Western-Carpathian mountain spruce woodlands at their southern margin: natural or anthropogenic origin?

Jsou horské smrkové lesy na své jižní hranici v Západních Karpatech původní nebo antropogenně podmíněné?

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Origin and dynamics of spruce woodlands in central Europe is an important topic due to the current disturbances triggered by bark beetle outbreaks and extreme climatic events. We focused on the Late Holocene development of spruce-dominated woodlands at their southern margin in the Western Carpathians. We analysed eight peat profiles along an altitudinal gradient of 730–1358 m a.s.l. and evaluated the pollen spectra separately for the period before and after the start of intense medieval or post-medieval human intervention in the landscape. We focused on the relative proportions of spruce, beech, fir and noble hardwood trees. Spatial variation in the proportions of beech and spruce exceeded the temporal variation, contrary to fir that declined generally. Proportion of spruce significantly increased over time but the effect differed among sites. Proportion of beech was highest at 800–1000 m a.s.l., while that of spruce increased linearly with annual precipitation rather than altitude and reached the highest values on windward slopes and in wet valleys. Different dominant trees at the two highest altitude sites indicate that altitudinal gradient was less important in the area studied. Although foresters consider spruce woodland on the highest summits as naturally monodominant, we found an apparent admixture of fir, together with a small admixture of beech, in the period before human intervention. An exact reconstruction of the proportions of individual climax trees in past vegetation is, however, not yet possible. Based on macrofossils, spruce unlike beech, has occurred directly on peatlands. Local occurrence of spruce might increase its proportion in a pollen spectrum. Indeed, after anthropogenic deforestation, its proportion decreased. It increased again as late as the establishment of spruce monocultures either by natural succession on abandoned pastures or by forestry. In addition to the effect of local spruce occurrence, modern pollen spectra further demonstrate an over-representation of spruce relative to beech and fir pollen even in a mixed woodland on the highest summit site. We conclude that spruce is a major natural component of mountain woodlands even at its southern margin. Contrary to previous expectation, we demonstrate that the proportion of spruce was not associated

with altitude but with mesoclimate and soil humidity. The natural spruce woodlands were mixed or existed as mosaics at all altitudes and the monodominant character of spruce woodlands in the area of summits is not natural.

Introduction

Norway spruce (*Picea abies*), a boreal-mountain climax species, is one of the most important trees in the European landscape (Obidowicz et al. 2004, Latalowa & van der Knaap 2006, Leuschner & Ellenberg 2017). Its environmental role, commercial use, susceptibility to recent air pollution, fire and climate change are the main reasons for studying the dynamics of climazonal mountain spruce woodlands (Schmidt-Vogt 1977, Saxe et al. 2001, Logan et al. 2003, Feurdean et al. 2017, Carter et al. 2018, Grindean et al. 2019, van der Knaap et al. 2020). In central Europe, large areas of old-growth spruce woodlands (*Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939) have persisted at high altitudes like those in the Western Carpathians (Korpeľ 1995, Obidowicz et al. 2004, Holeksa et al. 2007). This mountain range is a biogeographically transitional zone between deciduous and the coniferous biomes (Bálint et al. 2011). Its central southern part (Poľana, Veporské vrchy, Stolické vrchy and Volovské vrchy Mts) even lies on the southernmost natural limit of the distribution of spruce-dominated climazonal woodlands, although spruce itself rarely occurs in wet and mire habitats further south (Mikyška 1936, 1939, Michalko et al. 1986, Korpeľ 1989, 1995, Kukla et al. 1995, Miklós 2002). This region, including the Poľana Mts, whose mountain spruce woodland on andesite are unique within the whole of Slovakia (Korpeľ 1995, Kukla et al. 1995, Holeksa et al. 2007), might therefore be very important for understanding past, present and future dynamics of mountain woodlands dominated by spruce. However, the naturalness of spruce-dominated woodlands in this region has been frequently questioned, especially at altitudes below 1300 m a.s.l. The main doubts result from the current spread of *Fagus sylvatica* into spruce woodlands, which is documented by phytosociological data (Kučera 2012). A similar process is occurring not only in the Western Carpathians but also in other old-growth woodlands across Europe (Vrška et al. 2009, Bolte et al. 2014, Petritan et al. 2014). In addition, maps of potential natural vegetation indicate beech and beech-fir instead of spruce woodlands, with the exception of small fragments, at altitudes below 1300 m a.s.l. (Michalko et al. 1986).

Palaeoecological analyses (pollen and macrofossils) are crucial for determining the deeper history of recent spruce woodlands. Based on pollen data, glacial refugia for spruce were identified in the basins around the High Tatra Mts (Jankovská & Pokorný 2008) with a continual Holocene persistence of spruce woodlands suggested for central Slovakia (Abraham et al. 2016, Jamrichová et al. 2017). Nevertheless, the pollen data from the Western Carpathians mostly come from organic sediments accumulated in small mires where spruce used to grow or has grown locally (Pánek et al. 2010, Hájková et al. 2012, 2015, Šímová et al. 2019, Wiezik et al. 2019). A local presence may result in an overestimate of the abundance of spruce in a pollen spectrum (Hájková et al. 2019), making reconstructions based on a single or few sites unreliable.

To obtain more data in order to uncover the history of mountain spruce woodlands in the southern part of the Western Carpathians, we synthesized hitherto results of pollen-

based reconstructions from eight peat profiles distributed along an altitudinal gradient and supplemented them with modern pollen data. We ask whether the patterns in spruce dominance reflect macroclimatic differences in temperature, i.e. an altitudinal gradient, or differences in mesoclimate and local soil conditions. There are two principal hypotheses. The first postulates that the natural habitat of pure spruce woodlands is above the beech-fir vegetation zone, from ~1300 m a.s.l. (Zlatník 1959, Smutný 1969, Michalko et al. 1986, Korpeľ 1989, Kukla et al. 1995). In other words, this hypothesis stresses altitude, i.e. a macroclimatic temperature gradient. The second hypothesis postulates that all recent mountain spruce woodlands are of anthropogenic origin and monodominant spruce woodlands never existed (Kučera 2012) except in azonal and semi-zonal peaty habitats in wet basins, valleys and on alluvia (Dudová et al. 2018, Wiezik et al. 2019). This hypothesis stresses that humidity gradients may not coincide closely with altitudinal and temperature gradients. Contrary to large-scale studies working at quite coarse spatial grains (Abraham et al. 2016, Jamrichová et al. 2017), our focus on a smaller region where beech-fir and spruce woodlands meet, may determine whether there is support for either of these two hypotheses.

Material and methods

Distribution and ecology of Picea abies in the Western Carpathians

Typical spruce-dominated woodland (*Vaccinio-Piceetea*) in the Western Carpathians forms the upper montane forest zone approximately up to 1250–1500 m a.s.l. (Kučera 2012). In addition to their zonal occurrence, spruce forests can also occur azonally at low altitudes at the margins of bogs or in inverse valleys (Chytrý 2013). The centre of their occurrence within the Western Carpathians is in the northern part of Slovakia and adjacent part of Poland with the southernmost border near the Poľana Mts (Fig. 1).

