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A pollen-based quantitative reconstruction of the Holocene vegetation updates a perspective on the natural vegetation in the Czech Republic and Slovakia

Kvantitativní rekonstrukce holocenní vegetace na základě pylových analýz aktualizuje pohled na přirozenou vegetaci v České republice a na Slovensku

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The primary aim of this paper is to provide a pollen-based quantitative reconstruction of Holocene vegetation in order to update a perspective on natural vegetation in the Czech Republic and Slovakia. As a secondary aim we compare composition of this reconstructed Holocene vegetation with the composition of potential natural vegetation (PNV sensu Neuhäuslová et al. 1998) in the area studied. Based on 87 individual pollen sequences, we estimate the changes in Holocene vegetation that have occurred in nine circular regions, each 60km in radius. We obtained estimates of regional vegetation using the REVEALS model (Regional Estimates of VEgetation Abundance from Large Sites). This model considers pollen productivity, dispersal and taphonomic differences between taxa. The development of post-glacial vegetation can be divided into three general phases: Early, Middle and Late Holocene. Clustering of the interregional variability clearly separated lowlands from middle altitudes and mountains. The Early Holocene was dominated by semi-open pine forest in nearly all the regions studied. Mixed oak woodlands appeared in the Middle Holocene and only in the lowlands, while the rest of the area studied was dominated by spruce (> 32%) forest. The percentage of spruce remained high (> 19%) in fir-beech forests of the Late Holocene. The dominance and co-dominance of spruce at middle and high altitudes during the Middle and Late Holocene differs most from previous interpretations of pollen percentages. We attribute this to the climatic and edaphic conditions differing from those in other parts of central Europe at a similar altitude. Continuous presence of *Poaceae* (> 9%) and pioneer trees during the entire Holocene (*Pinus* > 6%) indicates an important role of factors sustaining their long-term abundance, be it herbivory, fire or other kinds of disturbance, natural and/or anthropogenic. The

PNV composition, compared to estimates of Holocene vegetation for AD 500–1000, assumes a larger representation of broadleaved taxa (*Fagus, Carpinus* and *Quercus*) at the expense of *Picea*. In spite of the high compositional difference between PNV and Holocene vegetation for AD 500–1000, we found a relationship between the naturalness of present-day vegetation as estimated by PNV and the compositional turnover from AD 500–1000 to the present day. This indicates that quantitative palynology and phytosociology have the potential to produce complementary results and their combination can contribute to a more integrated perspective on natural vegetation.

Keywords: Czech Republic, Holocene, pollen analysis, potential natural vegetation, REVEALS model, Slovakia, spruce, vegetation reconstruction

Introduction

A long-term perspective is crucial for understanding changes in present-day vegetation affected by changing climate, species invasions or by various kinds of human-induced disturbances. Revealing meaningful patterns in past changes in biodiversity and thresholds within natural variability might facilitate pertinent decisions in conservation management policies (Willis & Birks 2006). Some of the fundamental questions asked by vegetation scientists (including palaeoecologists) revolve around reconstructing the natural composition of vegetation.

When using pollen data as a proxy for vegetation, it is reasonable to criticize pollen analyses for their largely undefined spatial resolution (Loidi & Fernández-González 2012) and for the biases introduced by taxon-specific pollen production and dispersal (Loidi et al. 2010). This problem is inherent in palynological reconstructions, which are based on interpreting of pollen percentages. The Landscape Reconstruction Algorithm (LRA) (Sugita 2007a, b) overcomes these biases by using pollen productivity, pollen dispersal and the size and type of the sedimentation basin in order to estimate past abundances of different vegetation in a defined space. In this study, we focus on the first step of the LRA – the REVEALS model (Sugita 2007a), which estimates vegetation from the pollen records of many small sites (≤ 100 ha) or a few large sites (≥ 100–500 ha) across an area of 10^6 km^2. Pollen records were used in a REVEALS reconstruction (Gaillard et al. 2015, Trondman et al. 2015), which focused on the interactions between past climate and land-cover reconstruction at a continental scale for a particular period of time and used averaged parameters for the whole of northern Europe (Mazier et al. 2012). We concentrate on the entire Holocene vegetation history, its role in determining the natural vegetation and its distribution in particular regions of the Czech Republic (eight regions) and Slovakia (one region). We follow Rybníčková & Rybníček (1996), who synthesized the Holocene pollen data for this area, but interpret the “raw” percentages of pollen. Our main goal is to produce a pollen-based quantitative reconstruction of the vegetation using the REVEALS model with parameters previously validated by present-day vegetation in the same area (Abraham et al. 2014).

Inferring past natural vegetation from pollen data originating from periods before humans started to have a considerable impact (van Leeuwen et al. 2008, Connor et al. 2012) is often based in the tacit assumption that this started so late in the Holocene that natural changes (climate, soil development) can be neglected. Nevertheless, in central Europe humans were present during the whole prehistory in both the lowlands and highlands (Jiráň & Venclová 2008) and most probably had a profound effect on vegetation. Palaeoecology has already indicated that humans influenced vegetation directly by controlling the first spread of common trees and shrubs such as hazel (Kuneš et al. 2008) and oak (Kuneš et al. 2015), and indirectly by introducing a new anthropogenic environment, which altered the natural drivers of vegetation as early as the Neolithic (Gaillard et al. 2015). In the light of these considerations, in the present paper we need to extend the general meaning of "natural", i.e. a state determined by climatic and edaphic conditions or by biotic interactions, to include also some human contribution. This implies that we need to distinguish between (i) those kinds of human impacts that contributed to the development of the natural vegetation and (ii) those that started to be so intense or qualitatively different that natural vegetation disappeared from impacted areas and became fragmented. Full understanding of the natural vegetation requires not only a knowledge of the vegetation history until and after the breaking point between both regimes of human impact, but also a knowledge of the trends in succession in the area.

The map of potential natural vegetation of the Czech Republic (hereafter PNV sensu Neuhäuslová et al. 1998) indicates the composition of the vegetation at the hypothetical end-point of succession. The remaining fragments and attributes of natural vegetation in present-day landscapes provided phytosociological data for the PNV construction. The map of PNV soon became the most influential conceptual model for our study area, and several other parts of the world, and attracted conservation policy makers. Comparison of the PNV and the past vegetation may provide a more integrated perspective of the natural vegetation and mutual evaluation of the results obtained using both approaches.

A recent attempt to link palaeoecological data with PNV (Carrión & Fernández 2009) prompted debate about the relevance of such comparisons and the basic concept of PNV (Chiarucci et al. 2010). PNV, which represents a hypothetical state assuming current climatic conditions remain roughly constant, cannot be easily compared with palaeoecological data, because environmental conditions differed in the past (Loidi et al. 2010). In order to overcome this conceptual difference, we need to assume that site characteristics have some stability, i.e. there is a relationship between the vegetation that previously grew at a particular site not very far back in time and vegetation that might grow at the same site at the hypothetical endpoint of succession. The importance of palynological investigations is highlighted in the construction of the PNV (Neuhäuslová et al. 1998) and during the long development of the PNV concept in the Czech Republic, when palaeoecological results were gradually integrated into the various versions of the PNV reconstructions (Mikyška et al. 1968–1972, Peichlová 1979, Neuhäuslová et al. 1998, Pokorný 2002b). Here we extend this approach using newer data and quantitative methods.

In addition, PNV does not consider disturbances and their impacts on succession, which is why the representation of pioneer trees and forest-free areas is much lower in PNV compared to the Holocene vegetation estimates and present-day vegetation. For this reason we do not consider pioneer trees and forest-free areas in this comparison.

The primary goal of this paper is (i) to produce quantitative pollen-based reconstructed vegetation of the Czech Republic and Slovakia for a 500 year-long time window of the Holocene. As secondary aims we (ii) compare the PNV composition with the pollen-reconstructed vegetation for all time windows, and (iii) discuss possible contradictions revealed by this comparison in order to evaluate the natural vegetation in the study area.

Methods

Fossil pollen data

We extracted 87 sequences (Fig. 1, Table 1) from the Czech Quaternary pollen database (PALYCZ; Kuneš et al. 2009). Pollen types denoted by names of genera, except for *Pinus*, refer to all species within the given genus. *Pinus* in our data filtering refers only to species belonging to the subgenus *Pinus* (diploxylon pines). *Plantago lanceolata* is the only pollen taxon considered that is defined at the species level. *Poaceae* includes all wild grasses, except *Phragmites australis*. The genera *Triticum*, *Hordeum* and *Avena* were pooled into the group taxon *Cerealia*; pollen of *Secale* and *Zea* was excluded. The data contain some *Cerealia* pollen from the Early Holocene, which we assumed was pollen of *Glyceria maxima* misidentified as *Cerealia* pollen because of its similar size and all occurrences of *Cerealia* before 5500 BC were excluded from the analysis by setting pollen counts of *Cerealia* to zero (Electronic Appendix 1 and 2).

