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Palynologická syntéza pro Českou Republiku
Palynological synthesis for the Czech Republic

PhD thesis

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Contents

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Abstract

The present palynological synthesis is focused on the Holocene and partly on the period since the Late Glacial Maximum (LGM) in the Czech Republic and its close surroundings. The main aim is to gather pollen sequences and derive from them synthetic information on past species distribution and vegetation history. The synthesis of vegetation history was produced by applying the REVEALS model, which can filter out following factors influencing the relationship between pollen and vegetation: pollen taphonomy, pollen productivity and pollen dispersal. It was necessary to calculate and test those parameters, so the goals were partly methodical.

Pollen productivity estimates (PPEs) are calculated within the Relevant Source Area of Pollen (RSAP), which is one of the outputs of the computation and is influenced by vegetation structure. **Chapter 3** shows PPEs from the agricultural landscape of Central Bohemia. The RSAP distance of 1050 m is similar to the distance at which all taxa become present around all sites (1100 m). Unevenly distributed taxa therefore control the RSAP distance. Subsequent validation of those values in the area of the REVEALS model 10^4 km^2 and selection of additional values for lacking taxa created the best set of PPEs for the study area and moreover, **Chapter 4** explored the general importance of all parameters of REVEALS model.

The source fossil dataset for purposes of this synthesis is the newly developed Czech Quaternary Pollen database (PALYCZ). Non-direct multivariate analysis of pollen percentages including all taxa revealed a similarity between the end and the start of the current interglacial stage (**Chapter 1**).

The phylogeographic hypothesis that Alpine and Carpathian populations of *Lonicera nigra* survived the LGM in separate refugia is supported only by the Late-Glacial record. Nevertheless, unambiguous determination of this pollen type down to the species level is not possible. Pollen evidence covering the LGM from both the Alps and the Carpathians is still missing (**Chapter 2**).

Application of the best setting from **Chapter 4** on the fossil record from **Chapter 1** in nine regions produced REVEALS estimates for the whole Holocene. Dominance of spruce during the Middle Holocene at medium altitudes contrasts with most previous interpretations, which describe it as a period of mixed oak woodlands. The composition of reconstructed vegetation in the 750 AD time window is the most similar to the composition from Potential Natural Vegetation (PNV); however, quantities of individual taxa differ due to the methodological and conceptual background of PNV. Moreover, continuous presence of an open landscape (Poaceae >9 %) and/or pine (>6 %) in some lowlands highlights the role of possible natural drivers allowing their permanent abundance, be it herbivores, a dry climate or fire activity (**Chapter 5**).

Abstrakt

Předkládaná palynologická syntéza se zaměřuje na holocén a částečně na období od glaciálního maxima (LGM) v České Republice a blízkém okolí. Hlavním cílem je shromáždit pylové sekvence a získat z nich syntetickou informaci o historii vegetace a rozšíření druhů v minulosti. Na syntézu vegetační historie byl aplikován model REVEALS. Ve srovnání s tradičním použitím pylových procent, REVEALS zohledňuje následující faktory, které ovlivňují vztah mezi pylovým spadem a okolní vegetací: pylová produktivita, šíření a ukládání pylu. Bylo třeba spočítat a otestovat tyto parametry, takže cíl je částečně metodický.

Odhady produktivity pylu (PPEs) jsou vypočteny v okruhu relevantní zdrojové oblasti pylu (RSAP), která je jedním z výstupů výpočtu a která je ovlivněna strukturou vegetace. **Kapitola 3** ukazuje PPEs v zemědělské krajině středních Čech. Radius RSAP 1050 m je podobný vzdálenosti, ve které se všechny taxony dostanou do okolí všech lokalit (1100 m), což ukazuje, že nerovnoměrně rozptýlené taxony ovlivňují RSAP nejvíce. Následné ověření těchto hodnot v území pro model REVEALS 10^4 km^2 a výběr dalších PPEs chybějících taxonů vytvořilo nejlepší soubor pylových produktivit pro zájmovou oblast. **Kapitola 4** navíc prozkoumala obecný význam všech parametrů v modelu REVEALS.

Souborem fosilních dat pro účely této syntézy je nově vytvořená Česká Kvartérní Pylová Databáze (PALYCZ), která shromažďuje pylová data z více než 40-ti let palynologického bádání v České a Slovenské Republice. Nepřímá multivariační analýza pylových procent všech taxonů ukázala podobnost mezi koncem a začátkem současného interglaciálního cyklu (**Kapitola 1**) .

Fylogeografická hypotéza, totiž že alpské a karpatské populace *Lonicera nigra* přežily glaciální maximum v samostatných refugiích, je podpořena pouze pozdně glaciálním záznamem. Jednoznačné druhové určení pylu u tohoto rodu však není možné. Fosilní důkaz pro přežívání *Lonicera nigra* v glaciálním maximu v obou horstvech stále chybí (**Kapitola 2**) .

Použití nejlepšího nastavení z **Kapitoly 4** na fosilním záznamu v devíti regionech z **Kapitoly 1** vyprodukovalo vegetační odhady REVEALS pro celý holocén. Dominance smrku ve středním holocénu ve středních nadmořských výškách kontrastuje s většinou dřívějších výkladů, které vegetaci tohoto období popisují jako smíšené dubové lesy. Složení rekonstruované vegetace pro časové okno 750 našeho letopočtu je nejpodobnější složení z potenciální přirozené vegetace (PNV), ačkoliv proporce jednotlivých taxonů se zásadně liší kvůli metodickému a koncepčnímu pozadí PNV. Kontinuální přítomnost otevřené krajiny (Poaceae >9 %) a/nebo borovice (>6 %) v některých nížinách navíc zvýrazňuje roli přírodních faktorů, které umožňují jejich trvalé zastoupení, ať už to jsou býložravci, suché klima nebo požárová činnost (**Kapitola 5**).

Introduction

Palynological synthesis is a general term that should first be delimited by the period, geographical area, taxa and method used. The topic of the present thesis "Palynological synthesis for the Czech Republic" is mainly focused on the Holocene and partly on the period since the Late Glacial Maximum (LGM). Its geographic extent overlaps with the coverage of the Czech Quaternary Pollen Database (PALYCZ), i.e. the Czech Republic and its close surroundings. The aim of this thesis was to gather pollen sequences (**Chapter 1**) and derive from them synthetic information on past species distribution and vegetation history.

Lonicera nigra was selected as a model taxon for a comparison of palynological evidence with the phylogeographic pattern (**Chapter 2**). According to its present area of distribution, the extent to the sub-continental scale of this single-taxon synthesis was adjusted (Fig. 1).

Holocene development of vegetation dominants together with a map of potential natural vegetation (PNV) were used to evaluate the degree of naturalness of phases of the Holocene. Pollen signal of these taxa was treated quantitatively (**Chapter 5**), so the general historical aims of this thesis were extended to include methodological objectives in the field of palynological interpretation. Rather than new primary data collection, the work beside other things was devoted to the creation of the database, data cleaning (**Chapter 1**), calculation of interpretive parameters (**Chapter 3**) and model testing (**Chapter 4**).

General aspects of palynological interpretations

Pollen analysis is probably the most powerful tool for reconstructing past vegetation. Its methodological frame can be divided into three sequential phases:

Although pollen is deposited in huge quantities on the entire surface of the Earth, it can be preserved for the future only under wet conditions. The first, basic phase, "pollen data collection", includes localization of suitable sites, sampling, chemical preparation, pollen identification and counting. In the form of a pollen assemblage or stratigraphic sequence of pollen assemblages (usually depicted in the form of a pollen diagram), the results reflect the source vegetation, but this reflection suffers from taxonomic inconsistencies and several non-linearities. Four major factors influence the relationship between pollen and vegetation: the spatial pattern of source plants, pollen taphonomy, pollen productivity and pollen dispersal. The second phase, denoted here as "palynological interpretation", consists in filtering of above-mentioned factors and in obtaining information about vegetation from pollen data. The third phase, denoted here as "palynological synthesis", adds a valuable spatial dimension to the output, as it applies a consistent interpretation to a set of many sites within a defined geographical area. One can thus examine (dis-)similarities between selected sub-regions.

Data gathering, synthesis and interpretation are highly interlinked steps. All interpretative tools rely on certain assumptions, which are mostly based on uniformitarianism, to produce an interpretation, often informally called a story. However, they can differ in how complex and formalized these assumptions are, i.e. the level to which the transformations from pollen spectra to a vegetation model are under explicit control. The most basic and traditional approach is the author´s expert knowledge and narrative applied only to pollen percentages (observed from pollen diagrams). All assumptions are then expected to be generally and empirically known, so they are usually unstated and cannot be re-evaluated in hindsight. A little more formal variation to this approach is the use of thresholds values in pollen curves (von Post, 1918) as signal of regional presence and/or dominance of some taxa. An even more formal approach is when these values are previously tested on samples of the present vegetation (Lisitsyna *et al.*, 2011). Another formal way of reconstructing vegetation is the *modern analogue technique*. Samples from present vegetation types are assigned to the fossil record on some level of significance, so during the interpretation one can just describe the present vegetation of an assumed geographical analogue (the “space-for-time substitution” approach). However, more than one vegetation type can produce the same pollen assemblage (Jackson & Williams, 2004). The quantitative approach overcomes the four biases between pollen samples and surrounding vegetation by reducing their complexity into a few parameters or by transforming them into explicit assumptions. Without doubt, this very formal interpretation is oversensitive to minute parameter adjustments. However, vegetation history is reconstructed from vegetation estimates.

The interpretative tools employed in the present "Palynological synthesis for the Czech Republic" are of different levels of complexity. A traditional interpretation of pollen percentages was performed in the multivariate ordination of the whole database (**Chapter 1**). *Lonicera nigra* is extremely rare in pollen samples due to low pollen production and inefficient pollen dispersal. Thus in this case (**Chapter 2**), quantities of pollen were neglected and converted into presence or absence. Even rare occurrences of single pollen grains are considered to be evidence of the presence of the species in the past. This is underlined by the fact that the presence of *Lonicera* in a plant community does not guarantee its occurrence in the pollen assemblage, as evidenced by Pelánková & Chytrý (2009).

In the third case, I used a quantitative approach, which is described in the detail below. However, a classical intuitive interpretation of pollen percentages must precede it in order to exclude samples with taphonomy which deviates from the assumption of the dispersal model, i.e. that the prevailing pollen dispersal agent is wind blowing above the tree canopy. The cases were: very high proportion of *Alnus glutinosa*–type pollen originating from canopies above the site – gravity component; cereal grains in the core supposedly brought in by runoff from settlements - water component; and high proportion of resistant pollen of *Tilia* in the basal sample, which was interpreted as signal of poor pollen preservation (**Chapter 5**).

Quantitative approach

As already mentioned above, the quantitative approach can overcome three (in the case of the REVEALS model) or four (in the case of the LOVE model) factors biasing the translation from pollen to vegetation and vice versa: pollen productivity, pollen dispersal and taphonomy and spatial pattern of the surrounding vegetation.

Pollen productivity

Pollen productivity is a taxon-specific single-value parameter. Beside of the linear relationship to pollen loading and vegetation abundance, its key role resides in the fact that the reconstruction algorithm was developed as an inverse form of the algorithm for PPE calculation. Both deal with two steps and two spatial levels. PPEs are calculated from surface pollen samples and data on surrounding vegetation by the Extended R-Value (ERV) model (Parsons & Prentice, 1981; Prentice & Parsons, 1983; Sugita, 1994). The ERV model in the first step estimates the Relevant Source Area of Pollen radius, which represents the area of the vegetation used for subsequent PPE calculation. The area lying beyond the RSAP is assumed to be the source area of a certain proportion of pollen – the area of background pollen. The Landscape Reconstruction Algorithm (LRA; (Sugita, 2007a; b) is divided into the REVEALS model producing REgional Vegetation Estimates from Large Sites (>10^2 ha), which represents background pollen loaded at the regional scale (10^4-10^6 km^2), and the LOVE model, which reveals a LOcal Vegtation Estimates at a small site (<10-10^2 ha) by subtracting of the regional part from the previous step. ERV and LRA models have become a comprehensive toolbox for extracting species-specific reconstruction parameters and their application to the fossil record.

The ERV model was discovered already in the 1980s, but its use accelerated with the creation of the POLLANDCAL network (2001-2005). This scientific community was a platform for people applying these algorithms and solving practical issues of data collection (Gaillard *et al.*, 2008). A comparison of PPE values showed similarities, but also differences among many studies carried out in Europe (Broström *et al.*, 2008). One of the proposed reasons for these discrepancies were regional environmental characteristics (climate, vegetation structure). Thus, a region-specific PPE study for Czech Republic was needed.

The reliability of PPEs can be assessed from ERV results based on the length of the gradient of the input data, the proportion of background pollen, the likelihood function score or using simulation approaches. Before using PPEs in the LRA on fossil spectra, it is necessary to verify the validity of PPEs and the LRA. One of the validation criteria, the consistency between different sets of PPEs in the REVEALS model, was tested using the Czech Pollen Quaternary database (Mazier *et al.*, 2012), but the dissimilarity between model estimates and actual vegetation was not examined. Hellman et al (2008a) produced vegetation estimates using the REVEALS model that are very close to the real vegetation, however, in southern Sweden by using local PPEs. Some important trees are missing in the set of Czech PPEs (**Chapter 3**), so the actual regional vegetation and shallowest pollen samples from pollen profiles were used for select PPE values for taxa missing from available studies, and their PPEs were adjusted according to the regional pollen-vegetation relationship (**Chapter 4**).

Taphonomy and pollen dispersal

The bias of pollen taphonomy and dispersal is filtered by approximation with a dispersal-deposition function, which is used for a taxon-specific distance weighting of vegetation. According to the Prentice model (Prentice, 1985), pollen is transported only in the two-dimensional space (a plane), so trees as a pollen source have zero height. In this model, wind blowing above forest canopies is the prevailing component carrying pollen under neutral atmospheric conditions. Pollen is deposited in the centre of the circular sedimentation basin, which is free of all target taxa. Sugita's (1993) modification corrects for water mixing in lakes, so pollen from any part of the water surface contributes

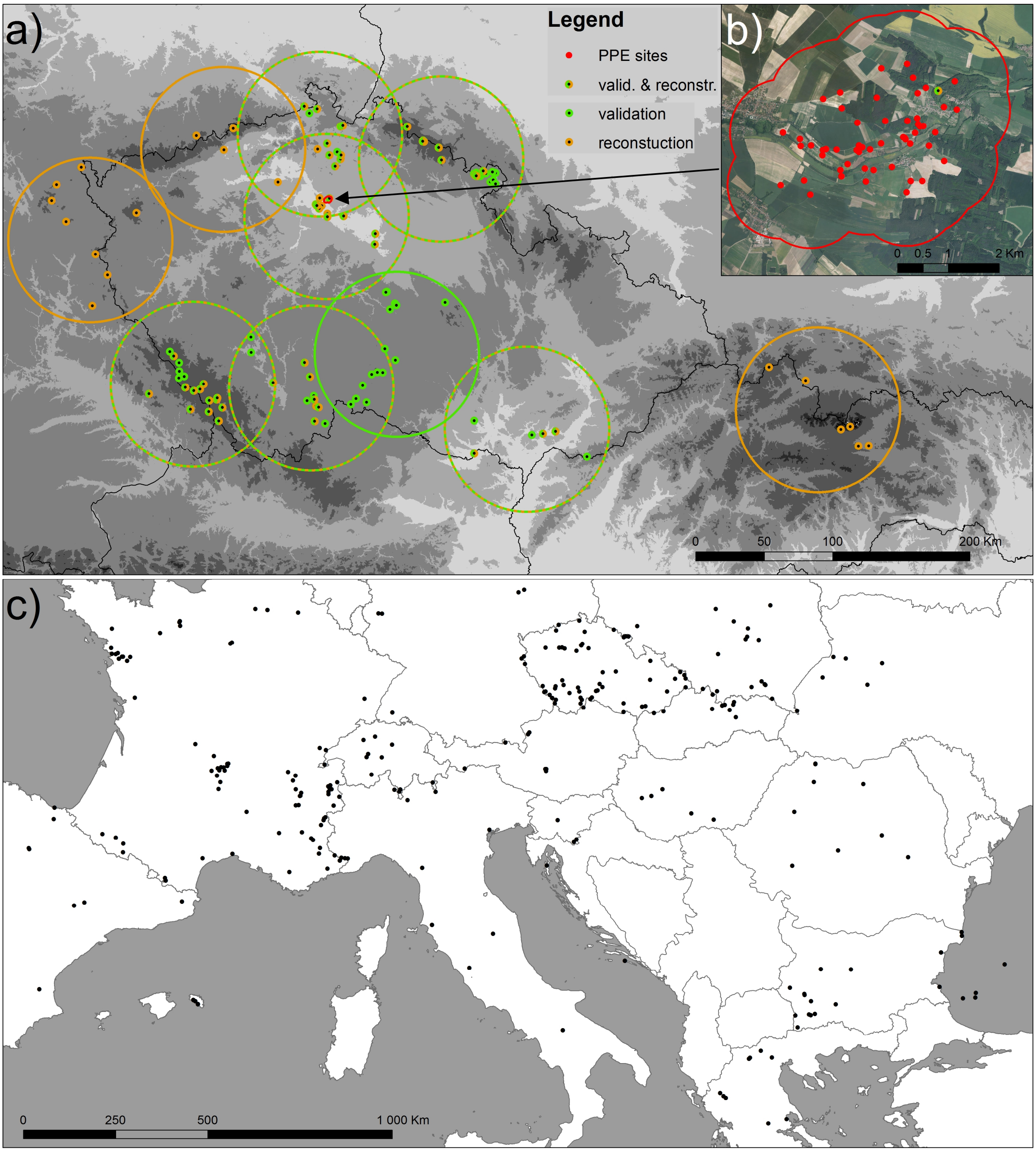

Figure 1: Spatial extent of the present synthesis and additional testing. **a)** sites used for parameter validation (**Chapter 4**) and Holocene reconstruction (**Chapter 5**); **b)** sites used for calculation of PPEs (**Chapter 3**); **c)** sites used for tracking of *Lonicera nigra* in the fossil record (**Chapter 2**).

to the sample. A dispersal-deposition function is applied to the vegetation in the area from the sedimentation basin to the RSAP or maximum extent of regional vegetation (Zmax), which corresponds to the area of the background component.

Let us now set aside the deeper challenges of the Prentice-Sugita model – e.g. concerning changes to the following parameters: atmospheric conditions (Jackson & Lyford, 1999), injection height of source plants (Sjögren *et al.*, 2010), and let us focus only on minor changes in the setting of the following parameters: maximum extent of regional vegetation, radius of the sedimentation basin and wind speed. According to Hellman et al (2008a), the maximum extent of regional vegetation can be approximated by the concept of characteristic radius (Prentice, 1988); however, this parameter itself has a very low effect on REVEALS estimates (**Chapter 4**). The size of the sedimentation basin in the case of moss polsters is set to 0.5 m. Normal or random distribution of the different sizes of lakes entering to the ERV model is necessary (Hjelle & Sugita, 2012). In cases of bogs

Table 1: Different consideration of landscape mosaics (Figure 2) by quantitative approach along the gradient of homogeneity and heterogeneity

	a	b	c
The ERV model considers it	homogeneous	heterogeneous (patchy)	heterogeneous (patchy)
The Prentice-Sugita model considers it	homogeneous (even)	homogeneous (even)	heterogeneous (uneven)
ERV model assumptions fulfilled?	no	yes	yes
Prentice-Sugita model assumptions fulfilled?	yes	yes	no

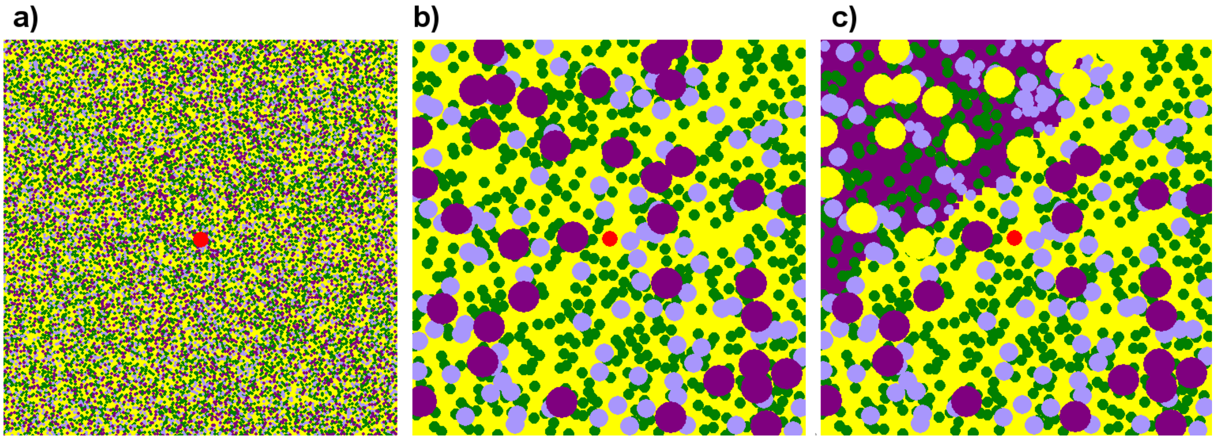

Figure 2: Landscape mosaics illustrating definition of homogeneity and heterogeneity according to the ERV model and the Prentice-Sugita model (Table 1). The red circle in the centre represents the sedimentation basin. Compare its diameter with the size of vegetation patches.

that are overgrown by target taxa, decreasing the radius of the sedimentation basin is an option to correct high pollen signal of local plants (*Alnus, Salix* and Poaceae) (**Chapter** 4). Fall speed of pollen is given by the size of the pollen grain. The theoretical range of wind speed of the canopy component is 2-6 m/s (Prentice, 1988), but 3 m/s is the widely used value. In the set of taxa with Cerealia as the taxon with the heaviest pollen grains (fall speed of pollen - 0.06 m/s), higher wind speed has no effect on the RSAP in the ERV model (Nielsen & Sugita, 2005). However, higher wind speed (4 m/s) can correct unrealistic REVEALS estimates, when taxa with even heavier pollen grains (*Abies* - 0.12 m/s) are included (**Chapter** 4). This is actually an "ad hoc" solution which overcomes the problem that the Prentice-Sugita model underestimates the dispersal of taxa with heavy pollen grains (Theuerkauf et al., 2013).

Vegetation structure and space in pollen analyses

Biases in the vegetation pattern bring ambiguity to the pollen record produced either by large populations far from the sampling site or by a few individuals close to it. Information with "regional" (10^6 km^2) and "local" (1-10 km^2) spatial resolution can be fully filtered only by performing both steps of the LRA: Pollen samples from large lakes are used for the calculation of regional composition, which is subsequently subtracted from small sites by the LOVE model. This theoretical concept is based on an empirical finding known since pioneering works (Andersen, 1970) that large sites better reflect regional spectra than smaller sites. Pollen samples from sites larger than 10 ha securely represent the vegetation of the whole region (Hellman *et al.*, 2008b).

The ERV model requires the opposite – that the size of the basin is smaller than the size of vegetation patches – in order to produce site-to-site variability in pollen loading for parameter estimation using the maximum likelihood method (Sugita, 1994). This prerequisite of vegetation heterogeneity or patchiness is easily met by moss polsters and by lakes provided that they are small. The Prentice-Sugita model assumes either that wind blows from all directions evenly or that vegetation is homogeneous. In this case it means even spatial distribution of vegetation patches, rather than their size (Fig. 2, Tab. 1). This assumption is hardly ever met in any real landscape; however, one can apply a modified dispersal function that includes the wind rose (Bunting & Middleton, 2005).

Vegetation structure strongly influences the RSAP. The RSAP is increased by large patches and rare or unevenly distributed taxa (Bunting *et al.*, 2004; Broström *et al.*, 2005; Hellman *et al.*, 2009b). Hellman et al (2009a) showed that the RSAP in a simulated landscape needs to be sufficiently large in order to attain sufficient vegetation cover of all taxa around all sites. An investigation in the real landscape with uneven distribution of patches indicates that this sufficient coverage means simply the presence of all taxa around all sites (**Chapter 3**).

However, the results depend not only the vegetation mosaic itself, but also on the locations of samples within the vegetation structure and the methods of the vegetation survey. For example, systematic sampling in the centre of patches (Broström *et al.*, 2005; **Chapter 3**) or combinations of different methods of recording the vegetation structure (Bunting *et al.*, 2013) can produce a non-stationary gradient between rings. Steep fluctuations in the ring proportions of some taxa can cause a non-asymptotic pattern in likelihood function scores and pose problems for the estimation of RSAP distances (Abraham unpubl., García-Prieto unpubl.).

Synthetizing palynological data

General aspects of gathering pollen data

Pollen data are usually extracted from individual cores by analysing several taxa at several depths. The original form of this kind of data is an individual spreadsheet for each core, where one dimension of the two-dimensional matrix represents taxa and the second represents depth. The practical objective of any synthesis is to link pollen types and depths from various cores. Depths are joined by chronology, but pollen types must be assigned to a uniform nomenclatoric system. Assigning objects to the correct places, times and biological taxa in palaeoecological databases and the development of tools for using the data are the challenges of the field of palaeoecoinformatics (Brewer *et al.*, 2012). Technically, there are two ways of storing data. With the first type of databases (Pangea), input, storage and export tables correspond to original spreadsheets, so synthetic work must be done outside of the database. Relational database systems (Neotoma, European Pollen Database - EPD and PALYCZ) perform this linking process already when data are imported, so synthesis-ready tables (e.g. a single taxon from all sites at a specific age) are easily accessible by querying the database.

Depth-age models

Creating chronologies entails interpolating age between dated depths. The most basic rule is the law of superposition, which states that deeper sediment layers are older than shallower ones. Historically, the first method of putting together two pollen cores was palynostratigraphy. Since the discovery of radiometric dating methods, especially ^{14}C dating, it has been possible to establish absolute chronologies independently of pollen stratigraphy. However, the use of pollen signal (peaks or troughs of pollen curves) as dating points can further improve absolute chronologies (**Chapter 5**). It is important to detect the correct pollen signal which undoubtedly occurred at both sites (the dated site and the undated site) synchronously. Various factors causing pollen signal, e.g. climatic changes, soil degradation or human impact, occur over different spatial scales (e.g. continental, regional or local), so their suitability as dating points differs accordingly. The use of pollen curves for dating purposes requires a sufficient number of dated control profiles. Pollen curves used for dating become unavailable for the analysis itself because their use would constitute circular reasoning. Uncertainties regarding pollen stratigraphical points vary from 150 to 500 years (Giesecke *et al.*, 2014). Besides pollen and radiometrically datable materials, some sections can contain archaeological objects (in the form of typologically datable artifacts), which can also be used for dating purposes (Juřičková *et al.*, 2014b).

Interpolating the age between two dated levels inevitably requires some assumption concerning sediment accumulation rates. Czech pollen records usually contain few dates per core, so I mainly used the CLAM script for classical depth-age modelling (Blaauw, 2010; R Development Core Team, 2013) presuming the easiest model – linear interpolation between dated levels. In cases of many dates or two slightly different reversed dates from close depths, I applied smooth-spline interpolation. The advantage of the CLAM script is that it can perform ^{14}C calibration and uses this probability distribution to plot the best curve of the depth-age model. Good reporting of ^{14}C dates and depth-age modelling constitutes a part of the reproducibility of palaeoecological results (Grimm *et al.*, 2014). An example is presented in the Supplemetary material of **Chapter 5.**

Nomenclature

Most pollen from Holocene deposits is assigned to pollen types based on the classification of modern pollen grains. So, in contrast to palaeo-palynological findings (e.g. *Normapolles*, Triporopollenites, etc.), names of living plants can cover the variability of pollen types from Holocene deposits. Still, there are certainly species which are already locally extinct. In spite of this advantage, the lack of precise reporting of some Holocene findings creates difficulties in communication between authors and readers, and complicates tracking of plant species by their pollen types and re-using pollen finding in a syntheses.

Systems of palynological nomenclature are hierarchically structured. They can substantially differ depending on the identification key used. The lack of precise reporting at the hierarchical level can be illustrated on the genus *Pinus*, which contains two pollen types corresponding to the subgenera *Haploxylon* and *Diploxylon*. Some authors can distinguish them, but report them as *Pinus* and the *Pinus cembra*-type. Luckily, I was interested only in the *Pinus Diploxylon* type comprising *Pinus sylvestris, P. mugo, P. nigra* and *P. rotundata* (Tab. 2). Pollen of the *Pinus cembra*-type pops up only in Slovakia (except for some very rare and disputable Late-Glacial finds in the Czech Republic), in the Late Glacial or in the last centuries as *Pinus strobus*, so even if the two taxa were not distinguished, the bias is minimal.

Species within pollen types in various identification keys can naturally differ because each nomenclature concerns a different geographical area and thus different modern sample collections ("pollen herbaria"). In cases of some characteristic pollen types, which determination key was used does not really matter. For example, the *Artemisia* pollen type always contains only *Artemisia* species, but sometimes species are assigned to different pollen types depending on the identification key. I was looking for fossil evidence of *Lonicera nigra* (**Chapter 2**). This species belong to the *Lonicera xylosteum*-type; however, depending on the determination key, other *Lonicera* species included in this pollen taxon differ. Luckily, how this taxon is referred to varies depending on the determination key used, so it was possible to at least guess which key was used in which case (Fig. 3).This last example illustrates how important it is to store the original names when gathering pollen data from different authors. Original names in the PALYCZ database are assigned names according Beug (2004) and PALYCZ nomenclature, which was adopted from the ALPine PAlynological DAta-BAse (*ALPADABA*) (**Chapter 1**).

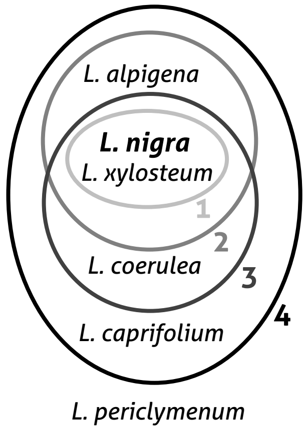

Figure 3: Which pollen type does *Lonicera nigra* belong to? Numbered circles represent pollen types enveloping all species belonging to them. Note the different spelling. **1)** *Lonicera xylosteum* type (Punt *et al.*, 1974), **2)** *Lonicera xylosteum*-type (Moore *et al.*, 1991), **3)** *Lonicera xylosteum*-Typ (Beug, 2004), **4)** Lonicera xylosteum t. (Faegri & Iversen, 1989).

Czech Quaternary Pollen Database (PALYCZ)

The data aggregation leading to the creation of an integrated database for the Czech Republic was started by Petr Kuneš, who downloaded around 40 sites from the EPD for the purposes of his PhD thesis. By the end of 2008 we gathered more than 150 sequences. Now their number exceeds 200. The database includes sites from eastern Slovakia to the Fichtelgebrige Mts beyond the westernmost border of the Czech Republic. Clusters of sites are usually connected with the investigative efforts of individual researchers or their project colleagues. The geographical pattern of sites in the PALYCZ database is given by the fact that many authors from the Czech Republic worked or still work also in Slovakia. Blank areas are due to a general lack of suitable sediments (e.g. the Czech Karst with calcareous deposits that do not preserve

Table 2: Target pollen types of the present synthesis and their corresponding species in the Czech Republic.

Pollen type	Species
Abies	*Abies alba*
Acer	*Acer campestre, A. platanoides, A. pseudoplatanus*
Alnus	*Alnus glutinosa, A. incana*
Artemisia	*Artemisia campestris, A. vulgaris, A. absithium*
Betula	*Betula (excl. Betula nana)*
Carpinus	*Carpinus betulus*
Cerealia	*Triricum, Hordeum, Avena,*
Corylus	*Corylus avellana*
Fagus	*Fagus sylvatica*
Fraxinus	*Fraxinus exclesior*
Chenopodiaceae	*Chenopodium, Atriplex, Amaranthus*
Lonicera xylosteum type	*Lonicera nigra, L. xylosteum*
Picea	*Picea abies, P. pungens*
Pinus	*Pinus sylvestris, P. mugo, P. nigra*
Plantago lanceolata type	*Plantago lanceolata*
Poaceae	Poaceae *(excl. Cerealia, Secale cereale, Zea mays)*
Quercus	*Quercus*
Salix	*Salix*
Sambucus nigra type	*Sambucus nigra, S. racemosa*
Tilia	*Tilia platyphyllos, T. cordata*
Ulmus	*Ulmus glabra, U. minor, U. leavis*

pollen), slow progress of investigations (e.g. the Frýdlant upland) or authors that decided not to contribute. The database stores data from the 1960s onwards. Sequences from the last three decades are the most valuable because they have strong chronologies, dense sampling and high pollen sums. Naturally, most of the samples fall into the Younger Holocene; however, sample density of the Early and Middle Holocene is also satisfactory.

Previous syntheses

The accumulation and availability of pollen data in the PALYCZ database started to meet the goals of palaeoecoinformatics in the Czech Republic. However, the Czech palylonological community functioned for decades without any database, and not all paleoecological research requires the use of informatics. Single-site datasets generated by individual investigators still continue to address fundamental ecological questions. Many key biogeographic issues can be solved by multiple-site syntheses without aid of a computer, as shown already by pioneer palynologists.

The first syntheses for the area of the Czech Republic originate from the work group of the German University in Prague, organized by Karl Rudolph and Franz Firbas. Their results are based on the classical interpretative method, i.e. comparison of pollen curves of tree taxa from several sites. They distinguished pollen curve maxima for each taxon and according to these maxima delimited phases of forest succession during the Holocene. The basic outline of their results is still valid, and the nomenclature of their succession phases is still in use. From the first synthetic work, one example can be cited: the idea of a synchronous increase of several pollen types (*Alnus*, *Corylus*) throughout Europe, rather than gradual migration from southern refugia (Rudolph, 1931), recently re-discovered using new data and radiocarbon dating (Giesecke *et al.*, 2011). The complete synthesis of the data accumulated by the whole pioneer generation is the cornerstone for knowledge about the vegetation history of Central Europe (Firbas, 1949).

Subsequent investigations have had the great advantage that suitable peat bogs were already localized by previous researchers. Many sites were re-cored and re-analysed with improved methodology (see **Chapter 1**). The question is, however, which of the many available studies to regard as "syntheses". This depends not only only on the spatial scale and the number of sites, but also the level of synthetic work. Some papers consist of separate diagrams whose synthesis and comparison with other proxies is hidden in the discussion whereas others contain join plots or some statistical analysis of the whole dataset and present readers with clearly articulated synthetic ideas. Both examples represent the extremes of a gradient, which to a certain degree correlates with the spatial scale and the decade of publication.

I divided all previous syntheses into three groups. The first group comprises all regional to national-scale syntheses touching the Czech Republic. Regional syntheses usually resulted from several sequences analysed for some thesis from a particular region. To separate case studies comprising several cores and small-scale syntheses, I picked out all publications containing five or more sequences from some region. National-scale syntheses mostly re-use already published data. The second group contains large-scale syntheses of sub-continental extent inferring migration routes and LGM refugia of trees from palynological and phylogeographic evidence. The third group encompasses syntheses using the REVEALS model.

Syntheses from the regional to the national scale

In the 1960s and 1970s Eliška Rybníčková and Kamil Rybníček together with their students formed a palaeoecological group at the Institute of Botany in Brno. The Bohemian-Moravian Highlands became the target for one of the most complete small-scale syntheses, which tells the story separately for all periods and for all pollen taxa (Rybníčková, 1974). Studies in those decades were led in the spirit of geobotanical mapping, so they provide many examples for comparisons with vegetation maps (Mikyška, 1968). However, palynological reconstructions do not always agree with the geobotanical idea of "natural vegetation". Evidence of fir, spruce and beech was found instead of indications of acidophilus oak woods in the Otava foothils (Rybníčková, 1973), and similar overrepresentation of oak and hornbeam as opposed to fir and spruce was reported by Peichlová (1979), who made an analogous comparison for the Broumovsko region. Save for one exception (site Vernéřovice), none of the sequences from those works could be used in the present thesis for the Holocene development due to the lack of any absolute dating (radiocarbon in this case). Moreover, some of the sequences were too short and comprised only a few samples (Broumovsko region, Otava foothils), or pollen events were not reliably synchronous with those in dated cores (Bohemian-Moravian Highland).

Luckily, this did not occur in the neighbouring area of southern Bohemia (Jankovská, 1980), where most pollen curves were so similar to each other that I could transfer dating points from other, absolutely dated sites (**Chapter 5**). Similarly as in Czechoslovakia, German doctoral students focused on specific areas for data collection, and three small scale syntheses appeared in Bavaria close to the Czech border. One thesis from the Bavarian Forest contains, besides usual sections of a classical synthesis, also a discussion of the natural distribution of spruce and the altitudinal zonation of vegetation in the Bavarian Forest (Stalling, 1987). The study from the Fichtelgebirge Mts is relatively brief (Hahne, 1992), but the synthesis from the Oberpfälzer Wald region is focused mainly on human impact and correlations between the pollen record and archaeology (Knipping, 1997). A thesis from the same decade carried out in southern Moravia is similarly oriented towards the impact of human activity (Svobodová, 1991).

Similarly to the theses mentioned above, other investigative projects were also devoted to particular regions. Publications dealing with the Šumava Mts (Svobodová *et al.*, 2002) and the Western Carpatians (Rybníček & Rybníčková, 2008) also include at least five sites and were therefore also regarded as syntheses. The present synthesis is based on most of the data cited in this section and also uses sequences from recently finished projects carried out in northern Bohemia and the Polabí lowland. The variability within the regions is outlined in **Chapter 5**; however, the results would merit a separate paper.

The area of former Czechoslovakia was the focus area for several national syntheses. The most complete one uses nine reference sites to describe vegetation development in six geomorfological units (Rybníčková & Rybníček, 1996). The same authors produced a reconstruction of vegetation types for three phytogeographic provinces in six time windows since the Late Glacial until 2000 BP (Rybníček & Rybníčková, 1994). When considering specific problems rather than the whole vegetation, it is necessary to highlight the existence of a synthesis that has produced results quite similar to mine. Geobotanical mapping by phytoindication methods reconstructed temperate broadleaved forests at middle altitudes (500-700 m a.s.l.); however, a joint analysis of pollen spectra from the Subatlantic period, historic data and toponomastic resources revealed fir and spruce forests at this surprisingly low elevation (Rybníček & Rybníčková, 1978).

Syntheses from the last two decades differ from earlier ones in that they use advanced statistical methods. Multivariate statistics are among the best methods to explore entire palynological datasets (Legendre & Birks, 2012). On the scale of the whole Czech Republic, ordinations were employed to detect human impact in the early Holocene (Kuneš *et al.*, 2008b), to assess the similarity between Last Glacial sequences and surface samples from Siberia (Kuneš *et al.*, 2008a), and to explore differences between Early- and High-Medieval urban deposits (Kozáková *et al.*, 2009), the general pattern of pollen spectra over the last 15 millennia (**Chapter 1**) and variability of pollen spectra in the 2000 BP time-window as a function of environmental factors (Pokorný, 2002). The last publication expands on the subject of earlier studies and compares the palynological interpretation with the geobotanical reconstruction.