Concerning ecological requirements, spruce grows in areas where the January mean temperature is lower than 0 °C and July temperature exceeds 18 °C (Zagwijn 1996). Spruce requires high humidity and soil moisture and is sensitive to an extreme continental climate and late spring ground frosts (Tranquillini 1979). Concerning its light requirements, spruce is a moderately shade-tolerant species and their seedlings can easily acclimate to various light conditions. The most favourable soil conditions are moderate to high moisture and moderate fertility, with a wide range in soil pH (Obmiński 1977, Tranquillini 1979).

The poor ability of spruce to compete with shade-tolerant species such as *Fagus sylvatica* and *Abies alba* is the most important factor limiting the natural distribution of spruce woodlands. Spruce flowers during May and June, whereas under unfavourable climatic conditions flowering can be suppressed for many years, for example at its alpine and polar limits (Hicks 2006) where mostly female flowers are produced (Kullman 2002, Rybníček & Rybníčková 2002).

Spruce is a wind-pollinated species but produces less pollen than pine, birch, alder, or hazel (Faegri & Iversen 1964). Owing to it producing little but heavy pollen (Sugita et al. 1999), its pollen is not dispersed over long distances in forested landscapes, but may be dispersed further in open landscapes (Birks & Birks 2000, Hicks 2006). The presence of a small amount of spruce pollen (< 0.6–2%) may, therefore, indicate the presence of small
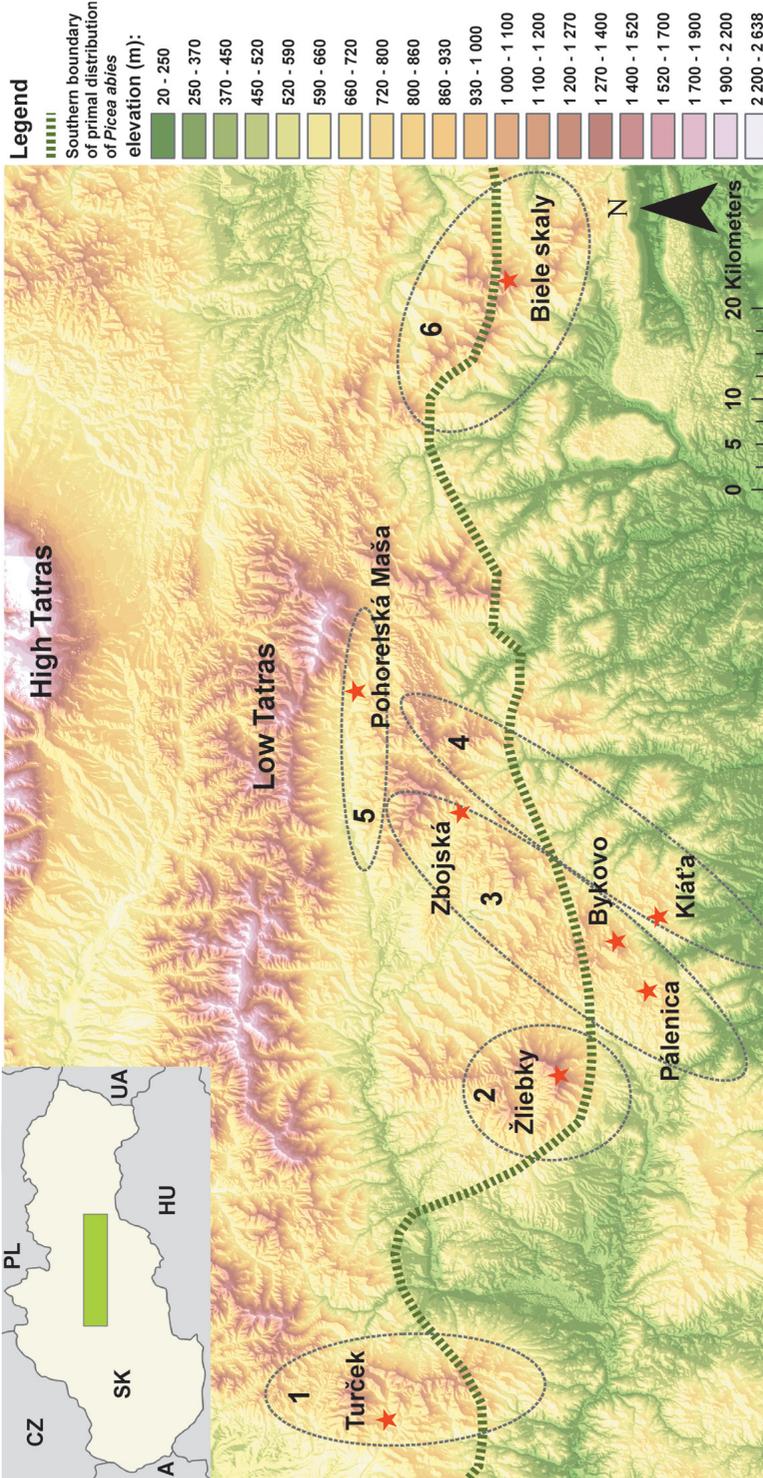
Fig. 1. – Map of the area studied with the southern limit of the primary distribution of *Picea abies* delimited according to the Landscape Atlas of Slovakia (Miklós 2002). Numbered ellipses indicate the regions mentioned in the text: 1 – Kremnické vrchy Mts, 2 – Poľana Mts, 3 – Veporské vrchy Mts, 4 – Stolické vrchy Mts, 5 – Horehronské podolie basin, 6 – Volovské vrchy Mts.

populations of spruce or even a single tree (Sŕodon 1967) resulting either from long-distance seed dispersal (Giesecke & Bennett 2004) or relict survivals (Rybníček & Rybníčková 2002). On the other hand, a high proportion of spruce in a pollen spectrum may not always indicate the dominance of spruce in climax woodlands in a region. Instead, it may mirror azonal spruce occurrence in wooded fens from which the pollen sequences were taken (Hájková et al. 2019).

Area studied

For the area studied there are eight peat profiles from along an altitudinal gradient of 730–1358 m (Fig. 1 and Table 1) in the Western Carpathians, within the Kremnické vrchy Mts (profile Turček), the Poľana Mts (Žliebky), the Slovenské Rudohorie Mts including Veporské, Stolické and Volovské vrchy Mts (Bykovo, Kláťa, Pálenica, Biele skaly, Zbojská) and Horehronské podolie basin (Pohorelská Maša). The climate varies from moderately warm in the lowest parts of the foothills to a cool mountainous climate. From the geological point of view, the bedrock in the area includes neovolcanite in the eastern part and meta-psammite, granodiorite and limestone in other parts (Miklós 2002). A more detailed description of the natural conditions at all the sites studied is presented in Table 1. In terms of potential natural vegetation the area is encroached by patchily distributed zonal spruce woodlands at the highest altitudes, while beech and beech-fir woodlands occur at middle altitudes and lime-maple woodlands occur on screes on steep and stony slopes (Michalko et al. 1986). Phytosociological studies indicate that the climazonal spruce woodlands occur mainly in the uppermost parts of Poľana Mts (Korpeľ 1995), Veporské vrchy Mts (Miadok 1969) including the Fabova hoľa Mt (Miadok 1988) and in the Muránska Planina Mts (Ložek 1991).