Chronologies were established by classical depth-age modelling (Blaauw 2010), mainly by linear interpolation of radiocarbon dates. Some chronologies in southern and north-western Bohemia were improved by palynostratigraphical dating with uncertainties of 250 years (Giesecke et al. 2014). For details see Electronic Appendix 2.

The Prentice-Sugita dispersal function (Prentice 1985, Sugita 1993) assumes that most pollen is transported from sources of zero injection height in a flat landscape. The prevailing dispersal agent, wind above the tree canopy, brings pollen into the circular sedimentation basin, which is free of target taxa in the wetland vegetation. Pollen deposited in the sedimentation basin by different vectors (e.g. runoff, redeposition) are a possible source of bias. Before aggregating samples into 500-year intervals, a traditional interpretation of pollen percentages (sensu Prentice & Webb 1986) is undertaken in order to exclude or adjust samples with taphonomy that deviates from the assumption of the dispersal model. Poor pollen preservation was the first reason to exclude samples. A high proportion of resistant *Tilia* pollen in basal samples was interpreted as a sign of poor pollen preservation. Before the initial stage of peat bog development, dry conditions may allow microbial processes to decompose most of the pollen grains (Havinga 1967). Secondly, both macroremains and high pollen counts of cereals in the same layers indicated post-taphonomic processes. Pollen taphonomy of assemblages at swamp site Zahájí was influenced by runoff from nearby settlements (as demonstrated by Albert & Pokorný 2012), thus we also excluded those samples.

At peat bog sites, bias of pollen originating from the local vegetation on the bog surface can be corrected by setting a very small radius of the sedimentation basin for sites with high pollen percentages of wetland taxa (Abraham et al. 2014). We opted for a similar approach by adjusting high pollen percentages directly.

Several target taxa in our dataset can bias the results by their local presence (e.g. *Poaceae*, *Pinus*). A threshold of 20% for *Alnus* pollen appeared to be the most suitable to distinguish pollen from a local source from that of *Alnus* outside the basin. When *Alnus* percentages within the samples exceeded this 20% threshold at a site, the regional average percentage of *Alnus* based on the percentages recorded at all other sites during the time window was calculated. Pollen counts of *Alnus* in the biased samples were adjusted to regional averages and subsequently summed with other samples within the time window. We applied this replacement to five cores from three regions: southern Moravia,

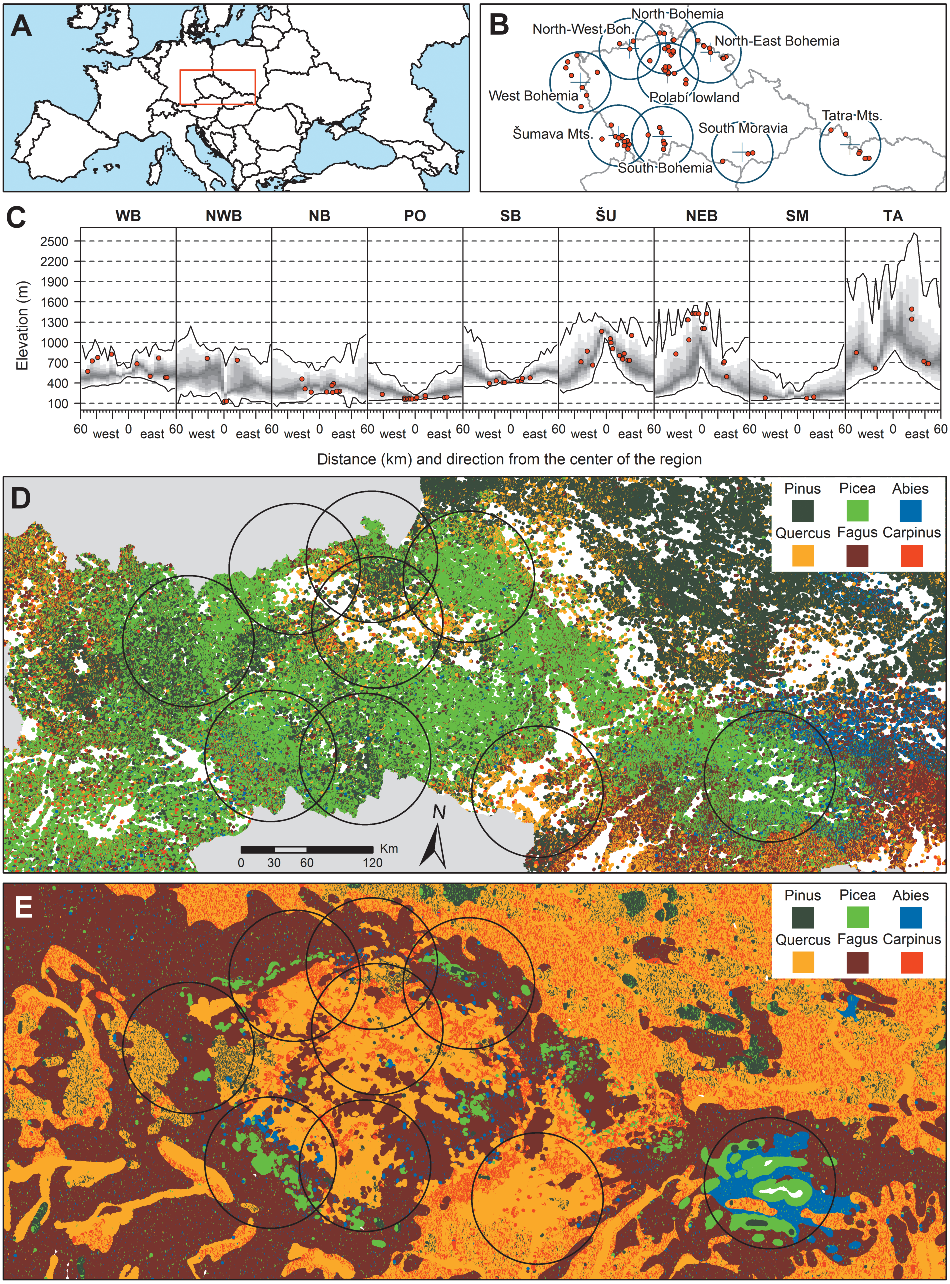

Fig. 1. – Geographical setting (A) of the area studied within Europe; (B) map of the sites (red) and the regions of 60 km radius; (C) distribution of the altitudes (grey) and of the sites (red) within the western and eastern part of each region, lines show the maximum and minimal altitude; (D) map of present-day vegetation, grey colour means lack of data; (E) map of PNV adopted from Neuhäuslová et al. (1998) and Bohn & Neuhäusl (2000–2003). Only *Pinus* (dark green), *Picea* (light green), *Abies* (blue), *Fagus* (darkbrown), *Quercus* (orange) and *Carpinus* (red) are shown; white colour represents bare land or areas with other taxa, colours correspond to Fig. 2.

Table 1. – Pollen sequences used for the analysis. Reg – REVEALS regions, R – radius of the sedimentation basin (metres), de – depositional environment (l – lake, b – bog). See further information in Electronic Appendix 2.

