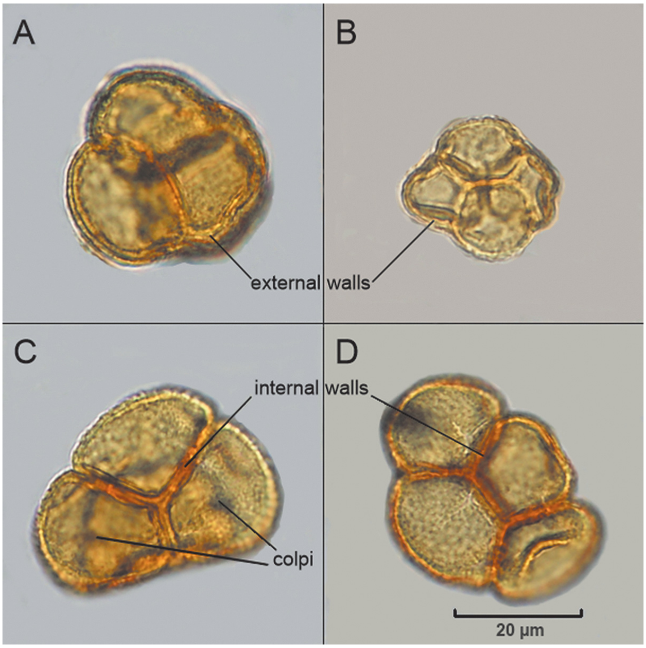

Fig. 7. Pollen grains of *Calluna vulgaris* from Křepelčí důl and Puklina; 1,000x magnification. Photographed by Tomáš Radoměřský.

internal and external walls are similar in thickness. The pollen grains were 34.0–48.0 µm in size and also have three colpi. (iii) *Vaccinium*-type pollen also has internal and external walls of the same thickness (Fig. 8A–D), but they are thinner than the walls of *Calluna vulgaris* pollen; all three colpi of *Vaccinium*-type are considerably longer and are straight (Fig. 7). The surface is psilate, scabrate and slightly cracked or very finely perforated. The size of *Vaccinium*-type pollen grains is in the range 37.0–50.5 µm.

Radiocarbon dating

To construct the chronologies of the peat profiles, three samples were collected from the Křepelčí důl core and three from the Puklina core (Table 1), which were dated using the ^{14}C radiometric method (accelerator mass spectrometry). Plant material of aboveground origin, mainly charcoal and seeds, was manually extracted from the sediment. In the absence of macrofossils, a bulk peat sample consisting of *Sphagnum* and moss stems was used. A standard acid-alkali-acid (AAA) pre-treatment was applied to remove humic and fulvic acids. All radiocarbon measurements were calibrated using the IntCal13 curve (Reimer et al. 2013) provided by OxCal, Version 4.2.4. (Bronk Ramsey 2009a, b) and reported in years before present (cal. BP). Age-depth modelling (Fig. 5) was done using the ‘clam’ 2.2 package (Blaauw 2010) in statistical software R (R Development Core Team 2013) by fitting a smoothing spline (smoothing parameter of 0.3, 1,000 iterations) to the radiocarbon-dated layers and interpolating them to obtain an estimate of the age of each layer of the core.

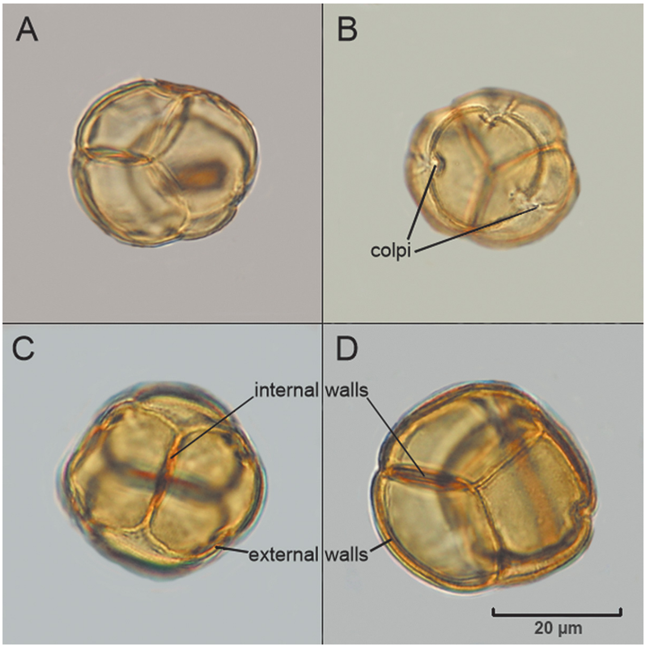

Fig. 8. Pollen grains of *Vaccinium*-type from Křepelčí důl and Puklina; 1,000× magnification. Photographed by Tomáš Radoměřský.

Charcoal analysis

To reconstruct past incidence of fires, macroscopic charcoal from 2 cm^3 of sediment were sampled at contiguous 1cm intervals. Samples were soaked in a 10% KOH solution for 24 hours, then all uncharred organic material was bleached with 10% hypochlorite (NaOCl). The resulting sample was washed through a sieve with a mesh of 125 µm and charcoal particles counted under a stereomicroscope. The recorded charcoal concentration (particles·cm^{-3}) was converted to charcoal accumulation rate (CHAR, particles cm^{-2}·yr^{-1}) using the estimated deposition time for a particular sample. CHAR values were used as a proxy for the biomass burned around the site without attempting to identify individual fires. A composite biomass burning curve (Bobek 2019) was used to compare regional fire activity in sandstone landscapes in northern Bohemia. This proxy synthesizes CHAR records at multiple locations to reveal periods of increased or decreased fire activity. All profiles used to calculate this proxy are within the current distribution of *R. tomentosum*.