Data sources, field sampling, pollen analyses and data processing

For this study, we compiled unpublished pollen data from four peat profiles (Poľana, Zbojská, Pohorelská Maša, Biele skaly) together with previously published results for the profiles recorded for Turček, Pálenica, Kláťa and Bykovo (Table 2). The sites are small spring-fed or percolation mires of a few dozen square meters, scattered in an otherwise largely forested landscape and surrounded by other wetland habitats of a total area of ~0.5–3.5 hectares. These fens have been encroached by trees in the past (Wiezik et al. 2019, 2020) and later managed as fen grasslands. Recently they have undergone succession to willow or alder carrs, tall herbaceous vegetation or fen woodlands or they are occasionally mown by nature conservancy authorities (Pohorelská Maša) or land owners (Zbojská). We therefore expected the pollen sedimentation basin to be small and the pollen records to reflect local (< 10 km^2) rather than regional sources of pollen, with the relevant source area for pollen not exceeding 1 km (Bunting et al. 2005, Sugita 2007).

All peat profiles, except for Turček (Rybníček & Rybníčková 2009), were cored using a gouge auger (100 × 6 cm). The description of the sediment was carried out in the field, along with colour determined by visual comparison or by Munsell Soil Colour Charts (Munsell 2000). Standard acetolysis for all peat profiles was used (Faegri & Iversen 1989). In all pollen samples, at least 300 pollen grains of terrestrial taxa were counted. The percentage values presented in pollen diagrams were calculated from total pollen sum (TS) including trees, shrubs, dwarf shrubs (AP) and herbaceous plants (NAP) using

Table 1. – Site locations and conditions

Locality	Coordinates	Geomorphological unit	Altitude (m a.s.l.)	Climatic zone	Mean annual temperature (°C)	Annual precipitation (mm)	Bedrock	Soils
1. Pohorelská Maša	20°01'35.4", 48°51'02.2"	Horehron basin	730	moderately warm	4-6	900	alluvial sediments with loess or loam cover (mainly sandy-loam gravel, loam)	dystric cambisols
2. Zbojská	19°51'16.6", 48°44'35.8"	Veporské vrchy Mts	772	moderately cool	2-4	1150	intrusive crystalline rocks (granite, granodiorite, diorite, gabbro)	dystric cambisols
3. Turček	18°56'16.0", 48°46'15.0"	Kremnické vrchy Mts	780	moderately cool	2-4	1050	massive neovolcanite rocks (andesite, rhyolite, basalts, melaphyre)	dystric cambisols
4. Pálenica	19°36'20.9", 48°33'09.2"	Veporské vrchy Mts	863	moderately cool	2-4	850	eluvio-deluvial sediments	dystric cambisols
5. Kláťa	19°43'01.4", 48°32'50.6"	Stolické vrchy Mts	914	moderately warm	4-6	750	eluvio-deluvial sediments	dystric cambisols
6. Bykovo	19°40'35.4", 48°35'10.7"	Veporské vrchy Mts	1053	moderately cool	2-4	1000	intrusive crystalline rocks (granite, granodiorite, diorite, gabbro)	dystric cambisols
7. Biele skaly	20°39'17.3", 48°43'45.3"	Volovské vrchy Mts	1206	moderately cool	2-4	950	metamorphic crystalline rocks (phyllitic slate, migmatite, amphibolite)	podzols adjacent to dystric cambisols
8. Žliebky	19°28'15.8", 48°37'54.2"	Poľana Mts	1358	cool mountainous	3.7	1069	massive neovolcanite rocks (andesites, rhyolites, melaphyres)	andosolic cambisols and cambisole-like andosols

the formula AP + NAP = 100. Pollen and spores of local plants (*Alnus*, *Salix*, *Cyperaceae*, *Caltha* t., *Equisetum*, *Lycopodium* undiff., *Polypodiaceae*, *Polypodium vulgare*, *Pteridium aquilinum*, *Bryales*, *Sphagnum*) and non-pollen objects were excluded from the TS, and their contribution was calculated as follows (TS) = AP + NAP + local taxa and spores = 100%. The pollen diagrams were constructed using C2 v. 1.7.7 software (Juggins 2016). Note that the analyses presented in this paper do not use these conventional percentage values (see below).

The nomenclature of taxa shown in the diagrams was consolidated according to Beug (2004). In addition to pollen grains we identified, in some of the sequences (Table 2), stomata according to the identification key by Sweeney (2004) and fossil needles according to Katz et al. (1977). Profiles used in the synthesis were radiocarbon dated and calibrated or recalibrated (Turček) using the IntCal 13 calibration curve (Reimer et al. 2013) in Oxcal 4.2 software (Ramsey 2009). The dates are shown as calibrated years BP (before present, i.e. before 1950). The age-depth models of the profiles studied were based on a P_Sequence with k_0=1 and $\log_{10}(k/k_0)$ equal to 1. The review of the dated material, calibrated years or number of dated layers and age-depth models for all profiles are shown in Electronic Appendices 1 and 3.

Collection and pollen analysis of surface samples of moss

For the more precise interpretations of the relationship between vegetation and its pollen rain, surface pollen samples, which aggregate several years of pollen deposition, are useful (Bunting et al. 2013). In a previous study (Hájková et al. 2019) we compared modern surface pollen samples from fens with and without spruce trees in another region of the Western Carpathians. In this study we supplemented these data with modern surface pollen samples from moss polsters collected directly in spruce woodland at the summit site Poľana-Žliebky. The main goal was a comparison of relative pollen abundance of spruce, beech and fir in the vegetation in the surrounding woodlands. For this purpose, we collected moss polsters from six sites in two seasons (May and October). The average of these two was used for comparison with recent vegetation in the surroundings. Samples were collected in the surroundings of the Žliebky profile. The sample POL1 was collected in a woodland opening located 50 meters from spruce woodland and 150 meters from mixed spruce-fir-beech woodland. The two samples (POL2, POL3) were collected in a forest opening 50 m from the POL1 sample, close to mixed spruce-fir-beech woodland. The remaining samples (POL4, 5, 6) were from under continuous tree canopy in the centre of the mixed spruce-beech woodland 300–500 meters from POL1. From the moss polsters 10 cm × 10 cm in size, we extracted their green apical parts. Standard acetolysis was used (Faegri & Iversen 1989). For the 18 samples at least 800 pollen grains of terrestrial taxa were counted. The recent proportions of spruce, beech and fir within the sum of their percentages were calculated for three different radiuses (200, 500 and 1000 m) using forest inventory data.

Assessment of change in proportional ratio of climax trees through time

We focused on the proportion of individual tree taxa within the group of climax species of mountain woodlands, specifically spruce, beech, fir and rarely admixed noble hardwood taxa as a whole (the sum of *Tilia*, *Ulmus*, *Acer*, *Fraxinus*). For comparison of changes

Table 2. – Details and references to the sites studied, which were included in the analyses. Age refers to the age of the oldest sample in a profile. The deforestation event refers to the end of Period 1 and is indicated by the AP:NAP ratio, increase in *Graminae* and decrease in climax trees.