Reg	Name	longitude	latitude	R	de	Reference
WB	Kulzer Moos XII	12.44278	49.39472	195	b	Knipping 1997
WB	Kulzer Moos XIV	12.44278	49.39472	195	b	Knipping 1997
WB	Sauborst	12.09961	50.27617	40	b	Hahne 1992
WB	Seelohe Profil 1	11.85900	50.02620	40	b	Hahne 1992
WB	Vlček	12.73226	50.03996	98	b	Švarcová 2012
WB	Weiherlohe	12.38750	49.72972	56	b	Knipping 1997
WB	Weissenstadter Forst	11.88185	50.13378	40	b	Hahne 1992
WB	Windbruch V	12.54278	49.60917	252	b	Knipping 1997
WB	Wolfslohe 1	12.04038	49.90756	56	b	Hahne 1992
NWB	Fláje - Kiefern	13.57987	50.68294	282	b	Jankovská et al. 2007
NWB	Komořanské j. PK-1-CH	13.51835	50.53507	2523	l	Jankovská & Pokorný 2013
NWB	Komořanské jezero 2	13.51835	50.53507	2523	l	Jankovská & Pokorný 2013
NWB	Mothhäuser Haide	13.21577	50.60000	399	b	Lange et al. 2005
NB	Česká Lípa	14.56457	50.67308	113	b	Kuneš unpubl.
NB	Držník	14.72170	50.60887	56	b	Svitavská-Svobodová unpubl.
NB	Jelení louže	14.27661	50.89261	25	b	Pokorný & Kuneš 2005
NB	Konvalinkový vršek	14.60465	50.59888	1262	b	Petr unpubl.
NB	Mařenice	14.67723	50.79509	18	b	Kozáková unpubl.
NB	Milčany	14.47319	50.62761	98	b	Petr unpubl.
NB	Okna	14.67593	50.53207	113	b	Abraham unpubl.
NB	Páchnivec	14.72334	50.58359	98	b	Svitavská-Svobodová unpubl.
NB	Pryskyřičný důl	14.40634	50.89304	25	b	Abraham & Pokorný 2008
NB	Voroněž	14.72334	50.58359	98	b	Novák et al. 2012
NB	Žába	14.70065	50.80245	18	b	Kozáková et al. 2015
PO	Borek	14.66256	50.21769	40	b	Kuneš unpubl.
PO	Hrabanovská černava	14.83158	50.21639	98	b	Petr & Novák 2014
PO	Hradištko	15.18186	50.06066	28	b	Kozáková et al. 2014
PO	Chrást u přejezdu	14.59368	50.26204	40	b	Petr et al. 2014
PO	Chrást	14.54406	50.26030	56	b	Břízová 1999
PO	Košátky-tvrz	14.66337	50.31878	98	b	Kozáková unpubl.
PO	Kozly 1	14.57220	50.24337	40	b	Petr unpubl.
PO	Kozly 2 Okrouhlík	14.57220	50.24337	40	b	Petr & Pokorný 2008
PO	Kozly 3	14.54406	50.26030	56	b	Petr unpubl.
PO	Libice	15.17312	50.12935	40	b	Kozáková et al. 2014
PO	Mělnický úval	14.56217	50.31092	564	b	Petr & Novák 2014
PO	Stará Boleslav čistička	14.66743	50.19793	56	b	Břízová 1999
PO	Tišice	14.53251	50.26691	56	b	Dreslerová et al. 2004
PO	Tišice 2	14.53251	50.26691	56	b	Petr unpubl.
PO	Zahájí 2	14.11555	50.37922	98	b	Pokorný et al. 2015
PO	Zahájí	14.11555	50.37922	98	b	Pokorný et al. 2015
SB	Barbora	14.83329	48.95584	40	b	Jankovská 1980
SB	Borkovická blata A	14.63270	49.23277	564	b	Jankovská 1980
SB	Branná	14.80529	48.95909	40	b	Jankovská 1980
SB	Červené blato A	14.81016	48.86078	282	b	Jankovská 1980
SB	Mokré Louky	14.77804	49.00221	1197	b	Jankovská 1987
SB	Švarcenberk	14.70482	49.14562	399	b/l	Pokorný 2002a
SB	Švarcenberk S3	14.70482	49.14562	399	b	Pokorný et al. 2010
SB	Zbudovská Blata	14.34901	49.07483	282	b	Rybníčková et al. 1975
ŠU	Březník A	13.48878	48.96231	56	b	Svitavská-Svobodová unpubl.
ŠU	Dösingerried	13.13913	48.88394	160	b	Stalling 1987
ŠU	Finsterauer Filz	13.57751	48.94813	156	b	Stalling 1987
ŠU	Heidemühle Beerenfilz	13.75340	48.82677	233	b	Stalling 1987

Reg	Name	longitude	latitude	R	de	Reference
ŠU	Hůrecká slať	13.32755	49.15222	445	b	Svobodová et al. 2002
ŠU	Chalupská slať	13.66286	49.00061	395	b	Svitavská-Svobodová unpubl.
ŠU	Knížecí pláně	13.63503	48.96455	126	b	Svobodová et al. 2001
ŠU	Mrtvý luh - Chlum	13.88292	48.86680	892	b	Svobodová et al. 2002
ŠU	Mrtvý luh	13.88292	48.86680	892	b	Svobodová et al. 2001
ŠU	Malá niva	13.81606	48.91376	455	b	Svobodová et al. 2002
ŠU	Plešné jezero	13.86571	48.77674	155	l	Jankovská 2006
ŠU	Sonndorf	13.57064	48.82519	98	b	Stalling 1987
ŠU	Stráženská slať	13.74226	48.89887	618	b	Svobodová et al. 2001
ŠU	Velká niva-Volary	13.81857	48.92412	691	b	Svobodová et al. 2001
NEB	Anenské údolí	16.11745	50.58873	18	b	Pokorný & Kuneš 2005
NEB	Bílé Labe A	15.71250	50.73889	178	b	Svobodová 2004
NEB	Bílé Labe C	15.71250	50.73889	178	b	Svobodová 2004
NEB	Černá hora	15.75586	50.66061	437	b	Speranza et al. 2000a
NEB	Černohorská rašelina	15.75586	50.66061	437	b	Svobodová 2002
NEB	Hala Izerska	15.36321	50.85019	56	b	Skrzypek et al. 2009
NEB	Labská louka A	15.54216	50.77075	160	b	Svitavská-Svobodová unpubl.
NEB	Labský důl	15.55222	50.76278	40	b	Engel et al. 2010
NEB	Pančavská louka	15.54102	50.76619	299	b	Speranza et al. 2000b
NEB	Teplické údolí	16.13153	50.58494	56	b	Kuneš & Jankovská 2000
NEB	Úpské rašeliniště Palza	15.71250	50.73889	178	b	Svobodová 2004
NEB	Úpské rašeliniště A	15.71250	50.73889	178	b	Svobodová 2004
NEB	Úpské rašeliniště B	15.71250	50.73889	178	b	Svobodová 2004
NEB	Úpská rašelina	15.71250	50.73889	178	b	Speranza 2000
NEB	Vernéřovice	16.19577	50.62165	69	b	Peichlová 1979
SM	Dvůr Anšov	16.42254	48.77728	98	b	Svobodová 1997
SM	Svatobořice	17.08188	48.95432	56	b	Svobodová 1997
SM	Vracov	17.20520	48.97784	271	l	Kuneš et al. 2015
TA	Bobrov	19.66053	49.44563	149	b	Rybníček & Rybníčková 2002
TA	Hozelec 2	20.33200	49.04641	149	b	Hájková et al. 2015
TA	Hozelec	20.33200	49.04641	149	b	Jankovská 1988
TA	Popradské pleso	20.07984	49.15350	144	l	Rybníčková & Rybníček 2006
TA	Spišská Teplica	20.23073	49.04075	56	b	Jamrichová unpubl.
TA	Štrbské pleso	20.05775	49.12277	239	l	Rybníčková & Rybníček 2006
TA	Zlatnická dolina	19.25833	49.50000	138	b	Rybníček & Rybníčková 2002

western and southern Bohemia. Samples are listed in Electronic Appendix 2. The pollen signal of *Alnus* in the Polabí lowland and in northern Bohemia exceeds this threshold at most sites. Even though we are aware that this pollen signal may originate from local individuals, pollen counts of *Alnus* remained unchanged there, making it almost impossible to obtain a reliable average of the regional signal (Electronic Appendix 2).

Pollen-reconstructed vegetation: model setting

We chose the same settings of the most important parameters for the REVEALS model as adopted in a previous study (Abraham et al. 2014). These settings, based on modern pollen samples, realistically estimate the present-day vegetation in the five regions studied. Pollen productivity estimates and fall speed of pollen are listed in Electronic Appendix 3. Wind speed was set 4 m/s and the value for the maximum range of regional vegetation was set at 60 km. Sites included in the analysis consist of various types, among which mires prevail, ranging from circular peat bogs in the mountains to large forested swamps in the valleys. At all sites the radius of the sedimentation basin (Table 1) was estimated as the radius of the largest inscribed circle accommodated by the morphometry of the site. Delimitation of the site was approximated by the current water surface in the case of lakes, and the treeless part of the bog or extent of the deposit in the case of forested sites. Vegetation cover was estimated from pollen counts using dispersal and deposition models: the Prentice model for bog sites (Prentice 1985) and the Sugita model for lake sites (Sugita 1993). REVEALS estimates were calculated from pollen counts for each time window using the script "reveals.v1.1.R" (Abraham et al. 2014) in R (R Core Team 2013). REVEALS estimates are percentages only for the target taxa, thus the result does not consider bare land or areas occupied by other taxa (e.g. *Larix, Juniperus*), even though the extent of these areas may be sometimes significant. In today's landscape, these areas constitute approximately 20% of forested areas and 40% of agricultural land (Abraham et al. 2014). Similarly, we obtained estimates for three herbaceous taxa (*Poaceae*, *Cerealia* and *Plantago lanceolata*) in order to quantify the minimum degree of landscape openness.