Geochemical analyses

The aim of the geochemical analyses was to trace changes in the past environment and thus provide independent information to complement the pollen analysis. Selected chemical elements in the core from Křepelčí důl were identified using X-ray fluorescence (XRF) spectrometry. Data on the elemental concentration of titanium (Ti), calcium (Ca) and iron (Fe) were added in order to ascertain the Ca/Ti and Fe/Ti values and better describe any environmental changes. The Ca-Ti ratio is ultimately a measurement of the relationship between biological productivity and physical erosion in the catchment area

Table 1. ^{14}C dates for Křepelčí důl (50.931874°N, 14.438233°E, 357 m a.s.l.) and Puklina (50.932394°N, 14.439768°E, 386 m a.s.l.).

Site	Lab code	Method	Depth [cm]	^{14}C age [yrs BP]	2σ error [yrs]	Material	Thickness [cm]
Puklina	DeA-10130	AMS	57	3017	27	*Picea abies* charcoal, single fragment	1
Puklina	DeA-10132	AMS	73	4644	30	*Pinus sylvestris* charcoal, single fragment	1
Puklina	DeA-10133	AMS	82	5727	32	*Picea abies* charcoal, 10 pieces	1
Křepelčí důl	DeA-10190	AMS	104	4044	31	bulk peat	1
Křepelčí důl	DeA-10128	AMS	122	6154	32	*Picea abies* charcoal, single fragment	1
Křepelčí důl	DeA-10191	AMS	197	11957	65	*Carex* sp. seeds, nine pieces	1

(e.g. Kylander et al. 2013), which decreases at transitions from warmer to colder periods and vice versa. Thus, the values approximate to warming or cooling of the local climate. In fact, Ca/Ti is the inverse of the Fe/Ti values. The Fe-Ti ratio is an indicator of reducing conditions in the profile. Possible post-depositional dissolution of Fe-Ti oxides can be discounted by comparing the distributions of chemically immobile Ti with those of Fe, which may be relatively mobile under reducing conditions (Rosenbaum et al. 1996). Fe/Ti values thus reflect wetness.

Species habitat suitability model

To identify local refugia, the information from the pollen analysis was downscaled using a habitat suitability model for *R tomentosum*. It was deterministically presumed that its distribution could be driven by the environmental conditions proposed by Hadincová et al. (2014), so five spatial grids (see Supplementary Table S1, S2) of uncorrelated (Pearson correlation < 0.7) topographic factors, representing the environmental conditions important for *R. tomentosum* (Table 2), were derived. Topographic factors were derived using a digital terrain model (DTM) based on LiDAR scanning data provided by the Institute of Photogrammetry and Remote Sensing at Dresden University of Technology. The original DTM was upscaled to a 5 m resolution to reduce fine scale, ecologically irrelevant bias. For topographical analysis, SAGA GIS 6.4.0. software (Conrad et al. 2015) was used. Statistics and modelling used R 3.3.4 software (R Core Team 2016) extended by the random Forest library 4.6-14 (Breiman 2001, Liaw & Wiener 2002). The well-established (Mi et al. 2017, Pecchi et al. 2019, Cerrejón et al. 2020) random forest algorithm with 500 trees was used and at each split random sampling of three out of five variables was allowed. To evaluate the performance of the model, Kohens Kappa was used, which corrects the overall accuracy of model predictions by considering occurrences happening by chance. The Kappa ranges from –1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random (Monserud & Leemans 1992, Allouche et al. 2006). The performance metrics were calculated with one fourth (0.25) of the data not included in model training. To assess the importance of environmental variables for determining the potential habitat suitability for *R. tomentosum*, the Gini index (e.g. Liu et al. 2009) was used. The sum over the number of splits (across all 500 trees) includes the environmental variable, proportional to the number of input occurrences (presences/absences) that it splits (Supplementary Fig. S2).

Table 2. Environmental input data used for modelling habitat suitability.

Variable	Description
Diurnal anisotropic heating	An approximation of the heat treatment index. This index is based on terrain morphology and sun position and describes the thermal balance of a site. It also similar to the humidity index.
Sky view factor	This factor indicates the degree of hemispheric shading of the sky by surrounding morphological features. Low values mean the view of the sky is obscured by barriers. The value generally decreases with the increasing height of rocks and increasing closure of the valley.
Topographic position index	The TPI (Guisan et al. 1999) expresses the relative height above or below the surrounding terrain according to a given search radius. This parameter represents an approximation of the degree of isolation from surrounding landforms and the distance from channels. The result is a marked moisture gradient and temperature gradient between the valley bottoms and the surrounding hills or rocks. A search radius of 30 m is able to identify rocks and rock edges in a sandstone relief. Positive values indicate a higher position of the site relative to the surrounding relief.
Topographic wetness index	This is a proxy for relative soil moisture and is calculated based on the size of the drainage basin above a specific locality.
Vertical distance to channel network	This index describes the vertical difference between the surface model based on channel network and terrain. It could be a proxy for potential wetness and potential radiation.

Occurrence data for habitat suitability modelling were based on known records from square mapping in Bohemian Switzerland (Hadincová et al. 2014), supplemented by the detailed mapping of 13 selected squares (350 × 350 m). Seven-hundred-twenty-three presences and 723 absences were used in the model. Based on field observation during detailed mapping of 13 squares, it was considered that any point in the 13 squares without a presence implies a real absence. Building on this, a 10 m buffer exclusion zone was created around each presence because of possible position error of the training points and generated 723 random absence points. This, resulted in a prevalence of 0.5 in the dataset, which is preferred value for modelling (Reese et al. 2005). For both the 723 presences and the 723 absences the mean value of environmental factors was calculated and used to estimate the effect the direction of the factors (Table 3).

Results

Habitat suitability model

The habitat suitability model for *R. tomentosum* performed well with Kappa higher than 0.7 (Monserud & Leemans 1992): Kappa = 0.72. Therefore, this model was used to predict potential refugia, that is, sites with highly suitable habitat (Fig. 9). It revealed that 2.3% of the area studied has a high probability (> 90%) for *R. tomentosum* occurrence. Habitat suitability prediction helped in downscaling the pollen evidence recorded at the Puklina and Křepelčí důl sites and thus the locating of local refugia. On the basis of topographic environmental factors, most suitable habitats were situated on north-facing rocky outcrops situated relatively high above the bottoms of valleys. Neither of the pollen sites, Puklina and Křepelčí důl, were potentially suitable for *R. tomentosum*, but potentially suitable sites for *R. tomentosum* did exist close to these sites (Fig. 9).