Site	Elevation (m a.s.l.)	Orographic unit	Depth (cm)	Age (cal BP)	Defores- tation (cal BP)	Analysed by	Stomata identified	Needles identified	Reference
1. Pohorelská Maša	730	Horehron basin	226	6514	85	L. Petr	yes	no	unpublished
2. Zbojská	772	Veporské Mts	100	6619	430	L. Petr	yes	no	unpublished
3. Turček	780	Kremnické vrchy Mts	105	3855	1125	E. Rybníčková	yes	yes	Rybníček & Rybníčková 2009
4. Pálenica	863	Veporské vrchy Mts	90	1568	536	M. Wiezik	yes	yes	Wiezik et al. 2019a
5. Kláťa	914	Stolické vrchy Mts	86	687	496	M. Wiezik	yes	yes	Wiezik et al. 2019a
6. Bykovo	1053	Veporské vrchy Mts	100	7836	647	M. Wiezik	yes	yes	Wiezik et al. 2019b
7. Biele skaly	1206	Volovské vrchy Mts	104	3766	undated	M. Wiezik	yes	yes	unpublished
8. Žliebky	1358	Poľana Mts	130	8002	296	V. Jankovská	yes	no	unpublished

between individual tree taxa found in fossil samples, we calculated the proportion of spruce, beech, fir and noble hardwood trees within the sum of their percentages for each of three consecutive periods. Such percentages are independent of which other pollen taxa are considered as local, i.e. excluded from the pollen sum when the pollen diagram is constructed.

The first period included the Late-Holocene period and ended with the start of intense medieval or post-medieval human intervention. Chronologically the period starts at 3800 cal BP (the oldest age that is shared among the profiles) and ends with the first abrupt anthropogenic change visible in a profile by the synchronized appearance of anthropogenic indicators and deforestation indicated by the AP:NAP ratio, increase in *Graminae* and decrease in climax trees. The time of this event differed among the profiles (Table 2). Anthropogenic intervention usually started between 13th and 19th centuries as a consequence of medieval mining and Wallachian or later colonization (Beňko 1973, Ratkoš 1980, Wiezik et al. 2019, 2020). The second period starts with the end of the first phase and ends with the beginning of spruce plantations indicated by a steep increase in spruce pollen and AP:NAP ratio in the uppermost parts of the sequences. Chronologically it may again differ among the profiles. The third phase starts with the end of the second phase and ends with the end of the sequence.

Statistical significance of differences in pollen proportions of spruce, beech and fir, respectively, among the three periods and sites (i.e. profiles) studied was tested by beta regression with logit link (R package betareg; Zeileis et al. 2012), which is designed for modelling of beta-distributed dependent variables, as proportions and rates are. Period and site were used as fixed effects in the analyses. To partition the variability in pollen proportions between both explanatory variables, we used two models with only one of

the explanatory variables, the model with main effect terms of both variables (Borcard et al. 2018), and the full factorial model with an interaction term. Significance of explanatory variables was assessed using function "joint_tests" from R package emmeans (Lenth et al. 2019). Post-hoc tests were not used because of the small number of replications. Analyses were done in R 3.6.0 environment (R Core Team 2019) using RStudio 1.2.1335 (RStudio Team 2018).

Non-metric multidimensional scaling

The taxon-by-sample matrix of the representation of individual tree taxa calculated as mentioned above was subjected to a NMDS analysis to show their compositional similarities along the two principal ordination axes. A logarithmic transformation of the relative abundance of pollen taxa was used to avoid overfitting by a single dominant tree. The two NMDS analyses were done using Canoco 5.0 (ter Braak & Šmilauer 2012), separately for the Periods 1 and 2+3. The sites were classified according to their position in the resulting scatter. Pollen sums of main trees corresponding to individual hypothetical types of vegetation (e.g. the sum of fir and beech representing beech-fir woodlands) as well as annual precipitation (Miklós 2002) were a posteriori plotted onto the resulting scatter.

Results

The change in the proportional ratio of climax trees through time

Based on proportions of climax trees (*Abies alba*, *Fagus sylvatica*, *Picea abies* and noble-hardwood trees) and their changes during the three periods studied, we classified individual profiles into two principal groups (Fig. 2). The first group includes sites where spruce pollen prevails over beech and fir pollen (Zbojská, Žliebky, Turček, Pohorelská Maša, and to a less extent also the Bykovo site). The second group includes sites where the proportion of spruce pollen is similar or lower than the proportion of beech and fir pollen (Kláťa, Biele skaly, Pálenica). However, during human intervention (Period 2), pollen abundance of spruce declined in some sequences (Žliebky, Bykovo, Pálenica, Turček) unlike in the sequences where it did not change (Zbojská, Pohorelská Maša, Biele skaly). Except for the Zbojská profile, the proportion of spruce pollen increased in all profiles in Period 3. The coincidence between the decline in spruce and increase in beech in Period 2 (preindustrial human intervention in woodlands) was recorded for Žliebky, Biele skaly, Bykovo, Kláťa, Pálenica and partially for Pohorelská Maša. Later, during the artificial planting of spruce in the most recent period, an abrupt decline in pollen of fir occurred at all the sites studied. Although noble hardwood trees were only marginally represented, their consecutive decline was recorded during the three periods. Nevertheless, the highest abundances of these trees were recorded for Bykovo, Kláťa, Pálenica and partially for Biele skaly profiles.

Beta regression (Table 3) revealed that the proportion of spruce was statistically significantly affected by the period, but the effect of period differed among sites (F = 4.582, P < 0.001; whole model: Z = 11.73, P < 0.001, R^2 = 0.79). Mean proportion of spruce statistically significantly increased from Late Holocene up to the recent period (F = 39.85, P < 0.001), but while the pure effect of period explained 6% of variability in the proportion
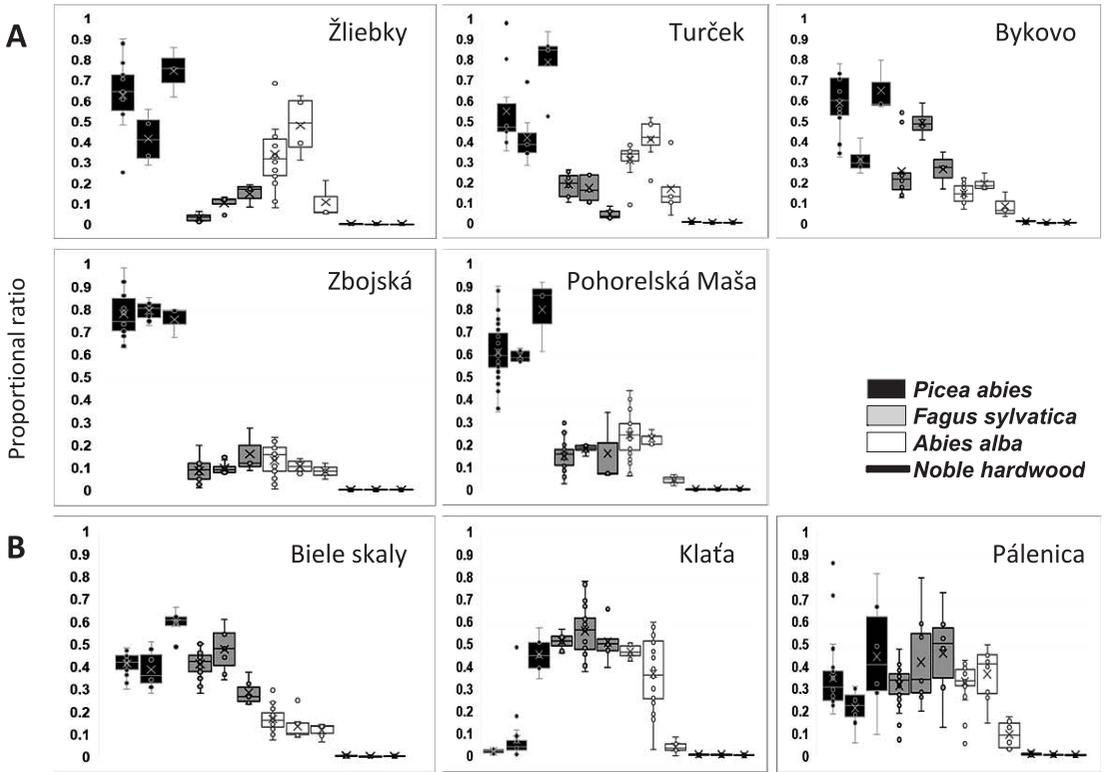
Fig. 2. – The variation in the relative proportion of individual tree taxa in the pollen records during the consecutive periods studied: the period of untouched late-Holocene climazonal woodlands (Period 1, left box), the period from the beginning of systematic human intervention (Period 2, central box) and the period of modern development of spruce plantations (Period 3). Group A includes sites where spruce pollen prevail over beech and fir pollen. Group B includes sites where the proportion of spruce pollen was similar or lower than the proportion of beech and fir pollen (Kláťa, Biele skaly, Pálenica). Boxes indicate the interquartile range, with the median (crossline), maximum and minimum values.