Zonation and cluster analysis

Several multivariate techniques in R (R Core Team 2013) were used to analyse the variability in the estimates. Biostratigraphic zones in each region were calculated based on the squared chord-distance matrix using the method of incremental sum of squares (Grimm 1987). The significant number of zones was determined by the broken stick method (Bennett 1996), calculated using the Rioja R package (Juggins 2012).

Interregional similarities between average compositions were determined using Ward's hierarchical clustering. Its exact input was a dissimilarity matrix of squared chord distances based on the mean composition of each significant zone. Clusters were cut at the height of 0.33. This threshold was sufficiently low to place zones from one region in different hierarchical clusters and at the same time indicated reasonable groups of vegetation.

Present-day vegetation

The main source of data was forest inventories for different administrative units of different spatial resolution in each country (in parentheses is the name of the unit and its average area): Bavaria (spatial planning region – 3929 km^2), Poland (forest management unit – 720 km^2), Slovakia (district – 621 km^2), Czech Republic (municipality with extended competence – 383 km^2). Forest composition (Fig. 1D) within these administrative units was joined to the CORINE Land Cover (CLC) classes 311, 312 and 313 (coniferous, deciduous and mixed forest). The total area of forest recorded in the inventories corresponded quite well with the area of forest depicted on the CLC map, except for Poland, where data from small landowners were probably not included. The Bavarian dataset has the coarsest taxonomic resolution: broadleaved trees were distinguished only as *Fagus* or *Quercus*. For the trees not recorded in neighbouring countries, their percentage was assumed to be similar to that in the Czech Republic, for which the dataset is the finest-grained. The abundance of *Corylus* was obtained from estimates based on habitat mapping (Abraham et al. 2014).

Potential natural vegetation

The area of PNV was calculated according to Neuhäuslová et al. (1998) in the Czech Republic and according to Bohn & Neuhäusl (2000–2003) in adjacent countries (Fig. 1E). Percentages of tree taxa within each mapping unit were based on results of typical vegetation relevés (Neuhäuslová et al. 1998), or mean values if more than one was available. Plant abundances in relevés were transformed using the following key: r = 0.1%, + = 0.5%, 1 = 3%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%. Typical relevés contain information about different degrees of forest openness (canopy cover) and the abundance of herbaceous plants inside the forest, but we selected only trees (including *Corylus* recorded in the shrub layer) and set them to cover the entire surface of a given relevé (= 100%). This decision follows from the assumptions of the Prentice-Sugita model that the prevailing source of pollen is the canopy, so non-arboreal taxa are considered only outside forests. Moreover, almost all PNV units in the area studied are covered by forests; only the tops of the Tatras and the Krkonoše Mts are covered by alpine treeless vegetation; here considered as bare land.

A few relevés were excluded, for example, *Brachypodio pinnati-Quercetum* (unit 30), because the tree layer is not natural according to the PNV interpretation (Neuhäuslová et al. 1998). Mapping units from both sources were assigned to 11 common classes defined according to the syntaxon and their dominant tree. Within these classes, the composition of mapping units was again averaged in order to obtain a tree percentage applicable to countries other than the Czech Republic. The assignation and averaging is summarized in Electronic Appendix 4.

Dissimilarity analyses

For dissimilarity analyses, only tree composition within the defined area of REVEALS reconstruction (radius 60 km) was used. Herbaceous plants and *Acer* were excluded from the REVEALS estimates, because herbaceous plants are not included in the PNV composition and forest inventory data for *Acer* are not reliable. Percentages were recalculated for remaining 12 taxa in all three datasets (REVEALS estimates, present-day vegetation and PNV).

A dissimilarity matrix was calculated using the squared chord-distance between all REVEALS and PNV assemblages in the Analogue R package (Simpson & Oksanen 2011). Time periods with the highest similarity of REVEALS result and PNV compositions were identified by the lowest mean squared chord distance observed. For this mean value, coefficients from all regions were averaged within the time windows. The most similar time period was extracted for further analysis and referenced as pollen-reconstructed vegetation (PRV).

We evaluated dissimilarity scores between PNV and PRV using the distances produced by reference comparisons, i.e. between present-day vegetation and PRV and between present-day vegetation and PNV. Additionally, abundance of each taxon in PRV was evaluated by visual comparison with that in PNV and present-day vegetation.

Finally, both distances to present-day vegetation were compared between each other in order to see in which regions present-day vegetation is closer to the PRV than PNV and vice versa. This comparison was tested using Spearman's correlation coefficient in the Hmisc R package (Harrell & Dupont 2012) to check whether there is a relationship.

Results

Vegetation reconstruction

Based on results of pollen-based reconstruction, the development of the vegetation cover during the Holocene in the Czech Republic and Slovakia (Fig. 2) can be clustered into eight different groups and three general phases: Early (9500–6500 BC), Middle (6500–2500 BC) and Late Holocene (2500 BC–AD 2000). Figure 3 shows that the first group of clusters on the left side (a–d) are recorded during the Early Holocene in all regions and during the Middle Holocene in lowlands. The second group of clusters on the right side (e–h) are recorded in the Middle Holocene in highlands and in the Late Holocene in all regions. The first group comprises semi-open pine forests (a), mixed oak woodlands (b), hazel woodlands (c) and semi-open coniferous forests (d). The second group includes two clusters with the presence of anthropogenic indicators (e–f), fir-beech forests (g) and spruce forests (h). Detailed compositions of the different classes of vegetation is displayed as a boxplot in Electronic Appendix 5

Comparison with the potential natural vegetation and present-day vegetation

The lowest average dissimilarity between REVEALS estimates and PNV occurs in the time window AD 500–1000 (Fig. 4), which was thus selected for defining the PRV. However, if we consider dissimilarities of each region separately, the dating of PRV ranges from 2500 BC to AD 1500. Only southern Moravia exhibits a closer relationship between PNV and present-day vegetation than between PNV and PRV in all Holocene time windows.

The results of PRV (Fig. 5) are generally closer to present-day vegetation than abundances in PNV (triangles are closer to the line of optimal fit than full circles). *Quercus*, *Fraxinus*, *Fagus*, *Ulmus* and *Carpinus* are overestimated in the PNV at the expense of *Picea*, *Abies* and *Alnus*, which are more abundant in PRV.

The fact that the composition of the present-day vegetation is closer to the past state (PRV) than PNV is also reflected by a lower dissimilarity coefficient (Fig. 6). Squared chord distances between present-day vegetation and PRV range from 0.05 to 0.37, whereas distances between PRV and PNV range from 0.23 to 0.84. Distances between PNV and present-day vegetation are similar or slightly higher, ranging from 0.24 to 1.14.

Generally, with increasing distance between present-day vegetation and PNV, the distance between present-day and past vegetation (PRV) also increases. The strength of this relationship measured using Spearman's rho is 0.62, which is a significant positive dependency (P-value 0.0769) for nine samples at alpha level 0.1. Southern Bohemia is the region with the highest dissimilarity between present-day vegetation and the PNV, probably due to the high mismatch of *Pinus* and *Quercus*. On the other hand, the present-day vegetation is most similar to PNV and PRV in the Tatras region, probably due to the high abundance of *Picea* and *Abies* in PNV, PRV and present-day vegetation. The distance from PNV is similar in the rest of the regions and the distance from PRV is greatest for north-western Bohemia due to the higher abundance of *Picea* and a lower abundance of *Fagus* compared to the past.