Table 3. Gini importance and direction of the effect of the environmental factors driving *Rhododendron tomentosum* potential habitat suitability in the area studied (+ effect means that the probable habitat suitability increases with increasing values of the factor and vice versa).

	Gini importance	Effect direction
Topographic wetness index	247.18	–
Diurnal anisotropic heating	202.84	–
Topographic position index	116.42	+
Sky view factor	79.65	–
Vertical distance to channel network	76.45	+

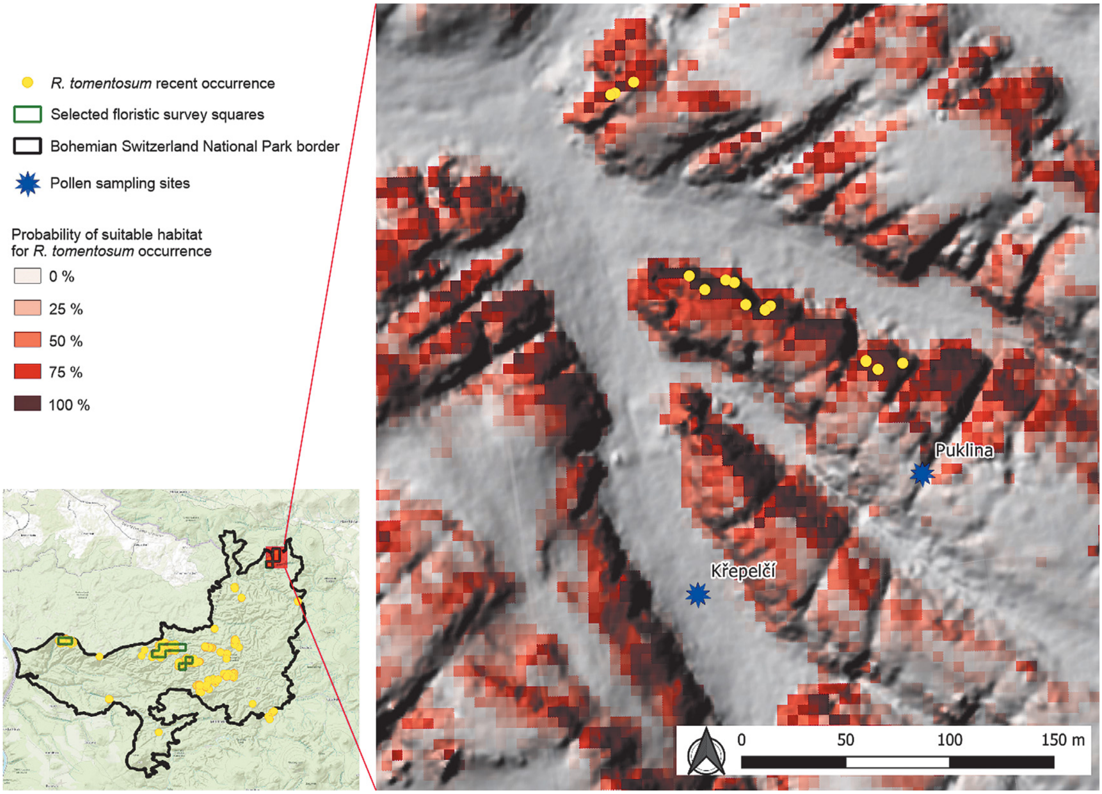

Fig. 9. Map of potential habitat suitability for *R. tomentosum* based on random forest prediction and environmental grids (Table 3). Zoom-in view of eight illustrative squares in the area sampled. Yellow points represent current occurrences of *R. tomentosum* based on field research. Prepared by Matěj Man.

Based on the habitat suitability model, the topographic wetness index and diurnal anisotropic heating were the most important environmental factors determining the potential habitat suitability for *R. tomentosum* (Table 3).

Description of the Křepelčí důl core

The top of the profile contains relatively bright peat composed of slightly-decomposed moss (Fig. 2). Generally, sediment compression increases with depth. From 25 to 110 cm, there are alternate dark brown and brighter layers of differently decomposed and compressed peat. From 110 to 123 cm, the peat contains a significant admixture of silt and scattered particles of charcoal, which makes the colour of the sediment darker. Macrocharcoal particles are scattered across the profile but also concentrate in one black layer 2 cm thick. Further, the well-decomposed and more compressed brown peat contains an alternating admixture of sand and silt or both of these components. Temporarily, the mineral component admixture disappears. The final depth of the core reaches 200 cm. Some layers also contain evidence of the presence of *R. tomentosum*.

Pollen evidence

The identification of pollen (Figs 3, 4), focused on tree species that probably have a significant effect on *R. tomentosum* populations, namely *Pinus* (including most probably only *P. sylvestris*), *Picea abies* and *Fagus sylvatica* (Fig. 10). Pollen of *Pinus sylvestris* is present in all layers, with two peaks in abundance: the first is between 12 and 8 ka cal. BP and the second in the last 1,500 years. After a significant decrease in *P. sylvestris* towards 7.5 ka cal. BP, there follows a gradual increase. Greater numbers of *P. sylvestris* pollen were recorded at Puklina, a natural habitat of *P. sylvestris*. The first evidence of *Picea abies* is recorded in the Late Glacial (in the profile before ~11.7 ka). *Picea abies* pollen numbers increased significantly before 8 ka, with a peak between 6.5 and 5 ka cal. BP at both sites and increase again in recent centuries. Higher pollen levels for *P. abies* are recorded at Křepelčí důl. *Fagus sylvatica* first appears in pollen spectra before 7 ka. There is a significant increase after approximately 5.3 ka cal. BP, with a peak from 5 to 4 ka cal. BP at both sites (Figs 3, 4). The subsequent trend is one of a gradual decrease. The number of pollen grains of *F. sylvatica* recorded at Křepelčí důl was higher (Fig. 10). Other tree species have a minor effect on the growth of *R. tomentosum*, particularly because of their lower representation in the vegetation.