Large-scale syntheses of postglacial migration and glacial refugia

Postglacial migrations were traditionally studied based on palynological findings, using the tool of isopollen maps. Three isopollen maps have already been produced for my study area for different sets of tax**a** at the following scales: the Czech Republic (Pokorný *et al.*, 2004), former Czechoslovakia for spruce, beech and fir (Rybníčková & Rybníček, 1988), and Europe (Huntley, 1988). A similar approach is taken by isochrone maps, which connecting sites where taxa appeared in same millennia, e.g. spruce in Central Europe (Latałowa & van der Knaap, 2006). Sometimes these maps show only ages when taxa arrived (Magyari, 2002). Alternatively, migration routes are displayed as raw pollen percentages or their threshold values in several time windows (Brewer *et al.*, 2002; Magri, 2008). Such works affirmatively sketch the directions from which tree taxa migrated, e.g. spruce and hornbeam entered the Czech Republic from the east or south-east whereas beech and fir first arrived at the southwestern border. Refugia of trees during the Last Glacial Maximum are thus shown to be situated further south or east. According to the traditional notion, temperate trees survived in the western part of the Balkan peninsula, in Italian mountains and in Spain (Bennett *et al.*, 1991) whereas boreal taxa could persist in the eastern part of Central Europe.

In the last two decades, this classical idea of southern refugia was confronted by the concept of cryptic refugia (Stewart & Lister, 2001). Temperate trees might have persisted much further north , e.g. the Pannonian Basin (Willis *et al.*, 2000; Willis & van Andel, 2004), in the Western Carpathians or even in the Bohemian Massif (Jankovská & Pokorný, 2008) and in Southern Moravia (Rybníčková & Rybníček, 2014). The development of molecular methods played a key role in the change of thinking. Refugia are characterized by relative ecological stability even under the influence of high-frequency and high-amplitude Quaternary climate oscillations. In areas with stable populations, evolution left greater genetic diversity and unique genotypes. By contrast, newly colonized regions are genetically uniform. Glacial refugia of temperate taxa in Central Europe are supported by phylogeographical studies on beech (Magri *et al.*, 2006), temperate forest grasses *Carex digiatata* (Tyler, 2002a) and *Melica nutans* (Tyler, 2002b), and various temperate animals (see citations in Stewart *et al.*, 2010).

The cold and dry climate of the ice age can be likened to southern Siberia and Mongolia, the closest recent analouge (Tarasov *et al.*, 1999). The little precipitation that there is falls on the windward sides of hills, so trees can grow there. Cryptic refugia must have been situated in mountainous or hilly landscapes, where rugged topography could create microclimatic conditions and shelter the biota from strong wind. The Western Carpathians were proposed for cryptic refugia based on the presence of forest mollusc species in LGM deposits (Juřičková *et al.*, 2014a) and on the phytogeography of species closely associated with the understorey of beech forests (Willner *et al.*, 2009). *Lonicera nigra* and *Rosa pendulina* are temperate shrubs distributed in the mountains of Central Europe. In both cases, molecular methods showed significant differences between populations from the Alps and the Carpatians (Fér *et al.*, 2007; **Chapter 2**).

Phylogeography reveals spatial patterns whereas palaeocological findings can date biogeographical events. This mutual complementarity made these two disciplines a powerful tandem tool for studying postglacial plant migrations. In the last year, however, all multidisciplinary evidnce (pollen, macroremains, phylogeography) of cryptic refugia in Central Europe was revisited and criticized (Tzedakis *et al.*, 2013). Authors of this review warned that the chronology of all key pollen sites in the Czech Republic and Slovakia (Podbaba, Jablůnka, Bulhary) does not cover the LGM. Dating at the Šafárka site ranges from 16,500 ^{14}C yr BP to infinite ages, but unluckily most of them are without stratigraphic context. Similarly, direct dating of charcoal and wood pieces determined in the context of Upper Palaeolithic sites in Central and Eastern Europe rarely fall into the interval of the LGM. Thus the 'cryptic fever' was cooled down again because direct and unambiguous palaeobotanical proof is still lacking.

Late-Glacial findings of temperate trees and shrubs in Central Europe are probably evidence of their rapid spread during warm oscilations, which in case of *Lonicera nigra* is dependent on endozoochoric seed dispersal by birds (**Chapter 2**).

Syntheses using the Landscape Reconstruction Algorithm

The most similar approach to my quantitative reconstruction was taken by members of the POLLANDCAL network as part of pilot testing in Switzerland: PPE calculation (Soepboer *et al.*, 2007), their evaluation (Soepboer *et al.*, 2008) and REVEALS reconstruction (Soepboer *et al.*, 2010). Since the development of the REVEALS algorithm, the number of studies using it to reconstruct past vegetation has nearly reached a dozen. Most of them emerged in the frame of the subsequent network LANDCLIM, whose main goal was to obtain vegetation estimates as a validation proxy for climate models. Unluckily, cooperation with climate modellers caused the loss of vegetation information in most LANDCLIM reconstructions (Gaillard *et al.*, 2010; Trondman *et al.*, 2014), because REVEALS estimates were merged into Plant Functional Types (Prentice *et al.*, 1992). Many of them deal with methodological issues: comparison of REVEALS estimates from multiple small sites or a few large sites (Sugita *et al.*, 2010; Fyfe *et al.*, 2013), pointing out the advantage over pollen proportions (Hultberg *et al.*, 2014; Marquer *et al.*, 2014) or comparison of LRA estimates with historical maps (Overballe-Petersen *et al.*, 2012; Poska *et al.*, 2014). More complex ecological questions were addressed in three studies: a statistical assessment of the importance of the climate and human impact on forest composition in Estonia (Reitalu *et al.*, 2013), the role of soil phosphorus in the interglacial cycle (Kuneš *et al.*, 2011) and a comparison of floristic richness and land-use evenness (Fredh *et al.*, 2013). The REVEALS algorithm was also employed to compare the fossil record with the map of potential natural vegetation. This aim follows the traditional effort of many previous studies (see section 'Syntheses from the regional to the national scale') but at the same time offers a great opportunity to produce a reconstruction of Holocene vegetation without biases in the relationship between vegetation and the pollen record. Use of quantitaive approach facilitates the identification of further methodological barriers in combining palynology with phytosociology (**Chapter 5**).

Summary - research questions

Chapter 1: Czech Quaternary Palynological Database (PALYCZ): review and basic statistics of the data.
Short title: PALYCZ database
Aims: data gathering, database creation
Questions: What is the general pattern and variability of all PALYCZ pollen spectra over the last 15 millennia?

Chapter 2: Phylogeography of *Lonicera nigra* in Central Europe inferred from molecular and pollen evidence.
Short title: *Lonicera nigra*
Aims: finding of palynological evidence for the survival of *Lonicera nigra* from available pollen databases and literature
Questions: Where are glacial refugia of *Lonicera nigra* situated?

Chapter 3: Relative pollen productivity estimates in the modern agricultural landscape of Central Bohemia (Czech Republic).
Short title: pollen productivity estimates
Aims: analysis of the relationship between surface pollen assemblages and surrounding vegetation at the local scale
Questions: What are the relative pollen productivity estimates?
How can the vegetation mosaic influence the relevant source area of pollen?
Does our our non-random sampling matter?

Chapter 4: Present-day vegetation helps quantifying past land cover in selected regions of the Czech Republic.
Short title: parameter validation for regional reconstruction
Aims: analysis of the relationship between surface pollen assemblages and surrounding vegetation at the regional scale, validation and adjustment of all reconstruction parameters
Questions: Which studies provide the most suitable PPEs for REVEALS reconstructions in the Czech Republic?
Besides PPEs, what are the best settings of the REVEALS model?
What is the general importance of additional parameters in this model?

Chapter 5: A pollen-based quantitative land-cover reconstruction in stages of the Holocene explains the naturalness of today's vegetation?
Short title: reconstructed Holocene vegetation
Aims: to obtain regional vegetation estimates and compare them with potential natural vegetation (PNV)
Questions: How do regional vegetation estimates change during the Holocene?
Which period is the closest to the PNV concept?
Which taxa show major differences in a comparison between PVN and reconstructed vegetation?

Chapter 1: PALYCZ database

Kuneš, P., **Abraham, V.**, Kovářík, O., Kopecký, M. & PALYCZ contributors (2009). Czech Quaternary Palynological Database (PALYCZ): review and basic statistics of the data. *Preslia* 81(3), 209–238.

Czech Quaternary Palynological Database – PALYCZ: review and basic statistics of the data

Česká kvartérní pylová databáze – PALYCZ: přehled a základní statistika

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Kuneš P., Abraham V., Kovářík O., Kopecký M. & PALYCZ contributors (2009): Czech Quaternary Palynological Database – PALYCZ: review and basic statistics of the data. – Preslia 81: 209–238.

This paper reviews the data on quaternary palynological sequences collected in the Czech Republic, attempts to store them in the Czech Quaternary Palynological Database (PALYCZ) and outlines a possible use for regional syntheses. Work on pollen stratigraphies done over the last hundred years has yielded a very large amount of data for this region. These data can be used globally for various types of environmental reconstructions and are of local importance, especially when combined with local databases. For data to be included in PALYCZ it has to meet certain criteria, the determination of the pollen of herbaceous plants must be well resolved and radiocarbon dated. As of 31 December 2008, we had reviewed 177 pollen profiles. Data from 152 sequences are already stored in PostgreSQL® in relational tables, which allow a broad range of queries to be addressed using the html protocol. The data collected since 1959 by 15 authors contain raw pollen counts together with ^{14}C dates and various metadata on locality. All the pollen samples were ordered using non-metric multidimensional scaling. Display of the ordination diagram incorporating the appropriate millennial time slices revealed a common pattern in all data. The quality of data is also discussed in the context of the history of the research and methods used. Database access can be found at http://botany.natur.cuni.cz/palycz.

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Keywords: data archive, Czech Republic, Holocene, multivariate analysis, pollen analysis, Pleistocene

Introduction

Research on pollen stratigraphies had quite a long tradition in the former Czechoslovakia. The adoption of a more rigorous determination of time and taxonomy in pollen analysis resulted in the data being frequently used for reconstructing changes in the postglacial environment. Recently, more scientists addressing specific questions have requested comparisons of pollen analytical data from several stratigraphies (Pokorný 2002b, Pokorný 2004, Kuneš et al. 2008).

At a continental scale, information on past vegetation has been used to answer questions about past climate change (Davis et al. 2003), the spread and distribution of woody species (e.g., Magri 2008) and potential future conservation of the environment (Anderson et al. 2006). Many studies could benefit from the European Pollen Database (EPD), where around 40 datapoints from the Czech Republic are already archived. These datapoints originated mainly from pollen sequences published in the 1970s and 1980s and some of them are core localities with well-established chronologies (e.g., Jankovská 1987, Rybníčková & Rybníček 1988a). However, during the last 15 years, Czech palynologists have analyzed and dated many new pollen sequences of high importance. Some of these sequences were published in international journals and therefore are well-known and readily available to authors (Pokorný 2002a, Svobodová et al. 2002, Pokorný et al. 2006, Rybníčková & Rybníček 2006). Others are, unfortunately, published in local journals and sometimes in local languages (Jankovská 1998, Svobodová 2004); others remain unpublished (Appendix 1).

Although global questions require integrated datasets, the existence of local and regional databases has advantages: database managers can benefit from their familiarity with the area of the Czech Republic; they know most of the researchers personally, the historical background and taxonomic concepts utilized by individual researchers. This automatically results in a high-level of accuracy of the data, which can be immediately checked, and database managers can easily track current research and encourage authors to submit their data, with communication occuring at a personal level.

Electronic databases enhance knowledge by providing large collections of information, which can be used in wider syntheses of data. In the region of Central Europe, there are several examples, ALPADABA (Bern), Polish Pollen Database (Ralska-Jasiewiczowa et al. 2004) and the Czech National Phytosociological Database (Chytrý & Rafajová 2003).

This encouraged us to compile a computer-based database of pollen stratigraphical data, which will provide: (i) an archive of raw data (pollen counts) and metadata; (ii) statistics for regional syntheses; (iii) support for the EPD; and (iv) a possible link with other local databases (archaeological database, modern pollen database, archaeobotanical database of plant macrofossils, phytosociological database), all of which would be a great contribution to future research (Fig. 1).

The aim of this paper is to review data from the Czech Quaternary Palynological Database (PALYCZ), which consists of pollen sequences analysed during the last 50 years in the Czech Republic, and indicate the basic statistical outputs and possibilities for further analyses. In addition, data analysed by Czech and Polish palynologists in Slovakia and a few sites near the border in Germany are also included into PALYCZ. Many researchers will benefit from this data in the future.

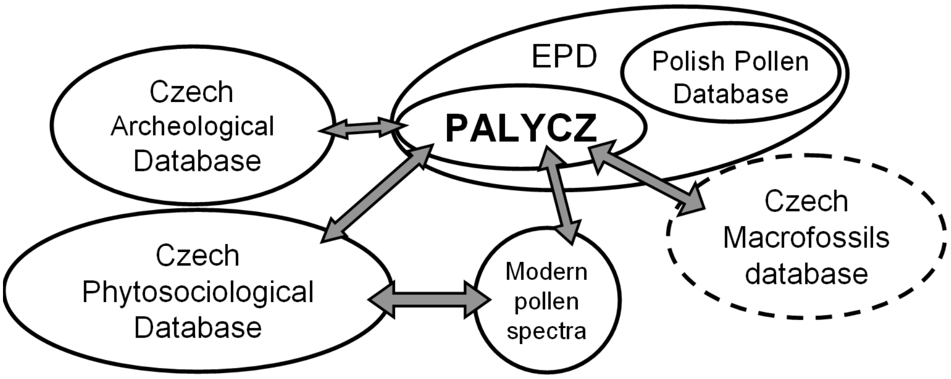

Fig. 1. – Schematic diagram of possible interactions between PALYCZ and other databases or datasets. Dashed indicates in progress.

PALYCZ from a historical perspective

Collecting data from palynological sequences had a long tradition in the former Czechoslovakia. Although the first investigation analysing an inventory of peat-bogs and a few macrofossils was published by František Ladislav Sitenský (1885, 1886, 1891), the real beginning of quaternary palynology is connected with Karl Rudolph (born 11. 4. 1881 in Teplice), who worked at the German University in Prague. He was inspired by attending the "IV. Internationale Pflanzengeographische Exkursion" in 1916 in Scandinavia, where he explored northern-European vegetation and met L. von Post, the leading pollen analyst at that time. Investigations first led K. Rudolph to the Třeboň Basin (S Bohemia) and the first publications of data for Široké blato, Příbraz and Mirochov (Rudolph 1917). Franz Firbas, Rudolph's first co-worker, focused on the Ploučnice region (Polzengebiet) in N Bohemia (Firbas 1927; see Fig. 2), where he analysed 25 sites. His students and colleagues continued research in the Jizerské hory Mts (Plail 1927), Cheb Basin (Funeck 1931) and Orlické hory Mts (Müller 1929) so intensively that by 1929 Rudolph could publish a review article summarizing these results (Rudolph 1929). Researchers from Rudolph's school also collected data outside the borders of Czechoslovakia – in the Pannonian Basin (Kinzler 1936), N Tatra Mts (Peterschilka 1927) and other areas (see Firbas 1949, 1952). The palynological workgroup educated many good students. Nevertheless, the outbreak of World War II inhibited further expansion of the group. Some of the students were killed (like Karl Preis; 1941 in Russia), while others were expelled from Czechoslovakia in 1945. Franz Firbas re-established his group at the University in Göttingen. In 1988, Hans Schmeidl, the last student of K. Rudolph, was still lecturing on vegetation history in Munich. After World War II, Hubert Losert (who worked at Komořanské lezero lake and in the Elbe Basin) and Hugo Salaschek (who worked on Moravo-Silesian peat-bogs) did not return to palynology but both became secondary school teachers. However, they analysed and published an outstanding number of profiles, which are still a great inspiration for modern palaeoecology (Fig. 2).

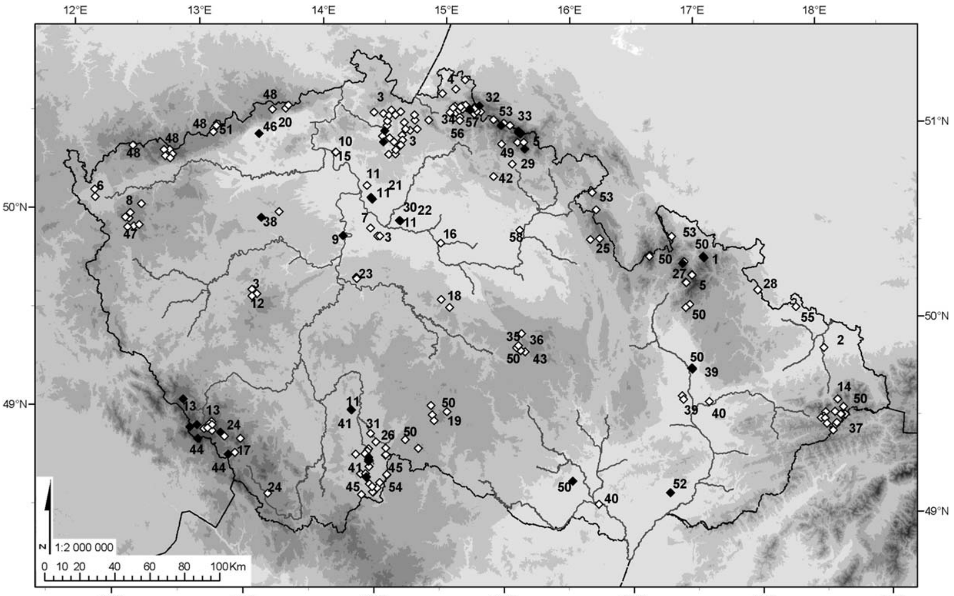

Fig. 2. – Map of palynological profiles not meeting the required standard of data quality. Black points indicate sites for which the results were included in the database only after the sites were revisited. References to numbers: 1 – Fahl 1926; 2 – Fejfar et al. 1955; 3 – Firbas 1927; 4 – Firbas 1929; 5 – Firbas & Losert 1949; 6 – Funeck 1931; 7 – Gough 1992; 8 – Granzner 1936; 9 – M. Kaplan, unpublished; 10 – Kern 1939–1940; 11 – Klečka 1926a; 12 – Klečka 1926b; 13 – Klečka 1928; 14 – Kneblová-Vodičková 1966a; 15 – Kneblová 1956a; 16 – Kozáková & Kaplan 2006; 17 – Kral 1979; 18 – Kriesl 1959; 19 – Križo 1958; 20 – Losert 1940a; 21 – Losert 1940b; 22 – Losert 1940c; 23 – Mráz & Pacltová 1956; 24 – Müller 1927; 25 – Müller 1929; 26 – Němejc & Pacltová 1956; 27 – Opravil 1959; 28 – Opravil 1962; 29 – Pacltová 1957; 30 – Pacltová & Hubená 1994; 31 – Pacltová & Špinar 1958; 32 – Plail 1927; 33 – Puchmajerová 1929; 34 – Puchmajerová 1936; 35 – Puchmajerová 1943; 36 – Puchmajerová 1944; 37 – Puchmajerová 1945; 38 – Puchmajerová 1947a; 39 – Puchmajerová 1947b; 40 – Puchmajerová 1950; 41 – Puchmajerová & Jankovská 1978; 42 – Purkyně & Rudolph 1925; 43 – Purkyně & Rudolph 1927, 44 – K. Rudolph, unpublished; 45 – Rudolph 1917; 46 – Rudolph 1926; 47 – Rudolph 1931; 48 – Rudolph & Firbas 1924; 49 – Rudolph & Firbas 1927; 50 – Salaschek 1936; 51 – Schmeidl 1940; 52 – Sládková-Hynková 1974; 53 – Stark & Overbeck 1929; 54 – Štěpánová 1930; 55 – Vodičková 1981; 56 – Wünsch 1935; 57 – Wünsch 1939; 58 – Žebera 1957.

To this generation of German palynologists we can also add a few scientists that worked at the Czech Agricultural University (Klečka 1926a, b) and the Czech part of Charles University (Puchmajerová 1929, Štěpánová 1930). The last-mentioned author was active until 1950. Pacltová (1957), Kriesl (1959) and Križo (1958) studied pollen analyses relevant to forestry, while Kneblová (1956) focused on geological questions. Opravil (1959) began with palynological studies in Keprník-Jeseníky, but later switched to archaeobotanical macrofossil analyses.

A comprehensive overview of all the data from this early period of research in the Czech Republic is illustrated in Fig. 2. Even though much of the primary data from this period are available in publications they are not included in the PALYCZ for reasons described below.

The modern palynological approach, which uses the determination of herb palynomorphs and ^{14}C dating, was founded at the Institute of Botany of the Academy of Sciences in Brno by E. Rybníčková. Since the 1960s, several palynologists have gone through this institute (M. Peichlová, A. Konětopský, H. Sládková-Hynková, H. Hüttemann and many others), including V. Jankovská (still active there) and H. Svobodová-Svitavská, who entered in the 1980s and subsequently moved to the Institute of Botany at Průhonice. Associated were quaternary palynologists among the geologists in Prague, namely V. Kneblová-Vodičková and E. Břízová, who is currently working at the Czech Geological Survey in Prague. During the 1970s and early 1980s the group established an internationally recognized palynological school in Central Europe, which is documented by a number of foreign exchanges and cooperative studies. For Slovakia E. Krippel published a comprehensive study of postglacial development of vegetation in that area (Krippel 1986). A summary of the major interactions and developments during the past century is shown in Fig. 3.

The first attempts to establish a Holocene pollen database for former Czechoslovakia were made by E. Rybníčková and K. Rybníček based on isopollen maps (Rybníčková & Rybníček 1988b, Rybníček & Rybníčková 1994) and profited from the wide synthesis published by Rybníčková (1985). Then, an advanced pollen database was created by Pokorný (2002b, 2004); however, much of the data were extracted directly from pollen diagrams by recalculating scanned pollen curves. Therefore, we decided to collect all the pollen data for the Czech Republic and store them in a unified database.

Data collection, database structure and nomenclature in PALYCZ

PALYCZ contains data from quaternary pollen sequences from the Czech Republic that were mainly analysed after the late 1950s. However, data are not included if: (i) the author is deceased and the data are lost, (ii) for some reason the data do not match pre-defined criteria (see the section Assessment of data quality) or (iii) they are is still undetermined for technical or other reasons proposed by the author. Additionally, we included into PALYCZ data from Slovakia collected by Czech and Polish palynologists and few sequences from bordering areas in Germany. All the pollen sequences were obtained directly from the authors or from original publications and where possible the raw pollen counts were stored with metadata from the locality. Metadata for each profile consists of author, a description of the locality (including geographic coordinates), type of sediment, radiocarbon dates, etc. A complete list of pollen profiles included in the database (as of 31. 12. 2008) is available in Appendix 1 and their geographical distribution is shown in Fig. 4.

The PostgreSQL® database software was used to store the data. This is an open source application, which offers easy implementation into html protocol. The structure of the database follows the EPD structure. Data are stored in relational tables to allow for a very broad range of queries, which may provide answers to very specific scientific questions. PALYCZ maintains original taxa names used by each pollen analyst. These names are then linked to two alternative nomenclatures: PALYCZ taxa, which is based on ALPADABA and includes details of the taxa designated by the original authors, and Beug taxa (Beug 2004), which merge some groups.

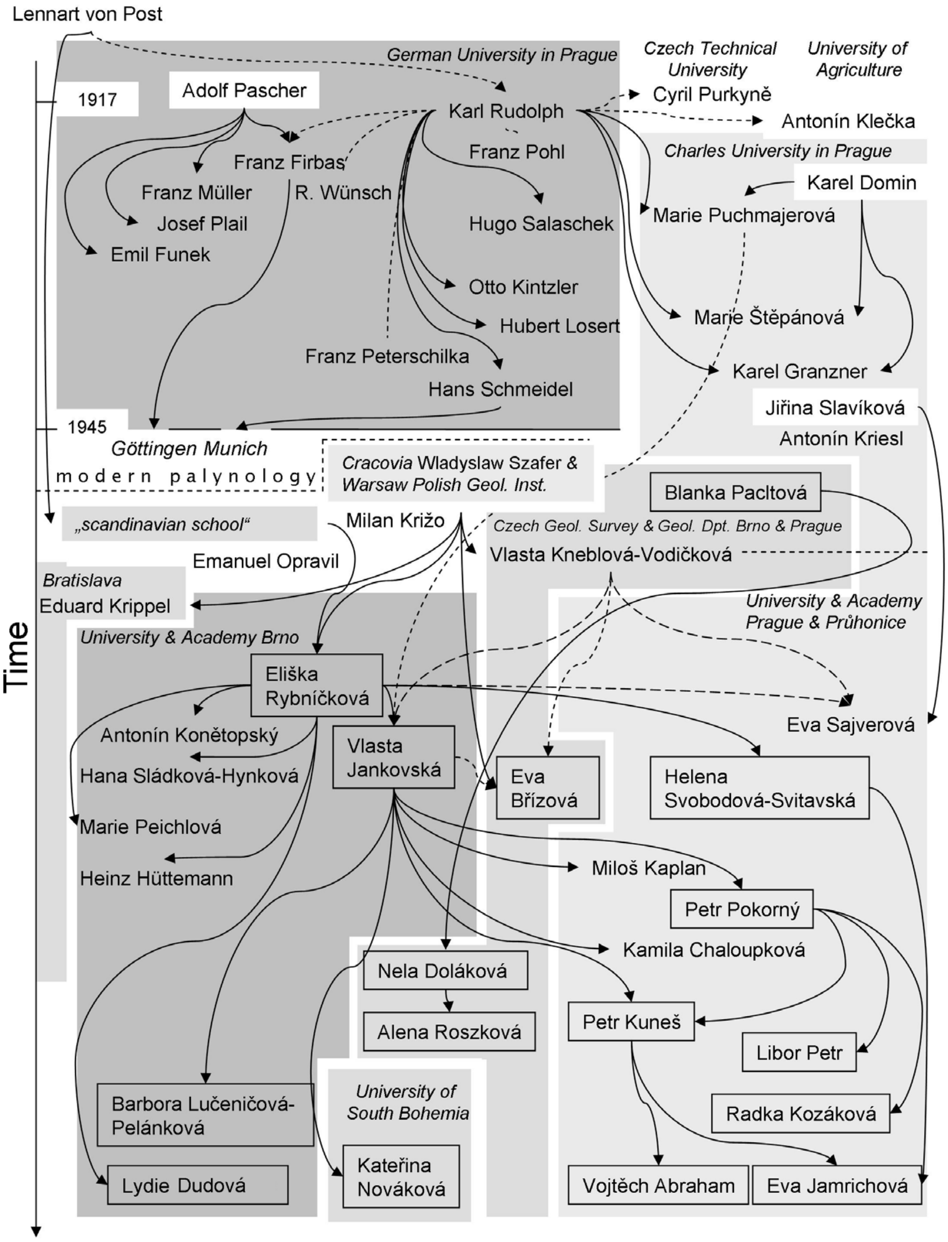

Fig. 3. – A summary of the interactions and developments in Czech quaternary pollen analysis (inspired by Birks 2005): full arrow: teacher (official)–student; dotted arrow: flow of inspiration or teacher (non-official)–student; italics – names of institutions; names in rectangle: living active palynologist, A. Pascher, K. Domin, J. Slavíková – official teachers of some palynologists.

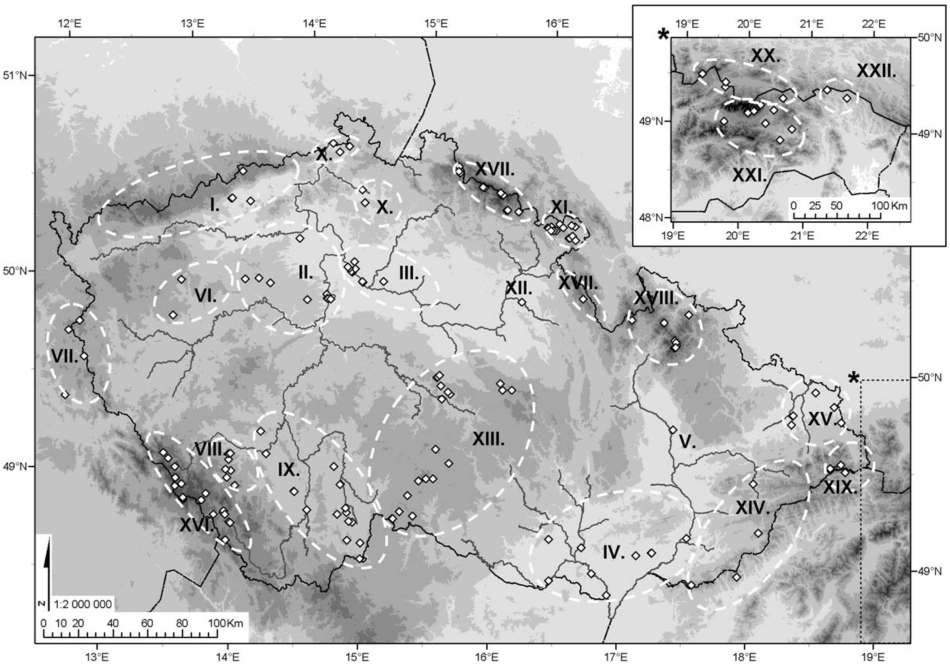

Fig. 4. – Location of all 120 sites projected on a hypsometric map of the Czech Republic and relevant neighbouring areas. For a complete list of localities refer to Appendix 1. Roman numerals refer to the main geomorphological regions in Appendix 1.

We developed the PALYCZ 1.0 utility for importing spreadsheets of pollen counts into the database structure and for matching original taxa names with PALYCZ taxa. An updated version of the database is accessible at http://botany.natur.cuni.cz/palycz.

PALYCZ is also designed for routine use by the palynological community. It allows for the submission of new profiles along with their metadata, which remain in the category "unfinished". Data are stored in the database under three different categories: open (can be publicly used), restricted (finished but not published) and ongoing (unfinished).

Chronologies

PALYCZ contains 292 ^{14}C and 6 ^{210}Pb dates for 76 profiles. In all, there are 27 entities with one or two dates only. When constructing depth-age models, calibrated BC/AD radiocarbon dates were mainly interpolated linearly between the midpoints using a 2σ range of error. For the construction of depth-age models, we used the application written by Maarten Blaauw (in prep.) for the R program (R Development Core Team 2008).

To demonstrate possibilities and weaknesses of depth-age models we provide four examples (Fig. 5). Poor chronological information on pollen sequence is quite a common problem with the data in PALYCZ, which results in it being only possible to predict (estimate) one or two dates using the depth age model (as in Fig. 5d).

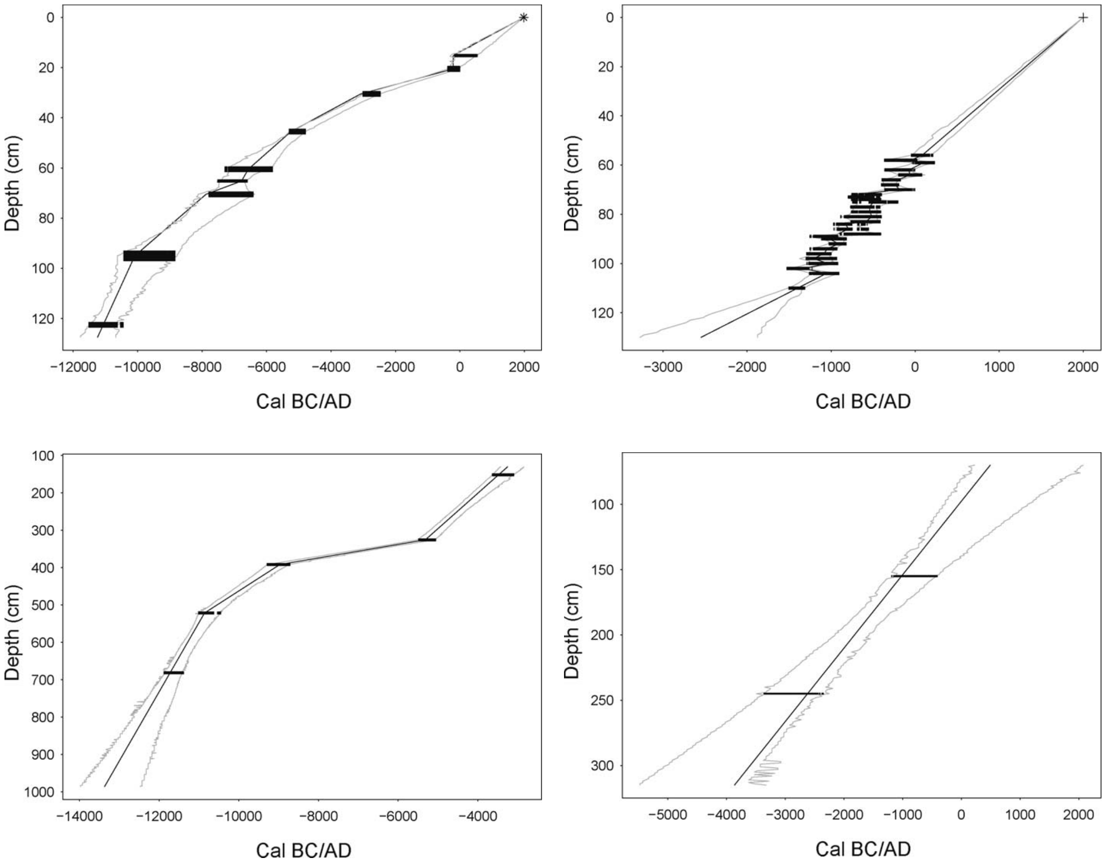

Fig. 5. – Depth-age models of four entities showing a good model that can be extrapolated (a), the best chronology but for a particular period only (b), the problem of making a long extrapolation into the late glacial (c), model based on two datapoints with linear interpolation and a large uncertainty interval (d).

Basic statistics of data

In total, 609,896 items (= count for profile, depth and taxa) from 5901 samples, 152 entities and 120 sites reported by 19 authors are currently included in PALYCZ. All items can be divided among: herbaceous pollen (51%), tree-shrub pollen (26%), aquatics (7%), spores of vascular plants and bryophytes (7%), non-pollen objects (fungal spores, animals, tertiary spores, etc.) 5% and algae (3%). Microscopic particles of charcoal were counted in 14 profiles.

A complete list of all the localities studied is presented in Appendix 1. We also recorded repeated research at localities and the 16 most revisited are presented in the following list (number in brackets indicates number of studies undertaken at each locality including of different profiles by the same author): Komořanské jezero (5), Pančavská louka (5), Hrabanovská černava (4), Malá Jizerská louka (4), Úpské rašeliniště (4), Barbora (3), Borkovická blata (3), Černá hora (3), Černovír (3), Červené blato (3), Keprník (3), Mělnický úval (3), Rejvíz (3), Švarcenberk (3), Velká Jizerská louka (3) and Vracov (3).

Assessment of data quality

If we disregard available metadata on location, dating, stratigraphy etc., the quality of any given sample is influenced by three main factors: (i) the level to which all objects were determined (palynomorphs, sporomorphs, non-pollen objects), (ii) pollen sum and (iii) pollen influx.

(i) The most important factors influencing quality of data are when the pollen analysis was done and its author. The criteria we used were that the profile must contain well identified herbaceous taxa and recorded at a time when radiocarbon dates were generally accepted as reliable. For this reason, we did not include the data of most early German authors (for review see Appendix 1) or from studies prior to 1959 (first analysed profile of Brušperk is in PALYCZ; see the section Data collection, database structure and nomenclature in PALYCZ). Authors influence the quality of taxonomic determination, especially of herbaceous taxa. Some authors only determine the families in particular cases, while others name species if possible. That is why there are several taxonomical levels in PALYCZ, e.g. *Pinus* at a high level contains two pollen types, *Pinus sylvestris* and *Pinus cembra*. In this case, it is possible to avoid several errors that might arise from detailed queries. The data source may also cause errors, especially when data are stored in an electronic form. We first collected sequences stored in the EPD, but counts and even metadata had to be corrected based on the original spreadsheets. For the types of errors encountered see Fyfe et al. (2009).

(ii) Pollen sum mainly depends on the preservation of the sediment from which the sample was taken, but also on the purpose of the study. In PALYCZ, 3% of the samples have a sum lower than 200 pollen grains, 21% between 200 and 400, 60% between 400 and 1000 and 16% more than 1000 pollen grains.

(iii) Adding and counting exotic markers in order to determine pollen influx was not widely used by Czech palynologists. An indicator (*Lycopodium* tablets) was used in eight profiles, totalling 398 samples, which is lower than 1% of the whole database. Only 17% of the samples for which pollen influx was determined lie between the recommended rates of 1:5 and 2:5 (Moore et al. 1991), while 25% of the samples have more indicators and 58% more fossil pollen.

Analysis of main pattern in data using multivariate methods

Multivariate statistical analysis was used to determine the main patterns in the data. We extracted all pollen samples from PALYCZ with percentages of pollen taxa related to total pollen sum, which was the sum of arboreal and non-arboreal pollen. The pollen nomenclature was standardized to conform to Beug (2004) and taxa were not included in the database if based on fewer than 30 pollen grains.

The samples were analysed by non-metric multidimensional scaling (NMDS; Kruskal 1964), the most robust and effective technique for the ordination of community data (Minchin 1987). NMDS orders samples in a specified number of dimensions, such that the distances among all pairs of quadrats in the ordination are, as far as possible, in rank-order agreement with compositional dissimilarities among the samples. We used two dimensions and the Jaccard quantitative index as measures of compositional dissimilarity. In order to reduce the weight of the dominant species the percentages of pollen taxa were

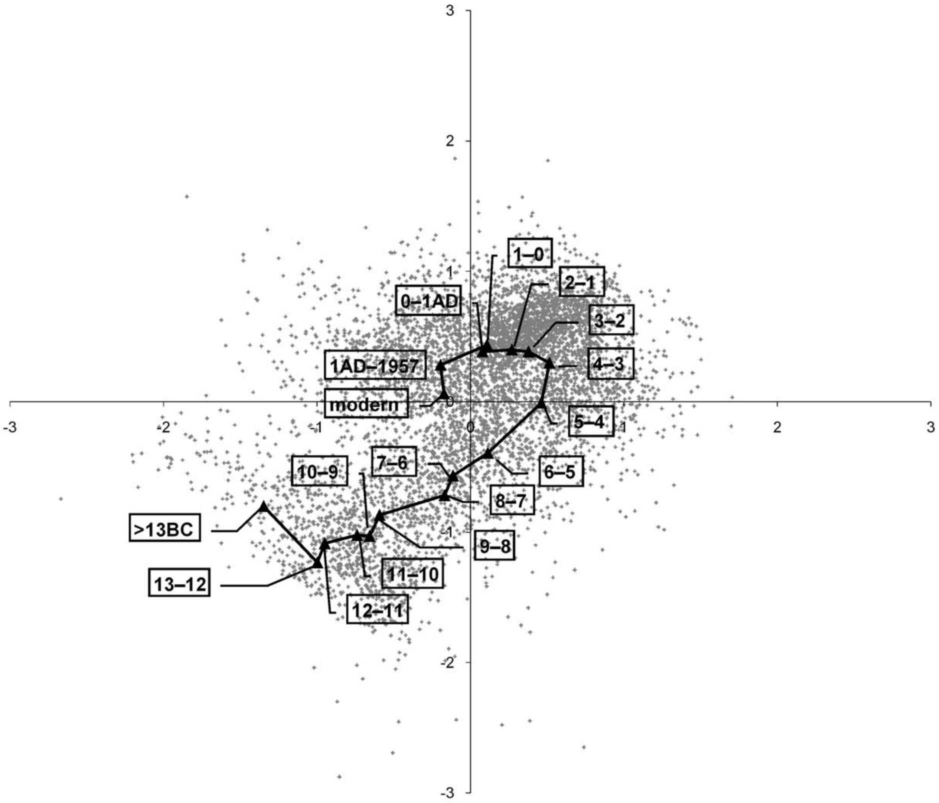

Fig. 6. – NMDS ordination scatterplot of samples. Grey dots indicate pollen samples, black triangles indicate averages of the scores for each stratigraphically connected time slice. Time is indicated in thousands of years BC or AD.

square-root transformed before computation of the Jaccard index. NMDS ordination was performed in PC-ORD program (McCune & Mefford 1999) with 50 random starts and a maximum of 100 iterations of each run.