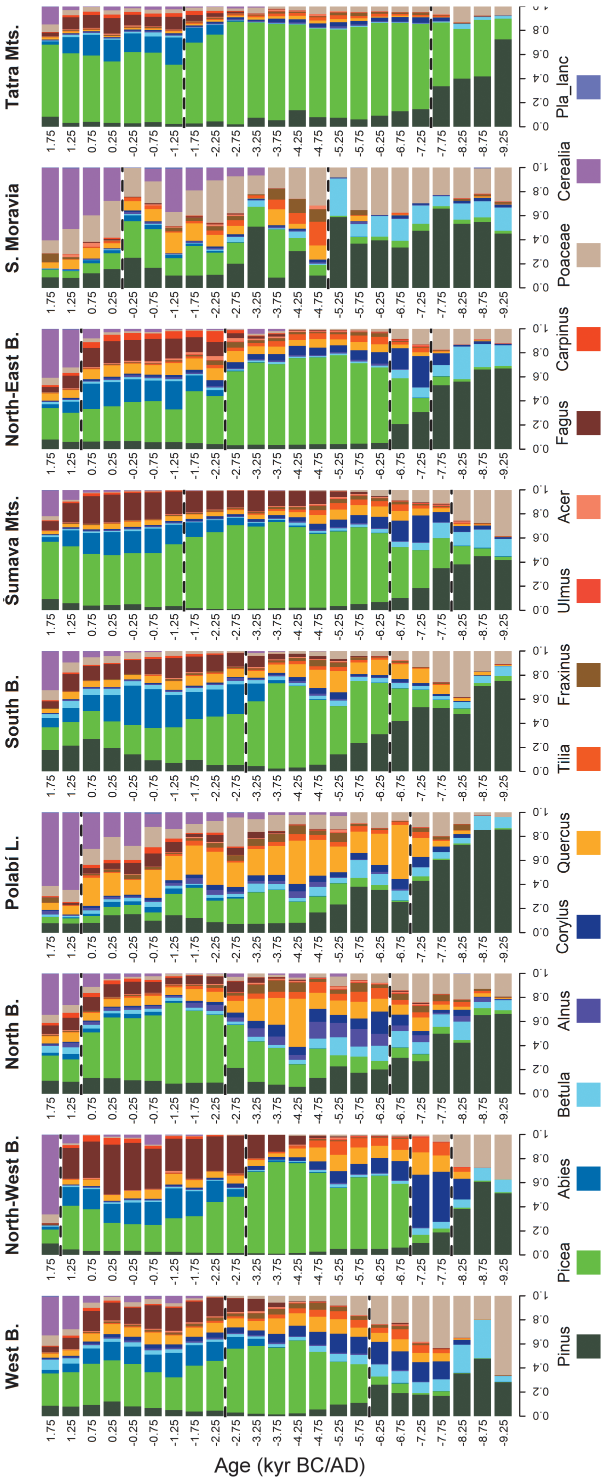

Fig. 2. – REVEALS estimates for nine regions and 23 time windows of 500 years (BC/AD). BC time windows marked with negative (-) sign. Dashed lines mark the position of significant vegetation zones. Order of the taxa in the graph follows the order in the legend. For detail plot of each taxa see Electronic Appendix 7. "Pla_lanc" refers to *Plantago lanceolata*-type. Colours correspond to Fig. 1.

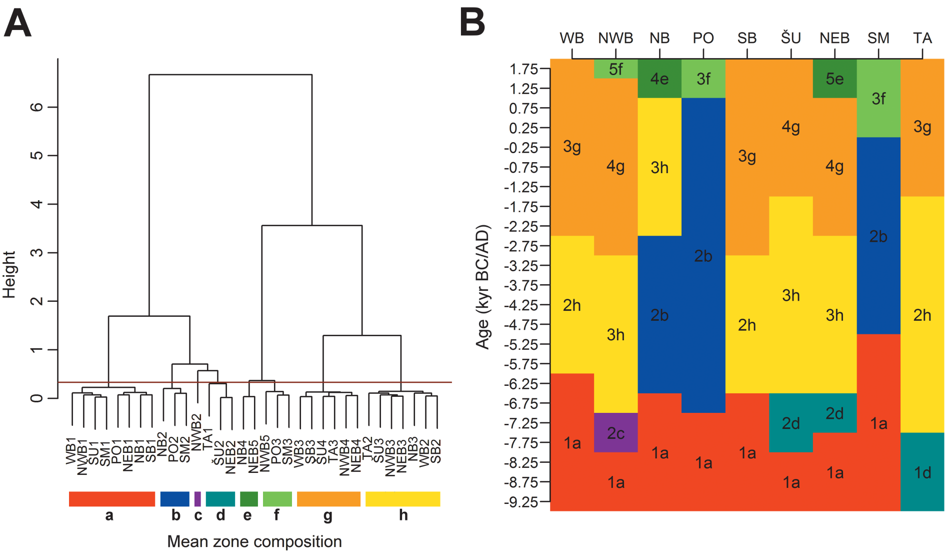

Fig. 3. – (A) Ward's hierarchical clustering of average composition of each vegetation zone, description of clusters indicated by different colours: a) semi-open pine forests; b) mixed oak woodlands; c) hazel woodlands; d) semi-open coniferous forests; e) vegetation subject to low human influence; f) vegetation subject to high human influence; g) fir-beech forests and h) spruce forests. (B) Time distribution of eight vegetation clusters in particular regions. Numbers represent significant pollen zones.

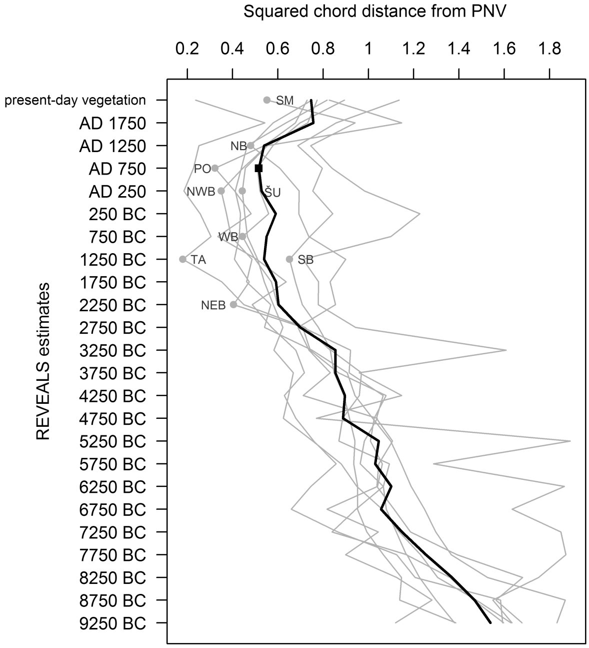

Fig. 4. – Changes in the dissimilarity coefficients calculated over time: between PNV and REVEALS estimates for the whole Holocene and between PNV and present-day vegetation; regions are represented by grey lines and their average by a black line; a black square marks the lowest average dissimilarity, while grey dots represent each region's lowest dissimilarity.