Table 3. – Percentage variation in the proportion of pollen of three species of trees based on beta regression models with one or two explanatory variables: Pure effects of period and site, respectively, are given in parentheses. Pure effects are calculated by subtracting the overall effect of site from the total variation explained by the two variables (Period + Site). All models were statistically significant at $P < 0.05$.

Explanatory variable	*Picea abies*	*Abies alba*	*Fagus sylvatica*
Period	13 (6)	13 (13)	5 (2)
Site	67 (60)	9 (9)	50 (49)
Period + Site	73	22	52
Period × Site	79	35	55

of spruce pollen ($Z = 11.73$, $P < 0.001$), the pure effect of site explained 60% of its variability ($Z = 11.91$, $P < 0.001$). Overall, the proportion of fir decreased during the three periods ($F = 63.03$, $P < 0.001$). The effect of period was more important than the effect of site, and the effect of interaction between period and site was more pronounced for fir
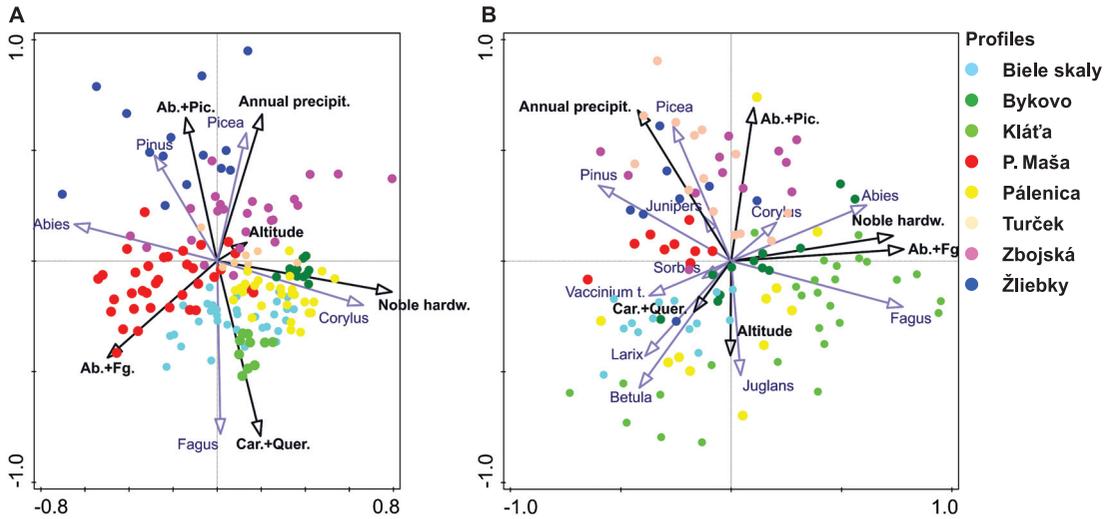
Fig. 3. – Scatterplots of NMDS analyses for the period (A) before (Period 1) and (B) after (Periods 2 and 3) the start of human intervention. Pollen taxa that were included in the analyses are in blue font. Pollen sums for the main trees corresponding to individual hypothetical types of vegetation (beech-fir, spruce-fir, oak-hornbeam and noble hardwood woodlands) and annual precipitation were a posteriori plotted onto the resulting scatter in black font.

than the other species of trees (Z = 11.62, P < 0.001). However, the amount of explained variation in the proportion of pollen was lowest for fir. Proportion of beech pollen was explained mainly by differences between the sites sampled.

Non-metric multidimensional scaling

The NMDS analysis for Period 1 sorted the individual sites along the first axis according to the abundance of *Abies alba* and noble hardwood trees, while the second axis was formed by changing abundance of the other main climax trees, *Picea abies* and *Fagus sylvatica*, along the gradient of annual precipitation (Fig. 3, diagram 1). After deforestation (Periods 2+3) the principal axis sorted profiles according to increasing proportion of beech, fir and noble hardwood trees (Fig. 3, diagram 2). Along the second axis the profiles were primarily arranged according to spruce and fir abundance, which change along the gradient of annual precipitation. Although in Period 1 the individual sites were largely clustered together, they overlapped mutually in Periods 2+3.

The results of the relationship between surface pollen samples and recent vegetation