Further, millennial time slices were determined according to calibrated radiocarbon years for localities for which there were depth-age models (see above). An average time was calculated for the ordination scores of all samples in each time slice (1000 years) and then displayed in the ordination diagram. A line connects the average points according to their position on the time scale (from the oldest to the youngest).

Results of the NMDS analysis of all pollen samples are shown in the ordination diagram (Fig. 6). The pattern in the data follows vegetation development from late-glacial cold steppes and open forests to Holocene forests dominated by broad-leaved tree species. During the Holocene, the vegetation development follows a typical interglacial pattern (Birks & Birks 2004), namely from forests dominated by pioneer deciduous trees and conifers, through mixed deciduous forests and back to conifers.

Concluding remarks

Over the last hundred years, a large amount of pollen analytical data was collected in the former Czechoslovakia. There was a significant increase in the quality of this data, especially over the last 50 years, as all data from this time attained current standards. Improvement in the methodological and conceptual approach of vegetational historical studies is clearly visible at reinvestigated sites. Scientists realized that they can reuse a unique sediment by improving taxonomic resolution and thus obtain a better chronology or higher resolution for answering specific questions more precisely. Some places were revisited several times, and this can be attributed not only to a desire for improving the quality of the data, but also to the uniqueness of such sites.

Data stored in PALYCZ can be used for testing ecological hypotheses and answering questions concerning species migration, human impact, or nature conservation. However, this ongoing research identified three main problems that should be addressed in future studies: (i) the very poor chronology of sequences, (ii) a lack of influx pollen counts, and (iii) temporal and spatial resolution of both samples and sites. We would like to encourage all quaternary pollenanalysts to join the common network, which is based regionally (PALYCZ) or internationally (EPD), and submit their data to the databases. We plan to develop PALYCZ in the future to include an administrative interface where authors can submit, edit and track their own data. We hope that the missing aspects highlighted in this paper will be finally filled and encourage authors to believe that such an endeavour would be to their advantage.

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We wish to thank all authors who have contributed or want to contribute their data to PALYCZ. Namely we thank Heinz Hüttemann, Kamila Chaloupková, Miloš Kaplan, Vlasta Kneblová-Vodičková, Antonín Konětopský, Marie Peichlová, Maurice Reille, Eva Sajverová and Alessandra Speranza, who are either deceased or inactive or unknown. We would also like to express our thanks to Magda Konzalová and Felix Bittmann for providing us with important texts concerning the history of palynology in Czechoslovakia. We thank Kamil Rybníček and František Krahulec for valuable comments, corrections and suggestions. PALYCZ was funded by the Grant Agency of Charles University, project no. GAUK 29407. Several projects have helped with the data collection: Grant Agency of the Czech Republic GA526/06/0818, Grant Agency of the Academy of Science of the Czech Republic IAAX00020701, IAAX00050801, IAA600050812, Ministry of Education MSM0021620828 and Academy of Sciences AV0Z60050516.

Souhrn

Článek reviduje data z kvartérních palynologických profilů, které vznikly na území České republiky, s cílem shromáždit je v České kvartérní pylové databázi (PALYCZ) a nastínit možnosti jejich využití při regionálních syntézách (databáze obsahuje též profily pořízených českými a polskými palynology na Slovensku a v příhraničních oblastech Německa). Práce na pylových stratigrafiích přinesly za posledních sto let výjimečné množství dat, která je možno využít pro různé typy rekonstrukcí prostředí. Ve spojení s dalšími místními databázemi mají tato data i značný lokální význam. Pro zahrnutí dat do databáze PALYCZ byla stanovena kritéria, že určování pylu musí zahrnovat detailnější rozlišení bylin a radiokarbonová data musí být již obecně dostupná. K 31. prosinci 2008 bylo revidováno 177 pylových profilů. Data ze 152 sekvencí jsou již uložena v relačních tabulkách PostgreSQL®, aby umožnila širokou škálu dotazů pomocí protokolu html. Od roku 1959 byla data analyzována celkem 15 autory; skládají se z originálních pylových počtů, ^{14}C dat and různých metadat o lokalitě. Data jsme analyzovali s použitím ordinace všech pylových vzorků pomocí nemetrického mnohorozměrného škálování (NMDS). Ordinační diagram s odpovídajícími tisíciletými intervaly odráží hlavní strukturu dat. Diskutována je též kvalita dat v kontextu s historií výzkumu a použitými metodami. Databáze je umístěna na adrese http://botany.natur.cuni.cz/palycz.

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Appendix 1. – Sites included in the Czech Quaternary Palynological Database. Revisited sites are in bold script, alternative names for the site are in brackets. E – number of entities at the site included in the database; * import of data is in progress due to technical reasons. D – number of datings (^{14}C and ^{210}Pb) per site, E10 – number of all entities within 10 km around the site (E included). Sites are grouped according to main geomorphological units (see Fig. 4). Arrows separate independent studies of revisited sites. Note that for additional sites in Germany (DEU) and Slovakia (SVK) no previous studies have been included (marked as –)

Site name	Country	E	D	Oldest ^{14}C date BP per site	Contributors	Citation to all cores from the site	Coordinates (WGS 1984)		E10	Citations to all other sites within 10 km around the site
							X	Y		
I. Ore Mountains and Podkrušnohorská Basin										
Fláje – Kiefern	CZE	1	3	9191	Jankovská	Jankovská et al. 2007	13.579870	50.682940	2	Rudolph & Firbas 1924
Komořanské jezero (Kommerner See)	CZE	5	4	7770	Jankovská	Rudolph 1926 → Losert 1940a → Jankovská 1983; Jankovská 1984 → Jankovská 1988a → Jankovská 2000	13.518350	50.535070	7	Jankovská 1995b
Most	CZE	1*			Jankovská	Jankovská 1995b	13.673780	50.533850	3	Jankovská 1983, Jankovská 1984, Jankovská 1988a, Jankovská 2000, Losert 1940a, Rudolph 1926
II. Central Bohemia										
Břve	CZE	1	3	2344	Pokorný	Pokorný unpubl	14.244920	50.071780	1	
Červená louka (U Olešné na Červené louce)	CZE	1*			Rybníčková	Puchmajerová 1947a → Rybníčková & Rybníček 1999	13.723220	50.131300	3	Rybníčková & Rybníček 1999
Klíčava	CZE	1			Rybníčková	Rybníčková & Rybníček 1999	13.833030	50.146160	5	Pokorný 2005, Puchmajerová 1947a, Rybníčková & Rybníček 1999
Praha-medieval archaeological context	CZE	16*			Jankovská; Kozáková; Pokorný	Kozáková & Pokorný 2007, Kozáková et al. 2009	14.428041	50.090262	3	Jankovská & Pokorný 2008
Praha-Podbaba	CZE	1	2	40418	Pokorný	Jankovská & Pokorný 2008	14.391670	50.112500	18	Kaplan unpubl, Kozáková & Pokorný 2007, Kozáková et al. 2009
Praha-Valdštejnská ulice	CZE	1*			Kozáková	Kozáková & Pokorný 2007	14.407350	50.089176	18	Jankovská & Pokorný 2008, Kaplan unpubl, Kozáková et al. 2009
Pražský hrad	CZE	1*			Kozáková	Kaplan unpubl → Kozáková et al. 2009	14.400448	50.090488	18	Jankovská & Pokorný 2008, Kozáková & Pokorný 2007, Kozáková et al. 2009
Rynholec	CZE	1* 1	4	10271	Břízová; Rybníčková; Pokorný	Rybníčková & Rybníček 1999 → Břízová 1999b → Pokorný 2005	13.929700	50.129280	3	Puchmajerová 1947a, Rybníčková & Rybníček 1999
Zahájí	CZE	1	5	4788	Pokorný	Pokorný 2005	14.115550	50.379220	1	

Site name	Country	E	D	Oldest ^{14}C date BP per site	Contributors	Citation to all cores from the site	Coordinates (WGS 1984)		E10	Citations to all other sites within 10 km around the site
							X	Y		
III. Polabí Lowland										
Hrabanovská černava (Moor bei Lissa-Hrabanow)	CZE	1	4	13630	Petr	Klečka 1926a → Losert 1940c → Pacltová & Hubená 1994 → Petr 2005	14.831580	50.216390	3	
Chrást	CZE	1	6	8630	Břízová	Břízová 1999a	14.544060	50.260300	9	Dreslerová et al. 2004, Dreslerová & Pokorný 2004, Klečka 1926a, Losert 1940b, Petr unpubl, Petr, 2005
Chrást u přejezdu	CZE	1	5	11523	Petr	Petr unpubl	14.593680	50.262040	11	Břízová 1999a, Dreslerová et al. 2004; Dreslerová & Pokorný 2004, Klečka 1926a, Losert 1940b, Petr unpubl, Petr 2005
Kozly	CZE	2			Petr	Petr & Pokorný 2008	14.563480	50.247050	11	Dreslerová et al. 2004, Dreslerová & Pokorný 2004, Gough 1992, Klečka 1926a, Losert 1940c, Petr unpubl, Petr 2005
Mělnický úval (Wschetater Urwiesen, Vsetater Moor)	CZE	1	2	14200	Petr	Klečka 1926a → Losert 1940b → Petr 2005	14.578110	50.299250	10	Dreslerová et al. 2004, Dreslerová & Pokorný 2004, Klečka 1926a, Petr unpubl
Stará Boleslav	CZE	2	4	1920	Břízová	Břízová 1999a	14.667430	50.197930	9	Dreslerová et al. 2004, Firbas 1927, Gough 1992, Petr unpubl
Tišice	CZE	1	2	4241	Pokorný	Dreslerová & Pokorný 2004	14.532510	50.266910	9	Klečka 1926a, Losert 1940b, Petr unpubl, Petr 2005
IV. Southern Moravian Basin										
Bulhary	CZE	1*	1	25675	Rybníčková	Rybníčková & Rybníček 1991	16.749920	48.837510	1	
Dvůr Anšov	CZE	1	4	8300	Svobodová-Svitavská	Svobodová 1992	16.422540	48.777280	1	Peschke 1977
Olbramovice (Wolframitz)	CZE	1	3	3825	Svobodová-Svitavská	Salaschek 1936 → Svobodová 1992	16.386600	48.990670	2	
Pohansko	CZE	2			Svobodová-Svitavská Roszková	Svobodová 1990 → Macháček et al. 2007	16.885850	48.734830	1	
Svatobořice-Mistřín	CZE	1	5	6620	Svobodová-Svitavská	Svobodová 1989	17.081880	48.954320	3	Rybníčková & Rybníček 1972, Sládková-Hynková 1974, Svobodová 1997
Uherské Hradiště	CZE	1*			Svobodová-Svitavská	Svobodová 1990	17.466250	49.070558	1	
Velké Němčice	CZE	1	1	1715	Svobodová-Svitavská	Svobodová 1990	16.650250	48.966930	1	

Site name	Country	E	D	Oldest ^{14}C date BP per site	Contributors	Citation to all cores from the site	Coordinates (WGS 1984)		E10	Citations to all other sites within 10 km around the site
							X	Y		
Vracov	CZE	3	7	11995	Rybníčková Svobodová-Svitavská	Rybníčková & Rybníček 1972 → Sládková-Hynková 1974 → Svobodová 1997	17.202360	48.977880	3	Svobodová 1989
V. Upper Moravian Basin										
Černovír (Olmützer Moor, V Černovírském lese)	CZE	1	1	12060	Jankovská	Salaschek 1936 → Puchmajerová 1947b → Jankovská 2003	17.275280	49.623880	5	Puchmajerová 1947b
VI. Plzeň Upland										
Hůrky u Úněšova	CZE	1	3	4435	Svobodová-Svitavská	Svobodová-Svitavská unpubl	13.192264	49.889102	1	
Vladař	CZE	1	6	2245	Pokorný	Pokorný et al. 2006	13.217560	50.079960	1	
VII. Upper Palatinate Forest										
Brentenlohe	DEU	1	3	8650	Knipping	Knipping 1989	12.462500	49.787220	2	Knipping 1989 –
Kulzer Moos	DEU	2	13	10740	Knipping	Knipping 1989	12.442780	49.394720	1	
Weiherlohe	DEU	1	4	9385	Knipping	Knipping 1989	12.387500	49.729720	2	Knipping 1989 –
Windbruch	DEU	1	5	10150	Knipping	Knipping 1989	12.542780	49.609170	1	
VIII. Bohemian Forest Foothils										
Bohumilice	CZE	1*			Rybníčková	Moravec & Rybníčková 1964, Rybníčková 1973	13.807910	49.098020	4	Moravec & Rybníčková 1964, Rybníčková 1973
Kraselov	CZE	1*			Rybníčková	Rybníčková 1973	13.808100	49.226260	4	Rybníčková 1973
Lštění	CZE	1*			Rybníčková	Moravec & Rybníčková 1964, Rybníčková 1973	13.878670	49.062860	4	Kral 1979, Rybníčková 1973
Mladotice	CZE	1			Rybníčková	Rybníčková 1973	13.795140	49.222750	5	Rybníčková 1973
Nahořany	CZE	1			Rybníčková	Rybníčková 1973	13.829940	49.137320	6	Moravec & Rybníčková 1964, Rybníčková 1973
Němčice	CZE	1			Rybníčková	Rybníčková 1973	13.801440	49.191870	5	Rybníčková 1973
Vacovice	CZE	1			Rybníčková	Rybníčková 1973	13.790160	49.140570	6	Moravec & Rybníčková 1964, Rybníčková 1973
IX. South Bohemian Basins										
Barbora (Revír Sv. Barbory, Svatá Barbora)	CZE	1			Jankovská	Štěpánová 1930 → Puchmajerová & Jankovská 1978 → Jankovská 1980	14.833290	48.955840	18	Jankovská 1980, Jankovská 1987, Nováková et al. 2008, Puchmajerová & Jankovská 1978, Štěpánová 1930
Borkovická blata (Veselská blata, Borkowitzer Moor)	CZE	3	4	11595	Jankovská	Klečka 1926a → Puchmajerová & Jankovská 1978 → Jankovská 1980	14.632700	49.232770	5	

Site name	Country	E	D	Oldest ^{14}C date BP per site	Contributors	Citation to all cores from the site	Coordinates (WGS 1984)		E10	Citations to all other sites within 10 km around the site
							X	Y		
Branná	CZE	1			Jankovská	Jankovská 1980	14.805290	48.959090	18	Jankovská 1980, Jankovská 1987, Puchmajerová & Jankovská 1978, Štěpánová 1930
Červene blato (Borská blata, Červené blato u Šalmanovic)	CZE	3			Jankovská	Štěpánová 1930 → Puchmajerová & Jankovská 1978 → Jankovská 1980	14.810160	48.860780	17	Jankovská 1996, Nováková et al. 2008, Puchmajerová & Jankovská 1978, Rudolph unpubl, Štěpánová 1930
České Budějovice	CZE	1*			Jankovská	Pokorný et al. 2002	14.466530	48.989170	1	
Halámky	CZE	1*			Jankovská	Jankovská 1996	14.916640	48.855820	17	Jankovská 1980, Nováková et al. 2008, Puchmajerová & Jankovská 1978, Rudolph 1917, Štěpánová 1930
Kožlí	CZE	1	3	8212	Pokorný	Pokorný & Kuneš 2009	14.020870	49.360060	1	
Mokré louky – North	CZE	1			Jankovská	Jankovská 1987	14.768910	49.024810	14	Jankovská 1980, Jankovská 1987, Němejc & Pacltová 1956, Puchmajerová & Jankovská 1978, Štěpánová 1930
Mokré louky – South	CZE	1	5	9630	Jankovská	Jankovská 1987	14.778040	49.002210	14	Jankovská 1980, Jankovská 1987, Němejc & Pacltová 1956, Puchmajerová & Jankovská 1978, Štěpánová 1930
Řežabinec	CZE	1	9	9095	Rybníčková	Rybníčková & Rybníček 1985	14.089680	49.250190	1	
Spolí	CZE	1			Jankovská	Jankovská 1980	14.710260	48.987100	13	Jankovská 1980, Jankovská 1987, Puchmajerová & Jankovská 1978, Štěpánová 1930
Švarcenberk	CZE	2	5	11750	Jankovská; Pokorný	Jankovská 1980 → Pokorný 2002a, Pokorný & Jankovská 2000 → Pokorný et al. 2008b	14.704820	49.145620	5	Klečka 1926a, Pacltová & Špinar 1958, Puchmajerová & Jankovská 1978
Velanská cesta	CZE	1 1*	2	8360	Jankovská; Nováková	Jankovská 1970 → Nováková et al. 2008	14.928290	48.774770	10	Jankovská 1996, Puchmajerová & Jankovská 1978, Rudolph unpubl, Štěpánová 1930
Zbudovská blata	CZE	2	4	10341	Rybníčková	Rybníčková et al. 1975, Rybníčková 1982	14.347080	49.076530	2	
X. Bohemian Switzerland and Ploučnice Region										
Česká Lípa (Schiessniger Heide)	CZE	1	2	4100	Kuneš	Firbas 1927 → Kuneš unpubl	14.564570	50.673080	11	Firbas 1927, Jankovská 1992
Jelení louže	CZE	1	5	5650	Pokorný	Pokorný & Kuneš 2005	14.276610	50.892610	3	Abraham 2006, Kuneš et al. 2007
Jestřebské blato (Habsteiner Moor)	CZE	1			Jankovská	Firbas 1927 → Jankovská 1992	14.598580	50.608780	10	Firbas 1927, Kuneš unpubl
Nad Dolským mlýnem	CZE	1	2	6000	Abraham	Abraham 2006, Pokorný et al. 2008a	14.338730	50.852330	3	Kuneš et al. 2007, Pokorný & Kuneš 2005

Site name	Country	E	D	Oldest ^{14}C date BP per site	Contributors	Citation to all cores from the site	Coordinates (WGS 1984)		E10	Citations to all other sites within 10 km around the site
							X	Y		
Pryskyřičný důl	CZE	1	8	2465	Abraham; Pokorný	Abraham & Pokorný 2008	14.413140	50.887570	3	Abraham 2006, Pokorný & Kuneš 2005
XI. Broumov Region										
Anenské údolí	CZE	1	4	7905	Kuneš	Pokorný & Kuneš 2005	16.117450	50.588730	11	Chaloupková 1995, Kuneš & Jankovská 2000, Peichlová 1977
Broumovské stěny	CZE	2			Peichlová	Peichlová 1979	16.282570	50.555750	11	Chaloupková 1995, Peichlová 1979, Stark & Overbeck 1929
Březová	CZE	1			Peichlová	Peichlová 1979	16.227400	50.606390	16	Chaloupková 1995, Kuneš & Jankovská 2000, Peichlová 1979, Pokorný & Kuneš 2005
Heřmánkovice	CZE	1			Peichlová	Peichlová 1979	16.324400	50.617670	9	Peichlová 1979
Hynčice	CZE	1			Peichlová	Peichlová 1979	16.292400	50.622170	10	Peichlová 1979
Kancelářský příkop	CZE	1*			Chaloupková	Chaloupková 1995	16.104038	50.596663	11	Chaloupková 1995, Kuneš & Jankovská 2000, Kuneš et al. 2007, Peichlová 1979, Pokorný & Kuneš 2005
Kraví hora	CZE	1*			Chaloupková	Chaloupková 1995	16.152404	50.584067	13	Chaloupková 1995, Kuneš & Jankovská 2000, Kuneš et al. 2007, Peichlová 1979, Pokorný & Kuneš 2005
Křinice	CZE	1			Peichlová	Peichlová 1979	16.309000	50.569560	10	Peichlová 1979
Martínkovice	CZE	1			Peichlová	Peichlová 1979	16.337790	50.547100	7	Peichlová 1979, Stark & Overbeck 1929
Rokliny	CZE	2*			Chaloupková	Chaloupková 1995	16.111560	50.594203	11	Chaloupková 1995, Kuneš & Jankovská 2000, Kuneš et al. 2007, Peichlová 1979, Pokorný & Kuneš 2005
Teplice nad Metují	CZE	1			Peichlová	Peichlová 1979	16.173620	50.585470	15	Chaloupková 1995, Kuneš & Jankovská 2000, Kuneš et al. 2007, Peichlová 1979, Pokorný & Kuneš 2005
Teplické údolí	CZE	11*	5	7504	Chaloupková; Kuneš	Chaloupková 1995 → Kuneš & Jankovská 2000	16.131530	50.584940	11	Chaloupková 1995, Kuneš & Jankovská 2000, Kuneš et al. 2007, Peichlová 1979, Pokorný & Kuneš 2005
Vernéřovice	CZE	2	9	11790	Peichlová	Peichlová 1979	16.195770	50.621650	16	Chaloupková 1995, Kuneš & Jankovská 2000, Peichlová 1979, Pokorný & Kuneš 2005
Vlčí rokle	CZE	1	4	10563	Jankovská	Kuneš & Jankovská 2000	16.128410	50.604500	11	Chaloupková 1995, Kuneš & Jankovská 2000, Peichlová 1979, Pokorný & Kuneš 2005

Site name	Country	E	D	Oldest ^{14}C date BP per site	Contributors	Citation to all cores from the site	Coordinates (WGS 1984)		E10	Citations to all other sites within 10 km around the site
							X	Y		
XII. Upper Labe Basin										
Na bahně	CZE	1	3	2020	Pokorný	(Pokorný et al. 2000)	15.961190	50.198880	1	
XIII. Bohemian-Moravian Highlands										
Bláto	CZE	2	2	11060	Rybníčková	Rybníček & Rybníčková 1968	15.190970	49.041740	7	Rybníčková 1974, Rybníčková & Rybníček 1975, Salaschek 1936
Doupě	CZE	1			Konětopský	Rybníčková 1974	15.424300	49.233980	5	Križo 1958, Rybníčková 1974, Salaschek 1936
Hojkov	CZE	1			Rybníčková	Rybníčková 1974	15.416010	49.388420	1	Rybníčková 1974
Horní Pole	CZE	1			Rybníčková	Rybníčková 1974	15.314780	49.213170	7	Križo 1958, Rybníčková 1974, Salaschek 1936
Hroznotín	CZE	1			Jankovská	Jankovská 1971	15.355380	49.758110	5	Jankovská unpubl, Jankovská 1971, Kriesl 1959
Chraňbož	CZE	2			Jankovská	Jankovská 1971	15.375340	49.770670	5	Jankovská unpubl, Jankovská 1971, Kriesl 1959
Kameničky	CZE	1	9	11070	Rybníčková	Rybníčková & Rybníček 1988a	15.963640	49.738670	4	Peichlová 1977, Puchmajerová 1943
Loučky	CZE	1	1	10225	Rybníčková	Rybníčková 1974	15.533550	49.324160	1	
Malčín	CZE	1			Jankovská	Jankovská 1989	15.459050	49.691590	5	Jankovská unpubl, Jankovská 1989
Palašiny	CZE	2	1	9530	Jankovská	Jankovská 1989	15.477960	49.681340	5	Jankovská unpubl, Jankovská 1989
Pfaffenschlag	CZE	2			Rybníčková	Rybníčková & Rybníček 1975	15.140770	49.001840	5	Rybníček & Rybníčková 1968, Salaschek 1936
Rváčov	CZE	1*			Peichlová	Peichlová 1977	15.868220	49.766500	4	Kneblová-Vodičková unpubl, Puchmajerová 1943, Rybníčková & Rybníček 1988a
Řásná	CZE	1	1	9610	Rybníčková	Rybníčková 1974	15.370830	49.230560	6	Križo 1958, Rybníčková 1974, Salaschek 1936
Stálkov	CZE	1			Rybníčková	Rybníčková 1974	15.300710	49.027650	4	Rybníček & Rybníčková 1968, Salaschek 1936
Suchdol	CZE	1			Rybníčková	Rybníčková 1974	15.241590	49.132800	2	Salaschek 1936
Zalíbené	CZE	1*			Kneblová-Vodičková	Kneblová-Vodičková 1961a, 1966b, 1970	15.891670	49.733250	6	Peichlová 1977, Puchmajerová 1943, Rybníčková & Rybníček 1988a
Závidkovice	CZE	1			Jankovská	Jankovská 1989	15.416670	49.650000	5	Jankovská unpubl, Jankovská 1989
Žebrákov	CZE	1*			Jankovská	Jankovská unpubl	15.397630	49.718380	8	Jankovská 1971, Jankovská 1989

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							X	Y		
XIV. Slovak-Moravian Carpathians										
Královec	CZE	1	2	1040	Rybníčková	Rybníček & Rybníčková 2008, Rybníčková et al. 2005	18.027780	49.131940	1	
Machová	CZE	1	1	890	Rybníčková	Rybníček & Rybníčková 2008, Rybníčková et al. 2005	17.540920	48.830810	1	
Tlstá hora	SVK	1	4	3920	Rybníčková	Rybníček & Rybníčková 2008, Rybníčková et al. 2005	17.888510	48.894150	1	
XV. Ostrava and Opava Basins										
Brušperk	CZE	1*			Kneblová-Vodičková	Kneblová 1958	18.212160	49.706830	3	Kneblová 1956b
Český Těsin	CZE	1*			Kneblová-Vodičková	Kneblová-Vodičková 1962	18.607790	49.738450	2	Břízová 1994, Kneblová-Vodičková 1961b
Stará Bělá	CZE	2*			Kneblová-Vodičková	Kneblová 1956b	18.217980	49.753160	4	Fejfar et al. 1955, Kneblová 1958
Stonava	CZE	1*			Kneblová-Vodičková Břízová	Kneblová-Vodičková 1961b → Břízová 1994	18.543430	49.815740	2	Kneblová-Vodičková 1962
Škrečoň	CZE	2			Kneblová-Vodičková	Kneblová 1965	18.383330	49.883330	2	
XVI. Bohemian Forest										
Březník (Blatenské slatě, Plattenhausenfilz)	CZE	2			Svobodová-Svitavská	Klečka 1928 → Svobodová-Svitavská unpubl	13.488780	48.962310	8	Klečka 1928, Rudolph unpubl, Svobodová et al. 2002
Hůrecká slať (Neuhüttenfilz)	CZE	1			Svobodová-Svitavská	Klečka 1928 → Svobodová et al. 2002	13.327550	49.152220	3	Svobodová-Svitavská unpubl
Chalupská slať (Seeheider Filz)	CZE	1			Svobodová-Svitavská	Müller 1927 → Svobodová-Svitavská unpubl	13.662860	49.000610	13	Klečka 1928, Müller 1927, Rudolph UNPUBL, Svobodová et al. 2002
Knížecí pláně	CZE	1	1	9120	Svobodová-Svitavská	Svobodová et al. 2001	13.635030	48.964550	12	Klečka 1928, Müller 1927, Rudolph UNPUBL, Svobodová-Svitavská unpubl
Malá niva	CZE	1	3	5125	Reille	Svobodová et al. 2002	13.816060	48.913760	9	Kral 1979, Reille unpubl, Rudolph unpubl, Svobodová et al. 2001, Svobodová et al. 2002
Mrtvý luh	CZE	2	10	9190	Svobodová-Svitavská Reille	Reille unpubl, Svobodová et al. 2001	13.872170	48.872280	7	Kral 1979, Svobodová et al. 2001, Svobodová et al. 2002
Nový Brunst	CZE	1			Svobodová-Svitavská	Svobodová-Svitavská unpubl	13.282750	49.177280	2	Svobodová et al. 2002

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							X	Y		
Plešné jezero	CZE	3	6	8264	Jankovská; Svobodová-Svitavská	Jankovská 2006 → Svobodová-Svitavská unpubl	13.865710	48.776740	3	Brande 1995
Prášily – pod Předělem	CZE	1			Svobodová-Svitavská	Svobodová-Svitavská unpubl	13.405310	49.058640	5	Klečka 1928, Svobodová et al. 2002
Prášily – Zadní chalupy	CZE	1			Svobodová-Svitavská	Svobodová-Svitavská unpubl	13.390690	49.114110	3	Klečka 1928, Svobodová et al. 2002
Rokytecká slať (Vietfelské slatě, Weitfallen Filz)	CZE	1			Svobodová-Svitavská	Klečka 1928 → Svobodová et al. 2002	13.412200	49.015300	6	Klečka 1928, Svobodová et al. 2002, Svobodová-Svitavská unpubl
Rybárenská slať (Fischerhüttenfilz)	CZE	1			Svobodová-Svitavská	Klečka 1928 → Svobodová et al. 2002	13.461890	49.031290	13	Klečka 1928, Rudolph unpubl, Svobodová et al. 2002, Svobodová-Svitavská unpubl
Stráženská slať (Wieherfilz bei Kuschwarda)	CZE	1	2	9680	Reille	Rudolph unpubl → Svobodová et al. 2001	13.742260	48.898870	7	Kral 1979, Svobodová et al. 2001, Svobodová et al. 2002
Velká niva	CZE	2			Svobodová-Svitavská	Svobodová et al. 2001, Svobodová et al. 2002	13.818570	48.924120	9	Kral 1979, Reille unpubl, Rudolph unpubl, Svobodová et al. 2001, Svobodová et al. 2002
XVII. Western Sudetes										
Bílé Labe (Moor auf der Weissen Aidse)	CZE	4	5	2900	Svobodová-Svitavská	Rudolph & Firbas 1927 → Svobodová 2004	15.697800	50.738890	20	Pacltová 1957, Puchmajerová 1929, Roszková 2007, Rudolph & Firbas 1927, Speranza 2000, Svobodová 2002
Černá hora (Černohorská rašelina)	CZE	2	9	2210	Speranza; Svobodová-Svitavská	Pacltová 1957 → Speranza et al. 2000a → Svobodová 2002	15.761270	50.662860	18	Puchmajerová 1929, Roszková 2007, Rudolph & Firbas 1927, Speranza 2000, Speranza et al. 2000b, Svobodová 2002, Svobodová 2004
Kunštátská kaple	CZE	2			Rybníčková	Rybníčková 1966	16.450000	50.250000	4	Müller 1929
Labská louka	CZE	2	5	4920	Svobodová-Svitavská	Svobodová-Svitavská unpubl	15.542160	50.770750	10	Jankovská 1970, Jankovská 2003, Jankovská 2004, Puchmajerová 1929, Rudolph & Firbas 1927, Speranza et al. 2000b, Stark & Overbeck 1929, Treml et al. 2008
Labský důl	CZE	1*	7	9572	Jankovská	Treml et al. 2008	15.554740	50.766060	12	Jankovská 2001, Puchmajerová 1929, Rudolph & Firbas 1927, Speranza et al. 2000b, Stark & Overbeck 1929, Svobodová-Svitavská unpubl

Site name	Country	E	D	Oldest ^{14}C date BP per site	Contributors	Citation to all cores from the site	Coordinates (WGS 1984)		E10	Citations to all other sites within 10 km around the site
							X	Y		
Malá Jizerská louka (Kleine Iserwiese)	CZE	1* 1*			Jankovská Sajverová	Plail 1927 → Puchmajerová 1936 → Sajverová 1981 → Jankovská unpubl	15.337610	50.823920	18	Plail 1927, Puchmajerová 1936, Sajverová 1981
Pančavská louka (Pančické rašeliniště Pantschemoor)	CZE	1 2*	35	7600	Hüttemann; Jankovská; Speranza	Rudolph & Firbas 1927 → Puchmajerová 1929 → Hüttemann & Bortenschlager 1987 → Speranza et al. 2000b → Jankovská 2001	15.541020	50.766190	10	Jankovská 2004, Puchmajerová 1929, Rudolph & Firbas 1927, Stark & Overbeck 1929, Svobodová-Svitavská unpubl, Treml et al. 2008
Rýchory	CZE	1*			Roszková	Roszková 2007	15.852673	50.660815	4	Pacltová 1957, Speranza et al. 2000a, Svobodová 2002
Stříbrná bystřina (Moor am Silberkamm)	CZE	1*			Roszková	Rudolph & Firbas 1927 → Roszková 2007	15.686060	50.748482	23	Jankovská 2001, Pacltová 1957, Puchmajerová 1929, Rudolph & Firbas 1927, Speranza 2000, Svobodová 2002, Svobodová 2004, Treml et al. 2008
Úpské rašeliniště (Moor am Koppenplan)	CZE	4	16	4490	Speranza; Svobodová-Svitavská	Rudolph & Firbas 1927 → Puchmajerová 1929 → Speranza 2000 → Svobodová 2002	15.712500	50.738890	20	Pacltová 1957, Puchmajerová 1929, Roszková 2007, Rudolph & Firbas 1927, Speranza et al. 2000a, Svobodová 2004
Velká Jizerská louka (Grosse Iserwiese)	CZE	1*			Sajverová	Plail 1927 → Puchmajerová 1936 → Sajverová 1981	15.326390	50.857400	18	Jankovská unpubl, Plail 1927, Puchmajerová 1936, Sajverová 1981
XVIII. Eastern Sudetes										
Barborka	CZE	1*			Rybníčková	Rybníček & Rybníčková 2004	17.229550	50.075070	8	Firbas & Losert 1949, Rybníček & Rybníčková 2004, Salaschek 1936
Keprník	CZE	1*	1	2090	Petr	Salaschek 1936 → Opravil 1959 → Treml et al. 2008	17.117439	50.170783	1	Opravil 1959
Mezikotlí	CZE	1*	1	528	Petr	Treml et al. 2008	17.231047	50.049755	9	Firbas & Losert 1949, Rybníček & Rybníčková 2004, Salaschek 1936
Mokrý hřbet	CZE	1*	1	4462	Jankovská	Jankovská unpubl	16.859470	50.168280	2	Salaschek 1936
Rejvíz (Moosebruch)	CZE	1*	6	7040	Dudová	Fahl 1926 → Salaschek 1936 → Navrátilová 2007	17.283340	50.210800	3	
Velká Kotlina	CZE	1*			Rybníčková	Rybníček & Rybníčková 2004	17.237580	50.060650	8	Firbas & Losert 1949, Rybníček & Rybníčková 2004, Salaschek 1936

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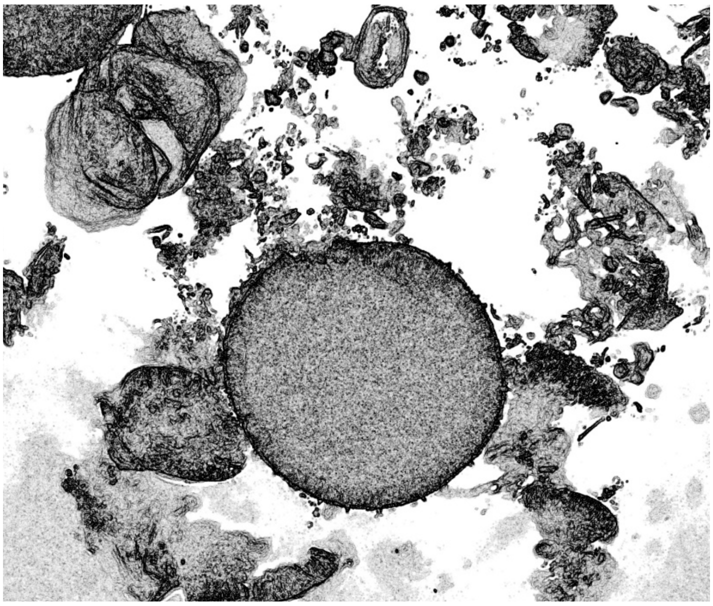
Velký Děd	CZE	1	4	4620	Rybníčková	Rybníček & Rybníčková 2004	17.218110	50.084770	9	Firbas & Losert 1949, Opravil 1959, Rybníček & Rybníčková 2004, Salaschek 1936
Velký Máj	CZE	1	4	1945	Rybníčková	Rybníček & Rybníčková 2004	17.220290	50.047390	9	Firbas & Losert 1949, Rybníček & Rybníčková 2004, Salaschek 1936
XIX. Western Beskids										
Horní Lomná	CZE	1	3	5130	Rybníčková	Rybníček & Rybníčková 2008, Rybníčková et al. 2005	18.630830	49.520560	7	Jankovská 1995a, Puchmajerová 1945, Rybníček & Rybníčková 1995, Rybníček & Rybníčková 2008, Rybníčková et al. 2005
Jablůnka	CZE	1	2	44872	Jankovská	Jankovská & Pokorný 2008	17.950000	49.383330	1	
Kubriková	SVK	1	1	1730	Rybníčková	Rybníček & Rybníčková 2008, Rybníčková et al. 2005	18.672220	49.484170	6	
Kysuca	SVK	1*			Rybníčková	Rybníček & Rybníčková 1995	18.551540	49.498320	13	Jankovská 1995a, Puchmajerová 1945, Rybníčková et al. 2005, Salaschek 1936
Súlov	SVK	1*			Rybníčková	Rybníček & Rybníčková 1995	18.547340	49.493530	13	Jankovská 1995a, Puchmajerová 1945, Rybníček & Rybníčková 1995, Rybníček & Rybníčková 2008, Rybníčková et al. 2005, Salaschek 1936
XX. Outer Western Carpathians										
Bobrov	SVK	1	13	10150	Rybníčková	Rybníček & Rybníčková 1985	19.660530	49.445630	2	Rybníček & Rybníčková 1985 –
Jedlová	SVK	1			Rybníčková	Rybníčková & Rybníček 1985	19.660530	49.397010	2	Rybníčková & Rybníček 1985 –
Sivárňa	SVK	1			Jankovská	Jankovská 1998	20.583330	49.316670	1	
Zlatnická Dolina	SVK	1	5	7450	Rybníčková	Rybníček & Rybníčková 1985	19.283330	49.516670	1	
XXI. Fatra-Tatra area										
Hozelec	SVK	1	3	11010	Jankovská	Jankovská 1988b	20.332000	49.046410	1	
Liptovský Ján	SVK	2	7	12960	Rybníčková	Rybníčková UNPUBL	19.677780	49.041670	2	
Podhorany	SVK	1			Jankovská	Jankovská 1972	20.470833	49.249167	1	
Popradské pleso	SVK	1			Rybníčková	Rybníčková & Rybníček 2006	20.135410	49.164340	2	Rybníčková & Rybníček 2006 –

Site name	Country	E	D	Oldest ^{14}C date BP per site	Contributors	Citation to all cores from the site	Coordinates (WGS 1984)		E10	Citations to all other sites within 10 km around the site
							X	Y		
Spišská Belá	SVK	1			Jankovská	Jankovská 1972	20.450000	49.184720	1	–
Šafárka	SVK	1	10	>52000	Jankovská	Jankovská & Pokorný 2008	20.575000	48.881950	1	–
Štrbské pleso	SVK	1			Rybníčková	Rybníčková & Rybníček 2006	20.044910	49.142450	2	Rybníčková & Rybníček 2006 –
Trojrohé pleso	SVK	1*	6	6050	Hüttemann	Hüttemann & Bortenschlager 1987	49.220140	20.226440	1	–
XXII. Lower Beskids										
Kružlová	SVK	1*			Wacnik	Wacnik 2001	21.583430	49.364170	1	–
Regetovka	SVK	1	5	6720	Wacnik	Wacnik 1995	21.279170	49.425000	1	–



Chapter 2: *Lonicera nigra*

Daneck, H., **Abraham, V.**, Fér, T. & Marhold, K. (2011). Phylogeography of *Lonicera nigra* in Central Europe inferred from molecular and pollen evidence. *Preslia* 83(2), 237–257.

Phylogeography of *Lonicera nigra* in Central Europe inferred from molecular and pollen evidence

Fylogeografická studie druhu *Lonicera nigra* se zaměřením na střední Evropu – kombinace molekulárních a paleopalynologických dat

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Daneck H., Abraham V., Fér T. & Marhold K. (2011): Phylogeography of *Lonicera nigra* in Central Europe inferred from molecular and pollen evidence. – Preslia 83: 237–257.