The first records of pollen of *R. tomentosum* occur at 14, 12.5, 11 and 10 ka cal. BP (Fig. 3). Approximately from 9 to 7.5 ka cal. BP (i.e. in the Boreal and Older Atlantic), this species is completely absent from the pollen spectra. At 6 ka cal. BP, the presence of *R. tomentosum* is again recorded and from 6 to 5 ka cal. BP, there is a significant increase in *R. tomentosum* pollen grains as a result of the addition of evidence from the Puklina site. From 5 to 4 ka cal. BP, there is a significant drop. From 4 to 2 ka, it increases rapidly, with a peak at 3 ka cal. BP at both sites. After a significant drop at 2 ka cal. BP, *R. tomentosum* occurs only occasionally and in recent centuries is absent. The number of pollen grains identified in each sample exceeded 3,000 (Fig. 10). The number of *R. tomentosum* pollen grains identified in samples from Puklina are considerably greater than in the samples from Křepelčí důl, which is likely to be a result of site selection: the Puklina site is probably located very close to a past population of *R. tomentosum*.

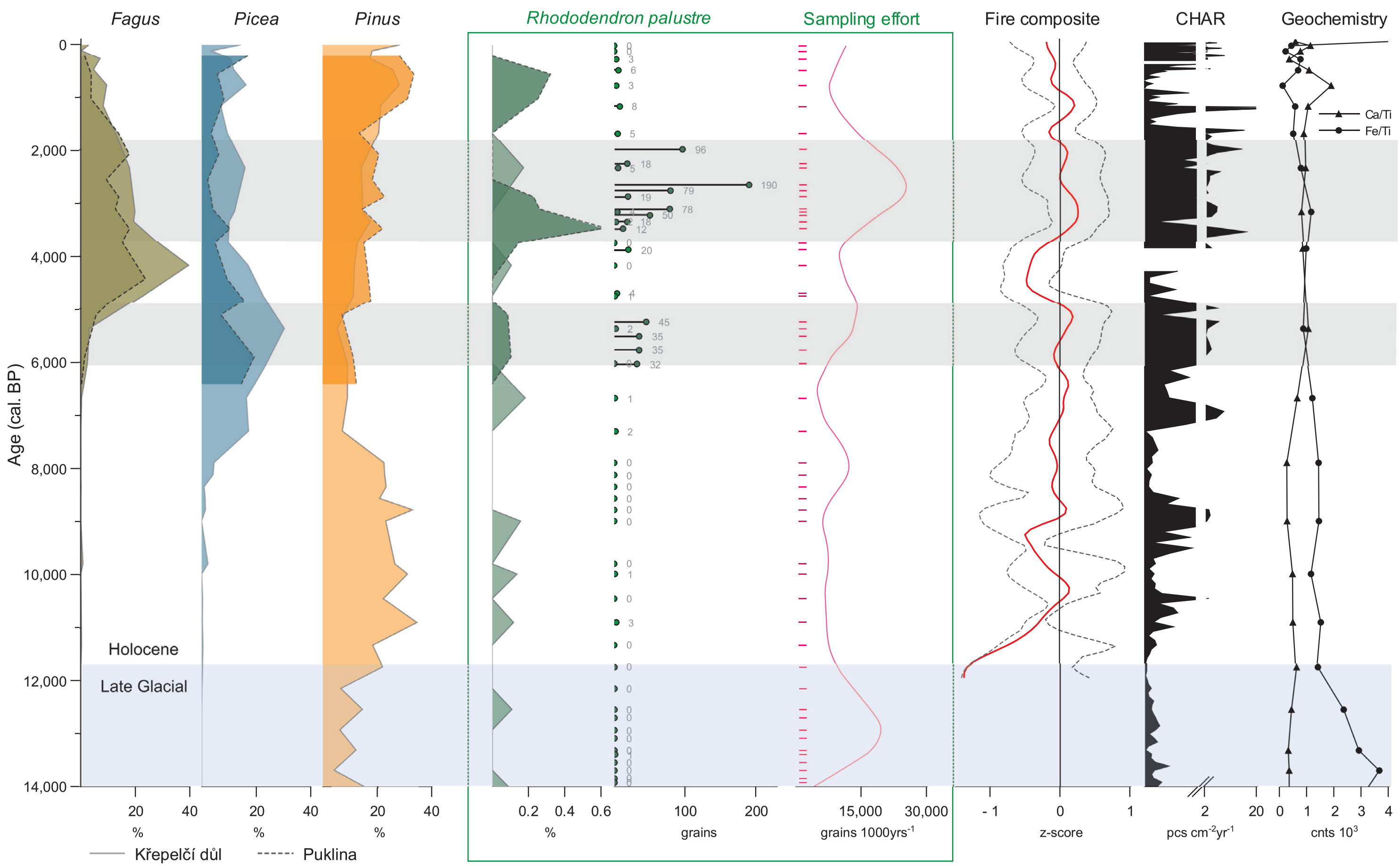

Fig. 10. Summary diagram comparing changes in the representation of major woodland species (*Fagus sylvatica, Picea abies* and *Pinus sylvestris*) with pollen evidence of presence of *Rhododendron tomentosum*. Sampling effort equals the number of pollen grains inspected (black line – rolling mean with 1,000-year window; red line – loess smoothing; red marks – locations sampled). The local fire history is depicted in terms of the accumulation of macrocharcoal (>125 μm). The content of trace elements (normalized Ti) in the Křepelčí důl core is displayed under Geochemistry. Grey layers represent periods of high numbers of *R. tomentosum* pollen grains. Prepared by Přemysl Bobek.