Of the six sites sampled and included in the analysis, only three (POL4, POL5, POL6) contained pollen grains. In the samples from POL1, POL2 and POL3, we recorded only a few pollen grains, and these samples were therefore excluded from the analysis. In three samples (POL4–6), all of which were collected under a closed tree canopy, the proportion of spruce pollen was higher than the proportion of spruce in the recent vegetation (Fig. 4). Beech showed the opposite pattern. The proportions of fir were similar in the pollen spectrum and vegetation. With increasing radius the proportions of spruce and beech in modern
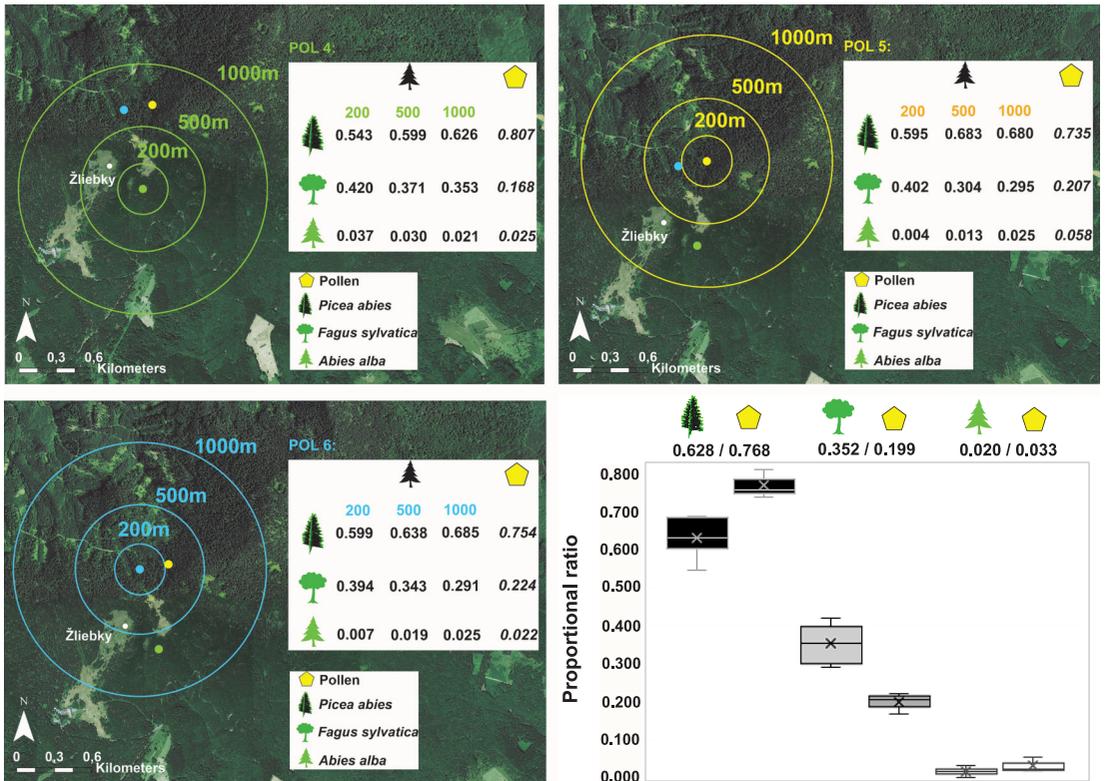
Fig. 4. – Aerial photographs and box-and-whisker plots describing the sample design and the differences in the proportional ratio of spruce, beech and fir in modern pollen samples, and the modern taxonomic composition of woodlands. Radiuses shown on the map (200, 500 and 1000 m) represent the area for which the recent proportions of trees in woodlands were calculated. The box-and-whisker plots show the variation in the ratio between recent pollen rain and vegetation for all sites sampled and radiuses merged. Left box-and-whisker plot describes the relative proportion of a species of tree in the modern woodlands while the one on the right describes its proportion in the pollen record. Boxes indicate the interquartile range, with the median (crossline), maximum and minimum values.

pollen samples became more similar to their proportions in the surrounding vegetation. For the exact pollen counts in individual samples see Electronic Appendix 4.

Discussion

Vegetation zonation or vegetation mosaic?

This regional study based on eight pollen profiles revealed a general decline in fir and increase in spruce in the course of the period of obvious medieval or post-medieval human intervention in the mountain landscape. Spatial variation in pollen abundances of spruce and beech exceeded the temporal variation. For spruce, however, this spatial variation did not coincide with altitude, but rather with annual precipitation and geomorphology.
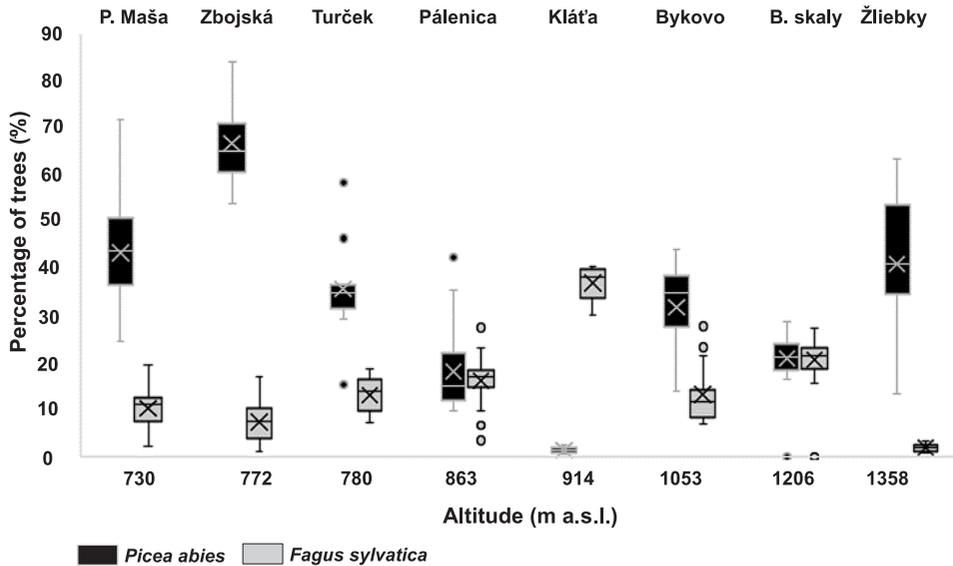
Fig. 5. – Changes in the relative representation of *Picea abies* and *Fagus sylvatica* (before systematic human intervention) along the altitudinal gradient in the area studied. Boxes indicate the interquartile range. Median is indicated by crossline, maximum and minimum values by whiskers, and outliers by dots. See Table 1 for the characteristics of study sites.

The highest proportion of spruce was found not only at the highest altitudes (Žliebky, 1358 m a.s.l.), but also in areas with high precipitation (Zbojská saddle on windward slopes; 762 m a.s.l.) or in peaty basins (Pohorelská Maša; 730 m a.s.l.) regardless of altitude (Fig. 5, Fig. 6). In contrast, some summit sites (Biele skaly, 1206 m a.s.l.) had a high representation of beech (22%). This pattern contradicts the hypothesis that stresses the dominant role of altitude, i.e. a macroclimatic temperature gradient, in the zonation of vegetation in the area studied, with pure spruce woodlands occurring above the upper distributional limit of beech and fir at ~1300 m a.s.l. (Zlatník 1959, Smutný 1969, Michalko et al. 1986, Korpeľ 1989, Kukla et al. 1995). Instead we found that the differentiation into spruce-rich and spruce-poor areas largely follows the moisture gradient (Fig. 6), corroborating the hypothesis of azonal or semi-zonal character of spruce woodlands (Dudová et al. 2018, Wiezik et al. 2019) and that the highest altitudes, although being locally extraordinarily rich in spruce, did not harbour pure spruce growths as observed today. The natural character of monodominant spruce woodlands at altitudes above ~1300 m a.s.l. (Michalko et al. 1986, Plesník 1989, Korpeľ 1995) is hence questioned by our results.