The phylogeographic pattern of the temperate shrub *Lonicera nigra* (*Caprifoliaceae*) in Europe was inferred from molecular and fossil data. Population samples and pollen data from most of the contemporary natural distribution were analysed. While chloroplast DNA sequences revealed no intraspecific variation, AFLP data show a non-random geographic pattern. Two genetically different groups, distinguished by Bayesian clustering, divided the distribution area of *L. nigra* into south-western and north-eastern regions with a contact zone situated approximately in the upper part of the Danube Valley. Iberian populations constitute an additional distinct genetic group. Pollen evidence supports the genetic data, indicating that *L. nigra* might have survived in glacial refugia located in Central Europe. Nevertheless, this evidence should be considered only as indicative and supplementary, as an unambiguous determination of the species is not possible based on the information on pollen in the literature.

Keywords: AFLP, Central Europe, contact zone, cpDNA sequencing, pollen evidence, postglacial history

Introduction

The present distributions of plant and animal species are a result of historical processes. Species distribution patterns are modified by large-scale environmental changes and may vary among species depending on their ecology. In Europe, Quaternary climatic fluctuations strongly influenced the current composition of biota (Taberlet et al. 1998, Hewitt 1999, 2001). Palaeoecological and molecular methods can be used to investigate the sequence of events leading to contemporary species distributions. Palaeoecological methods (such as palaeopalynology, or analyses of charcoal or other macro-remains) can directly document the presence of a given species in a particular area in the past. However, such data are generally discontinuous in space and largely missing or methodologically unavailable for many species due to limited resolution at the species level. Fossil evidence can also provide information about the likely composition of ancient vegetation, but it can be difficult to establish whether the documented species were widespread in the study area or whether they occurred only in isolated patches (Willis & van Andel 2004, Jankovská & Pokorný 2008). Thus, when testing hypotheses it might be advantageous to combine palaeoecological evidence with other types of data.

Molecular methods are widely used in studies on the history of the distribution of plant and animal species. The following two types of molecular data are generally used in plant phylogeography: (i) sequences of chloroplast DNA, which are used to define haplotypes and (since they are non-recombinant and maternally inherited in most angiosperms) to infer the origin of populations (Taberlet et al. 1998, Hewitt 1999); (ii) amplified fragment length polymorphisms (AFLPs), which provide data on genome-wide genetic variation and are frequently used to reconstruct changes in the postglacial distribution of particular species (Schönswetter & Tribsch 2005, Ehrich et al. 2007). Moreover, population analysis of AFLP data can give additional information about population divergence, e.g. by calculating DWs (frequency-down-weighted marker values, Schönswetter & Tribsch 2005), which use the accumulation of rare markers to reflect long-term population isolation.

The most commonly inferred main southern glacial refugia (the Balkan, Iberian and Apennine Peninsulas), common postglacial colonization routes and contact zones among different genetic lineages (the Pyrenees, the Alps, Scandinavia and Central Europe) are postulated (Taberlet et al. 1998, Hewitt 1999). Glacial refugia represent areas of relative ecological stability that provided habitats for species survival more or less in situ during periods of climatic instability (Tribsch & Schönswetter 2003), which is reflected in the greater genetic diversity and unique genotypes recorded in these areas. In contrast, newly colonized regions are genetically depauperate. More recently, the possibility of full-glacial survival of temperate species at northern latitudes (in so-called northern or cryptic refugia; Stewart & Lister 2001) was assumed for some species based on fossil data (Willis & van Andel 2004). However, there is little molecular evidence for the existence of such northern refugia in Central Europe or the Western Carpathians.

The postglacial spread of populations from refugia led to the contact of previously isolated genetic lineages, which resulted in the formation of contact (suture) or hybrid (transitional) zones with secondarily increased genetic diversity (Taberlet et al. 1998, Hewitt 1999, 2004). Such contact zones are usually defined as areas in which different lineages meet, mix or hybridize (Remington 1968, Taberlet et al. 1998). Suture zones of several species tend to cluster in certain geographical areas; nevertheless, the exact location and other characteristics of such zones seem to be specific to each particular species (Hewitt 1999, Willis & van Andel 2004, Magri et al. 2006, Fér et al. 2007, Magri 2008, Dvořáková et al. 2010).

Contact zones in Central Europe for a diverse assortment of organisms, including plants, fish, amphibians, birds and mammals have been detected (Taberlet et al. 1998, Hewitt 1999, 2004, Gum et al. 2005 and references therein). Among plants, there is the Central European contact zone for the widespread grass *Festuca pratensis* (Fjellheim et al. 2006), the annual herb *Rhinanthus angustifolius* (Vrancken et al. 2009) and the temperate shrub *Rosa pendulina* (Fér et al. 2007).

Phylogenetic data supported by palaeoecological information is rare for many plant species because their pollen is either undetectable in fossil pollen profiles or often cannot be identified to the species level solely based on morphology (Beug 2004). Hence, only genera for which it is possible to identify the pollen to species or a narrow species-group level are suitable for studies combining fossil and molecular evidence on species survival during the late glacial maximum, e.g. *Picea* (Tollefsrud et al. 2008), *Fagus* (Magri et al. 2006), *Abies* (Liepelt et al. 2009) or *Cedrus* (Cheddadi et al. 2009).

The temperate shrub *Lonicera nigra* L. (*Caprifoliaceae*) is a suitable species for such a study because its pollen is detectable in pollen profiles, even though such evidence is rare. Although pollen grains of *L. nigra* can be distinguished from those of *L. xylosteum* and other *Lonicera* taxa at high magnifications (Punt et al. 1974), the data compiled refer either to the *L. xylosteum*-type [which can include *L. nigra* and *L. xylosteum* (Punt et al. 1974), sometimes also *L. alpigena* and *L. coerulea* (Moore et al. 1991), or even also *L. caprifolium* (Faegri & Iversen 1989)] or *Lonicera*-type (that can include any *Lonicera* species). Pollen production and dispersal in *Lonicera* is low, due to its mode of pollination [entomogamy (Chrtek 1997) – flowers with concealed anthers and large pollen size (Punt et al. 1974)]. Thus, even rare occurrences of single pollen grains are considered to be evidence of a local presence of the species in the past. However, the presence of *Lonicera* in a plant community does not guarantee its occurrence in the pollen assemblage (Pelánková & Chytrý 2009). Unfortunately, preservation of macro-remains of the genus *Lonicera* is extremely rare; its wood is too thin to be preserved as charcoal and there are no other palaeoecological data for this genus.

Lonicera nigra is diploid (2n = 18; Browicz 1976, Chrtek 1997), self-incompatible, entomogamous and pollinated mainly by bumblebees (Willemstein 1987). Dark blue berries are dispersed by endozoochory, mainly by birds. In addition to sexual reproduction, clonal spread by root suckering or layering is recorded (Traiser et al. 1998). The distribution of *L. nigra* is restricted to Europe and extends from Central Europe to the Carpathians and Dinaric Alps in the south-east, to the Alps and Apennines in the south and to the Massif Central and Pyrenees to the south-west. This species reaches its northern limit of distribution in the Czech Republic. Being a submontane species, *L. nigra* is common in mountain regions and at low altitudes. It grows in forests and prefers forest edges and watersides (Browicz 1976, Chrtek 1997, 2002). Due to similar ecological requirements shared with other *Lonicera* species (*L. xylosteum* L. and *L. alpigena* L.), mixed populations may appear (Chrtek 1997, 2002). A hybrid between *L. nigra* and *L. xylosteum* (*L.* ×*helvetica* Brügger) is described, but there are no reliable data on its distribution (Browicz 1976, Bertová 1985, Chrtek 1997).

For the present study, cpDNA and AFLP genetic variation were analysed in populations from the entire range of *L. nigra* and palaeoecological data was compiled. The following questions were addressed by combining both types of data: (i) Does the molecular data indicate a phylogeographic pattern in the distribution of *L. nigra*? (ii) Is it possible to delimit contact zones between different genetic lineages? Where are these contact zones? (iii) Is it possible to delineate the probable glacial refugia of *L. nigra*? Is there any indication of full-glacial survival of this species in Central Europe? Is there a correlation between molecular and palaeoecological data? (iv) Is the phylogeographic pattern of *L. nigra* comparable with that of any other temperate, European plant species?

Materials and methods

Sampling

Leaf material of 150 individual plants from 31 populations (2–6 plants per population) of *L. nigra* was collected (Table 1). Sampling covered almost the entire contemporary natural range of this species. Field collections were conducted in 2006 and 2007. Material was collected from shrubs separated by at least 10 m in order to prevent the collection of leaves from the same individual. Young, intact leaves were immediately dried in silica gel. Voucher specimens were deposited in the herbarium PRC.

DNA extraction

Total DNA was extracted from approximately three dried leaves per individual plant (about 15 mg of plant material), using the CTAB protocol (Doyle & Doyle 1987). DNA concentration was measured photometrically using BioPhotometer 6131 (Eppendorf).

Sequencing of cpDNA

Six non-coding chloroplast (cp) DNA regions (*psb*A-*trn*H, *rpo*B-*trn*C, *psb*C-*trn*S, *trn*G-*trn*G2G, *trn*G2S-*trn*S and *trn*L-*trn*F) were screened for possible variation. A test-sample set included individuals from six populations covering the whole distribution area [Pyrenees (population 1, Estany de Sant Maurici, Spain), Alps (7, Steiermark, Austria), Czech Republic (30, Jizerské hory Mts), Western Carpathians (14, Vihorlat Mts, Slovakia), Eastern Carpathians (13, Mt. Hoverla, Ukraine) and Balkans (10, Bjelasica Mts, Montenegro)]. Universal cpDNA primers (*trn*L-*trn*F, Taberlet et al. 1991; *psb*C-*trn*S, Demesure et al. 1995; *trn*G-*trn*G2G, Ohsako & Ohnishi 2000; *psb*A-*trn*H, Tate & Simpson 2003; *rpo*B-*trn*C, t*rn*G2S-*trn*S, Shaw et al. 2005) were used for both PCR amplification and sequencing.

PCR amplifications were carried out in a total volume of 20 μl containing 5 ng of template DNA, 2 μl of 10× reaction buffer (Sigma-Aldrich), 0.2 mM of dNTP mix (Fermentas), 0.5 mM of $MgCl_2$ (Fermentas), 0.3 μM of each forward and reverse primers and 0.5 U of JumpStart RedTaq DNA polymerase (Sigma-Aldrich). Amplification was performed using an XP thermal cycler (Bioer Technology) with initial denaturation at 94°C for 60 s and 35 cycles of 94°C for 45 s, 60°C for 60 s and 72°C for 120 s. A final extension at 72°C for 10 min was performed. Amplification products were purified using the JetQuick PCR Product Purification Kit (Genomed).

Sequencing reactions were carried out using the BigDye Terminator 3.1 Cycle Sequencing Kit (Applied Biosystems) according to the manufacturer's instructions using the primers cited above. Purification of sequencing reactions was performed using an ethanol/sodium acetate precipitation provided with the sequencing kit. Purified reactions were run on an ABI 3130 Avant automated sequencer (Applied Biosystems).

AFLP

The double digestion was performed for 2.5 hours at 37°C. The reaction took place in a total volume of 5 μl containing 0.5 U of *Eco*RI/*Mse*I enzyme mixture (AFLP Core Reagent Kit, Invitrogen), 250 ng of total DNA and 1 μl of 5× restriction buffer (AFLP Core Reagent Kit, Invitrogen). Restriction was immediately followed by ligation for 12 hours at 37°C. With the addition of 0.2 U of T4 DNA ligase (AFLP Core Reagent Kit, Invitrogen) and 4.8 μl of adaptor ligation solution (AFLP Core Reagent Kit, Invitrogen) directly to the restricted sample, the reaction volume was increased to 10 μl. Preselective amplification was carried out in a total volume of 5 μl containing 4.0 μl of pre-amplification mix (AFLP Pre-Amp Primer Mix I, Invitrogen), 0.5 μl of 10× polymerase buffer with

$MgCl_2$ (Sigma-Aldrich), 0.1 U of JumpStart RedTaq polymerase (Sigma-Aldrich) and 0.4 µl of restricted/ligated sample. The pre-amplification mix included *Eco*RI-primer (5´– GAC TGC GTA CCA ATT C – 3´) and *Mse*I-primer (5´– GAT GAG TCC TGA GTA A – 3´). Pre-amplification proceeded under following conditions: 72°C for 120 s; 20 cycles: 94°C for 1 s, 56°C for 30 s, 72°C for 120 s and 60°C for 30 min.

Before selective PCR each pre-amplified sample was diluted 10×. The selective PCR reaction was conducted in a total volume of 10 µl containing 1.0 µl of 10× polymerase buffer with $MgCl_2$ (Sigma-Aldrich), 0.2 mM dNTP (Fermentas), 0.05 µM of fluorescence-labelled *Eco*RI-primer (Applied Biosystems), 0.25 µM of unlabelled *Mse*I primer (Applied Biosystems), 0.2 U of JumpStart RedTaq polymerase (Sigma-Aldrich) and 2.3 µl of diluted pre-amplified sample. The selective PCR conditions were as follows: 94°C for 120 s, 65°C for 30 s and 72°C for 120 s. Eight cycles were performed under the following PCR conditions: 94°C for 1 s, 64–57°C for 30 s (in each subsequent cycle, the temperature was decreased by 1°C), 23 cycles: 94°C for 1 s, 56°C for 30 s, 72°C for 120 s and 60°C for 30 min. In total 63 selective primer combinations were tested and the following three combinations were selected as they gave the clearest and most reproducible signal (fluorescent dye in brackets): (FAM)-*Eco*RI-ACT + *Mse*I-CAT, (NED)-*Eco*RI-AAC + *Mse*I-CAG and (HEX)-*Eco*RI-ACG + *Mse*I-CTC.

Two precipitations produced the final purification. First, PCR products with 1 µl of sodium acetate and 25 µl of 96% ethanol were chilled for 20 min at –20°C. Precipitated products were spun at 4°C for 30 min at 12,500 rpm and the supernatant was discarded. Second, 100 µl of 70% ethanol was added and samples were spun at 4°C for 5 min at 12,500 rpm. Purified products were desiccated at 65°C for 10 min. Just before the products were run on the sequencer, 10 µl of the mixture HiDi formamide: GeneScan-500 Rox (20:1, Applied Biosystems) was added to each sample. Fragment analysis was preformed on an ABI 3100 Avant automated sequencer (Applied Biosystems).

AFLP data analysis

Profile scoring was performed manually using the software GeneScan 3.7.1 (Applied Biosystems) and Genographer 1.6.0 (Benham 1999, Montana State University 1999 – http://hordeum.oscs.montana.edu/genographer). A presence/absence matrix of unambiguously scored AFLP bands was generated. In order to check reproducibility of the AFLP profiles, the whole AFLP procedure was repeated with 11 already analysed individuals and the error rate calculated as the ratio between the number of differences and the total number of compared fragments. This was done after suspicious and unreliable markers were deleted (Bonin et al. 2004). Afterwards, the presence/absence matrix of unambiguously scored AFLP bands was generated.

The isolation-by-distance pattern was investigated using Mantel tests (Legendre & Legendre 1998) implemented in ZT (Bonnet & Van de Peer 2002). The matrix of population pair wise F_{ST}-analogues (computed in Arlequin 3.01; Excoffier et al. 2005) was correlated with the matrix of inter-population geographic distances (computed using ArcGIS 9.0, ESRI). Significance was tested using 10,000 permutations.

The total number of AFLP fragments per population (FT, fragments total), the average number of fragments per individual (FA, fragments average), the number of unique fragments per population (EF, exclusive fragments) and the percentage of polymorphic fragments per population (%PF, polymorphic fragments) were computed. Since these values depend on the number of individuals analysed per population, the values were calculated by re-sampling the whole dataset (special case of bootstrapping, see Kučera et al. 2008 for details) in order to achieve the same sample size for each population and prevent any loss of information. In this analysis, four individuals per population were selected at each step and a mean value from 1,000 replicates was calculated. The re-sampling procedure was executed using a script in Scilab (http://www.scilab.org). Similarly, using the re-sampling procedure and the Scilab script mentioned in Kučera et al. (2008), the rarity of AFLP markers was determined using the DW index (frequency-down-weighted marker values). The DW value was calculated for each population as the number of occurrences of each AFLP marker in a particular population divided by the number of occurrences of this marker in the total dataset. Finally, these values were summed (Schönswetter & Tribsch 2005). Higher DW values are expected in populations where infrequent markers have accumulated due to mutations during long-term isolation (Paun et al. 2008). Shannon's diversity index for each population was calculated in FAMD 1.108 (Schlüter & Harris 2006).

Population genetic structure was inferred using STRUCTURE 2.2.3 (Falush et al. 2007). This program applies a Bayesian model-based clustering method, which uses a Markov chain Monte Carlo (MCMC) algorithm to organize genetically similar individuals into clusters using multi-locus genotype data. The admixture model was used and independent allele frequencies were assumed. As AFLPs are dominant markers, a recessive allele model was used. The number of clusters (K) was limited to 1 to 10. For each K, ten runs were performed to test the stability of the results. The length of burn-in period was set to 100,000, and the MCMC chains after burn-in were run through an additional 1,000,000 replicates (Falush et al. 2007). All computations were done on the freely available Bioportal (http://www.bioportal.uio.no). The R-script Structure-sum-2009 (part of AFLPdat; Ehrich 2006) was used to summarize the output files and to calculate similarity coefficients between the replicate runs (Nordborg et al. 2005). The optimum number of populations/groups (K) was the one with consistent results over ten repeats and high similarity coefficient. The software CLUMPP 1.1.1 (Jakobsson & Rosenberg 2007) and Distruct (Rosenberg 2004) was used to create graphical outputs. Because an analysis of the entire dataset indicated that only those runs in which K = 2 converged to a consistent solution in ten repeats, a subsequent, separate analysis of each of these two partitions was conducted using the same parameters. Clustering results were plotted using ArcGIS 9.0 (ESRI).

Analyses of molecular variance (AMOVA; Excoffier et al. 1992) were computed to compare variability within and among populations. In addition to testing the STRUCTURE clustering results, AMOVA analyses were used to compare within- and among-cluster variation. All analyses were computed in Arlequin 3.01 (Excoffier et al. 2005) and the significance of the results was obtained from 1,000 permutations.

Palaeopalynological data

To search for pollen evidence describing the past distribution of *L. nigra*, pollen data was obtained from the Czech Quaternary Palynological Database covering the Czech Republic and Slovakia (PALYCZ; Kuneš et al. 2009) and the European Pollen Database (EPD; Fyfe et al. 2009) covering the area 39–52°N to 2°30'W–30°E, which includes Austria, Bulgaria, Germany, Spain, France, Greece, Hungary, Switzerland, Italy, Poland, Romania and Ukraine (see Electronic Appendix 1). Additionally, data from the same area, which are not included in the PALYCZ or EPD databases, was also used (see Electronic Appendix 2). The area includes not only the entire contemporary range of *L. nigra* but also neighbouring areas. Chronologies proposed by both databases were used. For the sequences that lacked dates the periods proposed by their original authors were used. For many of the pollen profiles containing *Lonicera*, age was evaluated using a new depth-age model (linear interpolation between calibrated midpoints) constructed using Clam 1.0 (Blaauw 2010).

A map based on data from all the profiles examined was constructed, depicting the presence or absence of *Lonicera* or *Lonicera xylosteum*-type pollen grains. The records of *Lonicera* pollen were searched for the following periods: (i) Pleniglacial, 24–13 ky un-calibrated BP (–24 to –12.4 ky BC), (ii) Late-Glacial, 13–10 ky uncal. BP (–12.4 to –9.5 ky BC) and (iii) Early Holocene 10–7.5 ky uncal. BP (–9.5 to –6.4 ky BC) (Walker 1995, Brauer et al. 1999, Birks & Ammann 2000 and Tinner & Lotter 2001). The periods of time on the map show the oldest pollen record for each site and if there was at least one pollen grain recorded in an assemblage it is marked as a “presence”. Any site with no *Lonicera* pollen grain for all periods of time is marked as an “absence”.

Results

Molecular data

No variation was found among the 3,223 bp of six non-coding chloroplast DNA regions (379 bp in *psb*A-*trn*H, 426 bp in *rpo*B-*trn*C, 451 bp in *psb*C-*trn*S, 596 bp in *trn*G-*trn*G2G, 725 bp in *trn*G2S-*trn*S and 646 bp in *trn*L-*trn*F) in the sample of six populations covering the entire distribution range. A sequence of each region was submitted to the GenBank only once and the sequences are recorded there under the following accession numbers: GU076455 (*psb*A-*trn*H), GU076460 (*rpo*B-*trn*C), GU076465 (*psb*C-*trn*S), GU076470 (*trn*G-*trn*G2G), GU076475 (*trn*G2S-*trn*S) GU076480 (*trn*L-*trn*F). Thus, it is assumed that a single chloroplast haplotype occurs throughout the entire distribution area of *L. nigra*.

For the AFLP the three selective primer pairs that provided clearly readable profiles were selected (see Methods). In total, 205 unambiguously scored loci were selected from a range between 66 to 495 bp, of which 120 (59%) were polymorphic. The overall estimate of the error rate calculated from 11 repeated samples was 2.65%. The number of fragments per individual varied from 129 (population 28, Doupovské hory Mts, Czech Republic) to 154 (population 19, Českomoravské mezihoří Hills, Czech Republic). After re-sampling, the average number of bands per individual was 142.14. The lowest values (134.94) were recorded in population 8 (Primorie-Gorski Kotar, Croatia) and the highest (150.78) for individuals from population 19 (Českomoravské mezihoří Hills, Czech Republic). The percentage of polymorphic loci per population ranged from 5.60% (population 14, Mt. Vihorlat, Slovakia) to 11.44% (population 1, Catalan Pyrenees, Spain). These values correspond well with those of the Shannon index (Table 1).

There were no individuals with identical AFLP genotypes. Five populations contained one unique fragment: populations 11 (Kopaonik Mts, Serbia), 18 (Rychlebské hory Mts, Czech Republic), 19 (Českomoravské mezihoří Hills, Czech Republic), 24 (Brdy Mts, Czech Republic) and 28 (Doupovské hory Mts, Czech Republic). In these populations, each individual harboured a specific fragment, which was not found in any of the other populations studied.

Table 1. – List of *Lonicera nigra* populations studied, details of their localities, distribution of AFLP fragments and genetic diversity measures. No. – locality number, which corresponds to those in Figs. 1, 2 and 3; N – number of analysed individuals; FT – total number of AFLP fragments per population; FA – average number of fragments per individual; EF – number of unique fragments per population; DW – frequency-down-weighted marker value of a population; %PF – percentage of polymorphic fragments per population; H_{Sh} – Shannon's diversity index. Repeated resamplings were made to achieve the same sample size in each population (for details, see "Materials and methods" and Kučera et al. 2008) and resulting mean values are presented for FT, FA, EF, %PF and DW. Collectors' names: AB – Anna Bucharová (Mariánské Lázně), HD – Hana Daneck (Prague), JK – Jan Košnar (České Budějovice), JV – Jaroslav Vojta (Prague), LD – Lucie Drhovská (Prague), LE – Libor Ekrt (České Budějovice), VZ – Vojtěch Zeisek (Prague).

No.	Country	Locality description	Altitude (m)	Latitude	Longitude	Collector	N	FT	FA	EF	%PF	DW	H_{Sh}
1	Spain	Pyrenees, Catalan Pyrenees, Estany de Sant Maurici, river valley near Sant Maurici lake.	1900	42.35 N	1.02 E	HD	5	143.66	135.14	0.83	11.44	7.19	5.25
2	Andorra	Pyrenees, Ransol, banks of the Valira river.	1600	42.34 N	1.39 E	HD	4	147.24	142.78	0.35	6.40	7.63	4.35
3	Switzerland	Bern, Kaufdorf, 500 m NW of the village Hasli, Taanwald forest.	900	46.49 N	7.28 E	HD	5	142.45	137.18	0.01	7.35	5.33	4.62
4	Austria	Vorarlberg, Bludenz, near the tourist track, 1.5 km S of the village Raggal.	1600	47.11 N	9.50 E	HD	6	148.17	140.47	0.01	10.59	5.73	5.16
5	Germany	Bavaria, Tegernsee, 1 km W of the village Kreuth, tourist track to Mt. Leonhardstein.	870	47.38 N	11.44 E	HD	5	141.69	136.77	0.00	6.90	5.07	4.50
6	Austria	Lower Austria, Payerbach-Reichenau an der Rax, 3 km N of the town, near the tourist track.	900	47.43 N	15.51 E	HD	5	148.04	139.99	0.05	10.10	5.85	5.08
7	Austria	Steiermark, Graz, near the tourist track, 700 m E of the chalet Aiblwirt.	1100	46.57 N	15.07 E	HD	5	149.41	143.64	0.06	7.65	6.41	4.70
8	Croatia	Primorje-Gorski Kotar county, Delnice, close to road in direction of the National park Risnjak, 500 m from the town.	780	45.23 N	14.47 E	HD	6	142.36	134.94	0.04	10.44	5.82	5.11
9	Bosnia and Herzegovina	Bjelašnica Mts, 1.5 km W of the parking place at the ski centre.	1400	43.43 N	18.16 E	HD	6	143.79	136.18	0.05	10.45	5.68	5.14

No.	Country	Locality description	Altitude (m)	Latitude	Longitude	Collector	N	FT	FA	EF	%PF	DW	H_{Sh}
10	Montenegro	Bjelasica Mts, Kolašin, banks of the brook near the chalet Jezerine.	1400	42.49 N	19.37 E	HD	5	147.15	141.54	0.03	7.46	5.77	4.67
11	Serbia	Kopaonik Mts, ski-run in direction Duboka, banks of the brook.	1740	43.16 N	20.50 E	HD	4	149.80	144.76	0.81	6.19	6.74	4.44
12	Romania	Caliman Mts, Rastolita, road through the valley of the Tihuletul brook.	1100	47.53 N	25.51 E	JK	5	148.85	142.12	0.02	8.63	6.27	4.95
13	Ukraine	Ukrainian Carpathian Mts, by the path from the village of Hoverla to Mt. Hoverla, banks of the brook.	1000	48.08 N	24.45 E	VZ	5	149.20	141.38	0.02	10.07	5.98	5.11
14	Slovak Republic	Vihorlat Mts, near the peak of the Mt. Vihorlat.	1060	48.53 N	22.06 E	HD	2	150.92	146.49	0.05	5.60	6.28	4.09
15	Slovak Republic	Spiš, Branisko pass, Príkro ridge, 3 km E of the village of Poľanovce.	820	49.01 N	20.51 E	HD	6	150.77	143.03	0.00	9.89	5.71	5.19
16	Slovak Republic	Velká Fatra, Ľubochňa, near the road, W edge of the town.	520	49.06 N	19.09 E	HD	5	147.77	140.33	0.22	9.91	5.61	5.05
17	Czech Republic	Moravskoslezské Beskydy Mts, Hlavatá, behind the village, along the river Bílá Ostravice.	650	49.24 N	18.23 E	HD	3	146.20	139.88	0.07	8.04	5.61	4.71
18	Czech Republic	Rychlebské hory Mts, Nýznerovské vodopády waterfalls, banks of the brook.	460	50.16 N	17.31 E	LD	5	153.41	148.98	0.97	5.92	7.47	4.48
19	Czech Republic	Českomoravské mezihoří Hills, Lanškroun, close to the town along the road in the direction of Jakubovice.	400	49.55 N	16.34 E	HD	5	158.31	150.78	1.42	9.44	8.83	5.07
20	Czech Republic	Železné hory Mts, Seč, 1.5 km S of the village, the castle hill of the ruin Oheb.	500	49.50 N	15.39 E	HD	5	154.19	147.61	0.01	8.35	6.50	4.91
21	Czech Republic	Českomoravská vrchovina Mts, Jihlava – Kosov, 700 m N of the village, Kosovská hůrka hill.	480	49.23 N	15.38 E	HD	5	154.21	148.39	0.07	7.35	6.68	4.69

No.	Country	Locality description	Altitude (m)	Latitude	Longitude	Collector	N	FT	FA	EF	%PF	DW	H_{Sh}
22	Czech Republic	Českomoravská vrchovina Mts, Jindřichův Hradec, 1 km E of the railway station Jindřiš, Jindřišské údolí valley.	500	49.08 N	15.03 E	HD	5	152.92	146.52	0.24	8.55	7.22	4.92
23	Czech Republic	Šumava Mts, České Žleby, 1.1 km E of the town, Spáleniště hill.	955	48.52 N	13.47 E	LE	5	150.26	143.73	0.01	8.95	6.25	5.01
24	Czech Republic	Brdy Mts, Slavětín u Březnice, 1.5 km NW of the railway station, Špalková hora hill.	450	49.31 N	13.52 E	HD	5	149.33	142.12	0.35	9.86	6.16	5.04
25	Czech Republic	Slavkovský les Mts, Mariánské Lázně, Žižkův vrch hill, nearby the town.	720	49.58 N	12.47 E	AB	5	146.99	140.30	0.01	9.05	5.76	4.91
26	Germany	Thuringia, Thüringer Wald, Gehlberg, banks of the brook near the railway station Gehlberg.	600	50.41 N	10.45 E	HD	5	147.21	141.79	0.07	7.21	6.40	4.60
27	Germany	Thuringia, Schleiz, 700 m E of the castle Burgk, tourist track along the river Saale.	420	50.32 N	11.43 E	HD	4	142.08	137.01	0.22	7.39	5.45	4.49
28	Czech Republic	Doupovské hory Mts, Ostrov, 1 km SW of the town, Ostrovské rybníky nature reserve.	420	50.29 N	12.92 E	JV	5	149.72	141.19	1.07	11.01	7.16	5.25
29	Czech Republic	Lužické hory Mts, Česká Kamenice, 3 km E of the town, Pustý zámek natural monument.	400	50.48 N	14.27 E	HD	5	146.22	142.02	0.24	5.65	6.17	4.28
30	Czech Republic	Jizerské hory Mts, Oldřichov v Hájích, Viničná cesta road, along the watercourse.	500	50.51 N	15.08 E	HD	5	147.34	141.43	0.34	7.76	5.95	4.68
31	Czech Republic	Krkonoše Mts, Špindlerův Mlýn, Labský důl valley, along the tourist track near to the town.	850	50.44 N	15.36 E	HD	4	152.64	147.77	0.19	6.12	6.25	4.43

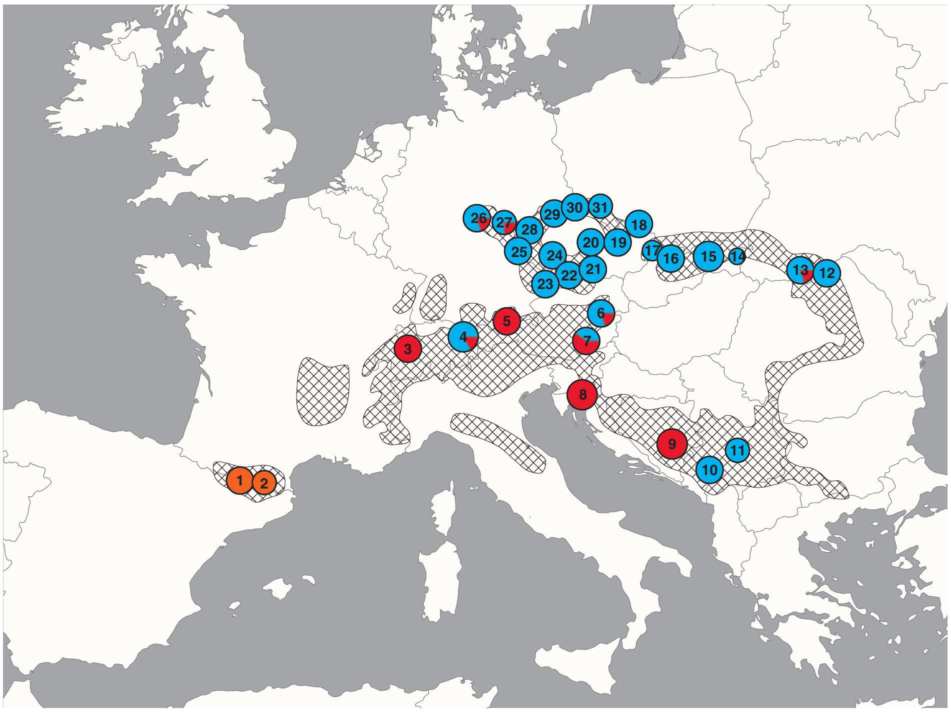

Fig. 1. – Distribution (crosshatched) of *Lonicera nigra* in Europe (taken from Meusel & Jäger 1992) and location of the 31 populations (Table 1) used for the molecular analyses. The colours of the dots refer to the three AFLP genotype groups (A1, A2, B) resolved using Bayesian analyses (Fig. 2).

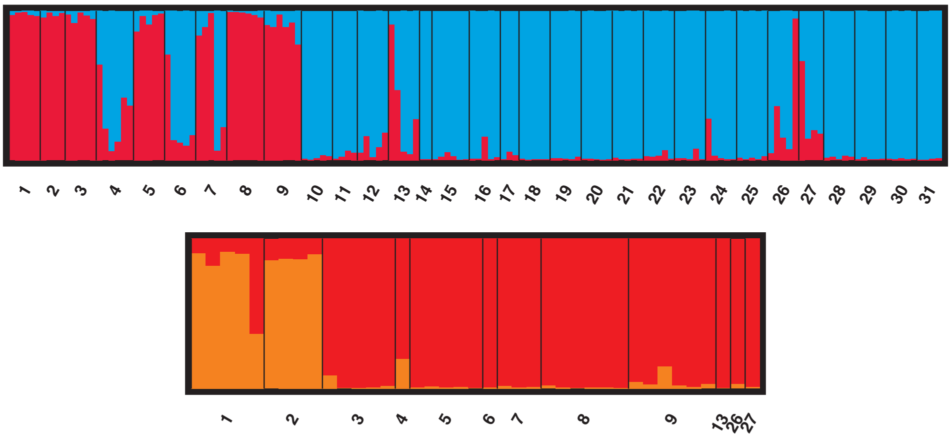

Fig. 2. – Graphical output of the Bayesian analyses showing the probabilities of (a) classifying all individuals in groups A and B; (b) classifying group A individuals in subgroups A1 and A2. Group colours are the same as in Fig. 1.

Fig. 3. – Frequency-down-weighted marker values for the 31 populations of *Lonicera nigra* studied. Dot sizes are proportional to the values (see Table 1 for exact values). The distribution of *L. nigra* in Europe is crosshatched.

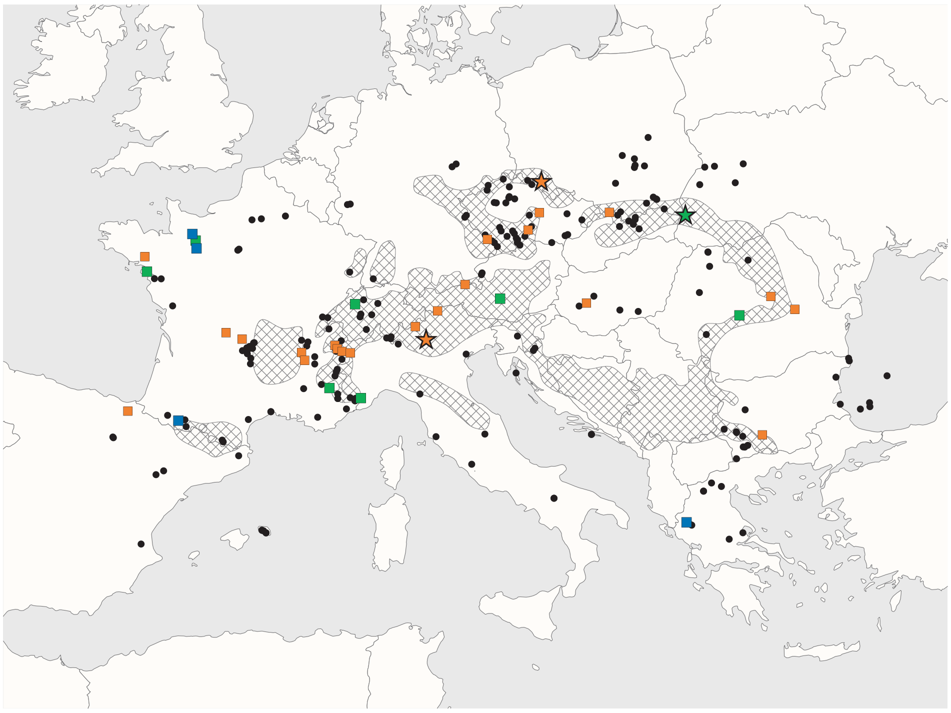

Fig. 4. – Locations in Europe from which the pollen data records studied came (absence of any *Lonicera* pollen – black dots, presence of *Lonicera sp.* pollen – squares, presence of *L. xylosteum*-type pollen – stars, Periodization: Pleniglacial – blue, Late-Glacial – green, Early Holocene – brown).

The re-sampled DW-index values ranged from 5.07 (population 5, Bavaria, Germany) to 8.83 (19, Českomoravské mezihoří Hills, Czech Republic), with an average of 6.29. The highest DW values were recorded in the Pyrenees (population 1, Catalan Pyrenees; 2, Andorra) and the Czech Republic (population 28, Doupovské hory Mts; 22, Českomoravská vrchovina Mts; 18, Rychlebské hory Mts). Populations with the lowest DW-values occurred primarily in the Alps (population 5, Bavaria, Germany; 3, Bern, Switzerland; 4, Vorarlberg, Austria), but also in the Carpathians (population 17, Moravskoslezské Beskydy Mts, Czech Republic; 16, Veľká Fatra Mts, Slovakia; 15, Spiš, Slovakia) and, surprisingly, on the Balkan Peninsula (population 9, Bjelašnica Mts, Bosnia and Herzegovina; 10, Bjelasica Mts, Montenegro). Two other populations with low DW-values were recorded on the western edge of the distribution range (population 27, Thuringia, Schleiz, Germany; 25, Slavkovský les Mts, Czech Republic) (Table 1, Fig. 3).

The Bayesian analysis of the complete dataset using STRUCTURE produced consistent results for only those runs in which K = 2 (similarity coefficient = 0.99, among 10 repeats; Fig. 2a). Individuals from the same population clustered together in the same group; only six populations [three populations from the Austrian Alps (population 4, Vorarlberg; 6, Lower Austria; 7, Steiermark), two from Germany (population 26, Gehlberg; 27, Schleiz) and one from the Eastern Carpathians (13, Hoverla Mt., Ukraine)] comprised a mixture of individuals that appeared in both groups (Fig. 2a). The first group (A; ‘Pyrenean-Alpine group’) includes the populations from the Pyrenees, the Alps, the western Balkan Peninsula and Thuringia (Germany). The easternmost individual of the group A was identified in the only mixed population in the Carpathians (population 13, Mt. Hoverla, Ukraine). The second group (B; ‘Balkan-Carpathian group’) includes all the populations located in the Czech Republic, the Carpathians (except one individual from Mt. Hoverla, see above) and the central part of the Balkan Peninsula. Some individuals were assigned by STRUCTURE to both groups A and B, but with different probabilities, suggesting they are of hybrid origin. These suspected hybrids were detected in mixed populations from Thuringia (population 26, Gehlberg; 27, Schleiz, Germany), the Alps (population 4, Vorarlberg, Austria) and the Eastern Carpathians (population 13, Mt. Hoverla, Ukraine). Each of these populations (except the population from Mt. Hoverla, Ukraine) is situated close to the border between the two clusters in Central Europe.