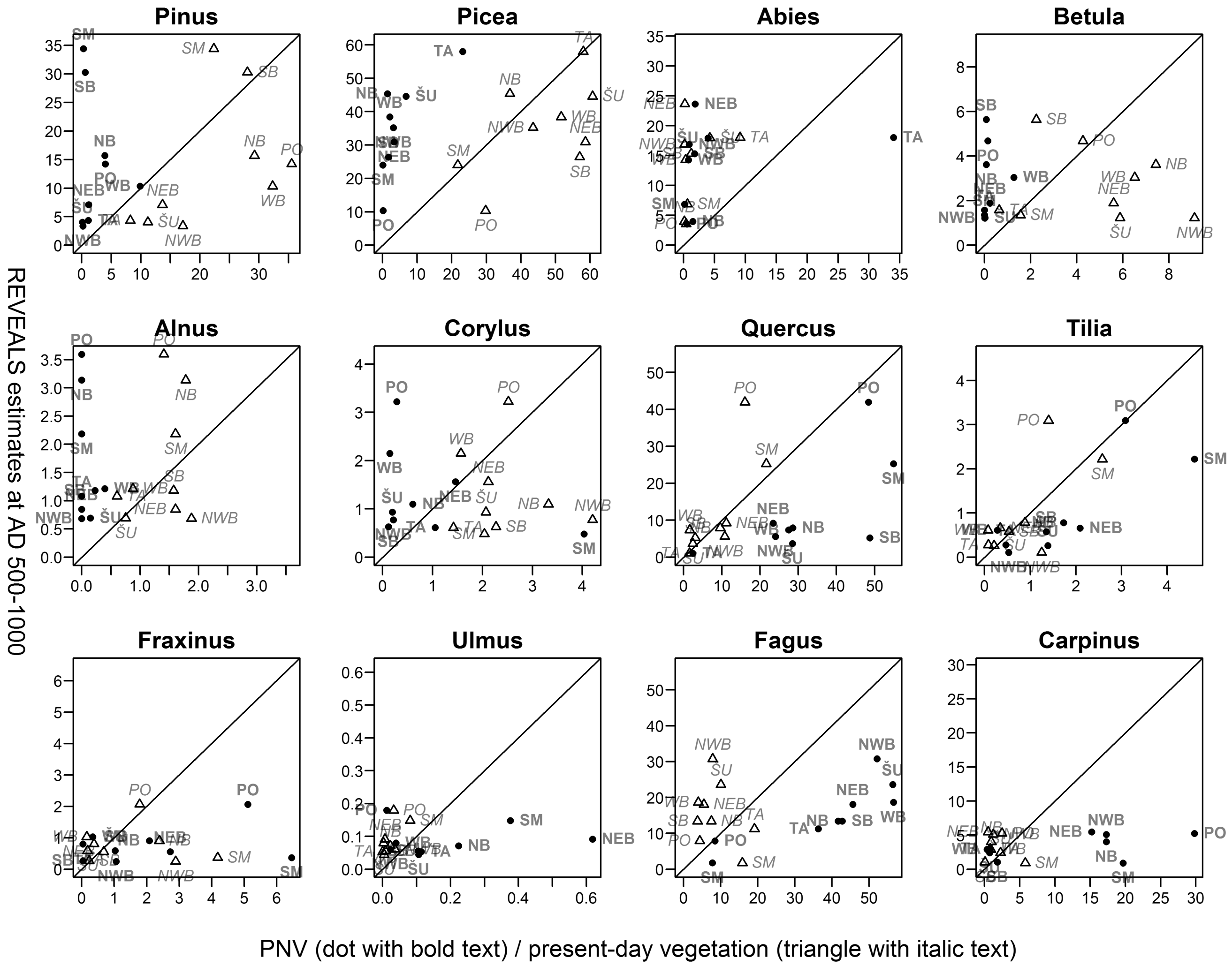

Fig. 5. – Scatter plots comparing REVEALS estimates at AD 500–1000 (PRV) with PNV (black circles) and PRV with present-day vegetation (red triangles). See Electronic Appendix 6.

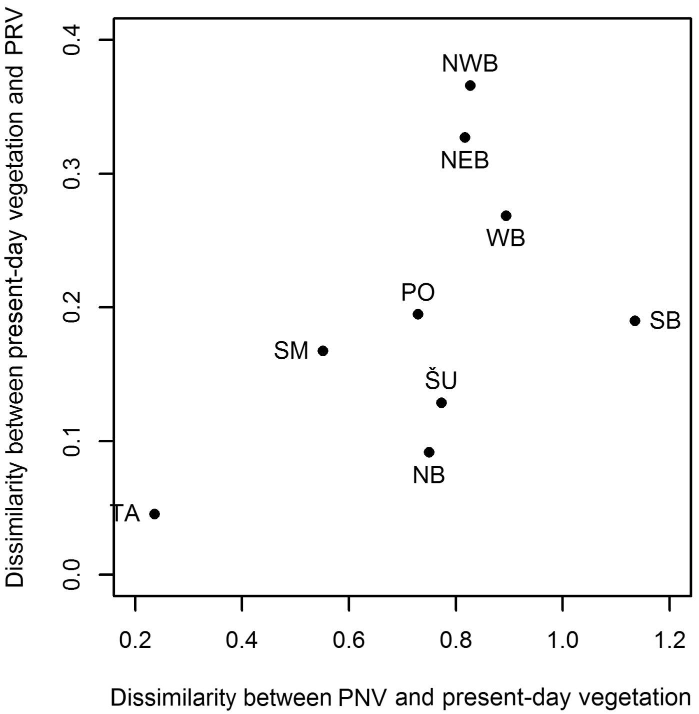

Fig. 6. – Scatter plots comparing squared chord distances between present-day vegetation and PNV with the squared chord distances between present-day vegetation and the REVEALS estimates (PRV) at AD 500–1000.

Discussion

Potentials and limits of REVEALS reconstructions

The REVEALS model provides robust estimates of vegetation much closer to reality than pollen percentages, and therefore can more realistically infer changes in vegetation (Fyfe et al. 2013, Marquer et al. 2014). This is why the reconstructed vegetation zones (Fig. 3) are slightly different from the general tree succession stages for central Europe proposed by Firbas (1949) based on pollen percentages. Earlier pollen analysts often discussed and considered pollen productivity in their reconstructions based on expert knowledge. Such an approach is generally difficult to reproduce.

Semi-open pine forests reconstructed for the Early Holocene and fir-beech forests for the Late Holocene match previous interpretations, but for most of the regions studied there is no indication of the Middle Holocene phase of hazel and mixed oak woodlands. The Early-to-Middle Holocene transitional phase dominated by hazel was distinguished in north-western Bohemia, probably due to the pioneer role of hazel in primary early postglacial succession in the Krušné hory Mts, where it is likely the near oceanic climate triggered its spread (Giesecke et al. 2011). Mixed oak woodlands expanded only in lowlands (northern Bohemia, Polabská nížina lowland, and in a reduced form also in southern Moravia) while the rest of the area studied was dominated by spruce in the same period of the Middle Holocene. In general, our REVEALS-based vegetation phases more closely follow the recently proposed subdivision of the Holocene into three phases (Walker et al. 2012).

This newly reconstructed history of the vegetation raises many questions regarding the diversity of herbaceous plants and soil conditions during such a long persistence of dark coniferous forests (spruce and fir-dominated ones). The chemical composition of spruce litter leads to soil acidification and subsequent podzolization (Emmer et al. 1998); however, most of the soils in the area studied are currently cambisols, which have supposedly evolved under deciduous forests.

When evaluating the results we allowed for some limitations of the REVEALS model. The use of a simple dispersal function may be a source of bias when dispersal conditions differ from the function's assumption, as is the case in mountainous regions. Electronic Appendix 1 for the Tatra region shows that the percentages of pollen of taxa characteristic of middle altitudes (*Quercus* and *Fagus*) are greater at the lake sites above 1300 m a.s.l. than at similarly sized bog sites around 650 m a.s.l. This effect of high mountains (Rybníčková & Rybníček 2006) may also affect the percentages of pollen of the different taxa in the bogs in the Krkonoše Mts in north-eastern Bohemia. Sites at high altitudes in the mountains receive pollen from high and windy layers of the atmosphere (Fig. 1C). Higher wind speed, which may be more realistic for such a high altitude deposition site, would also enlarge the source of pollen and thus consider the pollen load from lowland stands in the pollen spectra recorded at sites located at high altitudes.

After comparing curves of pollen percentages for all regions (Electronic Appendix 1), we are aware that the results for northern Bohemia, the Polabí lowland and southern Moravia are potentially affected by scarce sampling of very heterogeneous landscapes (which is mainly the case for northern Bohemia, the region where many pollen sites are located in sandstone landscapes characterized by steep geomorphological gradients). Pollen spectra for sites in the other regions are very similar, partly due to the large size of these sites and partly to the similarity of the landscapes around them.

Unstable pollen productivity is another source of possible biases. The model assumes that pollen productivity was constant during the entire Holocene. However, pollen productivity might have varied in the past as a consequence of changing climate, management practices (Theuerkauf et al. 2015) and temporary changes in the percentages of the different species of plants producing particular types of pollen. Apart from the temperature (Barnekow et al. 2007) vegetation structure might have played an important role. Solitary trees are better exposed to sunlight, so they produce more pollen than the similar individuals in closed forests (Aaby 1988). Taxonomic problems arise with pollen taxa of many plant species, especially within *Poaceae* and *Cerealia*. Species other than those used for PPE measurements (fitting the model using modern pollen spectra compared to present-day vegetation) possibly occurred in the past. The largest difference may have occurred during the High Medieval period, when autogamous cereals (*Triticum*) were replaced by anemogamous ones (*Secale*; Kozáková et al. 2014), but several pollen analysts did not distinguish between them. This is also the reason why the last time window (AD 1500–2000) contains more *Cerealia* than present-day vegetation (Abraham et al. 2014).

Generally, today's climate is more similar to that in the earlier periods of the Late Holocene, rather than Middle and Early Holocene. Since the parameters of the REVEALS model are adjusted to present-day vegetation (Abraham et al. 2014), the effect of the bias produced by different dispersal conditions and pollen productivity in the Late Holocene is considered to be low, which makes it reasonable to compare PNV and PRV compositions.

Spruce and fir dominance at middle altitudes

Despite the fact that the PNV composition is the most similar to the vegetation estimates for AD 500–1000 (PRV), the composition of the PNV is substantially different from any present or PRV (Electronic Appendix 6). When comparing the hypothetical state with real-world vegetation, we are aware of the conceptual differences and consider only reconstructed abundances of the most competitive dominants.