Beech was most abundant around 900 m a.s.l., corroborating the general pattern found in the Western Carpathians (Krippel 1986), but also that there was apparently no altitudinal limit and surprisingly a high representation around 1200 m a.s.l. A similar pattern is reported in the Jeseníky Mts, with the highest proportion of beech occurring close to the treeline rather than at middle altitudes (Dudová et al. 2018). We may conclude that our results support the hypothesis that stresses the crucial role of gradient in humidity in determining the pattern of vegetation in mountain woodlands. It means that the individual types of woodland have occurred naturally in a mosaic rather than in altitudinal zones.
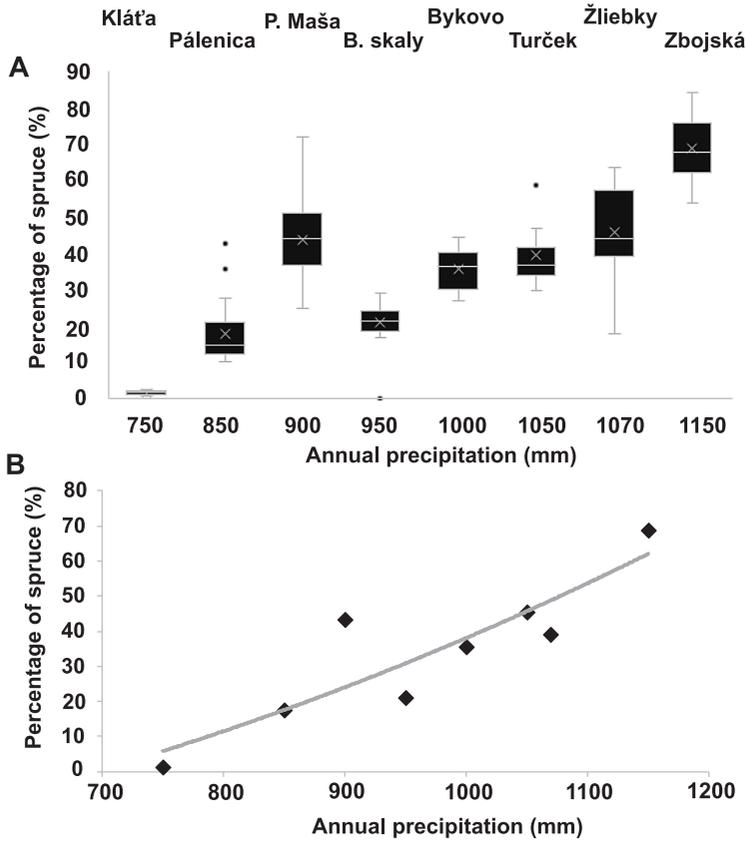
Fig. 6. – (A) Changes in the relative representation of spruce along the gradient of annual precipitation. (B) The relationship between the median values and annual precipitation fitted by a linear regression and tested by Spearman correlation (r = 0.77, P = 0.025). Boxes indicate the interquartile range. Median is indicated by crossline, maximum and minimum values by whiskers, and outliers by dots.

The high topographic heterogeneity in the area studied (Miklós 2002) could easily support fine-scaled alternation of individual dominant species of trees according to soil hydromorphism (Daněk et al. 2016, 2019). Spruce hence could dominate in flat terrain, where a colder and more humid microclimate occurred, while beech and noble hardwood trees could dominate on steep slopes. Our results indicate that such a mosaic occurred along the entire altitudinal gradient, but at the lowest altitudes spruce-dominated woodlands might be represented only by waterlogged fen woodlands (Neuhäuslová et al. 1998, Chytrý 2013).

How much spruce, beech and fir grew in mountain woodlands?

Another challenging question is to what extent did spruce dominate the reconstructed mosaic of vegetation in areas where it was highly represented in pollen samples. Our results from modern pollen samples from mixed spruce-beech woodland (Fig. 4) indicate a distinct under-representation of beech and over-representation of spruce (of about 15%)

as compared to their representation in modern vegetation. In a previous study in the Western Carpathians, Hájková et al. (2019) report an over-representation of spruce pollen of about 15–20% when spruce occurs directly in a fen where the pollen samples were collected. They found a good correspondence between the proportion of spruce in a pollen record and the proportion of spruce in surrounding vegetation only when spruce did not occur locally. In contrast, the current quantitative reconstruction models (e.g. Abraham et al. 2016, Szabó et al. 2017, Carter et al. 2018) mainly indicate the opposite pattern, i.e. under-representation of spruce in original pollen data (but see discussions in Hájková et al. 2019 and van der Knaap et al. 2020). Another source of bias may be an ability of summit mires to trap particles carried by winds from a wide region (Abraham et al. 2017), which questions our premise that all the mires studied reflect local rather than regional pollen rain. On the other hand, two of the summit mires studied (Biele skaly and Žliebky) have been encroached by spruce and are surrounded by woodlands that may limit long-distance wind dispersal. For these reasons, we cannot reconstruct the exact proportion of spruce, beech and fir in the past mosaic of vegetation. Nevertheless, we argue, based on the sites studied, especially their small area, forested surroundings and the local occurrence of spruce as evidenced by macroremains and stomata, that in fossil pollen spectra generally there is an over-representation of spruce and under-representation of beech.

The effect of the local occurrence of fir on its pollen percentages is not as clear as in the case of spruce and requires further study. There is an absence of modern pollen samples from the situations where fir grows azonally in a wooded fen while missing in the surroundings. Such situations are indeed quite rare in the Western Carpathians where fir usually admixes with beech in zonal woodlands and wetlands are rarely encroached by fir (Jaworski & Zarzycki 1983, Tomanek 1994) and even more rarely exclusively by fir. In our study, the highest proportions of fir pollen relative to other target trees were found at the opposite ends of the humidity gradient (Fig. 7). This pattern illustrates wide ecological amplitude of fir (Málek 1983) and perhaps also its poorer competitive ability in the central part of the gradient, where both major competitors (beech, spruce) are both abundant. Moreover, our results indicate an increase in proportions of beech (Kláťa, Pálenica, Biele skaly), fir (Turček) or both (Žliebky, Bykovo) when spruce declined in Period 2, during which anthropogenic intervention in forests are likely to have occurred (Fig. 2). Such increases may actually not indicate an increase in the proportion of beech and fir in climazonal woodlands, but that locally growing spruce no longer obscured the pollen rain coming from regional woodlands. This increase in fir relative to spruce, which is similar to an increase in beech, and the above-mentioned patterns in the abundance of fir, indicate that fir preferred non-peaty habitats and most of its pollen rain came from surrounding woodlands, although fir macroremains were found in some of the fens studied (see Electronic Appendix 2).