Bayesian analysis was repeated for each group separately. Analysis of group A produced consistent results for K = 2 (Fig. 2b) and separated populations from the Pyrenees (subgroup A1; ‘Pyrenean group’) from the rest of the group (subgroup A2; ‘Alpine group’). All models with higher K values produced inconsistent results with low similarity coefficients for the 10 runs. Analysis of group B revealed no structure (models for $K \geq 2$ produced results with very low similarity coefficients among runs).

The Mantel test resulted in a highly significant positive correlation between genetic and geographic distance (r = 0.276, P = 0.019), indicating an isolation-by-distance pattern. The AMOVA analysis revealed 36.78% variation among populations, whereas 63.22% was due to within-population variation (Table 2). The AMOVA analysis of groups based on the first STRUCTURE clustering results (Pyrenean-Alpine group vs. Balkan-Carpathian group) detected 13.43% variation between the two groups. Variation between the Pyrenean and Alpine groups was 24.27%, indicating a clear separation between these two regions.

Table 2. – Results of AMOVA (1,000 permutations) for (A) 150 individuals from 31 populations, (B) 150 individuals forming two clusters based on the first analysis using the program STRUCTURE (Pyrenean-Alpine vs. Balkan-Carpathian group), and (C) 38 individuals forming two clusters, based on the second analysis using STRUCTURE (Pyrenean vs. Alpine group). All values are highly significant ($P < 0.001$).

	Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	Fixation index F_{ST}
A	Among populations	30	925.20	4.71	36.78	
	Within populations	119	962.72	8.09	63.22	
	Total	149	1887.92	12.80	100.00	0.37
B	Among groups	1	117.08	1.86	13.43	
	Within groups	148	1759.47	11.97	86.57	
	Total	149	1876.55	13.83	100.00	0.13
C	Among groups	1	54.39	3.23	24.27	
	Within groups	36	362.38	10.07	75.73	
	Total	37	416.77	13.30	100.00	0.24

Palaeopalynological data

The palaeopalynological data (Fig. 4) confirmed the Pleniglacial presence of *Lonicera* in the north-western Pyrenees (Mardones & Jalut 1983), north-western France and Greece. Only the site in the Pyrenees is within the contemporary range of *L. nigra*. The presence of *Lonicera* pollen is documented at this site until the end of the Late-Glacial period. The other two Pleniglacial *Lonicera* pollen records are doubtfully for *L. nigra*.

During the Late-Glacial period, *Lonicera xylosteum*-type pollen (in the sense of Faegri & Iversen 1989) is documented only in the Eastern Carpathians (Poland, Tarnawa Wyżna; Ralska-Jasiewiczowa 1989), while *Lonicera*-type pollen grains are recorded for sites in the northern foothills of the Southern Carpathians (Romania, Avrig; Tantau et al. 2006) and at four sites along the entire length of the ridge of the Alps (Italy, Selle di Carnino and south-east France, Lac Saint Léger, Beaulieu, unpubl. data; Switzerland, Lobingensee, Ammann 1985; Austria, Dürrenecksee-Moor, Krisai et al. 1989). With the exception of the site at Avrig (where 14 Late-Glacial samples containing *Lonicera* pollen grains document the continuous presence of the genus at this locality), *Lonicera* pollen was confirmed just once at each site during the Late-Glacial period and just once during the Holocene.

Records of *Lonicera*-type pollen from the Early Holocene document its presence in the Bulgarian Rhodopes (Huttunen et al. 1992), the Carpathians (Rybníček & Rybníčková 2002, Tantau et al. 2003, 2009), the Bohemian Massif (Rybníčková 1974, Rybníčková & Rybníček 1988, Svobodová et al. 2002), the Alps (Rybníček & Rybníčková 1977, Oeggl 1988, Zoller et al. 1998, Clerc, unpubl. data) and the Massif Central (Guenet 1993). The *Lonicera xylosteum*-type from the Early Holocene in the sense of Moore et al. (1991) is recorded for the sandstone landscape of Broumovsko (Czech Republic; Pokorný & Kuneš 2005) and in the sense of Punt et al. (1974) in the Central Alps (Italy; Pini 2002).

Discussion

No plastid DNA variation detected in Lonicera nigra

Based on the molecular data there is little genetic variation in *L. nigra*. No variability was recorded in chloroplast DNA, although in many other species these regions are very variable (e.g. Shaw et al. 2005). Nevertheless, complete uniformity or very low variation of chloroplast non-coding regions at the continental scale is probably not exceptional as it has been recorded for *Carex pilosa* (Rejzková et al. 2008), *Corylus avellana* (Palmé & Vendramin 2002), *Fraxinus excelsior* (Heuertz et al. 2004), *Carex atrofusca* (Schönswetter et al. 2006) and *Carex curvula* (Pusçaş et al. 2008). The absence of genetic variation in *L. nigra* at northern latitudes (e.g. the Bohemian Massif) might be due to a rapid postglacial colonization resulting in homogeneity of cpDNA (cf. Hewitt 2004, Maliouchenko et al. 2007, Rejzková et al. 2008). However, in the case of this species no variation in chloroplast DNA has been recorded even in southern populations. Moreover, the extensive dispersal of the fleshy fruits of *L. nigra* could support the case of a rapid range expansion and lack of variation among populations, as is reported for several other taxa with fleshy fruits dispersed by birds or mammals (Mohanty et al. 2001, 2002, Hampe et al. 2003).

AFLP based phylogeographical pattern, delimitation of a contact zone

Although no variation in cpDNA was detected, AFLP analysis revealed a clear geographic structure in the variation, as three clusters of AFLP genotypes were identified using Bayesian clustering. The separation of the populations from the Pyrenees (confirmed by AMOVA analysis) is in accordance with their geographic isolation and presence of pollen of a *Lonicera* species in this area during the Pleniglacial and Late-Glacial periods. It is likely that plants from this refugium did not contribute to postglacial expansion into other parts of Europe. Similarly, a distinct genetic group of *Polygonatum verticillatum* is present in the Cantabrian Mountains (Kramp et al. 2009) and of *Alnus glutinosa*, *Fraxinus excelsior*, *Meum athamanticum* and *Rhinanthus angustifolius* in the Pyrenees (King & Ferris 1998, Hewitt 1999, Heuertz et al. 2004, Huck et al. 2009, Vrancken et al. 2009). While there is only a slightly different unique chloroplast haplotype of *Rhinanthus angustifolius* in the Pyrenean population; an analysis of AFLP data separates this population as a clearly differentiated group (Vrancken et al. 2009). On the Iberian Peninsula, there are also genetically different populations of several alpine plants, such as *Pritzelago alpina* (Kropf et al. 2003), *Cardamine alpina* (Lihová et al. 2009) and *Androsace vitaliana* (Dixon et al. 2009).

The remaining area of distribution of *L. nigra* is occupied by two genetically and geographically defined groups (Alpine and Balkan-Carpathian) separated by a contact zone in which there are mixed populations and individuals with intermediate genotypes (Fig. 1). This contact zone is located approximately in the upper part of the Danube Valley and reaches the north-western boundary of the distribution range of *L. nigra*. Towards the eastern part of Central Europe, the two above-mentioned genetic groups are divided by the Pannonian basin, which forms a natural barrier uninhabited by *L. nigra* due to inhospitable environmental conditions. This contact zone of *L. nigra* is present in a similar area to that of other plant species such as *Festuca pratensis* (Fjellheim et al. 2006) and *Rhinanthus angustifolius* (Vrancken et al. 2009). The contact zone between two main haplotype lineages of *Rosa pendulina* is also suggested to lie in the Danube Valley (Fér et al. 2007); however, subsequent analyses of the AFLP pattern in this species showed that the contact zone is wider, reaching the southern boundary of Austria (Daneck et al., in preparation).

Because admixed populations of *L. nigra* occur only south of the Danube and at the north-western edge of its range, it is hypothesized that the postglacial expansion from the contemporary northern or north-western part to the southern area of the range (Balkan-Carpathian lineage) reached the Danube Valley more quickly than the Alpine genetic lineage, which migrated from the south or southwest. Thus, it seems that only individuals from the Balkan-Carpathian genetic lineage crossed the Danube Valley, which probably constitutes a barrier to range expansion. In addition, it is also likely that the contemporary contact zone was established by the leading-edge colonization phenomenon (Hewitt 1993, 2004), suggesting that the northward migration of the Alpine lineage was prevented by the colonization of suitable habitat by the Balkan-Carpathian lineage.

Location of glacial refugia

Frequency-down-weighted marker values, which indicate long-standing isolation and consequent accumulation of rare markers, were used to detect divergent populations (Schönswetter & Tribsch 2005, Paun et al. 2008). This isolation may also indicate in situ glacial survival rather than a postglacial population origin. High DW values for some Central European populations (19, Českomoravské mezihoří Hills; 22, Českomoravská vrchovina Mts; 18, Rychlebské hory Mts) may thus indicate glacial survival of *L. nigra* in this area. Indeed, the presence of glacial refugia in Central Europe is suggested (based on molecular data) for several plant and animal species, e.g. *Saxifraga paniculata* (Reisch et al. 2003), *Cochlearia bavarica* (Koch 2002), *Carex pilosa* (Rejzková et al. 2008), *Clethrionomys glareolus* (Deffontaine et al. 2005) and *Ursus arctos* (Sommer & Benecke 2005).

Fossil pollen indicates that species of *Lonicera* occurred in Central Europe during the Late-Glacial period and Early Holocene. Nevertheless, this evidence should be considered only as indicative and supplementary, as this pollen data does not allow unambiguous determination of the species. The majority of the evidence refers only to the genus (*Lonicera*-type), but in three cases [the sandstone landscape of Broumovsko, Czech Republic (Pokorný & Kuneš 2005), the Eastern Carpathians (Ralska-Jaszewiczowa 1989), and Italian Central Alps (Pini 2002)] it is specific to *L. xylosteum*-type. The data for the *Lonicera xylosteum*-type from the Late-Glacial (Fig. 4) indicate possible glacial refugia for species of *Lonicera* in the Eastern Carpathians. On the other hand, the Early Holocene occurrences suggest either a very rapid postglacial spread or the glacial survival of *Lonicera* in the Bohemian Massif, and in the Alps and Carpathians, with subsequent population growth at the start of the warm period.

In addition, the genus level pollen evidence supports the hypothesis that some species of *Lonicera* survived in glacial refugia situated along the edge of the Alps. This accords with the existence of Central European glacial refugia for montane forest species and even some temperate broadleaf species (Willis et al. 2000, Jankovská & Pokorný 2008). In landscapes, where the topography is rugged, it is likely that most glacial refugia were located in mountain valleys or deep gorges, which offer protection against cold winds and where there is a high mesoclimatic humidity (Jankovská & Pokorný 2008).

In conclusion, molecular and palaeopalynological data indicate that *Lonicera nigra* may have survived in Central European glacial refugia located in the Carpathians and/or in the eastern perialpine region. Additional refugia north or south of the Alps or on the Balkan Peninsula cannot be excluded, but it was not possible to address this hypothesis using the data set presented. This data also indicates that despite low overall differentiation, the postglacial spread occurred along at least two migratory routes, which resulted in the contact zone in Central Europe.

See http://www.preslia.cz for Electronic Appendix 1, 2.

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Souhrn

Fylogeografická studie temperátního druhu *Lonicera nigra* L. (*Caprifoliaceae*) byla provedena s využitím molekulárních a pyloanalytických údajů, jejichž zastoupení v datových souborech pokrývá celý současný areál tohoto taxonu se zaměřením na oblast střední Evropy. Ačkoli sekvenování chloroplastové DNA odhalilo pouze jediný haplotyp v rámci druhu *L. nigra*, AFLP data vykazují genetickou variabilitu a její nenáhodné geografické uspořádání. Pro analýzu molekulárních dat byla použita Bayesova shluková analýza, jejíž výsledky ukazují rozdělení současného areálu druhu na dvě hlavní části (A; Pyrenejsko-Alpská a B; Balkánsko-Karpatská skupina) s kontaktní zónou probíhající zhruba v údolí horní části toku Dunaje. Doplňující analýza dále vyčlenila populace z Iberského poloostrova jako samostatnou geneticky odlišnou skupinu. Přestože pyloanalytická data nebylo možno určit na úroveň druhu, poukazují ve shodě s výsledky molekulárních analýz na možnost, že některé populace *L. nigra* mohly přečkat klimaticky méně příznivá období čtvrtohor v glaciálních refugiích ve střední Evropě. Důkaz na základě pylu je ovšem nutno pokládat za pouze doplňkový, vzhledem k nemožnosti přesného taxonomického rozlišení pylových zrn v rámci rodu *Lonicera*.

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Electronic Appendix 1: Sites used for the map in Fig. 4

Sites used for the map (Fig. 4) from PALYCZ database: http://botany.natur.cuni.cz/palycz/ (locality and latitude/longitude in brackets)

Anenské údolí (50.5887/16.1175), Barbora (48.9558/14.8333), Bláto (49.0417/15.191), Borkovická blata (49.2328/14.6327), Brentenlohe (49.7872/12.4625), Červené blato (48.8608/14.8102), Dvůr Anšov (48.7773/16.4225), Fláje - Kiefern (50.6829/13.5799), Horní Pole (49.2132/15.3148), Hozelec (49.0464/20.332), Hrabanovská Černava (50.2164/14.8316), Hůrecká slaĢ (49.1522/13.3276), Chrást (50.2603/14.5441), Jablůnka (49.3833/17.95), Jedlová (49.397/19.6605), Jestřebské blato (50.5989/14.6047), Kameničky (49.7387/15.9636), Klíčava (50.1462/13.833), Knížecí pláně (48.9646/13.635), Komořanské jezero (50.5351/13.5184), Kožlí (49.3601/14.0209), Liptovský Ján (49.0417/19.6778), Loučky (49.3242/15.5336), Mělnický úval (50.2993/14.5781), Mokré louky (South) (49.0022/14.778), Nad Dolským mlýnem (50.8523/14.3387), Palašiny (49.6813/15.478), Plešné jezero (48.7767/13.8657), Podhořany (49.2492/20.4708), Praha-Podbaba (50.1125/14.3917), Rokytecká slať (49.0153/13.4122), Rybárenská slať (49.0313/13.4619), Řásná (49.2306/15.3708), Řežabinec (49.2502/14.0897), Spišská Belá (49.1847/20.45), Šafárka (48.882/20.575), Švarcenberk (49.1456/14.7048), Velanská cesta (48.7748/14.9283), Vernéřovice (50.6217/16.1958), Vlčí rokle (50.6045/16.1284), Vracov (48.9778/17.2052), Weiherlohe (49.7297/12.3875), Zbudovská blata (49.0748/14.349), Zlatnická dolina (49.5167/19.2833)

Sites used for the map (Fig. 4) from EPD database: http://www.europeanpollendatabase.net/ (locality and latitude/longitude in brackets)

Aegelsee (46.6458/7.5433), Algendar (39.9406/3.9586), Altenweiher (48.0133/6.9944), Ampoix (45.6333/2.9333), Amsoldingersee (46.725/7.575), Amsoldingersee (46.725/7.575), Arkutino Lake (42.3667/27.7333), Aronde (49.4625/2.6911), Auneau (48.4561/1.7936), Avrig (45.7167/24.3833), Balladrum (46.0167/8.75), Banyoles (42.1333/2.75), Basse-Ville (47.1861/-1.8581), Bedlno (51.2042/20.2833), Bellefontaine (46.5753/6.0931), Besbog (41.75/23.6667), Biot (43.8/7.1), Black Sea (South) (42.0675/28.485), Black Sea (Southwest) (42.0675/28.8889), Black Sea (Southwest) (42.1842/28.9167), Black Sea (West) (42.8333/29.9167), Boehnigsee Goldmoos (46.2592/7.8431), Bois de la Masse (45.5/2.7333), Bois des Gardes (45.4167/2.7), Brugiroux (45.1472/2.8489), Burgmoos (47.1722/7.6744), Cala Galdana (39.9369/3.965), Cala'n Porter (39.8706/4.1314), Clapeyret (44.1472/7.2389), Col des Lauzes (45.7692/6.5333), Col du Pré (45.6892/6.6106), Colfiorito (43.025/12.925), Correo (44.5083/5.9831), Cristol Lake (44.9975/6.6333), Czajkow (50.7833/21.2833), Dry Lake II (42.05/23.5333), Dürrenecksee moor (47.1667/13.8667), Edessa (40.8181/21.9525), Embouchac (43.5664/3.9167), Etang d'Ouveillan (43.2667/3), Etang du Lautrey (46.5872/5.8639), Fuchsschwanzmoos (47.1167/13.9), Giannitsa B (40.6667/22.3167), Gorno (50.85/20.8333), Grand Ratz de Pellet (45.3417/5.6083), Grande Briere (47.3667/-2.25) Grosses Überling Schattseit-Moor (47.1667/13.9), Halos I (39.1667/22.8333), Hieres sur Amby (45.7908/5.2833), Hirschen Moor (47.8333/8.0917), Holzmaar (50.1167/6.8833), Hort Timoner (39.875/4.1264), Hoya del Castillo (41.25/0.5), Iezerul Calimani (47.3278/25.2736), Ioannina (39.65/20.9167), Ioannina (39.7625/20.7306), Ioannina II (39.6919/20.8397), Ivano-Frankovskoye (49.9167/23.7667), Jasiel (49.3728/21.8869), Jaslo (49.7833/21.4667), Khimaditis Ib (40.6167/21.5833), Khimaditis III (40.6125/21.5861), Kletnia Stara (51.635/21.6792), Krumpa (51.3/11.85), Kupena (41.9833/24.3333), La Taphanel (45.2744/2.6792), La Vie (48.5483/-0.2583), Lac Couve (45.6964/6.5347), Lac de Chambedaze (45.4506/2.8778), Lac de Perle (44.1417/7.6), Lac de Siguret (44.7917/6.55), Lac Long Inférieur (44.0578/7.45), Lac Mouton (44.0578/7.4447), Lac Noir (45.4536/2.6272), Lac Saint (44.42/6.3364), Lacs Noels (44.9731/2.8589), Lago dell'Accesa (42.9864/10.8833), Lago di Martignano (42.1167/12.3333), Lago Grande di Mont (40.9444/15.6), Lago Grande di Mont (40.9444/15.6), Lago Padule (44.2986/10.2147), Laguna Guallar (41.4/-0.2167), Lake Bala (46.8183/17.735), Lake Balaton (Centr (46.7444/17.4008), Lake Balaton (North (47.0017/18.1042), Lake Duranunlak (43.6667/28.55), Lake Racou (42.5542/2.0083), Lake Shabla-Ezeretz (43.5833/28.55), Lake Varna (Belosla (43.2/27.8333), Lake Xinias (39.05/22.2667), Le Fourne (48.4444/-0.1917), Le Grand (45.4733/5.4167), Le Grand Etang de S (44.35/5.2333), Le Marais St Boetie (49.6167/3.8167), Le Monal (45.5569/6.9286), Le Mont (45.5514/6.5489), Les Echets (45.8333/5), Les Saisi (45.7372/6.4769), Lignin Lake (44.1042/6.7086), Lignin Lake (44.1042/6.7086), Lobsigens (47.0319/7.2992), Loras (45.6639/5.2444), Lutiniere (46.4444/-0.8622), Madic (45.35/2.45), Mareuge (45.6219/2.8997), Meerfelder Maar (50.1/6.75), Mohos (46.0833/25.9167), Moulin de (45.8497/1.6458), Navarrés (39.1/0.6833), Peuil Peat Bog (45.125/5.6436), Peyreleva (45.7083/2.3833), Pla de Llacs (42.1742/-2.4769), Place du Commerce (47.2139/-1.5561), Plan du Clou (45.6997/6.5392), Plan du Jeu (45.6072/6.5322), Plan du Lac (45.3153/6.8167), Plan du Laus (44.2417/6.7022), Plateau de Prarion (45.8847/6.7494), Pré Rond (44.9189/6.5942), Puerto de (43.0333/-2.05), Puscizna Rekowianska (49.4833/19.8167), Puy de Pailleret (45.5167/2.8167), Rotsee (47.0756/8.3256), Roztoki (49.7167/21.5833), Sabbion (44.13/7.4733), Saint Julien de Rat (45.35/5.6233), Saint Sauveur (43.5664/3.9167), Saint-Urs (48.5194/-0.2533), Selle di (44.15/7.6944), Serrent (47.8094/-2.4681), Schwemm (47.65/12.3), Slopiec (50.7833/20.7833), Solokiya (50.4167/24.1667), Son Bou (39.9247/4.0272), Starniki (50.2667/26.0167), Stoyanov 2 (50.3833/24.6333), Suchedniow (51.05/20.85), Szymbark (49.6333/21.1), Tarnawa Wyżna (49.1/22.8333), Tarnowiec (49.7/21.6167), Tourbiere de Bresle (49.4/2.25), Tourves (43.5/5.9), Trumer Moos (47.9333/13.0667), Tschokljovo Marsh (42.3667/22.8333), Vallée de la Voise (48.4167/1.75), Vallon de Provence (44.3911/6.4042), Venice (45.5/12.25), Vitosha Mountains P (42.8333/23.8333), Voros-mocsar (46.4772/19.1908), Wasenmoos beim Zell (47.9833/13.1), Wolbrom (50.3833/19.7667), Zalozhtsy (49.75/25.45), Zirbenwal (46.8583/11.025), Zsombo Swamp (46.3614/19.9942)

Electronic Appendix 2: Additional sites

Additional sites which were not included in the PALYCZ and EPD datasets and which were used for pollen analyses. Abbreviations: Per. – periodisation, PG – Pleniglacial, LG – Late-Glacial, EH – Early Holocene.

Country	Site	Altitude (m)	Latitude	Longitude	Reference	Per.
Bulgaria	Lake Kremensko-5	2124	41.72° N	23.53° E	Atanassova & Stefanova 2003	LG
Bulgaria	Sedmo Rilsko lake	2095	42.22° N	23.31° E	Bozilova & Tonkov 2000	LG
Bulgaria	Ribno Banderishko	2190	41.73° N	23.47° E	Tonkov et al. 2002	LG
Bulgaria	Mozgovitsa	1800	41.42° N	23.12° E	Tonkov 2003	EH
Bulgaria	Lake Trilistnika	2216	42.2° N	23.32° E	Tonkov et al. 2006	LG
Croatia	Malo Jezero	23	42.78° N	17.36° E	Jahns & van den Bogaard 1998	EH
Croatia	Veliko Jezero	23	42.78° N	17.36° E	Jahns & van den Bogaard 1998	EH
Croatia	Lake Vrana (core VRA96)	40	44.85° N	14.38° E	Schmidt et al. 2000	LG
France	La Borde	1660	42.5° N	2.06° E	Jalut 1971	EH
France	Estarres	356	43.09° N	-0.38° W	Jalut et al. 1988	PG
France	Castet	850	43.03° N	0.37° E	Jalut et al. 1988	PG
France	Bious	1550	42.83° N	0.45° E	Jalut et al. 1988	LG
France	Biscaye	409	43.11° N	0.07° E	Mardones & Jalut 1983	PG
Germany	Zöchsen	100	51.38° N	12.05° E	Litt 1992	LG
Italy	Lago del Segrino	374	45.83° N	9.26° E	Gobet et al. 2000	LG
Italy	Pian di Gembro	1350	46.17° N	10.17° E	Pini 2002	LG
Romania	Steregoiu	790	47.81° N	23.54° E	Björkman et al. 2003	LG
Romania	Ponor	1020	46.64° N	22.83° E	Bodnariuc et al. 2002	EH
Romania	Iezerul Calimani	1650	47.33° N	25.27° E	Farcas et al. 1999	LG
Romania	Taul Zanogutii	1840	45.33° N	22.8° E	Farcas et al. 1999	LG
Romania	Preluca Tiganului	730	47.82° N	23.54° E	Feurdean & Bennike 2004	LG
Romania	Turbuta	275	47.37° N	23.5° E	Feurdean & Bennike 2004	LG
Romania	Bisoca	875	45.53° N	26.82° E	Tantau et al. 2009	EH
Slovenia	Griblje	160	45.57° N	15.28° E	Andrić 2007	LG
Slovenia	Mlaka	150	45.5° N	15.21° E	Andrić 2007	EH
Slovenia	Na mahu 1	-	45.98° N	14.54° E	Andrić et al. 2008	LG
Spain	Pla de Llacs	430	42.17° N	-2.48° W	Pérez Obiol 1988	LG
Spain	Sidera	440	42.16° N	-2.46° W	Pérez Obiol 1988	EH
Switzerland	Alpe Palü	1940	46.37° N	10.01° E	Zoller et al. 1998	EH
Switzerland	Lago di Muzzano	337	46° N	8.93° E	Gobet et al. 2000	LG
Switzerland	Hinterburgsee	1515	46.72° N	8.07° E	Heiri et al. 2003	LG
Switzerland	Balladrum	483	46.02° N	8.75° E	Hofstetter et al. 2006	LG
Switzerland	Bay of Geneve	357	46.23° N	6.17° E	Moscariello et al. 1998	LG
Switzerland	Lago di Origlio	416	46.06° N	8.95° E	Tinner et al. 1999	PG

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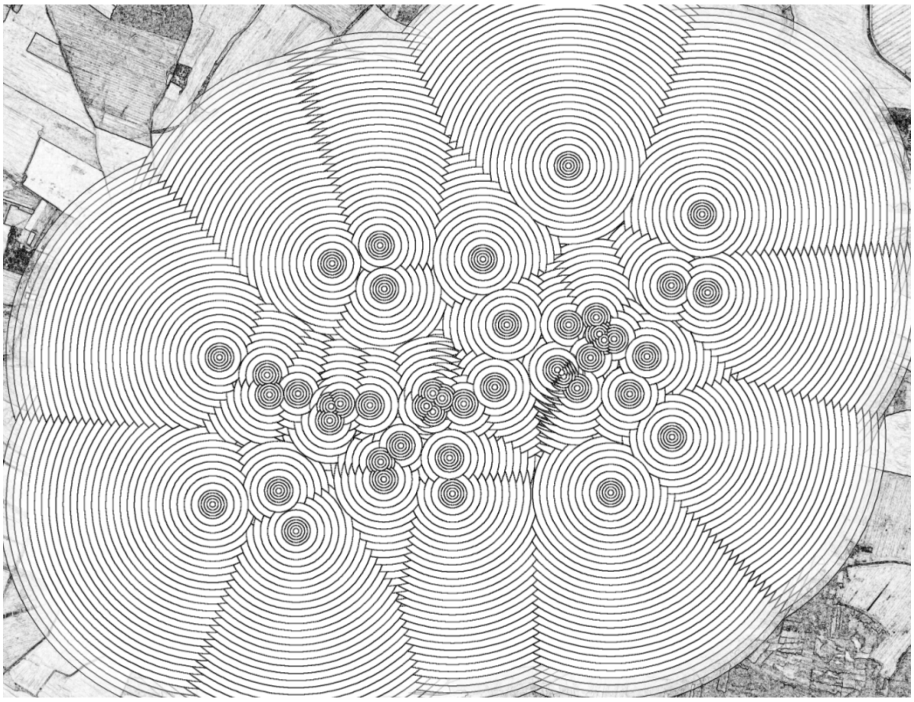

Chapter 3: pollen productivity estimates

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Research paper

Relative pollen productivity estimates in the modern agricultural landscape of Central Bohemia (Czech Republic)

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ABSTRACT

We estimated relative pollen productivity estimates (PPE), key parameters for the quantitative interpretation of pollen data, for 13 taxa using modern pollen assemblages from 54 sites and recent vegetation data. Vegetation mapping in the area covered a minimum radius of 2 km around each sampling site. Vegetation data were weighted by the Prentice model, i.e. weighting by distance and by the dispersal deposition parameters of different pollen types. PPE values were calculated by three submodels of the Extended R value model. ERV 1 produced the best goodness of fit. The PPEs for *Urtica* and *Sambucus nigra* are published here for the first time, and the PPE for the Chenopodiaceae represents the first estimate for Europe. Values for the other ten taxa (Poaceae, *Pinus*, *Salix*, *Fraxinus*, *Quercus*, *Tilia*, *Artemisia*, *Plantago lanceolata*, *Alnus* and Cerealia) are comparable with or fall within the ranges of values published in previous studies. Herb taxa produce ca 3 11 times more pollen than the Poaceae. Herbs produce even more pollen than trees, whose production is 1 6 times higher than that of the Poaceae. The lowest pollen producers are the Cerealia, producing 20 times less pollen than the Poaceae. Our estimate of the relevant source area of pollen (RSAP) of 1050 m is relatively high compared to other studies in semi open landscapes. This is possibly caused by the uneven pattern of some taxa in the vegetation mosaic (*Pinus*, *P. lanceolata*, *Salix* and *Alnus*). The distance of 1100 m, at which all taxa are present around each site, is similar to the RSAP distance (1050 m).

1. Introduction

The fossil pollen record can trace different environmental factors that caused vegetation changes in the past such as humans or the climate (Pokorný, 2005; Skrzypek et al., 2009). When the goal of palynological research is to know past vegetation abundances, it is critical to understand modern pollen vegetation relationships that can be used as a basis for quantitative vegetation reconstruction. One of the key parameters in this relationship is pollen productivity. Only percentage data are available for a majority of Czech pollen profiles (Kuneš et al., 2009), so we had to deal with relative pollen productivity, which is expressed as "relative pollen productivity estimates", hereafter referred to as PPE. The theoretical framework of its calculation was established with the introduction of the Extended R value model (further referred to as the ERV model; Parsons and Prentice, 1981; Sugita, 1994), in combination with the maximum likelihood method (Prentice and Parsons, 1983; Bunting et al., 2004), can be used to estimate the relevant source area of pollen (RSAP; Sugita, 1994). This is a breakthrough in pollen analysis because it makes estimates of pollen productivity much more appropriate and allows for the study of the effects of vegetation structure on pollen deposition (e.g. Hellman et al., 2009a). Hence, pollen data become the temporal and spatial proxy for the vegetation.

The complexity of the relationship between vegetation and the pollen assemblage is influenced not only by the surrounding vegetation and pollen productivity but also, for example, by the taphonomy and the dispersive characteristics of individual pollen types or atmospheric conditions. Dispersion and deposition of pollen can be described using these factors as parameters in a mechanistic model. In our study, we used the Prentice model (Prentice, 1985), which is applied as distance weighting for all taxa on vegetation data. This means that not only distance (the highest importance is given to the vegetation growing close to a site) but also taxon specific pollen dispersal properties (e.g. fall speeds) are taken into account.

Both the ERV model and the Prentice model were theoretically developed around the 1980s, but their use has risen mainly in the last decade. PPEs have now been calculated for many regions of Europe (Broström et al., 2008) as well as for North America (e.g. Calcote, 1995), Africa (Duffin and Bunting, 2007) and Asia (Li et al., 2011). In combination with the Landscape Reconstruction Algorithm (Sugita, 2007a,b) or the MultiScenario Approach (Bunting and Middleton, 2009), vegetation abundances have been estimated from the fossil pollen record in the Swiss Plateau (Soepboer et al., 2010), Southern Scandinavia (Nielsen

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and Odgaard, 2010; Kuneš et al., 2011) and northern England (Bunting et al., 2008).

The aim of the present study is to explore the relationship between pollen and vegetation in Central Bohemia and to produce reliable PPEs. Besides an early pioneer study in Bohemia (Križo, 1958), the modern pollen vegetation relationship has been studied only in the forested mountain ranges along the state border using pollen traps (Pidek et al., 2010). Our interest, however, lies rather in quantifying past human environment interactions in the central part of the country. This region has the longest human occupation history in all of Bohemia, which is also the reason why we focused on taxa classified as anthropogenic indicators (Behre, 1981). In Central Bohemia, archaeological exploration coupled with many pollen cores from abandoned meanders of the river Labe. All those studies offer a unique opportunity to combine archaeological knowledge with palaeoecological evidence of human impacts (Dreslerová and Pokorný, 2004).

A robust estimation of the relevant source area of pollen (Sugita, 1994) is critical for obtaining correct PPEs. However, the RSAP for sites of the same basin size under fixed atmospheric conditions is not controlled by different pollen productivity or the fall speed of individual taxa (Bunting et al., 2004), as one could expect, but by the spatial structure of the vegetation mosaic, as has been shown by previous simulations (Sugita, 1994; Sugita et al., 1999; Bunting et al., 2004; Broström et al., 2005; Gaillard et al., 2008; Hellman et al., 2009a,b). Since the spatial pattern and structure of vegetation affects the estimates of the RSAP using the ERV models, the two following assumptions have to be considered carefully in order to obtain reliable results. First, the ERV model requires vegetation heterogeneity to produce site to site variability in pollen loading, which is necessary for parameter estimation by the maximum likelihood method. The difference between heterogeneity and homogeneity is defined by the size of the patches surrounding a sedimentation basin their size should be larger than the size of the basin. Second, the ERV model requires similar overall proportions and patch sizes of major plant taxa among the regions of the sites included into the study (Sugita, 1994). If pollen is sampled from moss polsters in the real landscape, then the first assumption can be met easily. The second, however, is not easy to meet even in a single study region, where the composition of taxa can differ among patches. Thus, the second aim of the present paper is to examine the properties of the vegetation structure in the real landscape in consideration of their possible influence on the ERV model. Some of these properties (e.g. patch size, position of the sample within the patch) have already appeared as parameters in some past simulations (Sugita, 1994; Sugita et al., 1999; Bunting et al., 2004; Broström et al., 2005; Gaillard et al., 2008; Hellman et al., 2009a,b), so we aim to discuss the results from simulations and the real landscape in order to find the key parameter of the vegetation mosaic which controls the RSAP. We can summarize the aims of this paper as follows: (i) to calculate PPEs for the agricultural landscape of Central Bohemia, (ii) to explore the distance of the RSAP and find the main factor influencing it, and (iii) to discuss the relationship between the vegetation mosaic and the sampling strategy and its possible effect on the ERV model.

2. Methods and data collection

2.1. Taxon specific distance weighting

Prior to comparing vegetation with pollen data, vegetation can be weighted by either distance alone or by distance together with dispersal and deposition properties of different pollen types, which is what we have done by employing the Prentice model (Prentice, 1985). The Prentice model describes pollen dispersion by simplifying its transport from the source in the plane dimension, as if pollen is released at the same height as samples are collected, which means that tree pollen is assumed to come from the same height as pollen of herbs. The most important driver of pollen transport is wind above the tree canopy under neutral atmospheric conditions with no turbulences. The deposition basin is assumed to be a circular opening in the vegetation canopy without any source plants within the basin. Our parameters of the Prentice model were set as follows: (i) The deposition basin was a moss polster of 1 m in diameter, within which pollen does not mix. (ii) The wind speed was 2.5 m/s according to the year average for the region (Czech Hydrometeorological Institute, 2005). (iii) The pollen fall speeds were set to previously published values listed in Table 1. Values for four pollen taxa *Urtica*, the Chenopodiaceae, *Artemisia* and *Sambucus nigra* type were newly calculated according to Stoke's law (Gregory, 1961) using measurements of pollen grain diameters of each morphological type (Table 1). The density of pollen grain was set to 1 g/cm^3, the density of air to 0.00127 g/cm^3 and the viscosity of air to 0.00019 g/cm.s, following the settings of Broström et al. (2004). The pollen grains of *Urtica*, the Chenopodiaceae and *Artemisia* were assumed to be spherical. The fall speed of *S. nigra* type pollen was corrected using Falck's correction for ellipsoidal particles (Gregory, 1961; Duffin and Bunting, 2007). The cumulative value of distance weighted plant abundance at a certain distance from a sample (i.e. along a concentric ring), which is the sum of all rings inside it, not only depends on the model settings described above but also on the widths of the inner rings. We followed the suggestion of Broström et al. (2004) and set the ring width similarly. The ring widths were 0.5 m (between 0.5 m and 1 m), 1 m (between 1 m and 6 m), 2 m (between 6 m and 12 m), 4 m (between 12 m and 20 m), 10 m (between 20 m and 100 m) and 50 m (between 100 m and 2000 m). The taxon specific distance weighted plant abundance using the Prentice model was calculated automatically using the programme ERV.Analysis.v1.3.0.exe (Sugita unpubl.).

Table 1
Pollen types in the vegetation survey with basic parameters and a list of plant species included with overall percentages in the whole area of the vegetation survey. The fall speed of pollen was taken from previous studies or calculated according to Stoke's law (Gregory, 1961). The diameter of pollen grains was taken from: (1) (Beug, 2004) the average of intermediate values of species found in the Czech Republic; and (2) (Punt and Malotaux, 1984) intermediate values of a glycerol preparation.

Species	Pollen taxa	Diameter of pollen grains (μm)	Fall speed (m/s)	Reference cited for fall speed of pollen
Urtica dioica 99%, *Urtica urens* 1%	*Urtica*	15.50^2	0.007	This paper
Poaceae 100%	Poaceae		0.035	(Sugita et al., 1999)
Triticum sp. 98%, *Hordeum vulgare* 2%	Cerealia undif.		0.06	(Gregory, 1961)
Artemisia vulgaris 99%, *Artemisia absinthium* 1%	*Artemisia*	22.38^1	0.014	This paper
Chenopodium album 29%, *C. hybridum* 1%, *Amaranthus retroflexus* 60%, *Atriplex patula* 5%, *A. sagittata* 5%	Chenopodiaceae	25.45^1	0.019	This paper
Plantago lanceolata 100%	*Plantago lanceolata*-type		0.029	(Broström et al., 2004)
Tilia cordata 98%, *T. platyphyllos* 2%	*Tilia*		0.032	(Gregory, 1961)
Salix alba 95%, *S. caprea* 4%, *S. fragilis* 1%	*Salix*		0.022	(Gregory, 1961)
Alnus glutinosa	*Alnus*		0.021	(Sugita et al., 1999)
Fraxinus excelsior	*Fraxinus*		0.022	(Sugita et al., 1999)
Pinus sylvestris 95%, *P. nigra* 5%	*Pinus*		0.031	(Sugita et al., 1999)
Sambucus nigra 99%, *S. racemosa* 1%	*Sambucus nigra*-type	18.5×22.5^1	0.013	This paper

2.2. ERV analysis

To establish a relationship between pollen and vegetation, the spatial scale of the source area of pollen from similar sized sites has to be defined. This area is usually described as a radius from a sampling point or pollen core. The pollen coming from plant individuals within this radius contributes to the calculation of relative pollen productivity; pollen coming from beyond this radius is called background pollen (Andersen, 1970; Prentice, 1985). We used an already established Eq. (1) to represent this relationship (Prentice, 1985; Sugita, 1994).

$$y_{ik} = \alpha_i x_{ik} + \omega_i \tag{1}$$

Two sets of parameters are included in the linear equation for individual taxa (i) and sites (k): the slope of the equation (α), hereafter referred to as alpha, and the intercept, referred to as the background (ω). The independent variable in the linear equation is distance weighted plant abundance (x). Taking pollen loading (i.e. pollen counts) as the dependent variable (y), alpha represents pollen productivity relative to a reference taxon in the ERV models (Parsons and Prentice, 1981; Sugita, 1994). ERV models can correct for non-linear relationships between pollen and vegetation proportions (Fagerlind, 1952; Prentice and Webb, 1986) and provide reasonable estimates of alphas for individual taxa. These tasks of ERV models are integrated in the programme ERV.Analysis.v1.3.0.exe (Sugita unpubl.). For every distance, the programme solves the equation iteratively and records the likelihood function score as the goodness of fit between the data and the ERV model (Prentice and Parsons, 1983). The lowest likelihood function score represents the best goodness of fit. The distance at which the likelihood function score reaches the asymptote and does not improve any further is the radius delimiting the area of the background component and the relevant source area of pollen – the RSAP (Sugita, 1994). This distance was estimated by linear regression within a moving window between the log-likelihood (i.e. support function of the likelihood function score (Bunting et al., 2004; Sugita, 2007b)) and distance (length of the moving window). This method tests whether the slope of the regression line is statistically different from zero (Gaillard et al., 2008). We used the programme RSAP.estimate.MWLR.v1.0.exe (Sugita unpubl) with a 300 m long moving window. PPEs are then taken from the model with the lowest likelihood function score. The ERV model has three submodels, which differ in the input data and in the definition of the background component. ERV submodels 1 and 2 use pollen and vegetation proportions. ERV submodel 1 assumes that the background pollen percentage for each taxon is constant among sites (Parsons and Prentice, 1981). ERV 2 assumes that background pollen deposition at each site is a constant proportion of the total vegetation abundance surrounding each site to the total pollen loading of all taxa. ERV submodel 3 deals with pollen proportion and vegetation composition in absolute units (see below) and assumes constant background pollen loading among all sites (Sugita, 1994). For the purpose of the ERV 3 model, vegetation data were entered as the proportion of given taxa in a ring area including areas producing no pollen ("absolute vegetation abundance"). For the purposes of ERV 1 and ERV 2, vegetation data were entered as the proportions of given taxa in the sum of the areas of all selected taxa excluding areas producing no pollen (further referred to as the "vegetation proportion"). The programme weights these vegetation proportions using the Prentice model (Prentice, 1985) and then it again recalculates the weighted values for the proportions to ensure that the sum at each site equals to 1. These proportions, once weighted, are inserted into the ERV model and are hereafter referred to as "weighted vegetation proportions" to prevent any confusion. After the application of the ERV models, when the relationship between pollen and vegetation becomes linear, the naming of the two variables differs according to each of the ERV submodels: ERV 1 (pollen proportion, adjusted vegetation proportion), ERV 2 (adjusted pollen proportion, weighted vegetation proportion) and ERV 3 (relative pollen loading, absolute vegetation abundance).