Fire disturbances

Based on the number of macroparticles of charcoal in each layer (Fig. 10), there were fires at both Křepelčí důl and Puklina. The highest incidence of fires was recorded in around 3 ka cal. BP. In addition, periods characterized by numerous fires occurred from approximately 6 to 5 ka cal. BP and between 4 and 2 ka cal. BP, which coincide with peaks in *R. tomentosum.* In contrast, a low incidence of fires was recorded from 14 to 11 ka cal. BP. Significantly fewer fire events also occurred around 9 ka cal. BP and from 5 to 4 ka cal. BP.

Geochemistry

Geochemical analysis of the sediment from Křepelčí důl revealed changes in Ca/Ti and redox conditions in the sediment based on Fe/Ti values. There is a relatively stable trend in Ca/Ti in the profile from 14 to 8 ka cal. BP and again from 5.5 to 1 ka cal. BP (Fig. 10). The trend is for a slight increase from 8 to 5.5 ka cal. BP. There was then a strong increase in the trend, which peaked 1 ka cal. BP. Then, towards the present, the trend changes rapidly, but mostly declines. In fact, there is a weak inverse relationship between the Ca/Ti and Fe/Ti values throughout the profile (Fig. 10). A significant decreasing trend in Fe/Ti is recorded from 13.5 to approximately 11.8 ka cal. BP, followed by a long period of relative stability, with a slight decrease between 8 and 5.5 ka cal. BP. The lowest Fe/Ti values are recorded at 1 ka cal. BP, which coincides with a peak of Ca. A very strong increasing trend in the Fe/Ti values is recorded at present.

Discussion

Based on the results, populations of *R. tomentosum*, a plant that is demanding of both light and moisture, could have survived for long periods in local refugia situated on north-facing rocky outcrops. These microrefugia could have provided sufficient moisture during dry periods, for a number of reasons, such as low tree cover and greater wetness as a result of their northerly orientation, water movement inside the sandstone, or the presence of small wet depressions in the rocky outcrops. In addition, because the low plant cover on exposed rocky outcrops, these refugia could serve as ‘islands of light’ in periods otherwise characterized by closed tree canopy.

In recent centuries, the pollen data does not indicate the presence of *R. tomentosum* in the sedimentary record from Křepelčí důl. Evidence for Puklina is also missing in recent centuries, probably because of unfavourable conditions for organic matter sedimentation and pollen preservation. Despite the clear evidence of *R. tomentosum* in deeper layers of both pollen profiles, there is no evidence of the presence of recent populations of *R. tomentosum* close to the sites sampled. It was not expected that *R. tomentosum* would be currently growing at the sites sampled as they are forested with a closed canopy, which reduces the available light in the understory and makes the sites unfavourable for *R. tomentosum*. However, pollen grains of *R. tomentosum* were found at both these sites in periods when the forest canopy was probably also as closed as it is today. But when *R. tomentosum* was not growing in the bottom of valleys, then the source of pollen had to be close because of the generally small pollen source area of the forest hollows that were sampled (Sugita 1994, Calcote 1995). In addition, because *R. tomentosum* is adapted to insect pollination (e.g. Křísa 1990), its pollen grains fall close to the mother plant.

The habitat suitability model, based on high-resolution environmental topographic data (5 m), indicated the presence of potentially highly suitable habitats around the Puklina and Křepelčí důl sites (Fig. 9). Highly suitable habitats were situated on north-facing rocky outcrops high above valley bottoms. Despite the general landscape aridification or forestation, these sites could potentially serve as refugia for long-term stable populations of *R. tomentosum*. Close to the sites sampled, a source of the pollen signal was detected in sediments that could be considered to be refugia.

The current study is based on a similar approach to the downscaling of pollen data used by Theuerkauf & Joosten (2009), but the habitat suitability model was based on recent occurrence data. An alternative explanation is the possibility that pollen is transported over long distances, which would not be expected in entomophilic species. However, this was not considered because of the presence of topographic barriers and high surface fragmentation in the area studied, which probably blocks the movement of air masses over long distances.

The pollen record indicates that the relatively long-term survival of nearby populations was recently terminated. The closest population grows on north-facing rocky outcrops approximately 60 m north of the Puklina site (Fig. 9). Such outcrops are most likely to provide potentially suitable habitats. Despite the habitat suitability model, the initial view was that almost all north-facing rocky outcrops are potentially highly suitable.

These habitats characteristically have a low topographic wetness index and high values for diurnal anisotropic heating. However, a high topographic position and great vertical distance from a channel network indicates increased light reception on rocky outcrops. In addition, potentially suitable sites have a lower sky view factor typical of northerly and more humid slopes. This is consistent with the results of Hadincová et al. (2014), who conclude that *R. tomentosum* prefers higher light conditions (and is unable to grow under a forest canopy, despite other suitable factors). The low values for wetness and sky view might be seen to be in conflict with our conclusions (and those of Hadincová et al. 2014) that *R. tomentosum* prefers high levels of light and humidity. But a more detailed examination indicates a better fit – the places with high sky views are the plains and exposed rocks but *R. tomentosum* prefers north-facing outcrops. Similarly, although *R. tomentosum* prefers wet conditions, the potential habitat suitability model revealed a decreasing trend with increasing topographic wetness (TWI). The highest values of TWI are found at the bottom of valleys, which are not favourable for *R. tomentosum* because of closed canopy cover and terrain shading. Specifically, in the sandstone landscape in the area studied, TWI is probably not a good proxy for soil moisture, because of underground depressions in the bedrock and water movement through sandstone, which cannot be revealed using a digital terrain model (Jarecke et al. 2021, Riihimäki et al. 2021). Nevertheless, TWI in the models presented helped in the identification of suitable habitats as it is a potential proxy for microclimatic conditions and air movement.

Consistent with existing studies (e.g. Alba-Sánchez et al. 2010), the findings presented confirm that, combined with pollen data, topographic environmental factors could be useful for explaining the past distribution of species.