Modern spruce plantations

At most sites we recorded a retrogressive increase in the abundance of spruce pollen in the terminal parts of the peat sequences, allowing us to delimit a quite recent period of establishment of modern monodominant spruce plantations (Klimo et al. 2000). The establishment of modern spruce plantations is very visible in many pollen profiles across the Western Carpathians (Hájková et al. 2018, Kapustová et al. 2018, Šímová et al. 2019).
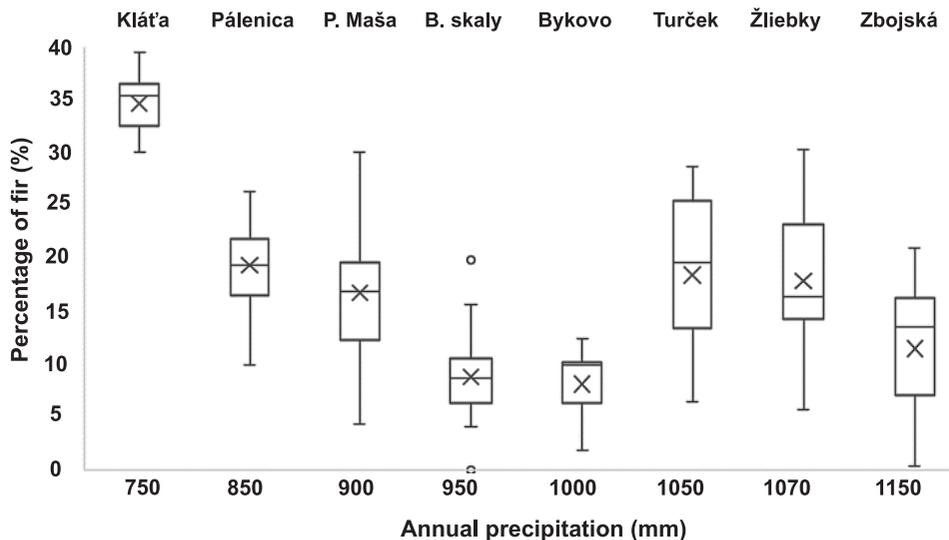
Fig. 7. – Changes in the relative representation of fir along the gradient of annual precipitation.

In the area studied, the modern increase in the proportion of spruce does not reflect only the establishment of spruce plantations in originally mixed woodlands, but also secondary succession of spruce on abandoned mountain pastures (Kučera 2012). Our data suggest extensive past deforestation even at the highest altitudes (see AP:NAP ratio in the pollen diagram for the Žliebky site, in Electronic Appendix 2). Deforestation was more extensive than the older studies indicate (Korpeľ & Saniga 1993, Korpeľ 1995, Podlaski 2004). After the cessation of grazing of mountain grassland a secondary succession of spruce started, as in other parts of the Western Carpathians where spruce is a pioneer tree (Dovčiak et al. 2008).

In the area studied, the proportion of spruce in the phase of modern spruce plantations is often much higher than that recorded in climazonal woodlands of the period before strong human intervention (Fig. 2). The question remains, however, to what extent did spruce monocultures add to pollen loading at the sites studied. Considering the absence of spruce macroremains in uppermost (i.e., recent or sub-recent) peat layers, we may hypothesize that most of the spruce pollen load comes from surrounding secondary spruce forests while the component due to pollen from far away is probably low (Sugita et al. 1999, Latalowa & van der Knapp 2006). There was an increase in the percentage of pollen of spruce of ~20% (10–30%) in the upper most layers of most of the sites studied. This corroborates the well-known ratio between recent (26.4%) and historical (4.9%) representation of spruce in Slovak woodlands, i.e. an increase of ~20% (Michalko et al. 1986, Schwarz et al. 2003). The pollen diagrams for small wetland sites in the Outer Western Carpathians where establishment of spruce plantations in the surroundings is well documented also indicate an increase in the percentage of spruce of ~15–40%, depending on the area of spruce plantations in the surroundings (Hájková et al. 2018, Kapustová et al. 2018, Šímová et al. 2019).

The most distinct change in the proportion of main climax trees was recorded for fir. It is apparent that fir was an important component of preindustrial woodlands at middle and high altitudes, but later it declined substantially not only in the area studied but throughout Europe (Senn & Suter 2003, Vrška et al. 2009, Diaci et al. 2011, Ficko et al. 2011). This decline is especially obvious at high altitudes in the area studied, where monodominant spruce woodlands currently occur (Electronic Appendix 2).

Conclusions

Although containing much spruce, the pre-industrial woodland landscape had a more mosaic character and higher local diversity than modern monodominant spruce plantations, which were established not only in formerly spruce-rich areas but often at places where there was a low abundance of spruce in the past. In terms of the two alternative hypotheses, our results support the humidity-oriented rather than temperature-oriented hypothesis, with annual precipitation and local waterlogging predicting the high abundance of spruce better than altitude or air temperature per se.

See www.preslia.cz for Electronic Appendices 1–4.

Acknowledgements

Souhrn

Původ a dynamika smrkových lesů ve střední Evropě je aktuálním tématem z důvodu jejich současného narušení kůrovcovými kalamitami a změnami klimatu. Zaměřili jsme se proto na pozdně holocenní vývoj smrkových lesů na jejich jižní hranici v Západních Karpatech. Analyzovali jsme osm pylových profilů z rašelinišť rozmístěných podél výškového gradientu (730–1358 m n.m.) a zahrnujících období před začátkem a po začátku intenzivního středověkého nebo novověkého vlivu člověka na krajinu. Zaměřili jsme se zejména na vzájemný podíl smrku, buku a jedle. Zatímco podíl buku a smrku se více lišil mezi lokalitami než mezi studovanými obdobími, podíl jedle po začátku intenzivního vlivu člověka na krajinu obecně, bez ohledu na lokalitu, klesal. Podíl smrku je naopak obecně vyšší v současnosti, ale ne na všech lokalitách. Zatímco pyl buku dosahoval největšího podílu v nadmořských výškách mezi 800 a 1000 m n. m., podíl pylu smrku lineárně narůstal podél gradientu ročního úhrnu srážek, spíše než podél výškového gradientu, a nejvyšších hodnot dosahoval na návětrných svazích hor a v podmáčených údolích. Méně výrazný vliv nadmořské výšky ilustruje to, že dva profily z nejvyšších poloh studovaného území se výrazně lišily. V jednom dominoval smrk (Poľana-Žliebky) a ve druhém buk (Biele skaly). Na lokalitě Žliebky se v současnosti vyskytuje čistý smrkový porost, jehož monodominantní charakter bez buku a jedle je považován za přirozený a podmíněný nadmořskou výškou. V profilu se ale v období před začátkem výrazného lidského vlivu výrazně uplatňuje jedle a méně výrazně i buk. Pomocí pylových dat ale zatím není možné spolehlivě rekonstruovat podíl jednotlivých klimaxových dřevin. Smrk se totiž, na rozdíl od buku, vyskytoval i přímo na studovaných rašeliništích, což dokazují nálezy jeho makrozbytků. Výskyt smrku na rašeliništi tak mohl navýšit podíl jeho pylu v záznamu. Po antropogenním odlesnění studovaných mokřadů podíl smrku v pylovém záznamu klesl a zvýšil se až po vzniku současných smrkových monokultur, který se udál buď sukcesí na opuštěných pastvinách nebo výsadbami. Nadhodnocení smrku v pylovém záznamu ukázala i analýza současných pylových spekter ze smíšeného lesa nejvyšších poloh. Naše data ukazují, že smrk byl i na jeho jižní hranici významnou součástí horských lesů. Oproti předchozím představám ale ukazujeme, že jeho podíl neodrážel těsně gradient nadmořské výšky, ale spíše mezoklimatickou a půdní vlhkost. Původní lesy byly pravděpodobně smíšené nebo mozaikovité podél celého výškového gradientu. Současný monodominantní charakter smrkových lesů v nejvyšších polohách studovaného území tedy nemůže být považován za přirozený.

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