2.3. Study area

The Košátecko region is a 50 km^2 area situated in the agricultural landscape of Central Bohemia. Elevation ranges between 180 and 280 m a.s.l. The geological bedrock is formed by Upper Cretaceous sandstones. Quaternary deposits vary from humolite to fluvial sands and clays at the bottom of valleys. Climatic conditions are characterized by long (50–60 days), warm (18–19 °C) and dry summers (350–400 mm), a very short transitional period before a slightly warm to warm autumn (7–9 °C), and a short (30–40 days), moderately warm (−2–3 °C) and dry to very dry winter (200–250 mm) (Quitt, 1970). The annual average wind speed varies from 2 to 3 m/s. Seasonal average wind speeds vary from 2–2.5 m/s in the summer and autumn to 2.5–3 m/s in spring and winter (Czech Hydrometeorological Institute, 2005).

Around 45% of Central Bohemia is covered by arable land. The half of all crops cultivated in Central Bohemia are cereals (excluding maize) with the following composition (average from years 2006, 2007 and 2008): rye (2.3%), oats (2.5%), barley (34.2%), triticale (3.2%) and wheat (57.8%) (Czech Statistical Office, 2009). The modern agricultural landscape is a mosaic of patches with varying openness and degrees of human influence. The basic landscape matrix is a mixture of arable fields where cereals prevail over vegetable cultivation. Villages Byšice, Čečelice, Kojovice, Krpy and Košátky host many ruderal and synanthropic species (e.g. *Artemisia vulgaris*, the Chenopodiaceae, *Rumex*, *Plantago lanceolata*). It is to be noted that the general trend concerning the expansion of nitrophilous taxa (van der Maarel, 2005; Csathó et al., 2007) (e.g. *Fraxinus*, *Sambucus nigra*, *Urtica*) is accentuated in this area by the fertilization of fields. The majority of woodland patches are formed by plantations of spruce and pine. Alluvial woodlands, oak–hornbeam, lime–oak and acidophilous oak woods are the only natural vegetation remaining, dispersed as small woodland fragments.

2.4. Pollen data

54 moss samples were collected for pollen analysis in the field by stratified random sampling in all vegetation formations (forests, meadows, baulks, ruderal sites and alluvial vegetation) present in the sampling area of 3 × 4 km where suitable material for pollen analysis was available (mosses, litter, soil from non-arable habitats). Soils from arable fields were assumed to be too mixed for the purposes of pollen analysis, so fields were sampled from grassy baulks between them. The minimum distance between each sample was 30 m. The position of every site was recorded using a GPS device with the precision of ± 5 m. All moss samples were treated by standard acetolysis (Moore et al., 1991). Pollen extracts were stored in glycerol and counted under 400× magnification to a minimum of 500 grains per sample. In each pollen sample, all sporo- and palynomorphs were identified using pollen keys (Reille, 1992, 1995, 1998; Beug, 2004).

2.5. Vegetation data

Vegetation data were obtained during the summer of 2008. Vegetation mapping was done in an area of ca 8 × 7 km, whose entire surface was surveyed thoroughly to ensure that each sampling point has a minimum 2 km buffer area around it (Fig. 1). Vegetation units, patches with same vegetation composition in the whole area, were distinguished in the field and immediately drawn into an orthophoto map. Plant abundance was estimated visually as the percentage cover

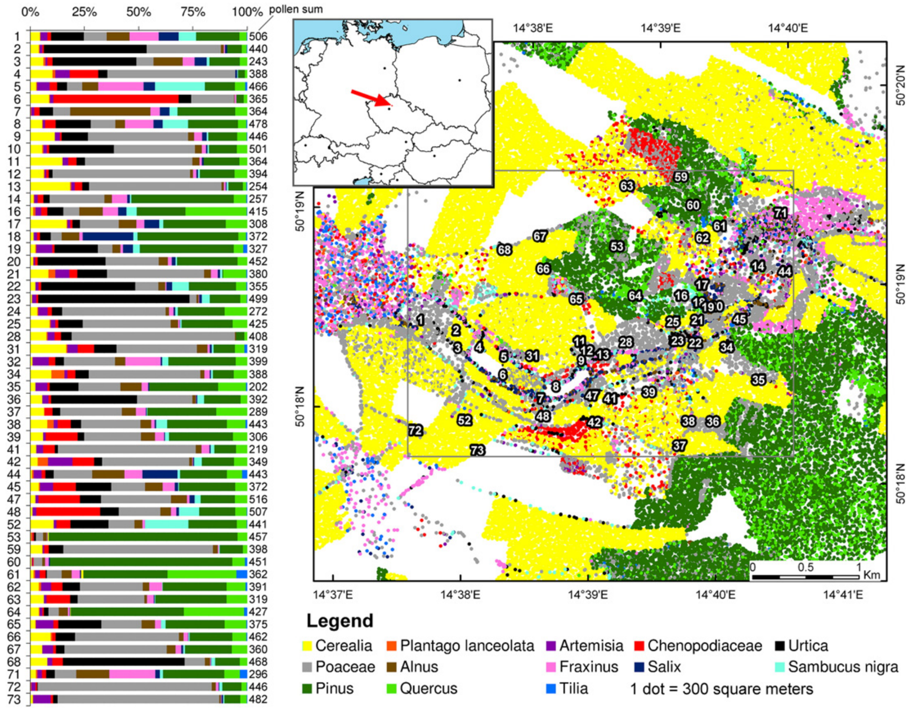

Fig. 1. Representation of taxa in pollen assemblages and the vegetation survey. The red arrow points to the location of the study area in Central Europe. The grey rectangle represents the sampling area, and the numbers are IDs of samples included in the ERV analysis. Vegetation cover density corresponds to the density of the dots. One dot represents 300 m^2 of a given taxon. White colour represents the vegetation cover formed by taxa that were not included in the survey (e.g. *Solanum tuberosum* or *Helianthus annuus*) or areas producing no pollen.

within each vegetation unit. Total cover values may exceed 100% because there are multiple vegetation layers. Species in the field were grouped into 24 pollen taxa.

The vegetation map was digitalized, creating a vector GIS layer, which is hereafter referred to as the "single part vegetation layer". The area occupied by each vegetation unit in every concentric ring was measured in ESRI ArcInfo version 9.2 by intersecting the single part vegetation layer with the ring layer. Attribute tables were loaded into R version 2.13.0, which proved to be the most efficient software package for handling matrices before and after the ERV analyses (area recalculation, plotting).

2.6. Taxa selection

24 taxa and 54 sites were entered into a two step selection analysis of taxa. First, we weighted the vegetation data for a maximum distance of 2000 m from the sites to ascertain the representation of all taxa in the pollen assemblages and their weighted vegetation proportions. The criterion for selecting a plant taxon was its presence in both the pollen assemblages and the surveyed vegetation at 27 or more sites (Broström et al., 2004). After the exclusion of taxa with too many zero values in the pollen or vegetation data, we checked the variation of weighted vegetation proportions. For instance, trees can contribute significantly to the sum of pollen; however, their individuals grow relatively far away from the sites. This usually causes a high background component (von Stedingk et al., 2008), which can decrease the reliability of PPE (Parsons and Prentice, 1981). We therefore introduced an additional criterion to prevent weak representation in the vegetation data: at the RSAP distance obtained during the preliminary ERV run, a minimum threshold of 0.0013 for weighted vegetation proportion had to be fulfilled by anemogamous trees at no less than 27 sites. Areas occupied by excluded taxa were considered as areas producing no pollen.

2.7. Analysis of the sampling pattern in the vegetation mosaic

The recommended and most often used way to place pollen sampling sites into the vegetation structure in pollen vegetation studies is random sampling. As shown by simulations, a random sampling design can prevent a non asymptotic pattern in likelihood function scores, so it can control RSAP and influence the final PPE (Broström et al., 2005). We thus tested whether our 54 stratified data points are clumped, dispersed or randomly placed within the sampling area of 3 × 4 km using the average nearest neighbour method. This method measures the distance between each point and its nearest neighbour. It then averages all these distances. If the average distance is smaller than the average for a hypothetical random distribution, the distribution of the points being analysed is considered to be clustered. If the average distance is greater than a hypothetical random distribution, the features are considered to be dispersed (Ebdon, 1985).

The second analysis focused on the description of the vegetation mosaic in order to obtain its quantitative parameters, which can be compared with simulated landscapes or used for their future creation. First, patches in our vegetation mosaic were classified into 8 groups according to size. As an approximation of the patches, polygons from the single part vegetation layer were considered. The classifying condition was that every size class had to contain the same number of patches. Vegetation data from the GIS layer were recalculated in the same way as the vegetation proportion for the ERV input (see above). We then calculated the following values for each patch class: mean percentage of selected taxa, mean number of taxa, mean diversity and mean evenness. As a measure of diversity and evenness we used Shannon's diversity index and Shannon's evenness (Shannon, 2001) following Hellman et al. (2009a). The number of taxa in all patches was calculated by converting the vegetation data to presence or absence.

The third analysis deals with the sampling design and the vegetation structure simultaneously. The relationship between the locations of the samples and the vegetation structure influences the result of the ERV analysis. For example, systematic sampling in the centre of patches can cause a non asymptotic pattern in the likelihood function scores and pose problems for the estimation of RSAP distances (Broström et al., 2005). For this reason, we tested the position of our stratified samples within the vegetation patches. First, we took patches occupied by sampling points and found centroids for each of them. Then, 54 random samples were generated within the same rectangle which envelopes the position of the samples in the area of 3×4 km. Finally, in each of these three layers of points stratified, centriod and random we measured the shortest distance between each point and the border of the closest vegetation patch. We then compared these distances among the three datasets by one way t tests at the alpha level of 0.05.

The fourth analysis examined the vegetation structure, measuring vegetation characteristics with increasing distance from the samples. The first approach considered each ring separately, so the increasing distance is labelled as “ring distance from samples”. In the second approach, the information from the inner ring was passed cumulatively to the outer ring, as when the vegetation is weighted, then the increasing distance is labelled as “distance from samples”. For both approaches, we used vegetation data from the ERV input, defined above as vegetation proportions. In order to scrutinize possible biases produced by stratified sampling, we extracted the vegetation data by the same means also from the random dataset used in the previous analysis. First, for both datasets (stratified and random) and all taxa, we visually compared the curves of mean ring Shannon diversity, mean ring evenness and mean ring vegetation proportion with increasing ring radius. We calculated the standard error for each mean value. The curve of mean ring vegetation proportions shows that the vegetation structure is related to the position of the sampling points, i.e. the mean distribution of patches with increasing distance from sampling points. If the curve shows no trend for common taxa, the vegetation structure is supposed to be stationary (Burrough, 1995). A no trend pattern of the mean curve can be produced not only by a homogeneous structure but also by a heterogeneous structure with many sites and sample spacing corresponding to the grain size. So, a heterogeneous structure sampled randomly, but with very small sampling area, can result to non stationary. The way this can happen is that rings of the same size containing different sites overlap each other, so they replicate the same parts of the mosaic, strengthening any pattern in the vegetation structure. In the case of some rare taxa, an initial increase can appear, which means that a larger area and distance from the sampling point are necessary to attain a mean for rare taxa in the mosaic. The purpose of the second approach to vegetation structure analysis is to find distances at which each taxon becomes present around all sites selected by stratified and random sampling. We therefore added vegetation proportions of inner rings to the vegetation proportions of outer rings for both datasets and converted them to presence/absence data, where every non zero value was taken as a presence.

3. Results

3.1. Selection of taxa

The following taxa (presence in pollen/presence in vegetation/ presence in pollen and vegetation) were excluded from the analysis since they were present in pollen and vegetation only at less than 27 sites: *Plantago media major* type (14/53/14), *Polygonum aviculare* (10/53/10), *Rumex acetosa* type (23/53/23), *Cornus mas* (12/53/12), *Ulmus* (19/35/12) and *Prunus* type (17/53/17). *Prunus* type pollen from 17 non zero pollen sites had the best variation in weighted vegetation proportion (0 0.3) of the taxa mentioned above, but it could not be included in our dataset because its pollen appeared at less than half of the sites.

The RSAP in the preliminary ERV 1 run was 1300 m. At this distance, we found a very low variation of weighted vegetation proportion of some anemogamous trees. The following taxa were therefore excluded from the second run (their range of pollen proportions/ number of sites at which the weighted vegetation proportion is higher than 0.0013): *Betula* (0.01 0.37/25), *Picea* (0 0.3/9), *Carpinus* (0 0.02/0), *Fagus* (0 0.02/0) and *Corylus* (0 0.08/7) since their weighted vegetation proportion was higher than 0.0013 at only less than half of all sites (<27). In the end, the ERV analysis was run with 13 taxa and 54 sites.

The pollen sums of the thereby included taxa comprise 49 85% of the original pollen sum at each site (these reduced pollen sums are listed in Fig. 1), which is sufficient for the ERV model, following Broström et al. (2004) and Mazier et al. (2008). These reduced pollen sums are mainly caused by the exclusion of *Betula* and *Picea*.

3.2. Vegetation mosaic

Stratified samples within the sampling area show a random pattern according to their mean distance from the nearest neighbour sample (223 m), which is not significantly different ($p = 0.9$) from the mean distance of the nearest neighbour in the hypothetical random dataset (220 m). Sample distances from the nearest patch border are on average 21 m, which is significantly lower than the mean distance for randomly generated dataset of 38 m ($p = 0.004503$). Our pollen samples are also significantly closer to the patch border than centroids, whose average distance is 44 m ($p = 0.005701$).

Table 2
Patch size classification to groups with the same number of patches. Abbreviations: G1 — *Salix*, *Alnus*, *Fraxinus*, *Sambucus nigra*-type, *Urtica*; G2 — *Plantago lanceolata*-type, Chenopodiaceae, *Artemisia*, *Tilia*.

								Percentage of each taxon within the classes					
Size class	Average size (ha)	Percentage in whole area	Number of samples	Number of patches	Diversity	Evenness	Count of taxa	*Quercus*	*Pininus*	Poaceae	Cerealia	G1	G2
0–0.23 ha	0.1	0.3	2	76	0.64	0.53	3.10	5	2	43	6	37	6
0.23–0.4 ha	0.3	1	8	76	0.62	0.51	3.12	11	2	42	3	39	4
0.4–0.7 ha	0.5	1	5	77	0.67	0.52	3.13	8	9	37	6	35	5
0.7–1 ha	0.8	2	8	75	0.62	0.51	3.01	5	8	40	5	38	3
1–1.6 ha	1.3	3	4	77	0.58	0.48	2.85	3	16	30	15	33	3
1.6–3 ha	2.2	5	5	75	0.56	0.45	2.79	6	18	38	15	20	4
3–8.5 ha	5	12	11	76	0.47	0.39	2.58	7	21	21	37	11	4
8.5–160 ha	30.6	75	11	77	0.41	0.36	2.46	5	18	5	66	3	3
Total		100	54	609									

The 476 different communities inhabit 609 patches of very different sizes (Table 2). The area of the intermediate sized patches, ranging from 0.4 to 3 ha (between the first and second quartile), occupies only 11%, whereas the majority of the area under survey (75%) consists of polygons larger than 8.5 ha. Vegetation composition changes with increasing patch size. The largest polygons are dominated by cereal fields and pine forests. As patch size decreases, Shannon's diversity and evenness as well as the mean number of taxa increase for the Poaceae, *Salix*, *Alnus*, *Fraxinus*, the *Sambucus nigra* type and *Urtica*.

The mean ring vegetation proportion shows a slight increasing trend in *Pinus* and *Tilia* with increasing distance from hypothetical random sites (Fig. 2, dashed line). Rare taxa (i.e. *Urtica*, *Artemisia* and partly *Plantago lanceolata*) increase rapidly within the first 80 m and then show no trend. The rest of the taxa do not exhibit any marked trend taking into account the standard errors and barring local fluctuations. The curve of the mean ring vegetation proportion for all taxa overlaps between the stratified random dataset and the random dataset from 500–750 to 2000 m (taking into account overlapping standard errors). Between 0 and 500–750 m, we can distinguish three types of patterns for both curves: (1) The first type is shared by *Quercus*, *Tilia* and the Chenopodiaceae because both curves of vegetation proportion for stratified and random sampling overlap and do not show any decreasing or increasing trend. (2) The second type is represented by Cerealia and *Pinus*, two vegetation dominants, which have a general increasing trend and gain a higher vegetation proportion by random than by stratified sampling. (3) An inverse pattern with a higher vegetation proportion obtained by stratified than by random sampling is observed in the rest of the taxa: *P. lanceolata*, the Poaceae, *Alnus*, *Salix*, *Sambucus nigra*, *Fraxinus*, *Urtica* and *Artemisia*. Differences between sites in vegetation proportion for each of the taxa and in each ring are shown by standard error bars (Fig. 2). Their length

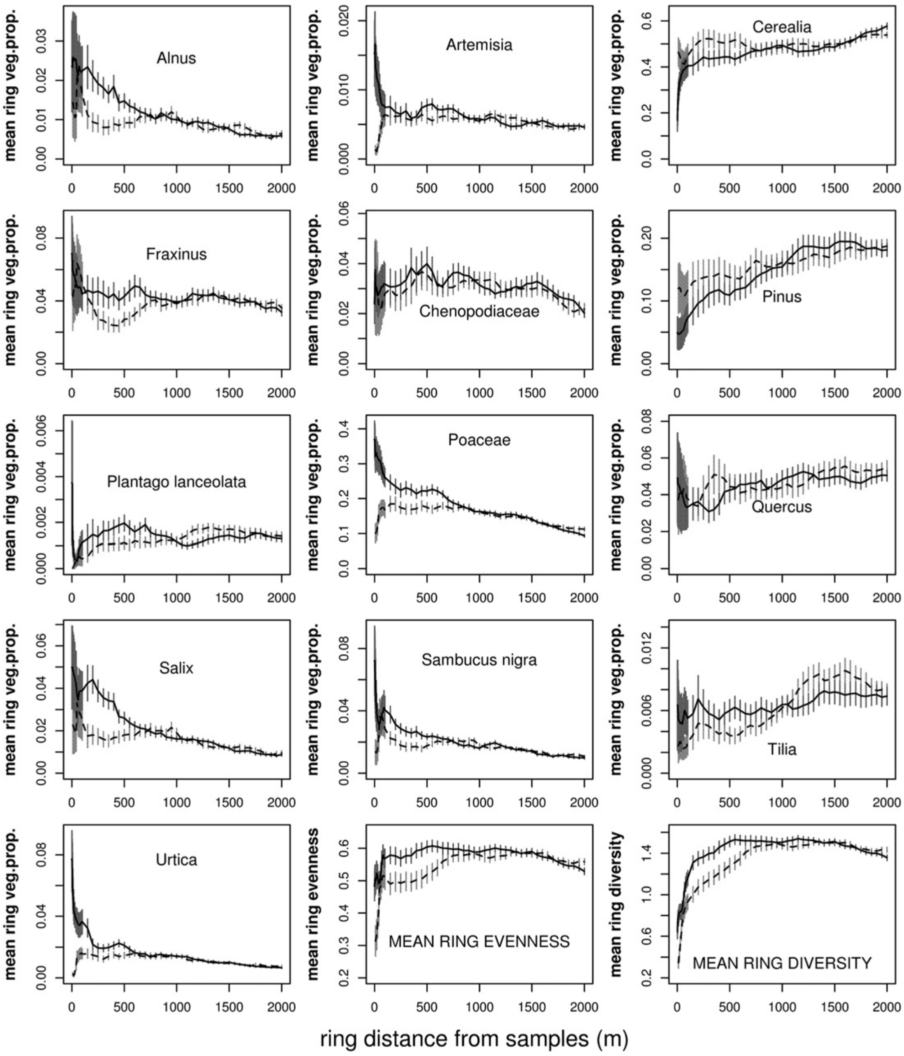

Fig. 2. Mean ring vegetation proportion for each taxon, mean ring Shannon's diversity index and mean ring Shannon's evenness with increasing distance from sampling sites. Solid line: stratified samples included in the ERV model; dashed line: hypothetical random samples. All values are calculated/taken from vegetation proportion for all rings at all sites and then averaged.

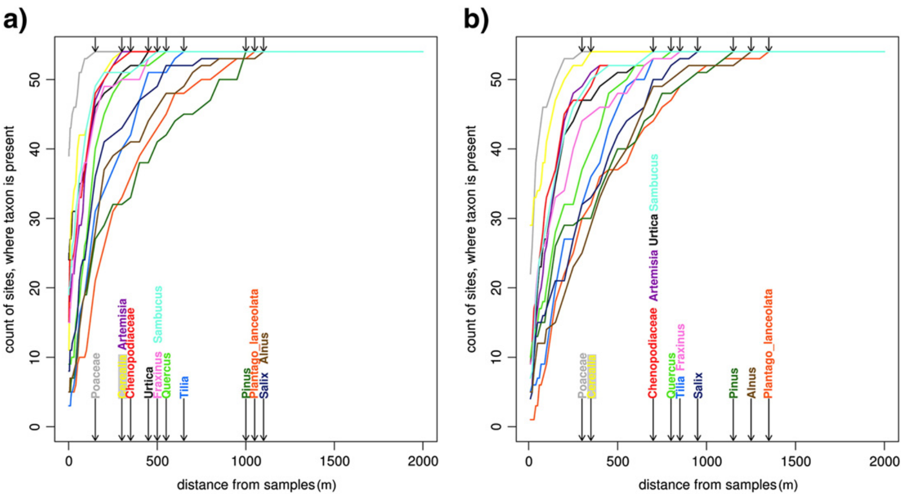

Fig. 3. Presence of taxa around sites with increasing distance from samples. The arrows point to the distance at which taxa become present around all sites. (a) — stratified samples, included in the ERV model, (b) — hypothetical random samples. The colour of each taxon corresponds to the colours used in Fig. 1.

is decreasing with increasing distance for both datasets. There are no substantial differences in the size of the error bars between both data sets. The average vegetation cover around the sites from random and stratified sampling is ca 80% and continually decreases to 68%. Mean ring Shannon's diversity and mean ring evenness increase up to 550 m, and both begin to decrease at 1500 m. The curve of evenness oscillates at the beginning and decreases in some sites between 20 and 50 m. The random dataset is less even and diverse until 600 m compared to the stratified one.

Distances at which all taxa become present around all sites do not differ substantially between the random (1350 m) and the stratified dataset (1100 m) (Fig. 3). However, distances for the hypothetical random dataset are 50 400 m larger than for the hypothetical stratified sampling dataset depending on the taxon. The only exception is *Salix* because it becomes present around all random sites within a smaller radius (950 m).

3.3. Relevant source area of pollen (RSAP)

The distance at which the likelihood function score reaches the asymptote varies between 1050, and 1300 m depending on the ERV model used (Fig. 4). Model 1 shows a much lower likelihood function score than ERV 2 and 3, meaning that it has the best goodness of fit between the model and the dataset (Sugita, 1994). This is why the RSAP of the study area is 1050 m and results from ERV 1 are selected for further comparison.

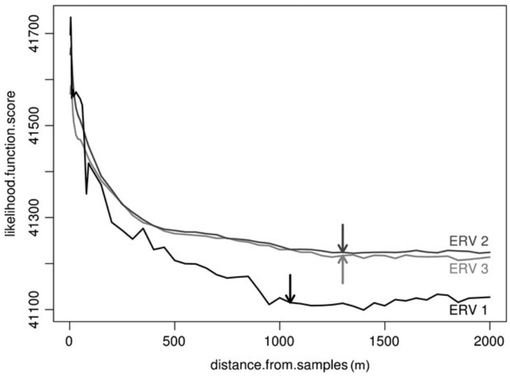

Fig. 4. Likelihood function score plot for different ERV models. The arrows show the radius of the RSAP identified by the moving window linear regression approach.

3.4. Pollen vegetation relationship

Fig. 5a shows the pollen vegetation relationship for selected taxa. Poaceae, Cerealia, *Quercus*, *Pinus* and *Urtica* have the longest gradients, ranging from 0 to 0.9, of pollen and/or weighted vegetation proportion. In the upper intermediate range are *Fraxinus* (0 0.7), *Alnus* (0 0.6) and *Salix* (0 0.5), while *Sambucus nigra* type and the Chenopodiaceae are in the lower intermediate range with values around 0 0.4. Taxa with the shortest range up to 0.15 are *Tilia* and *Artemisia*, the *Plantago lanceolata* type reaching only up to 0.08. The only continual gradients in terms of pollen and weighted vegetation proportion were for the Poaceae, *Urtica*, Cerealia, *Artemisia* and *Fraxinus*. The gradient of tree taxa is rather discontinuous; however, the ERV corrects the relationship in all taxa very well. Pollen productivity estimates are calculated relative to the Poaceae, which are set to 1. This decision was based on the fact that Poaceae is an intermediate pollen producer (Parsons and Prentice, 1981) and has good pollen and vegetation representation at all sites (Broström et al., 2004). The highest background components (Fig. 5b) are present in Poaceae 0.17 and *Pinus* 0.15. *Alnus*, *Quercus*, Cerealia and *Urtica* have intercepts between 0.04 and 0.05, while the rest of taxa have less than 0.02.

Alpha values and their standard deviations beyond the RSAP showed little variation. In order to smooth this variation out, final pollen productivities and their standard deviations (Table 3) were obtained by averaging all alpha values and standard deviations from the RSAP distance to the maximum extent of the vegetation survey (2000 m), following e.g. Soepboer et al. (2007).

4. Discussion and conclusions

4.1. Sampling and vegetation mosaic

4.1.1. The size of the sampling area

The absolute area of 56 km^2 of the vegetation survey ranks among the smaller areas used in other PPE studies (Broström et al., 2008). The area is rather small also in relation to the grain of landscape

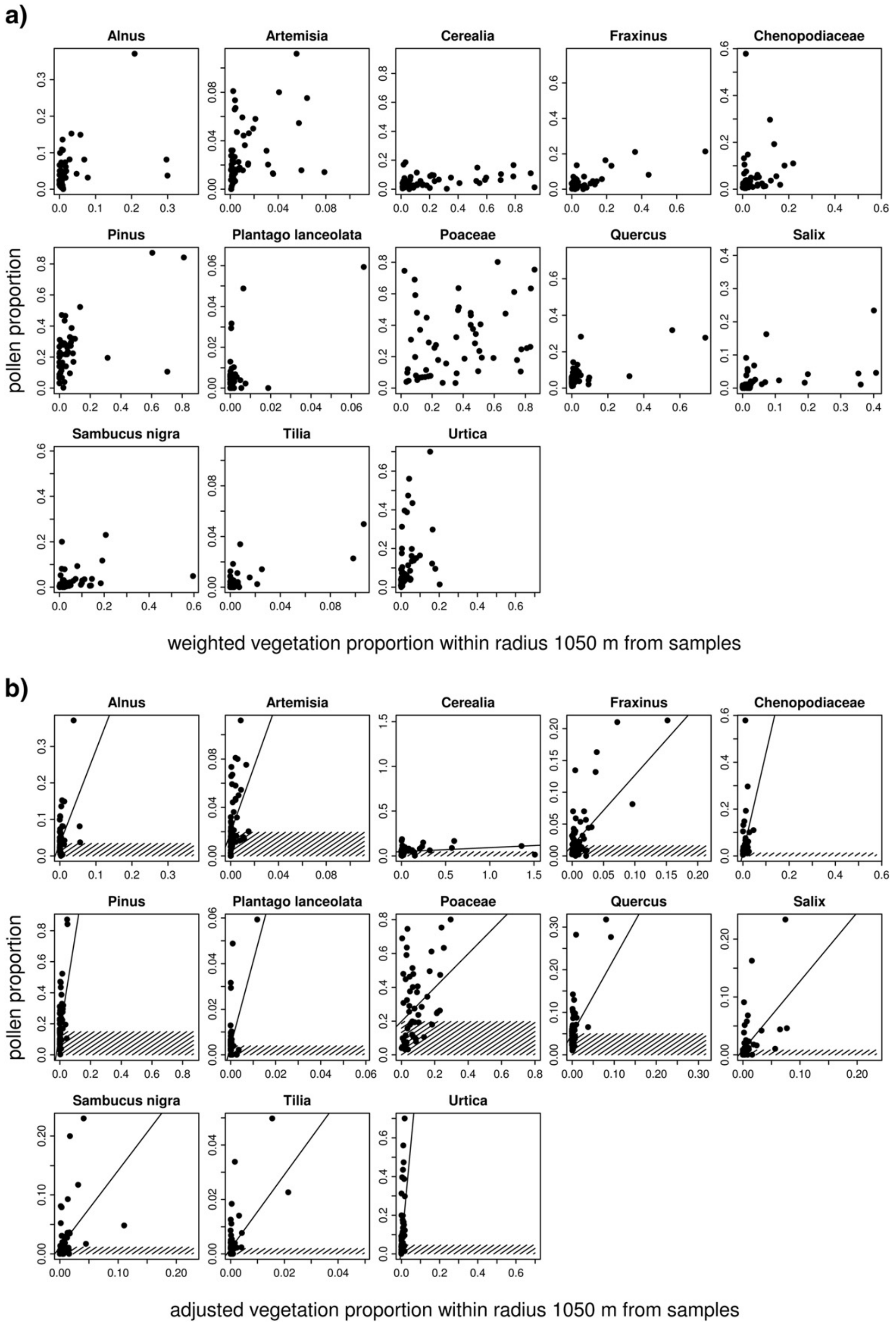

Fig. 5. Scatter plots of pollen and vegetation data within a 1050 m radius. (a) Pollen proportions and weighted vegetation proportions. These vegetation data were recalculated to vegetation proportions (see Section 2.2), weighted using the Prentice model (see Section 2.1) and again recalculated to proportions so that the sum at each site equals to 1. Note the same scale limits of both axes. Note that each taxon has a different scale. (b) Pollen proportions and adjusted vegetation proportion. The slope of the line represents pollen productivity, and its intercept, which is depicted by shading, represents the background component. Pollen proportions/percentages in Figs. 1, and 5a and b are of the same values.

Table 3
Comparison between pollen productivity estimates (with their standard deviations) calculated in this study and values published in previous studies (see citations in Section 4.5). Source data: Mazier, personal communication.

Region	Central Bohemia	Finland	C Sweden	S Sweden	England	Swiss Jura	Estonia	Denmark	Swiss Plateau
ERV model	ERV 1	ERV 3	ERV 3	ERV 3	ERV 1	ERV 1	ERV 3	ERV 1	ERV 3
Alnus	2.56 (0.32)			4.20 (0.14)	8.74 (0.35)		13.93 (0.15)		
Artemisia	2.77 (0.39)						3.48 (0.20)		
Cerealia	0.0462 (0.0018)			3.20 (1.14)			1.60 (0.07)	0.75 (0.04)	0.00076 (0.0019)
Fraxinus	1.11 (0.09)			0.67 (0.03)	0.70 (0.06)				1.39 (0.21)
Chenopodiaceae	4.28 (0.27)								
Pinus	6.17 (0.41)	8.4 (1.34)	21.58 (2.87)	5.66 (missing, 0.00)			5.07 (0.06)		1.35 (0.45)
Plantago lanceolata	3.70 (0.77)			12.76 (1.83)				0.90 (0.23)	0.24 (0.15)
Poaceae	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)
Quercus	1.76 (0.20)			7.53 (0.08)	5.83 (0.00)		7.39 (0.20)		2.56 (0.39)
Salix	1.19 (0.12)		0.09 (0.03)	1.27 (0.31)	1.05 (0.17)		2.31 (0.08)		
Sambucus nigra-type	1.30 (0.12)								
Tilia	1.36 (0.26)			0.80 (0.03)					
Urtica	10.52 (0.31)								

mosaic because the heterogeneous vegetation structure even with hypothetical random sampling has produced slight general trends in vegetation proportion of some taxa, especially trees (*Pinus* and *Tilia*). RSAP areas around some sites overlap, so we had to take note of this repeated sampling of the vegetation mosaic. Possible biases arise from the replicated vegetation samples because plant individuals come from an area of only 22 km^2; this is an area 10 times smaller than if there were no overlaps (216 km^2), so it has to be kept in mind that any differences among local population (in species composition or pollen productivity) are potentially enlarged.

4.1.2. Sampling strategy

All taxa except *Quercus*, *Tilia* and the Chenopodiaceae show different trends in mean ring vegetation proportion. The close surroundings of the sampling sites are to a larger extent covered by alluvial woodlands or ruderal communities (higher abundance of *Alnus*, Poaceae, *Salix*, *Sambucus nigra*, *Urtica*, *Artemisia* and *Plantago lanceolata*) and less by cereal fields and pine plantations (Fig. 2). This pattern is caused rather by stratified sampling than by repeated sampling (small sampling area) because the curve of the stratified dataset is much more different from the no trend pattern than the curve of the random dataset, although both factors do contribute. Our stratified sampling avoided cereal fields due to the absence of mosses and thus suitable material for pollen analysis. Instead, we preferred grassy baulks (Poaceae, *Artemisia*, *P. lanceolata*, etc.) and also small patches and sites close to the patch border, which provided a more suitable material. These sites have higher evenness and diversity than sites selected randomly. This sampling strategy allowed us to obtain a good representation of the majority of the taxa under study, especially the rare ones. It, however, produced some non stationary patterns in the vegetation data. There are two kinds of such patterns. The first is site to site variation in the overall proportion of all taxa, which is shown as standard error in Fig. 2. Their presence itself already contradicts the ERV assumption of similar overall proportions of major taxa because this variation causes biases in alpha values (Sugita, 1994). However, these standard errors are not substantially larger than standard errors resulting from random sampling. We can thus reckon that, in this case, stratified random sampling does not introduce any additional error to our ERV results above the error that would be introduced by random sampling. The second kind of non stationarity, which shifts weighted vegetation proportion, is represented by trends exhibited by some taxa. The interaction between this non stationarity and the ERV model together with possible biases must be the subject of future simulations.

Random sampling in such an uneven landscape includes more sites located in very large patches of one or two taxa (e.g. cereal fields and pine plantations). We are, nevertheless, aware that this does not satisfy the criteria for selecting sites and major taxa into the ERV analysis; Brostrom et al. (2004) describes that no species should have zero values in vegetation and/or pollen data within more than half of the sites. This could eventually cause a non asymptotic pattern in the likelihood function score. Similarly, a non asymptotic pattern of the likelihood function score has already been observed in simulations in which sites were placed systematically in the centre of grassland patches in a semi open landscape (Broström et al., 2005) or when sites were placed randomly in a very uneven semi open landscape (Hellman et al., 2009a). It therefore seems that stratified sampling was the only way to obtain PPE values for our 13 taxa structured in such an uneven landscape mosaic a combination of large patches with one or two taxa and small patches containing high diversity.

4.2. Relevant source area of pollen

RSAP varies between 1050 and 1300 m depending on the ERV model used. This estimate is similar to those found in open agricultural regions in Denmark and the Swiss Plateau or even semi open landscape of the eastern Baltic region. All these studies, however, were dealing with lake sediments (Nielsen and Sugita, 2005; Soepboer et al., 2007; Poska et al., 2011). Similar RSAP values of ca 1000 m were obtained by Räsänen et al. (2007) from moss polsters in the tundra ecosystem of northern Finland. We expected much smaller RSAPs, comparable with studies based on material from moss polsters in open or semi open landscapes, such as 400 m in an agricultural landscape, 300 m in a pastoral landscape (Broström et al., 2005) or 450 m in a forest tundra ecotone (von Stedingk et al., 2008). This relatively small RSAP in the case of Broström et al. (2005) could result from the exclusion of trees in their data, but this can hardly be taken as the only possible explanation because von Stedingk et al. (2008) included trees.

Our relatively large RSAP could be explained by the vegetation structure. Broström et al. (2005) worked in Southern Sweden, where the size of the largest patch was 30 ha, whereas in our study this is the average patch size for 75% of the area. This is because some rare taxa that occupy small patches can turn up, due to large patches in between them, further away from the sampling sites. Therefore, the other important factor affecting the size of the RSAP is the positioning of samples within vegetation patches. The suggestion of Hellman et al. (2009b) that the longer the distance from each sampling site needed to obtain sufficient cover of all taxa within the landscape, the larger the RSAP fits our observations. Moreover, this “sufficient cover” in our case means simply “the presence of all taxa at each site” because the distance (1100 m) at which all sites contain all the taxa under study is similar to the RSAP distance (1050 m). By comparing these distances from Fig. 3 with the map of vegetation structure (Fig. 1), we can conclude that taxa becoming present around all sites within smaller distances are evenly dispersed in the landscape structure. By contrast, taxa requiring larger distances to become present around all sites are unevenly clumped in some part of the mosaic. This fact is not influenced by the total abundance of the taxon, so we can find similar distances for rare (e.g. *Plantago lanceolata*) and dominant taxa (e.g. *Pinus*). The most unevenly distributed taxa in our study are *Pinus*, *P. lanceolata*, *Salix* and *Alnus*. The distance obtained by stratified sampling (1100 m), at which all taxa become present around all sites, is not substantially different from the distance obtained by randomly distributed samples (1300 m) (Fig. 3). We can thus conclude that our RSAP is not affected by the non-random sampling strategy.