Abies was relatively abundant in the past, but it declined around Early Modern times, or even earlier (High Medieval) in some places. In the case of the Czech Republic, its Holocene dynamics seem to be closely connected with human impact (Kozáková et al. 2011). Nowadays, reintroductions of *Abies* are unsuccessful, and the low expectations of its spread are correctly indicated by its low abundance in PNV. Tatras is the only region with high representation of *Abies* today, yet the PNV suggests it could be much higher. Regarding the compatibility of the phytosociological approach with pollen-based reconstructions, regions with abundant *Abies* in PRV (13–25% north-eastern Bohemia, Šumava Mts and southern Bohemia) overlap with areas of fir forests (*Galio rotundifolii-Abietetum albae*, *Luzulo-Abietetum albae* and *Vaccinio myrtilli-Abietetum albae*) and no relevés linked with fir forests were found in regions with low *Abies* in PRV (see maps in Chytrý 2013).

Picea and *Alnus* are listed among taxa that are expected to spread (Neuhäuslová et al. 1998), so their representation should be higher in the PNV than PRV. Nevertheless, our results indicate the opposite. While the high representation of *Alnus* in PRV in the Polabí lowland and northern Bohemia is caused by local presence at most sites (see Methods), the same explanation does not apply elsewhere.

Spruce occurs naturally in the Czech Republic above 800 m a.s.l. and, additionally, in wet depressions in the lowlands (Chytrý 2012). Contemporaneous spruce growths in the highlands and at middle altitudes supposedly originate from artificial reforestation, because spruce became a popular forestry tree at the end of the 18th century (Nožička 1957). This is clearly reflected in the representation of spruce in the PNV (1–7%). Spruce estimates in PRV are much higher (26–45%) at middle and high altitudes and relatively stable during the Late Holocene. Its late expansion in the sandstone landscapes of northern Bohemia is connected with Late Holocene soil acidification (Pokorný & Kuneš 2005). A similarly late dominance of spruce is recorded in other peripheral areas of its distribution (Latałowa & van der Knaap 2006). We do not see any evidence of spruce introductions, because the time windows are probably too coarse, and even the original pollen data in the present dataset rarely show an increase in spruce in recent centuries, and it is only recorded at the following two sites for which there is a relatively fine time control: Pryskyřičný důl in northern Bohemia (Abraham & Pokorný 2008) and, to a lesser extent, Černá hora in north-eastern Bohemia (Speranza et al. 2000a). Although recent forestry interventions are not noticeable in the fossil record, the present-day percentage of spruce (36–60%) indicates it must have occurred. Beside introductions, selective logging of beech wood may have played a role. The Czech part of the Šumava region has a lower percentage of *Fagus* than the Bayerischer Wald (Fig. 1D); however, *Fagus* on the Czech side of that region is well documented in historical forestry data (Brůna et al. 2013).

The predominantly cultural origin of spruce over the last two centuries recorded in the literature clearly results in a strong underestimation in the PNV. Our estimates of spruce cover can be magnified by growth of spruce on mires at middle altitudes, but we think that this kind of bias has affected the spruce results less than e.g. the *Alnus* estimates in the Polabí lowland and northern Bohemia. Besides the high percentage of spruce in the results based on quantitative interpretation of pollen, there is ample evidence of the presence of spruce at middle altitudes before the period of modern forest management. These studies were generally neglected during the potential natural vegetation mapping, although they include traditional pollen-analytical interpretations and toponomastics (Rybníček & Rybníčková 1978), as well as utilization of written sources on forest composition of close-to-natural stands (Pokorný 1955, Nožička 1972). More recent studies document spruce at middle altitudes based on subfossil charcoal (Kozáková et al. 2011) and archival evidence (Szabó et al. 2016). The original distribution of natural spruce and spruce-fir forests is placed between the fir-beech and oak or oak-hornbeam vegetation belts (Szabó et al. 2016). Such forests remain as negligible fragments considerably affected by recent forest management (Rybníček & Rybníčková 1978).

The reasons for hornbeam, beech and oak dominance in the assumed PNV composition probably stem from presumed ecological characteristics, usually plotted as Ellenberg's ecograms (Ellenberg 1988). Hornbeam is the strongest arboreal competitor in the lowland and supracoline belt in the Czech Republic, whereas oak preferentially occupies drier sites (Chytrý 2012). Beech is described as the most competitive tree from the submontane to the montane belt; north-westwards of its Czech distribution, beech would dominate even at lower altitudes, whereas in the Carpathians it would only occur at higher altitudes (Bohn & Neuhäusl 2000–2003). This model generally underestimates the ecological characteristics of spruce at middle altitudes, because the assumptions adopted from Ellenberg (1988) are based on field observations in Germany, which might differ from the conditions in the Czech Republic due to both geographic, edaphic, climatic and historical factors.

The reasons for the quantitative differences between PRV and PNV reside partly in the PNV methodology. Biases in the representativeness of the results are common for any phytosociological methodology, and have already been pointed out by many authors (e.g. Ewald 2003, Roleček et al. 2007). Usually non-random sampling is preceded by interpretation of vegetation in the field, such that the placement of phytosociological relevés in the vegetation is influenced by authors' preferences. Any preconception about what natural vegetation is can magnify the representation of particular vegetation units.

The exact method of extrapolation of the vegetation units to PNV is somewhat hidden from the end-user. The use of expert knowledge could shift current PNV towards broad-leaved taxa because too many coniferous stands are interpreted as secondary (mostly plantations). Finally, typical phytosociological relevés might not optimally represent the abundances of taxa in PNV. The few (1–3) relevés we used to represent the whole unit cannot capture the variability of the whole plant community. We are aware that evaluation of the original expression of PNV by using a few typical relevés decreases the robustness of our comparison between PNV and PRV. Thousands of available relevés for forest communities in the phytosociological database (Chytrý & Rafajová 2003) could have provided statistically stronger estimates of vegetation cover for each PNV unit. In spite of this, we expect that the trends in the over-/under-representation of taxa between PNV and PRV would be similar.

PNV (if compared to PRV) assumes quantitatively different percentages of the above mentioned taxa, but interestingly this difference is consistent with the interregional gradient of taxa percentages in PRV, e.g. regions with a high abundance of spruce in PRV are also covered by relatively high abundance of spruce in PNV (Fig. 5). This similarity in interregional gradients of abundances of different taxa inferred from PRV and PNV is also reflected in the positive relationship between distances of present-day vegetation to PNV and PRV (Fig. 6). Even though this relationship is not very strong, the result is satisfactory considering the quality of the data compared. It indicates that those fragments of natural vegetation in present-day landscapes that were identified by PNV are related to the PRV. Relationship between the naturalness of present-day vegetation in the sense of PNV and the change in composition from the past until now implies that both palynology and phytosociology can jointly identify natural vegetation, i.e. these approaches are complementary.

Past non-equilibrium vegetation states

A broad and stable cover of *Pinus* during the Holocene is documented for Polabská nížina lowland, southern Moravia and northern Bohemia. In southern Moravia and the Polabská nížina lowland, we obtained regional estimates of *Poaceae* exceeding 9% throughout the Holocene. Both belong to taxa of young successional phases, therefore their high percentage in the past and also in present-day vegetation could be explained as human-dependent, but it is inconsistent with their stable percentage in those regions subject to different intensities of human activity.

In order to describe natural occurrences of *Pinus* and *Poaceae* abiotic factors need to be taken into consideration. These regions have sandy soils, which are suitable for the growth of pine. Dry climate in southern Moravia and the Polabská nížina lowland (Tolasz et al. 2007) can restrict the distribution of some trees, so *Poaceae* might be favoured. On the other hand, present-day experience shows that most of the grasslands or pine forests in southern Moravia and Polabí lowland tend to develop into oak and hornbeam forest, which are also in the PNV composition. This contrasting fact can be explained either by recent changes in climate and high nitrogen deposition or by the time scale over which the vegetation dynamics was measured. When considering millennial rather than a decadal perspective, dynamic factors (windstorms, fires, herbivores) can become more important drivers of the natural vegetation than abiotic factors (soil, topography, climate) or biotic interactions (tree competition).

Vegetation is not only influenced by disturbances, but feedback between vegetation composition and disturbance frequency is also important. The balance between spruce and pine determined by soil conditions and their ecological competitiveness can change with increase in frequency of disturbances (e.g. wind throw, insect outbreaks, fires). Regular fires favour pine over spruce in the boreal zone (Gromtsev 2002, Tryterud 2003) and fire has also been considered an important natural driver in the lowland temperate zone (Novák et al. 2012, Bobek 2013, Adámek et al. 2015). Our result pointing to stable percentages of *Pinus* in the lowlands supports this new consideration. Higher levels of disturbances would be indicated also by the presence of *Betula*, which has remained stable (1–6%) since it decreased around 6500 to 5000 BC. The long-term openness is likely due to grazing pressure by large herbivores, be they wild or domestic (Vera 2000).