Pleistocene and Early Holocene dynamics of Rhododendron tomentosum

During the glacial periods, the sandstone landscape of northern Bohemia was exposed, arid and almost devoid of woodlands. There is no direct pollen evidence of *R. tomentosum* from these times because the creation of sedimentary records was limited by strong erosion and the absence of organic detritus. However, based on Hadincová et al. (2014) and the knowledge presented on how *R. tomentosum* responds to environmental variables, it is suggested that the type of environment where *R. tomentosum* could survive was probably valley bottoms under steep north-facing slopes and on protected outcrops exposed to little direct sunlight and with high substrate humidity resulting from prolonged snow cover. A combination of exceptional environments therefore offered protection from the regional climate and the effects of climate change and enabled this species to persist despite a regionally unfavourable environment (Gavin et al. 2014).

Nevertheless, higher temperatures and increased precipitation after the LGM improved abiotic conditions at many previously unfavourable sites for most plants, including *R. tomentosum*. Sparse and more or less open cover with *Pinus sylvestris* dominant developed in the wetter valleys (e.g. Svoboda et al. 2018) and steppes on plateaus (Walter 1974, Ermakov et al. 2000). During this time, *R. tomentosum* could have dispersed from several isolated sites. In addition, the potential for preservation of its pollen increased because of the formation of numerous sedimentary basins. Therefore, according to the pollen record from Křepelčí důl, *R. tomentosum* first occurs as early as 14 ka BP. Such an early occurrence of *R. tomentosum* pollen indicates the proximity of a glacial refugium that could also be affected by fires. The charcoal record in the peat profile is lacking, but the possibility of unrecorded Late Glacial fire events that affected exclusively herbaceous vegetation cannot be excluded (Bobek et al. 2018).

At the beginning of the Holocene (~11.7 ka BP; Walker et al. 2012), because of the significant increase in average temperatures and precipitation, semi-open boreal communities began to spread into all accessible habitats. At certain sites high above the valley floor, assuming stable and increased humidity, the beginning of the process of plant litter accumulation caused a gradual change from predominantly mineral soils to more organic soils and probably, therefore, resulted in habitats suitable for *R. tomentosum*.

The results from Křepelčí důl indicate that during Early Holocene (~11.7 ka BP to ~8.2 ka BP; Walker et al. 2012), the presence of *R. tomentosum* was relatively low and intermittent, probably as a result of this species becoming extinct at this site due to deteriorating conditions. It is also possible that the soil conditions were still not favourable for *R. tomentosum*, probably because of high pH values. The spread of *R. tomentosum* back to this site from other sites may then have been blocked by, for example, strong competition or the presence of a geographical barrier (Hirzel et al. 2002). At the same time, progressive afforestation of the landscape resulted in a dramatic deterioration in conditions for *R. tomentosum* at its original sites in the valleys due to increase in competition (tree shading), which resulted in *R. tomentosum* occupying more suitable north-facing rocky outcrops more exposed to light high above the valley floor. During the environmental changes in the Quaternary, *R. tomentosum* probably repeatedly occupied habitats at different heights above the valley floor.

Furthermore, climate reconstructions for the Early Holocene in central Europe reveal periodic decreases in annual rainfall and warmer summer conditions (Litt et al. 2009), which might have resulted in prolonged droughts and an increase in the incidence of fires. Fire events are recorded by the presence of charcoal particles scattered in the peat profile (Fig. 2) and in some places concentrated in layers (Fig. 10). Available data on soil charcoal also indicate the high abundance of conifers from the beginning of the Holocene up to 6.3 ka BP (Bobek et al. 2018). There are no prominent peaks in the macrocharcoal record from Křepelčí důl, but indications of infrequent low-intensity fires. A mixed-intensity fire regime is also confirmed by a composite record of fires from multiple sites in the North Bohemian sandpit area (Bobek 2019).

The trend in Ca/Ti between 14 and 8 ka BP is stable and indicates a relatively cold climate, which contrasts with the results of the pollen analysis. Nevertheless, the amount of Ca in older layers of the profile could have been affected by humidity-induced leaching from the profile typical of the wet Middle Holocene period. In addition, Fe/Ti values indicate a decrease in humidity up to 12 ka BP followed by stable humidity conditions.

Rhododendron tomentosum in the Middle Holocene

The dominant ecological factor in the Middle Holocene (~8.2–4.2 ka BP; Walker et al. 2012) was afforestation, which resulted in strong selection (Pokorný et al. 2015), especially in the Older Atlantic period (~8.2–6.5 ka BP; e.g. Šída & Pokorný 2020). Palaeoecological data indicate that coniferous forests, which also prevailed in Bohemian Switzerland during the Early Holocene, were replaced by more competitive deciduous and mixed forests (e.g. Pokorný & Kuneš 2005, Kuneš et al. 2007, Pokorný 2011, Novák et al. 2019). The spread of broadleaved trees with a strongly increasing trend in *Picea abies* and strong decrease in *Pinus sylvestris* (Fig. 10), could have resulted in a dramatic decline in the diversity of the undergrowth (including *R. tomentosum*) as a result of tree crown shading, leading to numerous extinctions (Chytrý et al. 2010). This afforestation process also resulted in a decrease in fire events and therefore created a bottleneck effect for *R. tomentosum*, which gradually reduced the number of favourable sites. This process is recorded at Křepelčí důl by the episodic presence of *R. tomentosum*.

At this time, improvement in climate is associated with the early expansion of agriculture in central Europe during the Neolithic period around 7.5 ka BP (Bonsall et al. 2001, Bogaard 2004). Based on the weak influence of humans on the dynamics of erosion and sedimentation and the absence of anthropogenic indicators in the pollen spectra, however, it is assumed that this did not occur in the area studied. Generally, the low influence of human activity in Bohemian Switzerland has always been due to the pronounced relief dynamics and absence of large flat areas of loess-derived soils that are the most suitable for agriculture. These factors coincide with the opposing trends in Ca-Ti ratio and Fe/Ti in the peat profile, which document a gradual warming and drier climate during the Older Middle Holocene (Fig. 10).