4.3. Prentice model

We obtained good ranges of pollen and weighted vegetation proportions for a majority of the taxa under study, anthropogenic indicators in particular. By contrast, the ranges of weighted vegetation proportions of tree taxa (*Pinus*, *Alnus*, *Quercus* and *Tilia*) are limited. Only a few sites have a higher (between >0.08 and >0.15 depending on the taxa) weighted vegetation proportion. The reason for this is the scarce sampling in woodlands (Fig. 1) although the huge difference in weighted vegetation proportion (Fig. 5a) between forest and non-forest samples is given by taxon specific distance weighting (Prentice, 1985; Sugita, 1993). The dispersal model is highly leptokurtic, which means that critical importance is given to the vegetation touching the sedimentation basin. This can be demonstrated by the weighted vegetation proportions of *Pinus* at four sites where the values exceeded 0.2 (Fig. 5a). Sites number 66 and 59 (with a lower pollen proportion), located between a forest and a field, are within the value range of sites 53 and 60 inside the forest (with a higher pollen proportion). The rest of the sites with lower weighted vegetation proportions of *Pinus* (<0.2) are outside the forest, but some are very close to it (Fig. 1). A similar drop in weighted vegetation proportion between sites inside the forest stand or just adjacent to it and sites outside the stand (even very close to it) was observed in a previous simulation of a small *Picea* population (Gaillard et al., 2008).

4.4. Robustness of the ERV model

As to the background component of each of the taxa, our data meet the assumptions of the ERV-1 model. ERV-1 is robust when the background pollen deposition for each taxon is a small proportion of the total pollen deposition at each site (Parsons and Prentice, 1981). The ERV-1 model therefore works optimally when the pollen proportions of each site are higher than the intercept for each taxon (Fig. 5b). Our dataset contains many sites that contradict this assumption (i.e. they fall into the shaded field in Fig. 5b). Still, the background component for each taxon is generally low and is comparable with other empirical studies (Jackson and Kearsley, 1998; Soepboer et al., 2007). We can thus consider the ERV-1 model to be sufficiently robust. This assumption also contributed to our decision to exclude *Betula* and *Picea* after the preliminary ERV-1 run. The background component of these two taxa was around 0.1, and their pollen proportion ranged from 0 to 0.3, which would lead to very unreliable pollen productivity estimates.

4.5. PPE values

It is always difficult to compare PPEs from different studies. One problem is the different methodologies used when collecting vegetation data (Bunting and Hjelle, 2010). However, the majority of vegetation surveys listed in Broström et al. (2008) are based on vegetation cover data, except the survey from Norway (Hjelle, 1998), in which the vegetation data are based on non-distance weighted vegetation frequency data within square metre plots. So, if we assume that all vegetation cover data approximate real vegetation, we can compare them. In this way, our PPEs from ERV-1 are comparable with values from other studies. The lowest pollen production of Cerealia (0.05) is from the autogamous species wheat and barley, which are the only cultivated and observed species in the survey area. Regional reports on the composition of cereals, however, indicate a low percentage of oats, rye and triticale (Czech Statistical Office, 2009). A similar pollen-vegetation relationship, with small amounts of Cerealia type pollen in samples and many crop fields around, was observed in the Swiss Plateau (0.0008; Soepboer et al., 2007). PPE values of Cerealia in northern Europe, where anemophilous rye is cultivated more often, are much higher: 1.27 (Nielsen and Sugita, 2005), 3.2 (Broström et al., 2004) and 4 (Poska et al., 2011). In any case, we should not forget about the possible biases inherent in our data. Pollen samples were taken outside of cereal fields because no useful material was available for sampling on the surface of cultivated land. We can also expect yearly field alternation, which would mostly not only affect cereals, but also the Poaceae and annual weeds from the Chenopodiaceae family. The pollen assemblage of annual plants can be biased by annual changes in the vegetation cover because the time span of the pollen record retained by moss polsters varies greatly. Even using a single method, it can vary from one year to up to several years (Räsänen et al., 2004; Pardoe et al., 2010). The different material used for the present pollen analysis in the case of this study can also bias this time span (Räsänen et al., 2004).

Shrubs and trees, having an alpha value of around 1, are among taxa producing intermediate amounts of pollen. This group, which contains *Salix*, *Sambucus nigra* type and *Fraxinus*, is common throughout the area of the vegetation survey (>0.02 of mean ring vegetation proportion – Fig. 2) and therefore shows a wide variation in the data (Fig. 5a). This, combined with a low background component, produces reliable pollen productivity estimates (Parsons and Prentice, 1981; Broström et al., 2004). The *Fraxinus* PPE value of 1.10 is slightly higher than the closest value for *Fraxinus* from England (Bunting et al., 2005). The PPE for Salix (1.19) is slightly lower in our case than in the two other studies from temperate Europe, which could have been caused by the fact that different taxa were included in the pollen type. The intermediate value of 1.30 for the *S. nigra* type is expected since it is a large entomogamous shrub. Our PPE for *Tilia* (1.35) is higher than that found in Sweden, which could be caused by our scarce sampling in the forest. The same applies to the value for *Quercus* (1.76), which would be expected to be much higher, the closest being the value from the Swiss plateau (2.65; Soepboer et al., 2007).

The last group consists of three high pollen producers, *Alnus* (2.56), *Pinus* (6.17) and *Plantago lanceolata* type (3.70), for which the closest values are from the southern Sweden (Broström et al., 2005). The PPE results for these latter three groups, especially *P. lancelata* type, could possibly be biased by the gradient which exists in our data, in which pollen and/or vegetation percentages are low at many sites and high at only a few. The PPE values for the Chenopodiaceae (4.28), *Artemisia* (2.77) and *Urtica* (10.52) are also among the higher ones, as all taxa are anemogamous. When attempting to reconstruct the past, we have to keep in mind that the Chenopodiaceae pollen type also includes neophyte taxa (e.g. *Amaranthus retroflexus*, native in North America).

Summing up, herb taxa (except Cerealia) produce ca 3–11 times more pollen than the Poaceae, which is more than the pollen production of trees (producing 1–6 times more pollen than the Poaceae). This fact, which might seem to be in disagreement with a pollen counter's intuition, is given by our set of taxa. Trees and shrubs comprise a mixture of entomogamous (*Sambucus nigra* type, *Tilia* and *Salix*) and anemogamous (*Pinus*, *Quercus*, *Fraxinus* and *Alnus*) taxa, whereas all of our herbs (*Plantago lanceolata* type, *Urtica*, Chenopodiaceae and *Artemisia*) are anemogamous.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.revpalbo.2012.04.004. These data include Google maps of the most important areas described in this article.

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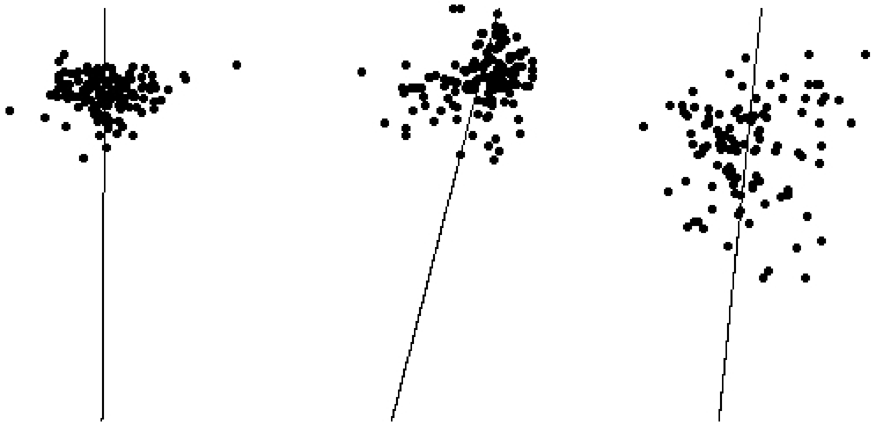

Chapter 4: parameter validation for regional reconstruction

Abraham, V., Oušková, V. & Kuneš, P. (2014). Present-Day Vegetation Helps Quantifying Past Land Cover in Selected Regions of the Czech Republic.(Bond-Lamberty, B., Ed) *PLoS ONE* 9(6), e100117.

Present-Day Vegetation Helps Quantifying Past Land Cover in Selected Regions of the Czech Republic

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Abstract

The REVEALS model is a tool for recalculating pollen data into vegetation abundances on a regional scale. We explored the general effect of selected parameters by performing simulations and ascertained the best model setting for the Czech Republic using the shallowest samples from 120 fossil sites and data on actual regional vegetation (60 km radius). Vegetation proportions of 17 taxa were obtained by combining the CORINE Land Cover map with forest inventories, agricultural statistics and habitat mapping data. Our simulation shows that changing the site radius for all taxa substantially affects REVEALS estimates of taxa with heavy or light pollen grains. Decreasing the site radius has a similar effect as increasing the wind speed parameter. However, adjusting the site radius to 1 m for local taxa only (even taxa with light pollen) yields lower, more correct estimates despite their high pollen signal. Increasing the background radius does not affect the estimates significantly. Our comparison of estimates with actual vegetation in seven regions shows that the most accurate relative pollen productivity estimates (PPEs) come from Central Europe and Southern Sweden. The initial simulation and pollen data yielded unrealistic estimates for *Abies* under the default setting of the wind speed parameter (3 m/s). We therefore propose the setting of 4 m/s, which corresponds to the spring average in most regions of the Czech Republic studied. Ad hoc adjustment of PPEs with this setting improves the match 3–4-fold. We consider these values (apart from four exceptions) to be appropriate, because they are within the ranges of standard errors, so they are related to original PPEs. Setting a 1 m radius for local taxa (*Alnus*, *Salix*, Poaceae) significantly improves the match between estimates and actual vegetation. However, further adjustments to PPEs exceed the ranges of original values, so their relevance is uncertain.

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Introduction

Pollen-based quantification of past land cover is important for understanding vegetation-climate interactions and human induced changes [1]. The Landscape Reconstruction Algorithm (LRA) [2,3] is a robust method for quantitative vegetation reconstruction, and is therefore widely used for studying Holocene sequences [4–9] and interglacial deposits [10]. The LRA can be used in combination with other data, for example, to estimate the spatial extent of cereal fields [7], to examine the role of different factors on long-term vegetation changes [11] or as input for climate reconstructions [12].

The necessary parameters include taxon-specific relative pollen productivity and parameters of the pollen dispersal function (such as the size of the basin, size of the region, fall speed of pollen and wind speed). Various model parameters have been shown to vary significantly among regions [13]. To provide Holocene vegetation estimates for the Czech Republic, we therefore need to examine the model parameters in light of modern pollen assemblages at fossil sites and compare them with actual vegetation composition. In the present paper, we focus only on the first step of the LRA: REgional Vegetation Estimates from Large Sites (REVEALS) [2]. This model estimates vegetation for large regions (10^6 km^2) based on single or multiple pollen sites and provides a baseline for the second step of the LRA: LOcal Vegetation Estimates (LOVE), which produce single-site vegetation proportions for a limited local area (few km^2) [3].

Actual vegetation data for large areas can be compiled from various sources: forest inventories, crop statistics, land-cover information and remote sensing data such as aerial or satellite images [14]. Until now, Czech vegetation has not been reconstructed on a quantitative basis, although its components have been examined separately to solve certain partial problems such as land cover changes in the last two decades [15]. Here it is important to note that detailed qualitative overviews of vegetation in the Czech Republic are available (e.g. [16]).

The REVEALS algorithm was originally developed for large sites, as they better reflect regional vegetation than small ones (e.g., [17]). However, simulations and empirical data show that good mean estimates of regional vegetation can be attained even when many small sites are simultaneously included in a REVEALS model [2,18]. Many studies have already successfully employed the REVEALS algorithm using the Prentice-Sugita dispersal-deposition model, but always in areas with large lakes [4]. One exception are pilot tests carried out by Sugita *et al.,* [18], who used many same-sized small bogs. This model assumes that no taxa of interest grow within the sedimentation basin. Yet, most Czech palynological records come from bogs, which differ in size and in the number of taxa of interest growing within their sedimentation basins, depending on the region. The size of the sedimentation basin influences the size of the region, hence the term "characteristic radius" [19]. Previous testing suggests that the extent of a vegetation survey (region) has little effect on model validation [20].

Apart from this dispersal-deposition consideration, it is necessary to work with correct relative pollen productivities (PPEs) for all taxa. This parameter has already been calculated for many parts of Europe, and differences in methodology (lakes vs. moss polsters) or environmental setting (climate, landscape structure) cause substantial variations [13]. Since PPEs of 13 pollen taxa from moss polsters are available for Central Bohemia [21], any methodological and environmental biases associated with taxa under study should theoretically be reduced to a minimum. However, PPEs of missing target taxa (*Picea*, *Fagus*, etc.) must be filled in with data from other areas. It has been shown that averaging different values from Europe [22] yields applicable results using the dataset from the Czech Quaternary Palynological Database [23]. These averaged PPEs, in spite of their slightly different input parameters (type and size of basin, set of taxa), assure the consistency among REVEALS estimates of past vegetation. Which PPEs are the most appropriate for actual vegetation remains uncertain, however.

The main goal of our present study was to ascertain the best REVEALS settings and adjustments of parameters for producing a reliable quantitative vegetation reconstruction. We therefore i) examined actual vegetation data for the Czech Republic, ii) tested the effects of taxa growing in peat bogs and iii) identified the best set of PPEs. We particularly addressed questions related to the effects of wind speed and the characteristic radius of regional vegetation.

Theoretical Assumptions

The LRA [2,3] is the inverse form of the ERV model [24–26]. Both methods therefore deal with space in a similar way. The whole space is divided into a sedimentation basin (R), a relevant source area of pollen (RSAP) and an area of background pollen.

No taxa producing pollen are assumed to grow in the sedimentation basin. Its radius and type are set as parameters prior to the analysis. The size of the radius can range from 0.5–1 m (e.g. in studies of moss polsters using the ERV model) to several kilometres, as in the case of some large lakes.

According to the ERV model, the area of the background pollen is defined as the source area of a certain proportion of pollen which lies beyond the RSAP and does not have an exact extent. The REVEALS model produces vegetation estimates pertaining to the area from the edge of the sedimentation basin to the maximum range of the regional vegetation (Zmax). This is an input parameter. The size of the background area is generally 10^5 km^2; however, the REVEALS model deals with PPEs from a much smaller area. We therefore need to validate our selection of PPEs in a REVEALS model.

PPEs are not the only parameters for translating pollen data into vegetation proportions when using the REVEALS model. As already mentioned above, the maximum range of the regional vegetation (Zmax), the radius of the sedimentation basin (R) and also parameters of the deposition function – wind speed (u) and fall speed of pollen (v_g) – each play a significant role. We could have adhered to widely used settings of these parameters (see Methods for default settings) but decided to explore how changing these parameters affects the final results of simulations. A similar approach to testing the effect of changing radius was taken in Norway [27].

Secondly, we tested selected settings on real data and, finally, adjusted PPEs according to the dataset. Adjustment of PPEs is based on the following general assumptions: (1) The REVEALS algorithm with selected deposition function describes realistic conditions; (2) The fall speed of pollen (v_g) is universally valid; (3) The given sets of pollen assemblages represent regional pollen rain; and lastly (4) Vegetation data reflect actual vegetation. If input parameters (u, R, Zmax) are chosen correctly, we can use the dataset to recalibrate PPEs.

Characteristic Radius

The maximum range of the regional vegetation (Zmax) can be approximated as the characteristic radius, assuming homogenous vegetation [20]. The characteristic radius is a distance (z) from which part of the pollen loading ($F_i(R,z)$) of taxon i arrives at the sedimentation basin with radius R (Equation 1). Taxon specificity is given by parameter b_i that depends on how fast pollen is lost from the atmosphere. Parameter γ was set to $\sim 1/8$, which corresponds to typical daytime conditions. The term b_i is given approximately by 75 v_g/u, where v_g is the fall speed of the pollen and u is the wind velocity [19].

$$F_i(R,z) = 1 - \left(e^{-b_i z^{\gamma}} / e^{-b_i R^{\gamma}}\right) \tag{1}$$

REVEALS Model

A REVEALS estimate (V_i) is the proportion of regional vegetation composition belonging to taxon i. It is defined for one site (k) as pollen counts of taxon i (n_i) weighted by its pollen productivity (α_i) and dispersal term (K_i), divided by the sum of weighted pollen counts for all taxa [2]. In the case of multiple sites (Equation 2), sums of weighted pollen counts of taxon i from all sites are divided by the total sum of the same sums of weighted pollen counts for all taxa (j) at all sites (k) (Sugita, pers. comm.).

$$V_i = \frac{\sum_{k=1}^{q} \left(n_{i,k}/\alpha_i \, K_{i,k}\right)}{\sum_{k=1}^{q} \sum_{j=1}^{m} \left(n_{j,k}/\alpha_j \, K_{j,k}\right)} \tag{2}$$

The dispersal term (K_i) can be substituted by any dispersal function. We used the Prentice model (Equation 3), which considers the distance of source plants (z), dispersal properties of pollen and the type of sediment where pollen is deposited without mixing (bog model). The distance is considered from the edge of the sedimentary basin (R) to the edge of the maximum range of the regional vegetation (Zmax). A sedimentary basin is defined an area of a peat bog or lake where no plants of interest grow. However, this assumption can be violated if the size of a peat bog vegetated by target species is set to the size of the sedimentary basin. We thus propose that this fact is taken into account by considering the ecology of each taxon. For all extra-local taxa, the site radius should be set according to the size of the sedimentary basin; for local taxa, this radius should be decreased. Optimally, we would obtain a matrix of different radii for all taxa at all sites per region ($R_{i,k}$); however, we do not have data about distances of local taxa from the centre of the sedimentation basin. We therefore suggest that the R of local taxa be approximated by the radius used in studies of the pollen/vegetation relationship based on pollen trapped in moss posters (i.e. 1 m).

$$K_{i,k} = \int_{R_{i,k}}^{Zmax} g_i(z)dz = e^{-b_i \cdot R_{i,k}{}^{\gamma}} - e^{-b_i \cdot Zmax^{\gamma}} \qquad (3)$$

Methods

Characteristic Radius

We designated 70% of the pollen loading, following [19,20], as a representative part of the major source area of pollen collected at a certain point in the canopy. Its radius is further referred to as the "characteristic radius 70". Using the wind speed of 3 m/s and the corresponding fall speed of pollen from Table 1, we get parameter b_i. We calculated distances corresponding to the "characteristic radius 70" for all taxa at all sites (120). There is an advantage to performing separate computations for all sites instead of just working with mean values: Instead of a single number, we obtain a distribution of "characteristic radii 70" that follows the distribution of site radii and reflects the dispersal properties of all taxa included in the study.

REVEALS Simulation Setting

(Table 2) We simulated the effects of increasing four parameters. Each simulation scenario has a pair scenario with control settings. In each simulation, we thus consider two effects: i) gradual changes of REVEALS estimates along the x axis and ii) changes against the control scenario. To ensure comparability between scenarios, all control simulations share the same setting at one reference point. This reference setting used the following parameters: original PPEs listed in Table 1, radius of the sedimentation basin R = 100 m and maximum range of the regional vegetation Zmax = 60 km; an even pollen assemblage of 100 pollen grains per taxon was used as the dataset. We used the Prentice model to devise the pollen dispersal-deposition function, using $b_i = 75\ v_g/u$, where v_g (terminal velocity) is listed in Table 1 and u (wind speed) equals 3 m/s.

We asked the following questions: Simulation A – What is the effect of increasing R on REVEALS vegetation estimates of each taxon? How is it influenced by higher wind speed? Simulation B – What is the effect of increasing Zmax on REVEALS vegetation estimates of each taxon? How is it influenced by higher wind speed? Simulation C – How do REVEALS vegetation estimates change when we calculate them for two sites differing in size? Simulation D – Can approximation of R by the moss polster size of 1 m for local taxa improve REVEALS vegetation estimates when local taxa have higher pollen proportions than other taxa? We expected the results to be influenced by PPEs and fall speed of pollen. We therefore selected *Picea* and *Alnus* (see their values in Table 1) as local taxa in simulation D. This combination represents the tree layer of the wetland community *Thelypterido palustris-Alnetum glutinosae* [28].

Table 1. Fall speed of pollen (v_g), relative pollen productivity estimates (PPE) and their standard error (SE).

	v_g	original PPEs			adjusted PPEs	
	(m/s)	PPE	SE	citation	$u = 4$ m/s	$R_{(local\ taxa)} = 1$ m
Abies	0.12	9.92	2.86	[40]	12.77	20.62
Acer	0.056	0.32	0.1	[41]*	0.22	0.38
Alnus	0.021	4.2	0.14	[89]**	4.2	6.46
Betula	0.024	2.42	0.2	[40]	2.62	4.31
Carpinus	0.042	2.106	0.0405	[48]***	0.5	0.92
Cerealia	0.06	0.0462	0.0018	[21]	0.046	0.08
Corylus	0.025	1.4	0.042	[89]**	1.4	2.15
Fagus	0.057	1.2	0.16	[41]*	1.2	1.85
Fraxinus	0.022	0.667	0.027	[89]**	0.18	0.28
Picea	0.056	0.57	0.16	[40]	0.47	0.83
Pinus	0.031	1.35	0.45	[40]	2	3.23
Pla_lanc	0.029	0.897	0.235	[90]**	0.9	1.38
Poaceae	0.035	1	0		1	1
Quercus	0.035	1.76	0.2	[21]	0.42	0.65
Salix	0.022	2.31	0.08	[91]	2.31	3.55
Tilia	0.032	0.8	0.029	[89]**	0.5	0.92
Ulmus	0.032	1.267	0.05	[89]**	6	9.23

*) in [22], **) in [7], ***) recalculated to Poaceae.
Footnotes by original PPEs indicate the source of the values. PPEs were adjusted according to the results of REVEALS model under higher wind speed (u) – S4MS_P and lower radius of the sedimentation basin (R) for local taxa – S4MSR_P.
doi:10.1371/journal.pone.0100117.t001

Table 2. Input parameters for simulations of REVEALS vegetation estimates.

	u	Zmax	R (m) of the first site		R (m)	n (pollen counts)	
	(m/s)	(km)	rest of taxa	*Picea, Alnus*	second site	rest of taxa	*Picea, Alnus*
A control*	3	60	1–1000	1–1000	–	100	100
scenario	4	60	1–1000	1–1000	–	100	100
B control*	3	1–1000	100	100	–	100	100
scenario	4	1–1000	100	100	–	100	100
C control	3	60	1–1000	1–1000	1–1000	100	100
scenario*	3	60	100	100	1–1000	100	100
D control*	3	60	100	100	–	100	100–1100
scenario	3	60	100	1	–	100	100–1100

*) includes calculation of standard errors.
All calculations were performed with original PPEs (Table 1) using the Prentice model.
doi:10.1371/journal.pone.0100117.t002

Pollen Data

We used the shallowest sample from every core in the Czech Quaternary Pollen Database (PALYCZ, accessed 01.07.2013). However, these samples were not collected in the same year as the vegetation data (see Table S1), but within the last 40 years, and not all of them have exactly 0 cm depth. Still, we assume that they are the closest representation of recent pollen deposition. Centroids of regional circles were placed visually around the spatial clusters of the sites. When two regions overlapped, certain sites fell into both of them at the same time. In these cases, the region was assigned according to the environmental conditions surrounding the core (vegetation, altitude, climate, etc.) (Figure 1). The pollen sum of selected taxa was limited to 100 pollen grains per sample, but only seven sites had less than 200 grains per sample; the average pollen sum of all 120 sites is 542 grains per sample (Table S1). Names of genera, except *Pinus*, used to denote selected pollen types refer to all species within the given genera. The name *Pinus* refers only to species belonging to the subgenus *Pinus* (diploxylon pines). *Plantago lanceolata* is the only pollen taxon defined at the species level. Poaceae encompass all wild grasses, and Cerealia comprise the genera *Triticum*, *Hordeum* and *Avena*; if distinguished, pollen of *Secale* and *Zea* was excluded.

Data Sources of Actual Vegetation

To establish the proportions of all target taxa in actual vegetation (Table 1) and the size of each regional circle (Figure 1), we extracted data from various sources. Distribution and abundance information is available for two groups of taxa. Data on the first group (crops and trees) can be relatively easily obtained because its biomass is ascertained periodically, as they directly benefit mankind. Data on the second group of taxa (Poaceae, *Plantago lanceolata* and *Corylus*) are available thanks to the habitat mapping project coordinated by the Nature Conservation Agency of the Czech Republic, which was initiated for delimiting Natura 2000 sites and is continually updated for the purpose of reporting under the Habitats Directive (92/43/EEC). We used the habitat mapping layer (Nature Conservation Agency of the Czech Republic, unpublished data) – a large dataset containing spatial and tabular data from habitat surveys (species presence or abundance) – to estimate the proportion of taxa in the second group. The first results (number of segments and area of every habitat) have already been published [29].

We used several data sources to obtain the most reliable data on regional vegetation cover. The CORINE Land Cover (CLC) map from 2006 [30] served as a spatial basis for most of the area. Areas under farm crops from 2006 [31] in the resolution of administrative regions (average area 5,637 km^2) were included in CLC class 211 (Arable fields). Forest inventory data from 2006 [32] in the resolution of municipalities with extended competence (average area 383 km^2) were joined with CLC classes 311, 312 and 313 (coniferous, deciduous and mixed forest). Areas of forested and arable land provided by numerical and spatial data (statistics and CLC) were compared at the corresponding resolution.

Processing of Habitat Mapping Data

We combined the CLC map with habitat mapping data (see below) to obtain average abundances of Poaceae, *Corylus* and *Plantago lanceolata*. The following reasons made us select these taxa: Poaceae are the key taxon of open landscapes, *Corylus* became subdominant in pollen assemblages during the Early Holocene, and *Plantago lanceolata* is classified as an anthropogenic indicator [33]. These taxa allow us to reconstruct landscape openness, Early Holocene vegetation and the magnitude of human impact. The habitat mapping layer consists of two datasets: (i) a map of natural

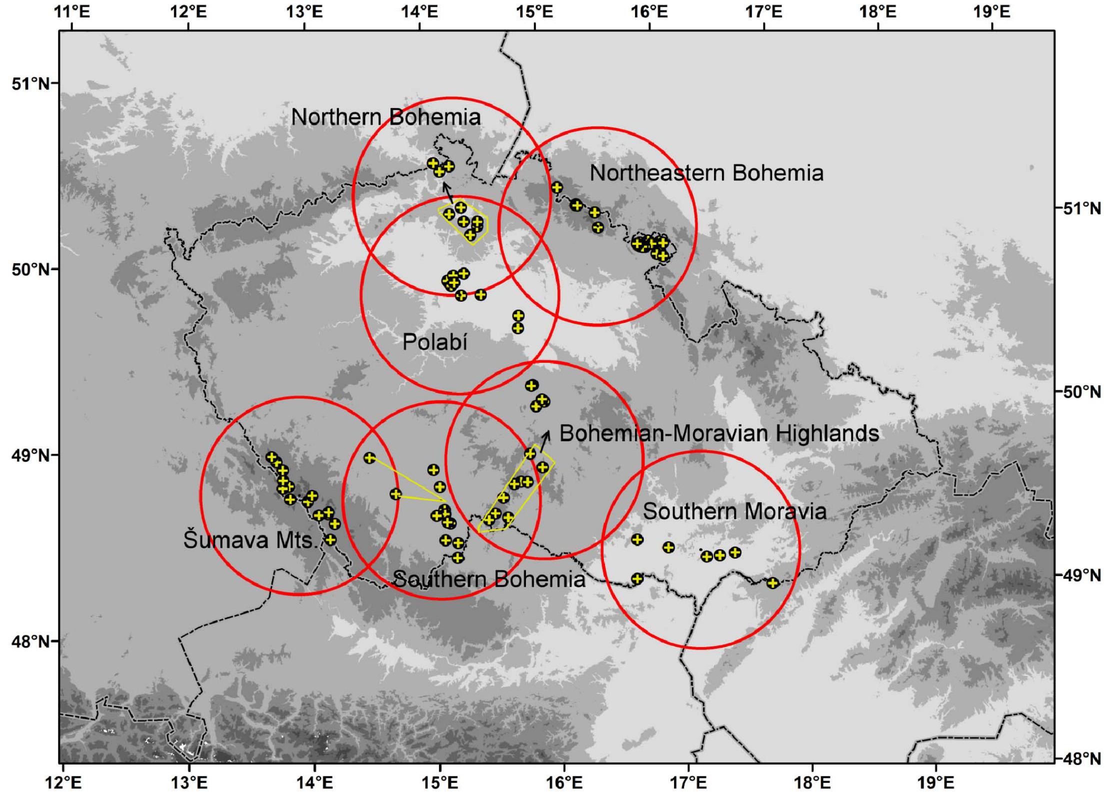

Figure 1. Map of the Czech Republic with pollen sites (yellow crosses) and assigned regions (red circles). Northern Bohemia [49–53], Northeastern Bohemia [49,54–63], Polabí [64–67], Southern Bohemia [68–73], Southern Moravia [74–79], Bohemian-Moravian Highland [80–85], Šumava Mts. [86–88]. Yellow lines and arrows show the allocation of sites to regions in cases when sites are situated in two overlapping regions.
doi:10.1371/journal.pone.0100117.g001

habitats covering 20% of the Czech Republic obtained by a field survey carried out between 2000 and 2011; and (ii) the presence or abundance of taxa estimated in some segments (0.4% of the total area for Poaceae, *Corylus* and *Plantago lanceolata*) collected between 2008 and 2011. The whole map of habitats was intersected with the CLC map. Abundance data were averaged and extrapolated to all habitats and CLC classes.

The details of the method of habitat mapping are described elsewhere [29]; however, it is helpful to mention its most important aspects. Recorded taxa include vegetation dominants and taxa of interest for nature conservation. In segments with habitats categorized as "natural", abundances of diagnostic or typical species were recorded using the Braun-Blanquet scale. In segments with transitional or human-influenced biotopes, only the presence of target species was recorded. The Braun-Blanquet scale was converted into percentages according to the following key: "r"–0.1%; "+"–0.5%; "1"–3%; "2"–15%; "3"–37.5%; "4"–62.5; "5"–87.5%. The total cover of segments had to be standardized due to the presence of multiple vegetation layers (more than one species recorded as "5"). If the total cover of a segment was less than half the standard value, the record was treated as a mere presence. The standard total cover was obtained from [34,35].

The extrapolated cover of *Corylus*, Poaceae and *Plantago lanceolata* was calculated by bootstrapping from random resampling from all segments with replacement. We then calculated the average percentage for segments containing abundance data of the habitat/CLC class and multiplied it by its proportional presence in all segments. Bootstrap calculations ($N = 5000$) of these weighted means permitted estimation of variances for each habitat/CLC class and standard deviation in each region (see Table S2, S3, S4 in Supporting Information). Due to the focus of vegetation mapping on natural and semi-natural biotopes, the surface of some CLC classes suitable for vegetation mapping was estimated as follows: 35% – discontinuous urban fabric, industrial or commercial units (121, 112), 10% – forests (311, 312, 313) and 5% – arable land (211). Herb taxa (Poaceae and *Plantago lanceolata*) were considered only in non-forest and shrub vegetation (excl. T, K, X9, X8 sensu [36]).

The layer was intersected with circles representing regions. Some of the circles extended beyond the borders of the Czech Republic. We therefore extrapolated the vegetation composition in parts of the circles within the country to parts of the circles overlapping into neighbouring countries. Similarly, we assumed regional proportions of bare land and areas vegetated by plants beyond our interest to be zero. We converted absolute plant abundances into vegetation proportions to compare them with vegetation estimates.

Data Analysis

REVEALS estimates were calculated by the REVEALS.v4.2.2.-Tallinn.wks.exe binary (Sugita unpublished) and by a script written in R [37] (Text S1). Unlike our script, the original programme calculates standard errors, but offers only limited parameter settings. These default settings together with our initial parameters include: Prentice's [38] model as the dispersal function using $b_i = 75\ v_g/u$, the fall speed of pollen (v_g) extracted from previously published works [39–41] and wind speed ($u = 3$ m/s). The radius of the sedimentation basin (R) was set to the size of the peatbog, a parameter extracted from the Czech Quaternary Palynological Database (Figure 2, Table S1). The maximum range of the regional vegetation Zmax was set 60 km.

We selected PPEs during preliminary REVEALS calculations. Assuming environmental similarities, we first picked PPEs for all available taxa in Central Bohemia; PPEs for missing taxa were completed from other studies with the following priority Swiss Plateau, Swiss Jura and Southern Sweden. PPEs of taxa not matching vegetation estimates were substituted by other values until we reached the best set of PPEs. A change of one PPE value shifts the estimates of all taxa; however, rare taxa have a smaller effect than abundant ones, so we began by evaluating abundant taxa. We first assessed the goodness of fit visually and then calculated two kinds of dissimilarities, hereafter referred to as "dissimilarity A" and "dissimilarity B". The two dissimilarity indices highlight differences of REVEALS model from pollen proportions and also differences among alternative scenarios (representing expected improvements over widely used settings). Dissimilarity A was calculated by subtracting estimates (or pollen proportions) from actual vegetation values and summing the results of this subtraction for each taxon across all regions. As regards dissimilarity B, the results obtained by the previous subtraction (calculated for dissimilarity A) were squared, summed together for each taxon and divided by the sum of squared residuals from a linear regression calculated between the two variables for each taxon. To keep dissimilarity B close to 1, the linear regression line should be close to the line of best fit (one-to-one line). Another particularity of dissimilarity B is that it can be very high when both variables are linearly related, albeit far from the line of best fit.

We hypothesize that the results of our regional vegetation reconstruction in the study area can be biased by individuals growing in the sedimentation basin and by wind speed. Wind speed (u), the radius of the sedimentation basin (R) and PPEs were adjusted in a three-step process considering alternative scenarios. After every step, we assessed the goodness of fit between REVEALS estimates and actual vegetation proportions. First, we ran the REVEALS model with two different wind speeds: 3 m/s and 4 m/s (scenarios S3MS and S4MS, respectively). Average seasonal wind velocity in spring varies from 2.5 m/s in lowlands to 4.5 m/s in mountains [42]. In this first step, it was assumed that no taxa of interest grow in the sedimentation basin, whose size corresponds to the default setting.

In the second step, we added the wind speed setting which better matched actual vegetation proportions to the alternative setting representing the radius of the sedimentation basin. The presence of local taxa was estimated by comparing pollen percentages, general wetland vegetation of the regions and the ecology of species corresponding to our pollen taxa. Approximation using the size of moss polster sites (radius of the sedimentation basin R = 1 m) was applied to *Alnus*, *Salix* and Poaceae at all sites within the following regions: Southern Moravia, Southern Bohemia, the Polabí lowland and Northern Bohemia; *Alnus* and Poaceae were also considered local in the Bohemian-Moravian Highland.

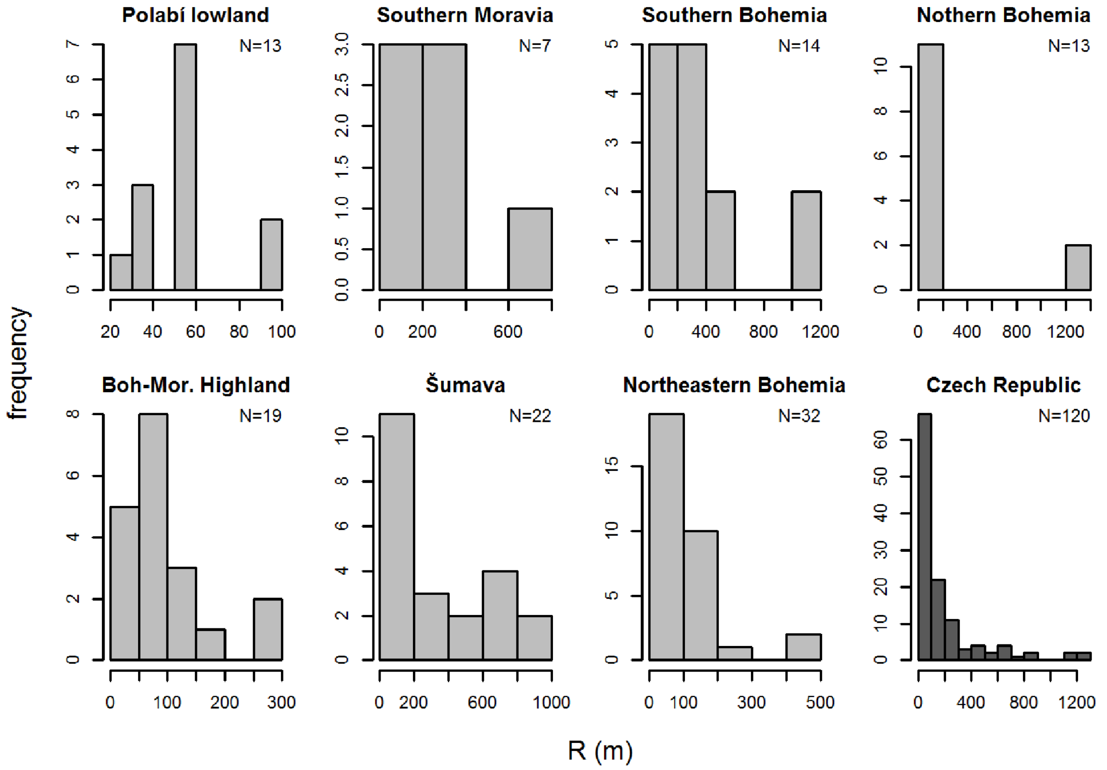

Figure 2. Histograms of sizes of sedimentation basins in different regions. The number of sites included is indicated at top right.
doi:10.1371/journal.pone.0100117.g002

Finally, the two scenarios with the lowest sums of both dissimilarities were used for the adjustment of PPEs. As we approached the optimal set of adjusted PPEs, dissimilarity A tended to decrease to 0, while dissimilarity B decreased towards 1. PPE values of mismatching taxa were adjusted until the best match was obtained. If the PPE of Poaceae (reference taxon = 1) needed to be adjusted, all values were adjusted accordingly to keep the value of Poaceae at 1. This was done to retain comparability with other studies.

To test the robustness of REVEALS vegetation estimates, we applied a leave-one-site-out approach. Following [22], we calculated non-parametric Spearman rank-order correlation coefficients and their statistical significance for the relationship between estimates for all sites (default scenario) and estimates with one site omitted. We tested the null hypothesis (H0) that there is no association between the two types of estimates and used a two-tailed test with the significance level of p = 0.01. Additionally, we calculated scores of Principal Component Analysis (without transformation) for all leave-one-site-out samples and their corresponding estimates for all sites. For each region, we compared the variability of all leave-one-site-out samples and also their distances from the default scenario. We expected the site radius to have a substantial influence, so we plotted each leave-one-site-out sample as a symbol whose size indicates the radius of the corresponding site.

Results

Characteristic Radius

(Figure 3) The maximum "characteristic radius 70" refers to the distance of approximately 250 km pertaining to all taxa at all sites. This large distance is given by the size of the largest sedimentation basin (1,262 m) and by taxa with light pollen (*Alnus*, *Fraxinus* and *Salix*). However, most of the "characteristic radii 70" are accumulated within the first 60–80 km. Within this distance fall also the maximum characteristic radii of taxa with medium-weight to heavy pollen grains. The reason behind this result is that the distribution of site radii is skewed towards smaller radii, with quartiles ranging from 30 to 250 m (Figure 2).

REVEALS Simulation

(Figure 4) Pollen productivity and the dispersal term are inversely proportional to REVEALS estimates. Hence, the highest REVEALS estimates are those for Cerealia, which have the lowest PPE. However, *Abies*, the taxon with the highest PPE, does not have the lowest REVEALS estimates because it has a low dispersal term. The first two simulations (Figure 4A, 4B) show how parameters of the dispersal term – wind speed (*u*), fall speed (v_g), radius of the sedimentation basin (R) and maximum range of the regional vegetation (Zmax) – influence REVELS vegetation estimates. Taxa within each simulation show a similar pattern to taxa with similar fall speed of pollen. *Alnus*-*Capinus*, *Picea*-Cerealia and *Abies* delimit three groups of taxa corresponding to three ranges of terminal velocities of pollen: slow (0.021–0.042 m/s), medium (0.056–0.06 m/s) and fast (0.12 m/s). All remaining taxa fall within one of these ranges (Table 1).