The continuous open landscape in southern Moravia and the Polabská nížina lowland sheds light on classic biogeographical questions regarding central Europe. Both regions host certain disjunctive floristic elements of continental steppes, which survived the Holocene thermal optimum before the beginning of the Neolithic (Kajtoch et al. 2016). Regardless of the putative drivers and possible complexity of their interactions, which could keep the areas unforested, we can contribute to answering these questions by quantifying the minimal degree of landscape openness (> 9% of *Poaceae*). The strongest palaeoecological proof of continuous forest-free patches comes from fossil assemblages of snails that live exclusively in open landscapes (Juřičková et al. 2013, Pokorný et al. 2015). The widespread presence of chernozem soils in both regions may also indicate landscape openness, because genesis of chernozem soils is hypothesized to be dependent on a dry climate restricting the expansion of forests (Antoine et al. 2013). One justified objection to our results is that *Poaceae* pollen can originate from local grasses such as *Phragmites australis*, which often covers lowland mires and shores of shallow lakes. In this case it is difficult to filter out local pollen; however, peat bogs in northern Bohemia are also overgrown by local grasses, yet a strong evidence of continuous openness is lacking.

Natural vegetation undergoing long-term anthropogenic transformation

The increase in the abundance of *Pinus* during the Late Holocene in western and southern Bohemia (Electronic Appendix 7) is likely to be due to an anthropogenic disturbance. Fluctuations of pine in southern Bohemia correlate with the intensity of human occupation; noticeable peaks in the estimates of pine occurred around 2000–1500 BC and 500–1 BC, which coincide with the Early Bronze Age and Late Iron Age. It is likely that plantations during the 18th and 19th century caused the increase of *Pinus* in the most recent time window. However, other human impacts like fire, wood cutting and livestock grazing provoked very similar responses to natural disturbances (e.g. wildfires, windstorms, herbivores), so it is difficult to determine the particular factors that were important in the past.

Our results show that the most recent time window when the pollen-reconstructed past vegetation was most similar to the hypothetical composition of current PNV (AD 500–1000) falls within the Early Medieval period (AD 580–1200). The subsequent time window includes the High Medieval (AD 1200–1500); thus it is probable that this result is influenced by a dramatic increase in human impact. A considerable increase in human population led to the colonization of highlands and triggered deforestation (Kozáková et al. 2014). It is important to note that the High Medieval transition is not only a milestone in terms of the magnitude of human impact, but especially in terms of the relationship of humans to nature, which was changed by social and economic transformations (Le Goff 2005). Prehistoric fields were replaced by new modes of resource exploitation by humans. Clearly defined ownership of land shifted activities to more organized interventions (inter-connected with urbanization), central planning and assignment of landscape functions (Sádlo et al. 2005).

We infer that the vegetation under the human impact prevailing in the Early Medieval is still acceptable as a natural baseline. However, pollen-reconstructed vegetation for any period of time or PNV should not be understood as a target composition in forest management and nature conservation, because it consists of static percentages of taxa per unit area (Jackson 2013), whereas real vegetation is always inherently dynamic. It is made up of shifting patches at different stages of succession. Historical ranges in the variability of different taxa need to be estimated for the area studied. One of the potential tools for revealing small-scale vegetation variability in the past would be the LOVE model, the second step in the Landscape Reconstruction Algorithm (Sugita 2007b).

Conclusions

Three general vegetation phases were distinguished by the REVEALS estimates of vegetation: Early, Middle and Late Holocene. Clustering interregional variability clearly divided lowlands from highlands and mountains. Oak was the most prevailing taxon in the lowlands during the Middle Holocene, and spruce was dominant (> 32% in the REVALS estimates) at middle altitudes and in mountainous regions. The percentage of spruce also remained high (> 19%) in the fir-beech forests during the Late Holocene. The high percentage of spruce contrasts with some previous vegetation reconstructions, which did not consider the low pollen productivity and low pollen dispersal of spruce.

The closest match between PRV and PNV compositions was recorded for the time window AD 500–1000. PRV emphasizes the underestimation of *Picea* in PNV at the benefit of *Fagus*, *Quercus* and *Carpinus*, which are unlikely to be important constituents of natural vegetation as PNV assumes. This mismatch may be caused by two factors: overemphasis of introductions of spruce by foresters since the end of the 18th century and disregard for the different climatic and edaphic conditions compared with other (especially lowland) areas of central Europe.

The present-day vegetation in southern Bohemia can be considered the least natural according to the PNV composition, because *Pinus* is more abundant and *Quercus* less abundant than PNV assumes. The present-day vegetation in north-western Bohemia is the least preserved according to the PRV composition, because *Picea* is more abundant and *Fagus* less abundant than in PRV. The most natural vegetation according to PNV and the most preserved vegetation according to PRV grows in the Tatras region, because high abundances of *Picea* and *Abies* are recorded in PNV, PRV and present-day vegetation. The relationship between the naturalness of the present-day vegetation as estimated by PNV and the compositional turnover from AD 500–1000 to present suggests that quantitative palynology and phytosociology have the potential to produce complementary results and their combination can contribute to a more integrated view of natural vegetation.

For the lowlands, there were high percentages of *Pinus*, *Betula* and *Poaceae* in the PRV reconstruction using REVEALS. Their stable representation during the entire Holocene stresses the greater importance of possible drivers that maintained their abundances during the Holocene, such as herbivory, fire or human impact. Since these disturbances are not incorporated in the PNV, we propose to describe and conserve the natural vegetation in a more dynamic way by assembling the ranges of variability of the current plant communities together with the variability of the plant abundances in the past and the long-term disturbance dynamics. The present REVEALS estimates represent one example of historical ranges for the area studied, providing an overall view, coarse in spatial and temporal resolution, yet one that has the potential to be refined and informed by complementary sources of information.

See www.preslia.cz for Electronic Apendices 1–7.

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Souhrn

Hlavním cílem práce je kvantitativní rekonstrukce vývoje vegetace v průběhu holocénu na základě pylových analýz, zejména pro aktualizaci pohledu na přirozenou vegetaci v České republice a na Slovensku. Z tohoto důvodu jsme si vytyčili i vedlejší cíl a srovnali jsme složení této pylově rekonstruované vegetace (PRV) s předpokládaným složením potenciální přirozené vegetace (PNV sensu Neuhäuslová et al. 1998) v této oblasti. Pro výpočet zastoupení jednotlivých druhů ve vegetaci jsme použili 87 pylových sekvencí z devíti regionů, každý o poloměru 60 km, a model REVEALS, který zohledňuje rozdílnou pylovou produktivitu, šíření pylu a jeho ukládání do mokřadních sedimentů. Rozlišili jsme tři základní vegetační fáze: raný, střední a pozdní holocén. Shluková analýza variability mezi regiony jasně oddělila nížiny od středních nadmořských výšek a hor. V raném holocénu téměř ve všech regionech převládaly poloотevřené bory. Smíšené doubravy se objevily ve středním holocénu a jen v nížinách, zatímco ve středních a vyšších polohách převládal smrk (> 32 %). Jeho podíl zůstal vysoký (> 19 %) i v jedlobučinách, které dominovaly v pozdním holocénu. Výrazné zastoupení smrku vyšlo na základě započtení jeho nízké pylové produktivity a nízké šiřitelnosti pylu. Výsledek kontrastuje s některými předchozími rekonstrukcemi, které tyto faktory dostatečně nezohledňují. Přirozeně hojný výskyt smrku ve studovaném území přikládáme klimatickým a půdním poměrům, které se zde mohou lišit od zbytku střední Evropy. Kontinuální zastoupení lipnicovitých (> 9%) a pionýrských dřevin v průběhu celého holocénu (borovice > 6%) indikují důležitou roli dynamických faktorů, které udržovaly jejich dlouhodobou přítomnost. Mohli jimi být herbivoři, požárová aktivita nebo jiné typy přirozených a člověkem řízených disturbancí. PRV v období 500–1000 n. l. ukazuje více smrku na úkor listnatých klimaxových druhů mírného pásu (dub, buk, habr), které dominují v předpokládané PNV. I přes tento výrazný rozdíl jsme našli vzájemný vztah mezi přirozeností současné vegetace ve smyslu PNV a změnou složení vegetace od 500–1000 n. l. směrem do současnosti. To znamená, že oba přístupy, kvantitativně-palynologický a fytocenologický, mají potenciál dojít k velmi podobným výsledkům a jejich kombinace může přispět k celistvějšímu pohledu na přirozenou vegetaci.

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