In the Younger Atlantic period (~6.5–4.2 ka BP; e.g. Šída & Pokorný 2020), especially the first half, a peak in *Picea abies* and its predominance over deciduous trees in the pollen profile was recorded at both sites and high levels of shading by *P. abies* would have had an adverse effect on habitat suitability for *R. tomentosum*. Furthermore, *Pinus sylvestris* decreased to its minimum in the pollen record. Based on the pollen evidence from Puklina, however, there was relatively continuous and significant representation of *R. tomentosum* from 6 to 5 ka BP. These results are supported by the charcoal analysis.

The species composition associated with the charcoal corresponds most closely to semi-shaded forest dominated by *Pinus sylvestris* (Bobek 2013) and its acidophilous undergrowth, including *R. tomentosum*. This disagreement is significant and can be explained only by the coexistence of more types of vegetation. The results of many palaeoecological analyses from different areas of central Europe indicate that the Middle Holocene Forest optimum was not fully realized everywhere (Tinner et al. 2000, Brown & Giesecke 2014, Pokorný et al. 2015, Bobek et al. 2018) as sites repeatedly affected by fire are held in an early stage of succession (Brown & Giesecke 2014). Therefore, fire most likely facilitated the survival of *R. tomentosum* during the Middle Holocene because it prevents the spread of fire-sensitive deciduous tree species, which are often excluded from these communities (Tinner et al. 2000).

During the second half of the Younger Atlantic, however, climatic conditions suitable for the growth of nutrient-demanding woodland species started to deteriorate as a result of an increased number of climate oscillations and decrease in temperature and precipitation. Geochemical analysis accord with the pollen analysis. The Ca/Ti and Fe/Ti values indicate that a long-lasting gradual warming turned into a weak cooling event and a reversal in hydrological conditions during the Younger Atlantic period and point to climate change. In addition, after 4.7 ka BP a significant period of soil acidification occurred in Bohemian Switzerland (Pokorný & Kuneš 2005).

At the same time, *Fagus sylvatica* became dominant in the forest canopy (Fig. 10). The predominance of *F. sylvatica* tends to gradually eliminate fires from forest disturbance dynamics (Feurdean et al. 2017). Based on the evidence from Křepelčí důl, the peak in *F. sylvatica* corresponds well with a significant decrease in fire events. A dramatic decrease in *R. tomentosum* was recorded at both sites. This combination of a low incidence of fires and a peak in *F. sylvatica* (and high canopy shading) resulted in another bottleneck for *R. tomentosum*.

The rapid increase in *R. tomentosum* after the Middle Holocene afforestation indicates that its survival in Bohemian Switzerland was in all likelihood a product of a mosaic of different types of vegetation on the rugged sandstone hills and the cyclic effect of fires.

Late Holocene dynamics of Rhododendron tomentosum

During the Middle and Late Holocene transition at 4.2 ka BP (Walker et al. 2012), together with the onset of substantial climate instability (Novák et al. 2019), the advanced retrogressive succession process caused an abrupt change in vegetation. These nature-driven processes resulted in more favourable conditions for less nutrient-demanding species such as *R. tomentosum*. The spread of coniferous trees such as *Pinus sylvestris*, *Picea abies* and *Abies alba* in broadleaved forests is also reliably documented (e.g. Pokorný & Kuneš 2005, Novák et al. 2019). These facts are consistent with the results presented, which indicate a sudden increase in pollen of *R. tomentosum* from 4 to 2 ka BP. In addition, a peak of *R. tomentosum* at 3 ka BP, which is recorded in samples from Křepelčí důl and Puklina, coincides with the culmination of the period of acidification (Pokorný & Kuneš 2005). Acidification favoured the colonization of new habitats (and recolonization of former habitats) by *R. tomentosum* at the end of the Middle Holocene period, which is in accordance with the assumption that degraded soil, which is typically acidic, provides the most suitable conditions for the germination and growth of *R. tomentosum*. It is confirmed, therefore, that the colonization of suitable habitats in Bohemian Switzerland culminated at this time.

The Late Holocene increase in the abundance of *R. tomentosum* pollen could also be a result of numerous intense fires (Fig. 10) that probably facilitated the survival of *R. tomentosum* (Bobek 2013). However, the high representation of *R. tomentosum* is in contrast with the increased pollen levels of *Fagus sylvatica*. During this age, *F. sylvatica* was a significant competitor for many light-sensitive species due to the shading of its canopy. Therefore, *F. sylvatica* probably made many otherwise suitable sites unfavourable for *R. tomentosum*. In addition, this time was also characterized by the spread of *Abies alba* in central-European forests (e.g. Bobek et al. 2018). *Abies alba* is also significant in terms of the high shading of its canopy and thus a potential competitor for *R. tomentosum*. However, *A. alba* is often associated with livestock grazing in forests (Vrška et al. 2009, Kozáková et al. 2011) and, in Bohemian Switzerland, but was never dominant in the pollen record, probably because of the limited human influence on natural processes.

Although the results of many pollen analyses reveal significant environmental changes, based on the relatively stable Ca/Ti values throughout the Late Holocene no warming or cooling occurred during this period. In contrast, the noticeable decrease in Fe/Ti values may therefore testify to a gradual drying-out of the sediment. It is interesting that ages with high representation of *R. tomentosum* correlate well with a decreasing trend in Fe/Ti values (Fig. 10), i.e. with the gradual drying-out of sediment.

Rhododendron tomentosum in the last 2,000 years

The presence of *R. tomentosum* from 2 ka BP is relatively low and episodic (Fig. 10). By contrast, the representation of *Pinus sylvestris,* which is usually positively associated with *R. tomentosum*, reached a peak, while that of *Fagus sylvatica*, which usually has an adverse effect on *R. tomentosum*, decreased. In addition, the presence of *R. tomentosum* is exclusively linked to particular fire events.

The results of charcoal analysis indicate that the frequency of fires is relatively high and increases towards the present, especially in the last 1 ka. This documents the introduction of a new factor, in addition to nature-driven processes – the presence of humans. The growth in the number of fire events is partly a product of better resolution in the upper, less compressed layers of the profiles, but also probably a consequence of gradually increasing human activity in the region. This assumption is supported by the results of the pollen analysis, which indicate a gradual increase in plants associated with the presence of humans (Figs 3, 4).

The results of geochemical analysis document significant changes in the Ca/Ti and Fe/Ti values (Fig. 10). The most marked peak was reached around 1 ka BP, which may be related to the mediaeval temperature maximum. After that, there was a rapid fall, indicating a possible effect of the Little Ice Age. Finally, recent significant fluctuations in Fe/Ti indicate habitat drainage (and the contribution of humans) rather than any possible climate change.

Moreover, the most intensive transformation of woodlands occurred at the end of 18th century, when there was intensive and planned forest management based on clear-cutting and planting dense monocultures of *Picea abies* and non-native species (Kačmar 2013). Forests all across Bohemian Switzerland were thus gradually transformed into homogeneous plantations with *P. abies* dominant. Natural mixed woodlands only survived on rugged rocky slopes high above the bottoms of valleys. In addition, as dominant *P. abies* may exclude some light-sensitive species in the undergrowth (Chytrý et al. 2010), its spread is therefore associated with numerous extinctions of *R. tomentosum*.

Today, a managed transition to mixed forests dominated by *Fagus sylvatica* is being carried out across huge areas of the National Park. In addition, bark beetles have extensively damaged the stands of *P. abies*. *Fagus sylvatica* could fundamentally change the lighting conditions, which may result in an undesirable reduction in the population of *R. tomentosum* in this relict habitat. A similar reduction is seen in its pollen record between 5 and 4 ka BP at the maximum of *F. sylvatica* expansion.

Rhododendron tomentosum is abundant in some other areas of Czechia. Any rugged foothills are potentially suitable habitats for *R. tomentosum*, but its distribution is still largely concentrated in a few sandstone areas. It is assumed that the positive effect of frequent and significant fires in sandstone areas is associated with the favourable effect of the early onset of intensive acidification. Nevertheless, *R. tomentosum* also survived in completely different, lowland areas in the Třeboňská pánev basin, which is covered with coniferous forests. The stable but inhospitable environmental conditions in this basin, hard winter frosts and waterlogged soils, with the formation of peat sediments, prevented the spread of deciduous forest and thus enabled *R. tomentosum* to survive throughout the Holocene. However, the dynamics of *R. tomentosum* have not been studied here and our model was not designed for lowland areas.

Species distribution models were used as a tool for detecting the sites in rugged landscapes where *R. tomentosum* occurred during interglacial ages, including the Holocene. After establishing a connection between information on the actual occurrence of *R. tomentosum* and knowledge of the factors that determine its presence, it was assumed that the same factors probably worked similarly in the past and a certain level of stability occurred during this period of time. The model does not, however, consider treeless landscapes that had a significant role in the Quaternary. In this respect, the model is less valid for the cold phases of Quaternary cycles. The results of this study are nonetheless valid for interglacial periods and represent a potentially valuable source of information for the protection of the natural environment. For example, it is possible to identify sites in rugged terrain where *R. tomentosum* is present and to protect these habitats by managing the land in such a way as to avoid its further deterioration.

Conclusion

The findings presented demonstrate that sandstone landscapes provide valuable habitats for the long-term survival of *Rhododendron tomentosum*. Based on pollen data, *R. tomentosum* survived the Middle Holocene afforestation in the area of Bohemian Switzerland. It is likely that the long-term stability of natural habitats and repeated forest disturbances have been vital for the survival of *R. tomentosum*. The data presented reveal rapid population growth associated with ecosystem acidification at the beginning of the Late Holocene, resulting in a population maximum. The distribution model successfully predicted the suitability of each habitat for the occurrence of *R. tomentosum*. Floristic research proved that the species is currently extinct in many suitable sites. This species occurs in the pollen record and indicates that human-induced transformation of the natural environment worked in synergy with unfavourable environmental changes to produce the current situation. These results highlight the importance of the type of environment in which *Rhododendron tomentosum* is likely to survive environmental changes in the Quaternary.

Supplementary materials

Fig. S1. Distribution of *Rhododendron tomentosum* in Czechia.
Fig. S2. Density plots of topographic environmental variables in presence and absence sites of *Rhododendron tomentosum.*
Table S1. Technical details of the topographic environmental variables.
Table S2. Correlation of five environmental variables used in the distribution modelling.

Supplementary materials are available at www.preslia.cz

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Modelování interglaciálních mikrorefugií pro druhy přizpůsobené chladu: poznatky z reliéfem podmíněného rozšíření *Rhododendron tomentosum* v mírném pásmu střední Evropy

Některé pískovcové oblasti poskytují nepostradatelná stanoviště pro dlouhodobé přežití *Rhododendron tomentosum*. Na základě pylových údajů dokládáme, že *R. tomentosum* v modelové oblasti Českého Švýcarska přežil kritické období vrcholného zalesnění ve středním holocénu. Tvrdíme, že dlouhodobá stabilita přírodních stanovišť spolu s opakovanými disturbancemi lesa je určujícím předpokladem pro přežití *R. tomentosum*. Naše data dále odhalují relativně rychlý populační růst spojený s acidifikací ekosystému na počátku pozdního holocénu s dosažením holocenního populačního maxima. Distribuční model úspěšně předpověděl, do jaké míry je konkrétní stanoviště vhodné pro výskyt *R. tomentosum*. Výsledky mapování rozšíření druhu ukazují, že v současnosti je tento druh vyhynulý na mnoha vhodných lokalitách, kde jsme však přítomnost *R. tomentosum* prokázali v pylových záznamech. To naznačuje, že člověkem vyvolaná přeměna přirozeného prostředí fungovala v součinnosti s nepříznivými změnami životního prostředí. Naše výsledky svědčí o důležitosti vztahu mezi *R. tomentosum* a jeho stanovišti během změn životního prostředí v kvartéru.

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