Light pollen grains show a significantly decreasing trend. Medium-weight pollen grains indicate no trend or one that is only slightly decreasing or increasing. Heavy pollen grains of *Abies* show a significantly increasing trend. Higher wind speed increases REVEALS estimates of light pollen grains, decreases estimates of heavy pollen grains and has no significant influence on medium-weight pollen grains. In general, decreasing the radius of the sedimentation basin has a similar effect as increasing the wind speed parameter from 3 to 4 m/s.

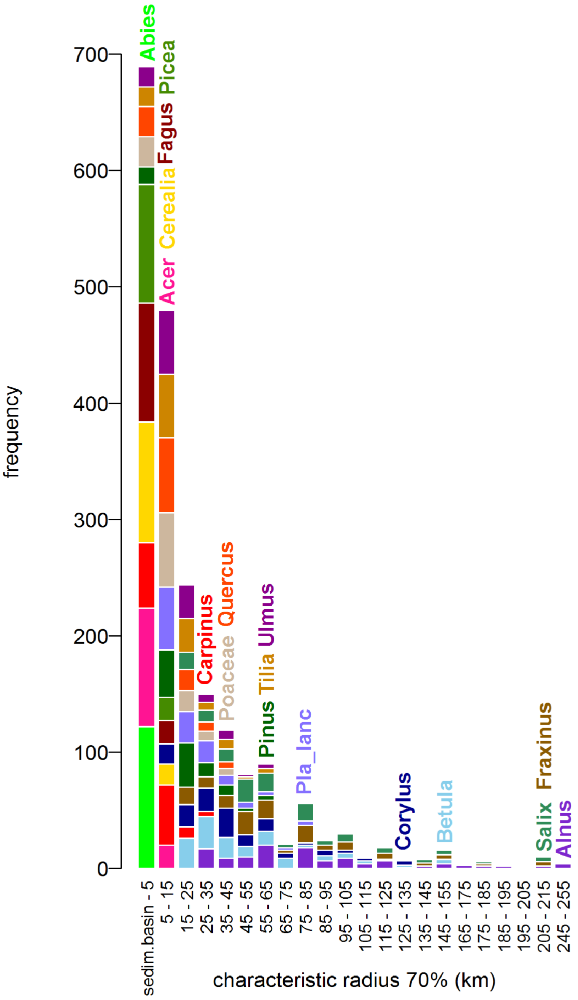

Figure 3. Histogram of "characteristic radii 70" (km) for all pollen taxa (17) at all sites (120). Note the different distribution of taxa with light pollen grains (e.g. *Alnus* – purple) and heavy pollen grains (e.g. *Abies* – light green). The wide distribution is given by the variability of the radii (see Fig. 2). The name of each taxon is placed at the maximum distance given by the maximum sedimentation basin (1,262 m).
doi:10.1371/journal.pone.0100117.g003

Within the reasonable Zmax ranges of ca. 10–500 km, the increasing maximum range of the regional vegetation has very little effect on REVEALS estimates for all taxa.

When a combination of two differently sized sites is used (Figure 4C), REVEALS estimates of *Abies* and light-pollen taxa are similar to REVEALS estimates calculated for the larger site only (or two sites the size of the larger one). Our comparison of standard errors from the first and third simulation shows that combining two sites differing in size increases standard errors. The standard errors grow with the size difference in taxa on which the size of the site has a notable effect (e.g. *Abies* and, to a lesser extent, light-pollen taxa).

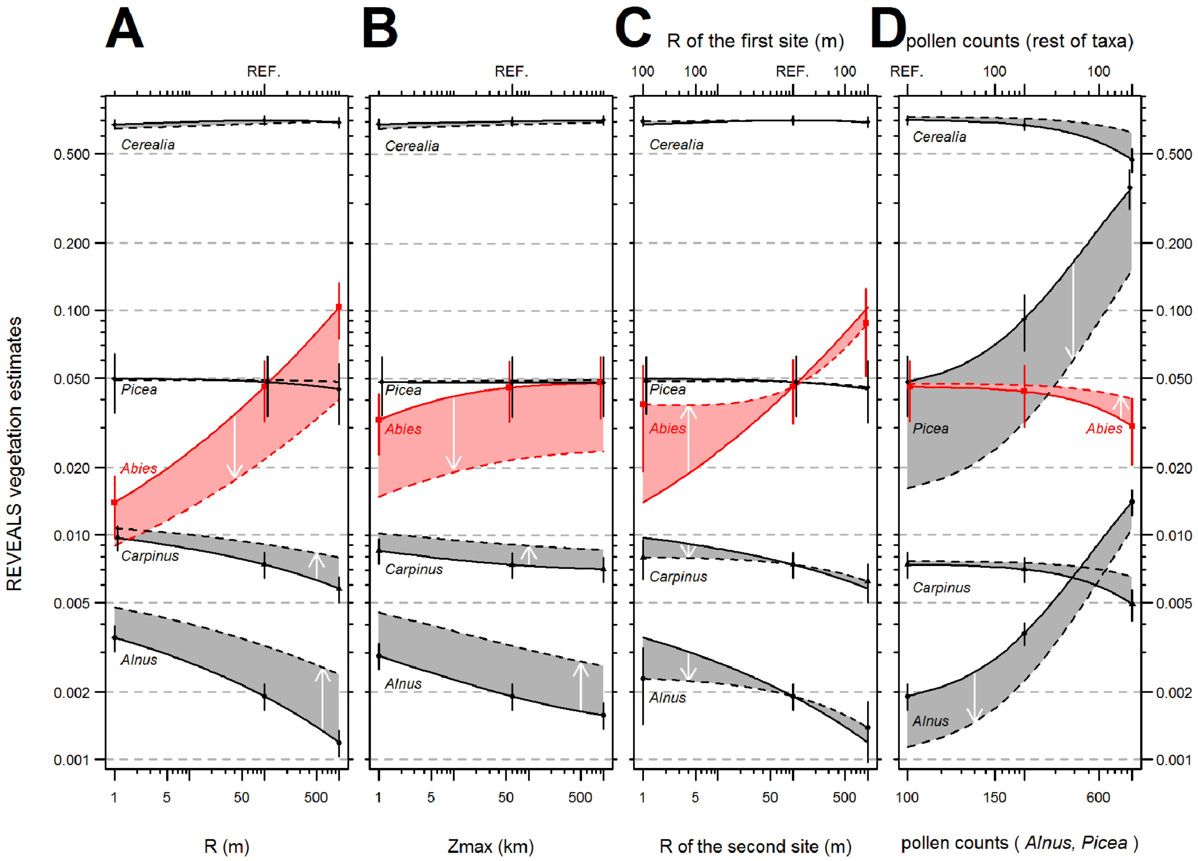

Figure 4. Simulation of REVEALS estimates (proportion in log scale). *Alnus-Capinus*, *Picea*-Cerealia and *Abies* delimit three groups of terminal velocities of pollen: slow, medium and fast, which also represent the pattern of the rest of taxa not plotted here. Arrows show the change of estimates from control (full line) to scenario (dashed line); for details, see Table 2. (A) Simulation A: Increasing radius of the sedimentation basin under two wind speed velocities (B) Simulation B: Increasing radius of the area of the background pollen under two wind speed velocities. (C) Simulation C: Fixed versus increasing radius of the sedimentation basin of the second site. (D) Simulation D: Increasing pollen counts of *Alnus* and *Picea* under two radii of the sedimentation basin. The reference setting common to all control simulations is marked on the secondary horizontal axis by "REF".
doi:10.1371/journal.pone.0100117.g004

Decreasing the site radius of *Picea* and *Alnus* (100 m → 1 m) decreases the REVEALS estimates of these taxa (Figure 4D). This effect is stronger for *Picea* than for *Alnus* because a pollen assemblage with a site radius of 1 m and 210 more *Picea* grains or more 70 *Alnus* grains than the rest of the taxa produces similar REVEALS vegetation estimates as an assemblage with a 100 m radius and equal pollen counts for all taxa. It is important to note the difference against the first simulation; in other words, when the site radius decreases for all taxa, REVEALS estimates of *Alnus* increase.

It is necessary to note the log scale of the vertical axis. Changes in the vegetation estimates of *Alnus* (Figure A–C) are actually very low (<0.5%). Similarly, however, although the decreases in control simulation D of Cerealia, *Abies* and *Carpinus* seem similar; Cerealia exhibit the highest absolute decline (70 → 47%).

Actual Vegetation Cover Derived from CLC and Habitat Mapping

(Figure 5, 6) Areas of arable land and forests derived from two different sources yield similar results and are thus combinable (Figure 5). There is a slight trend towards overestimating forest and arable land in CLC mapping with increasing size of the municipality or region.

The selected taxa cover 56% of the area of the Czech Republic, dominants being Cerealia, *Picea*, Poaceae and *Pinus*; the remaining taxa never reach 2%. The taxa reach similar proportions in all regions (Figure 6). The selected taxa cover only 35–57% of the surface of the regions studied (60 km radius circles). The remainder of the circles is bare land, land covered by other taxa or land outside the Czech borders. Standard deviations of regional proportion of Poaceae, *Plantago lanceolata* and *Corylus* turned out to be lower than the plotting limit (<0.1%), so they are only listed in Table S4.

Pollen-based Estimated Vegetation by REVEALS Model

(Figure 7, 8) Table 3 shows both measures of dissimilarity between REVEALS estimates and actual vegetation. Their sums (0.32–1.6 and 64–957) are several times lower than in the case of pollen proportions (7.31 and 4875). According to both dissimilarities, scenario S4MS better matches actual vegetation than the original setting (S3MS). Considering the taxa individually, *Abies*, Poaceae and Cerealia show the best improvement in these three scenarios; on the other hand, the match of *Pinus* and *Picea*

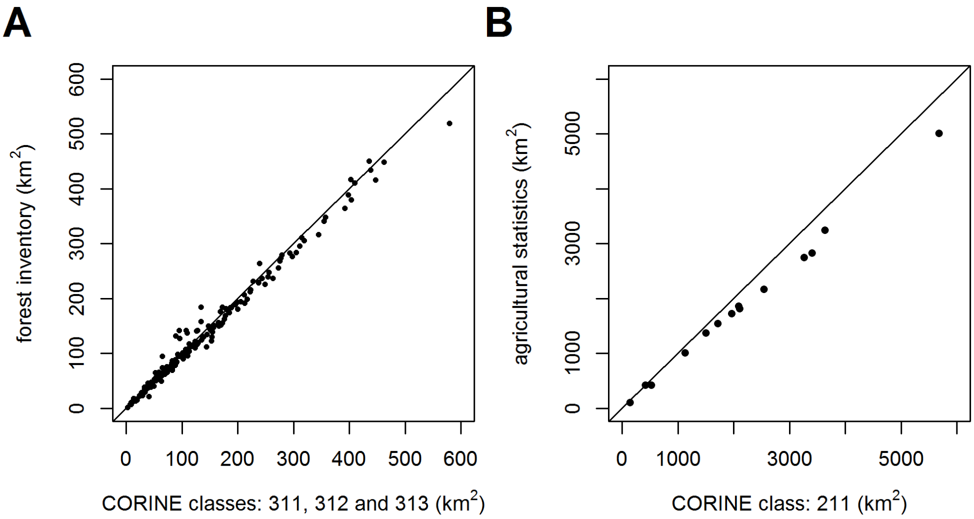

Figure 5. Comparison of the area derived from the CLC map [30] **and numerical data sources.** (A) Forest area within municipalities with extended competence [32]. (B) Arable land within regions [31].
doi:10.1371/journal.pone.0100117.g005

deteriorates. The setting from scenario S4MS was used in cases of local taxa with small radii (Poaceae, *Salix*, *Alnus*).

Scenario S4MSR generally yields brings estimates which are closer to actual vegetation because the sum of both dissimilarities is lower than in scenario S4MS; individually, however, Poaceae and Cerealia perform worse. The lowest dissimilarities appear in scenarios S4MS and S4MSR, so both settings (i.e. wind speed of 4 m/s and wind speed of 4m/s together with the reduced radius for local taxa) are used to adjust the PPEs.

Initial PPEs and their geographical origins are summarized in Table 1, which also shows adjusted values for both alternative scenarios. Considering scenario S4MS, adjusted PPEs exceed the ranges of previously published values for *Fraxinus* 0.18, *Ulmus* 6, *Quercus* 0.42 and *Carpinus* 0.5. In the cases of Cerealia (0.046), *Pinus* (2), *Abies* (12.77), *Tilia* (0.5), *Picea* (0.47), *Acer* (0.22), *Betula* (2.62) and *Plantago lanceolata* (0.9), adjusted PPEs stay in the ranges of standard errors or close to them. Most of adjusted PPEs using settings from scenario S4MSR are higher than the initial PPEs and out of the range of their standard errors. This is because adjustment decreased the PPE of Poaceae. The sums of the two dissimilarities for both scenarios of adjusted PPEs (S4MS_P, S4MSR_P) are very similar (0.32 vs. 0.38 and from 64.5 vs. 70.2, respectively; Table 3).

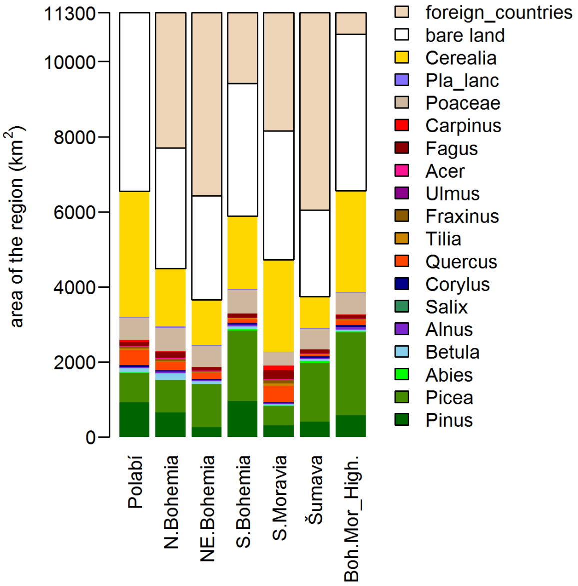

Figure 6. Vegetation cover in selected regions.
doi:10.1371/journal.pone.0100117.g006

All REVEALS estimates calculated by the leave-one-site-out approach across all regions are significantly correlated with corresponding values calculated for all sites (p<0.01). We therefore reject the null hypothesis. The PCA (Figure 8) shows that the highest variability among leave-one-site-out estimates lies within Northern Bohemia, Southern Bohemia and Southern Moravia. Moreover, the variability within Northern Bohemia is caused by large sites. In other words, REVEALS estimates deviate far from the mean when a large site is excluded.

Discussion

Accuracy of Actual Vegetation Data

Agricultural statistical data and forest inventories. Areas obtained from CLC classes (211, 311, 312 and 313) tend to be overestimated when compared with areas derived from forest and agricultural statistics. Such discrepancies are caused by small-scale owners of forests and arable land, who are not required to maintain forest inventories or to provide data for agricultural statistics. This lack of accuracy becomes apparent in larger areas because of accumulated noise. Another reason behind the overestimation of forest CLC areas is that military zones, although abandoned and overgrown by forests, are registered as non-forest areas. Even though there is a tendency to overestimate forest CLC areas, some municipalities have underestimated them. Such municipalities are located within regions with high forest regeneration, since young forests do not show up as forested areas in remote sensing. Fortunately, these kinds of errors do not on average exceed 6% in the area

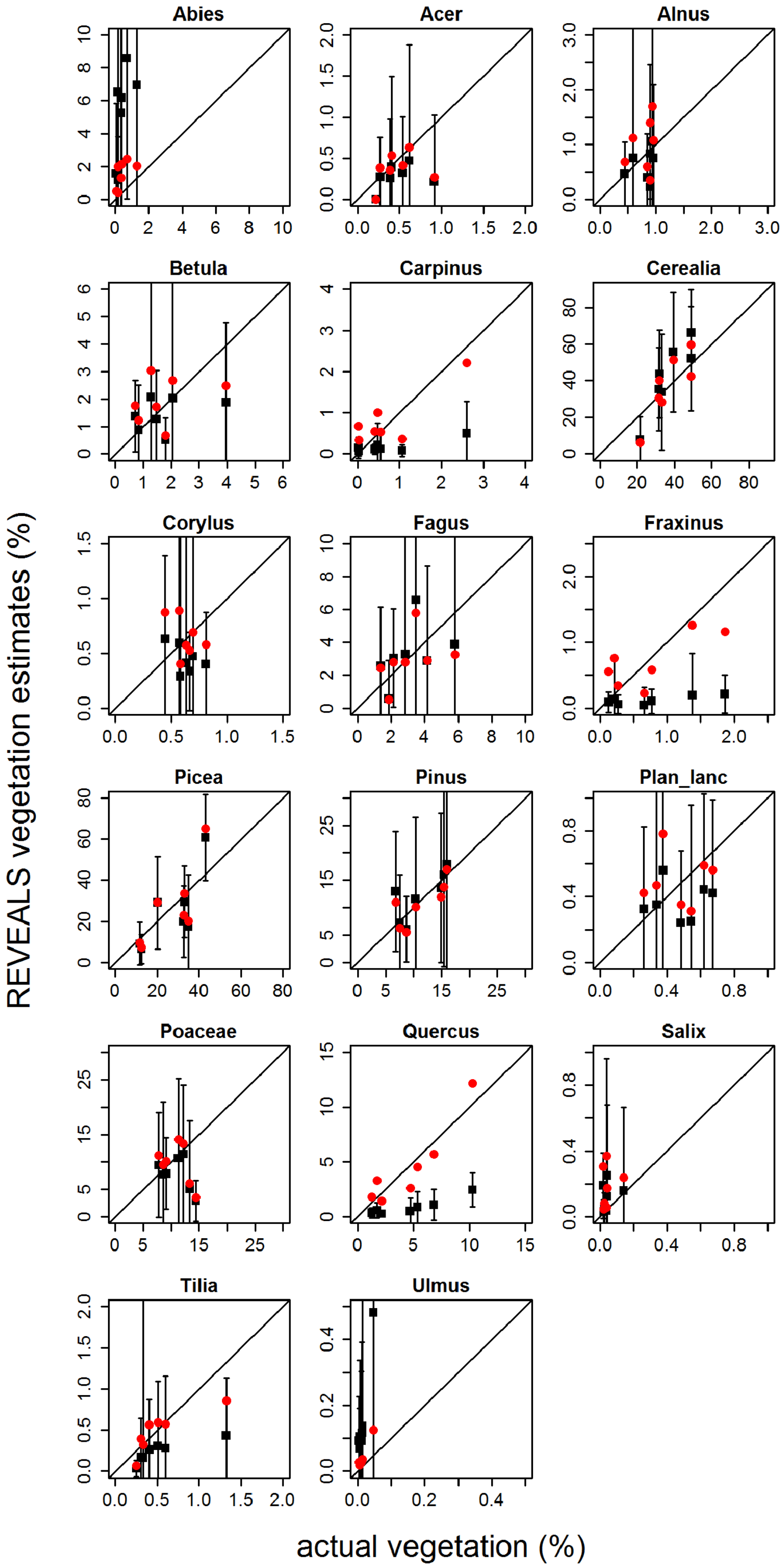
REVEALS vegetation estimates (%)
actual vegetation (%)
Abies
0 2 4 6 8 10
Acer
0.0 0.5 1.0 1.5 2.0
Alnus
0.0 1.0 2.0 3.0
Betula
0 1 2 3 4 5 6
Carpinus
0 1 2 3 4
Cerealia
0 20 40 60 80
Corylus
0.0 0.5 1.0 1.5
Fagus
0 2 4 6 8 10
Fraxinus
0.0 1.0 2.0
Picea
0 20 40 60 80
Pinus
0 5 15 25
Plan_lanc
0.0 0.4 0.8
Poaceae
0 5 15 25
Quercus
0 5 10 15
Salix
0.0 0.4 0.8
Tilia
0.0 0.5 1.0 1.5 2.0
Ulmus
0.0 0.2 0.4

Figure 7. Comparison of actual regional vegetation with REVEALS estimates. Settings: original PPEs under wind speed of 3 m/s - S3MS (black squares, confidence intervals show their standard errors); adjusted PPEs under wind speed of 4 m/s - S4MS_P (red dots). Both settings deal with original sizes of the sedimentation basin. The diagonal line shows the position of the optimal fit of the model to expected values.
doi:10.1371/journal.pone.0100117.g007

considered here. Forestry data on taxa deemed marginal for timber production may lack accuracy and should therefore be considered unreliable, particularly in cases of rare tree taxa with actual vegetation data below 0.1% (*Carpinus* in two regions, *Ulmus* and *Salix* in six regions, *Abies* in one region).

Habitat mapping. This third source of vegetation data was used for extrapolation. Habitat mapping covers a high number of independent observations over a relatively large area; however, the number of records for Poaceae, *Corylus* and *Plantago lanceolata* differs (Table S2). These variations are due to different frequencies of these three taxa in the vegetation, but we must point out certain biases introduced by methodological aspects of the mapping. The taxon Poaceae consists of dominants or diagnostic species of many important habitats and plant communities (e.g. *Corynephorus canescens*, *Molinia caerulea*, *Arrhenatherum elatius* and *Bromus erectus*). These species were recorded relatively well, at least when it comes to their presence. *Corylus avellana* is favoured by nature protection, so it was a well recorded taxon in all habitats where it was present and not only in habitats where its recording was compulsory (K3, L3.1, L3.2, L3.3, L8.2 and S1.5 sensu [36]). On the other hand, mapping of *Plantago lanceolata* was the least accurate because it is utterly uninteresting from the standpoint of nature conservation and thus its recording was compulsory only in a few habitats (T1.3, T3.5A, T3.5B and T5.5) [43]. Its mean values are nevertheless based on 7,363 segments with recorded abundances and 21,319 segments with recorded presence, which we consider sufficient.

Reveals

Generally, estimates of the REVEALS model from all scenarios are several times closer to vegetation data than mere pollen proportions (see Table 3 and Figure 7). However, *Abies* and *Quercus* matches were poorer worse when using the REVEALS model with standard settings ($u = 3$ m/s) than simple pollen proportions.

Maximum Range of the Regional Vegetation (Zmax)

The general grain of the landscape mosaic in Central Europe is sufficiently fine to fulfill the assumption of vegetation homogeneity for the area of the background pollen [19]. Landscape heterogeneity can matter if we get for a comparison with REVEALS estimates different regional vegetation at different radiuses, for example if there is an altitudinal gradient of vegetation. The centre of the Šumava region is situated in forested mountains, but the peripheral part of the circle reaches lowlands with a cultural landscape. On the other hand, Zmax (as a one of the REVEALS parameters) has little effect on vegetation estimates in accordance with Hellman *et al* [20]. So in practice, when comparing regional vegetation estimates and regional vegetation data, setting the Zmax parameter is more important for the vegetation survey. Heterogeneous mosaics are inevitable in real landscapes, but the theoretical size of the region can be at least approximated using characteristic radius concept. Most "characteristic radii 70" of our set of taxa and set of sites are smaller than 60 km; i.e. the length we set as the maximum range of the regional vegetation.

Wind Speed (u)

The REVEALS settings with the wind speed parameter of 4 m/s decreased the sums of dissimilarity A and dissimilarity B compared to the default settings. The lower sum of dissimilarity A can also be attributed to the decrease in the dissimilarity of *Abies*. Our simulation shows that lower REVEALS estimates for *Abies* can be attained using the same pollen counts provided that either the sedimentation basin is smaller or wind speed is faster.

To decrease the mismatch of *Abies* caused by the default settings, we could have also decreased the sedimentation radius, either for *Abies* or for all taxa. Although *Abies* can grow in wet subtypes of phytosociological associations [44], it is not a typical tree of wetlands. Decreasing the radius would entail neglecting the size of

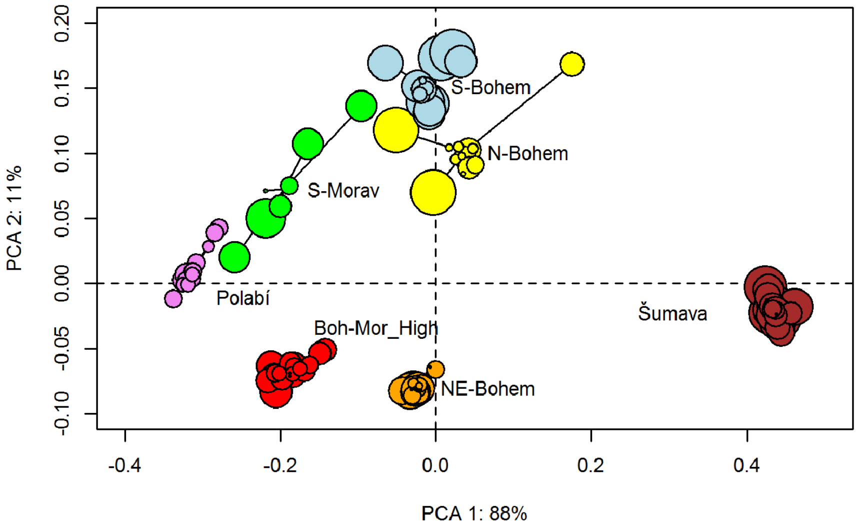

Figure 8. Principal Component Analysis of REVEALS estimates. Colours cluster all leave-one-site-out runs to their corresponding regions. The size of each sample reflects the size of the site which was left out.
doi:10.1371/journal.pone.0100117.g008

Table 3. Two measures of dissimilarity between actual vegetation and REVEALS estimates or pollen proportion.

	dissimilarity A						**dissimilarity B**					
	sum of simple differences						**sum of quadratic differences/sum of quadratic residuals**					
		step 1		**step 2**	**step 3**			**step 1**		**step 2**	**step 3**	
	pollen	**S3MS**	**S4MS**	**S4MSR**	**S4MS_P**	**S4MSR_P**	**pollen**	**S3MS**	**S4MS**	**S4MSR**	**S4MS_P**	**S4MSR_P**
Abies	−0.11	−0.33	−0.12	−0.1	−0.08	−0.09	3.4	6.7	5.4	9.7	4.3	4.3
Acer	0.03	0.01	0.01	0.01	0.01	0.01	59.1	5.1	5.3	1.8	2.2	2.5
Alnus	−0.5	0.01	−0.02	0	−0.01	0	4.3	1.6	1.3	1.2	1.2	1.1
Betula	−0.53	0.02	−0.03	−0.05	−0.01	−0.02	6.3	3.8	2.2	2.2	2.2	2.1
Carpinus	0.01	0.04	0.04	0	–0.01	0	7.4	152.9	106.6	2.4	2.0	2.3
Cerealia	2.43	−0.38	−0.11	−0.22	−0.03	0.03	4626.4	2.4	1.5	1.5	1.3	1.3
Corylus	−0.08	0.01	0	−0.01	0.00	−0.01	4.3	6.7	2.4	1.5	2.6	2.7
Fagus	0.01	−0.01	0	−0.04	0.01	−0.01	1.4	1.2	1.3	1.1	1.4	1.3
Fraxinus	0.03	0.04	0.04	0	0.00	0	41.7	382.5	123.3	2.0	3.0	2.2
Picea	1.01	0.15	0.25	0.2	0.00	0.06	10.8	1.1	1.1	1.4	1.1	1.1
Pinus	−1.86	−0.06	−0.36	−0.08	0.04	−0.01	31.3	1.2	3.1	1.1	1.2	1.0
Pla_lanc	−0.03	0.01	0	−0.01	0.00	−0.01	2.5	3.5	1.8	1.4	1.9	2.0
Poaceae	−0.44	0.22	0.07	0.33	0.09	0.09	21.9	5.1	3.1	107.4	3.0	4.4
Quercus	0.12	0.26	0.24	−0.03	0.01	−0.03	19.7	274.7	131.8	1.1	1.0	1.2
Salix	−0.06	−0.01	−0.01	−0.01	−0.01	−0.01	3.5	2.0	2.5	2.9	2.4	2.6
Tilia	0.01	0.02	0.02	0.01	0.00	0.01	4.5	42.0	15.7	4.7	2.5	3.1
Ulmus	−0.03	−0.01	−0.01	0	0.00	0	26.8	64.9	63.3	24.6	31.3	34.8
sum of absolute values	**7.31**	**1.6**	**1.33**	**1.09**	**0.32**	**0.38**	**4875.1**	**957.2**	**471.7**	**168.0**	**64.5**	**70.2**

Note the improvement of sums against previous steps. Abbreviations code the REVEALS settings: S - wind speed, R - radius of local taxa decreased to 1 m, _P - pollen adjusted.

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the sedimentation basin as an important theoretical concept of pollen analysis.

We also tried to keep default setting (S3MS) and adjusted the PPE for *Abies* in one of the preliminary analyses, which resulted in a PPE of *Abies* higher than 20. However, such a high PPE for *Abies* is well out of any range of PPEs published so far and does not seem very realistic.

We thus decided to correct the mismatch of *Abies* by setting the wind speed parameter to 4 m/s. This finding corresponds to observations of pollen trapping, which show that heavy pollen grains fall closer to their trees and that only a small part of them is able to reach air currents high enough above the canopy and thus contribute to the regional component of pollen rain [45].

Moreover, this value falls within the theoretical range of wind speeds blowing above the canopy [46]. In most of the regions considered, the average wind speed is approximately 4 m/s. Winds in the Polabí lowland and in South Bohemia are somewhat slower [42]. The wind speed of 4 m/s corresponds better to pollen and regional vegetation data in this study, especially because *Abies* is included in the set of taxa.

Combining Different-sized Sites for REVEALS Estimates

A correctly set radius of the sedimentation basin becomes important when *Abies* or light-pollen taxa are included in the dataset. Changes of the site radius do not affect REVEALS estimates of taxa with intermediate fall speed of pollen (Cerealia, *Picea*, *Fagus*). The simulation also showed the expected pattern – larger sites have a stronger influence. This effect is again the strongest for taxa with the heaviest and lightest pollen grains. As radii of our sites within each region vary substantially, we could expect high variability between estimates from each leave-one-site-out run. However, taxa with intermediate fall speed of pollen represent dominants of actual regional vegetation, so our results appear to be robust. Even when we omitted one large site from the analysis, the estimates remained significantly similar to those provided by the analysis of all sites in the dataset. The variability of leave-one-site-out out runs for Northern Bohemia showed a pattern that agreed with the simulation. Omitting a large site yielded the most aberrant results.

Alternative Radius of Sedimentation Basin (R) for Local Taxa

Setting a small radius of the sedimentation basin for local taxa decreases their REVEALS estimates, which would otherwise be too high because of their high pollen proportion. In accordance to this simulation result, the setting had the same effect on real data. Their estimates are even closer to actual vegetation than in the S4MS scenario (Table 3). This possibly confirms our initial hypothesis that the presence of local taxa in the sedimentation basin can be corrected by a smaller radius.

One could object that this technique is too subjective, because the decision as to which pollen is assumed local is made based on the high pollen proportion. We argue that it can be a way of formalizing certain *a priori* information that is well known among palynologists. This knowledge can be obtained from the fossil record either by establishing pollen percentage thresholds or combining pollen and macrofossil data [47].

Selection of PPEs

PPEs of half of the taxa giving the best match between REVEALS estimates and regional vegetation were determined on the Swiss Plateau [40] (*Pinus*, *Picea*, *Abies* and *Betula*) or in other regions of Central Europe [21,41,48] (*Fagus*, Cerealia, *Carpinus*, *Quercus* and *Acer*). PPE values of *Alnus*, *Salix*, *Plantago lanceolata*, *Corylus*, *Ulmus*, *Fraxinus* and *Tilia* originating from northern Europe do not differ substantially (less than two-fold) from values ascertained in Central Europe.

The close semblance between Swiss and Czech PPE data is due to the geographical proximity of the regions under study and the similarity in their climatic conditions, especially when compared with Northern Europe. Apart from the climate, similarities between the landscape mosaics in the Czech and Swiss studies may also play an important role. Both studies deal with plantations of *Pinus* and *Picea*, which create dense and shadowy stands. This explains the lower pollen productivities than those determined in Northern Europe. Moreover, the similarity with the Swiss Plateau also exists on the taxonomic level. Czech and Swiss Cerealia are dominated by autogamous *Triticum* whereas north-European fields host anemogamous *Secale*. Furthermore, we extracted the most suitable PPEs for main vegetation dominants in our study, including both the highest and lowest pollen producers from the study carried out on the Swiss Plateau. PPEs of the remaining taxa (except *Carpinus* and *Ulmus*) are comparable to this data set. This demonstrates the consistency among different PPE studies.

The unexpectedly bad suitability of PPEs from Central Bohemia might be caused by the small size of the sampling area. The PPEs were calculated for an area of 56 km^2 [21], which can magnify any local anomaly. By contrast, sampling sites on the Swiss Plateau and in southern Sweden are scattered over an area which corresponds to the background pollen area (10^4–10^5 km^2).

Adjustment of PPEs

Most adjusted PPEs calculating the wind speed setting of 4 m/s remain within the range of standard errors of original values. The PPE of *Ulmus* exceeds this range whereas adjusted PPE values of *Fraxinus*, *Quercus* and *Carpinus* are lower than published values. Such discrepancies might be caused by the scarcity of data (one or two) for *Ulmus* and *Carpinus*. The value for *Quercus* is significantly lower than northern European data, but still reasonably close to Central European data.

A problem arises, however, with adjusted PPEs calculated using the lowered setting of the radius for local taxa (S4MSR_P). The values of these PPEs fall well out of the ranges of original PPEs and seem very improbable. Their relationship to PPEs from pollen/vegetation studies and the ERV model remains unclear. A simulation of PPEs in a heterogeneous landscape with a gradient of local taxa might prove interesting.

Conclusions

Our simulation shows that changing the site radius influences substantially the REVEALS estimates of taxa with very heavy (*Abies*) or light pollen grains. Decreasing the site radius has a similar effect as increasing the wind speed parameter. We conclude that the initial mismatch between the estimates of *Abies* and its actual proportion was caused by an inappropriate setting of the wind speed parameter. We propose that wind speed should be set to 4 m/s, which is the average wind speed during the flowering season in most regions of the Czech Republic [42].

We found the best set of PPE values and adjusted them to make them as appropriate as possible for estimating present-day vegetation using the REVEALS algorithm. Most PPE values originate either from Central Europe (Swiss Plateau and Central Bohemia) or do not markedly differ from those values (more than two-fold). Ad hoc adjustment of PPEs with respect to present vegetation under the setting of wind speed 4 m/s improves the match 3–4-fold. We consider these values to be appropriate, because all except four of them fall within the ranges of standard errors of original PPEs and retain their relationship with original PPEs. The fact that even adjusted PPEs are cohesive with natural values confirms the theoretical assumption that PPE values from different studies are compatible.

Our initial hypothesis that the effect of local taxa can be corrected by decreasing the radius of the sedimentation basin is correct; however, satisfactory adjustments of PPEs to this setting remain to be identified.

Supporting Information

Table S1 List of pollen sites used for REVEALS estimates of present-day vegetation.
(XLS)

Table S2 Table of mean values of the cover of Poaceae, *Corylus* and *Plantago lanceolata* extrapolated into habitat classes. Codes of habitats correspond to [36]. Standard total vegetation cover was taken from [34,35,35]. ''Segments total'' means all segments of habitats distinguished during the mapping with presence or abundance data. ''Average abundance'' was calculated from segments with abundance data and presence data.
(XLS)

Table S3 Table of mean values of the cover of Poaceae, *Corylus* and *Plantago lanceolata* extrapolated into CORINE classes. For further information, see Table S2.
(XLS)

Table S4 Actual vegetation (%) in each region. The brackets show standard deviation.
(XLS)

Text S1 REVEALS model in R-script.
(DOC)

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Author Contributions

Conceived and designed the experiments: VA. Performed the experiments: VA. Analyzed the data: VA. Wrote the paper: VA PK. Provided vegetation data and edited the manuscript: VO. Designed the software used in analysis: VA PK.

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Table S1

region	longitude	latitude	sigle	R (m)	year of sampling	depth (cm)	pollen sum	citation
N-Bohemia	14.56457	50.67308	c_lipa	113	2005	20	106	Kuneš unpubl.
N-Bohemia	14.27661	50.89261	jeleni	25	2004	0	612	[52]
N-Bohemia	14.33873	50.85233	ndosky	13	2006	2.5	733	[53]
N-Bohemia	14.41314	50.88757	prysky	25	2004	0	456	[54]
N-Bohemia	14.60465	50.59888	jestre	1262	1986	0	473	[55]
N-Bohemia	14.67593	50.53207	okna	113	2007	2	370	Abraham unpubl
N-Bohemia	14.72334	50.58359	prachn	98	2009	0	281	Svitavská in prep
N-Bohemia	14.72334	50.58359	vorone	98	2009	20	398	Svitavská in prep
N-Bohemia	14.7217	50.60887	drznik	56	2009	0	485	Svitavská in prep
N-Bohemia	14.60465	50.59888	konval	1262	2009	1	508	Petr unpubl
N-Bohemia	14.67723	50.79509	mareni	18	2010	0	603	Kozáková unpubl
N-Bohemia	14.70065	50.80245	zaba	18	2010	0	150	[56]
N-Bohemia	14.67897	50.62591	ploucb	25	2012	0	426	Abraham unpubl
NE-Bohemia	16.11745	50.58873	anensk	18	1999	0	400	[52]
NE-Bohemia	16.28257	50.55575	broum1	10	1979	0	654	[57]
NE-Bohemia	16.28257	50.55575	broum2	10	1979	0	449	[57]
NE-Bohemia	16.2274	50.60639	brezov	10	1979	0	979	[57]
NE-Bohemia	16.3244	50.61767	herman	10	1979	0	682	[57]
NE-Bohemia	16.2924	50.62217	hyncic	10	1979	0	815	[57]
NE-Bohemia	16.309	50.56956	krinic	10	1979	5	455	[57]
NE-Bohemia	16.33779	50.5471	martin	10	1979	0	520	[57]
NE-Bohemia	16.17362	50.58547	teplic	10	1979	0	580	[57]
NE-Bohemia	16.13153	50.58494	tep_uk	56	1999	0	440	[58]
NE-Bohemia	16.19577	50.62165	verne2	69	1979	0	474	[57]
NE-Bohemia	16.12841	50.6045	vlci_r	25	1993	0	683	[58]
NE-Bohemia	16.19577	50.62165	verner	69	1974	0	1076	[57]
NE-Bohemia	16.10404	50.59666	kancel	10	1995	0	1231	[59]
NE-Bohemia	16.1524	50.58407	krav_h	10	1995	0	1320	[59]
NE-Bohemia	16.11156	50.5942	roklin	10	1995	2.5	1243	[59]
NE-Bohemia	16.13153	50.58494	tep_uc	56	1995	0	1160	[59]
NE-Bohemia	15.7125	50.73889	blab_a	178	2004	0	225	[60]
NE-Bohemia	15.7125	50.73889	blab_b	178	2001	0	375	Svitavská unpubl
NE-Bohemia	15.7125	50.73889	blab_c	178	2004	0	241	[60]
NE-Bohemia	15.7125	50.73889	blab_d	178	2001	0	143	Svitavská unpubl
NE-Bohemia	15.75586	50.66061	c_hora	437	2000	1	254	[61]
NE-Bohemia	15.75586	50.66061	cernoh	437	2002	20	370	[62]
NE-Bohemia	15.54216	50.77075	lab_la	160	2001	0	332	Svitavská unpubl.
NE-Bohemia	15.54216	50.77075	lab_lb	160	2001	50	240	Svitavská unpubl.
NE-Bohemia	15.55474	50.76606	labsky	40	2004	20	740	[63]
NE-Bohemia	15.54102	50.76619	pancav	299	1996	1	359	[64]
NE-Bohemia	15.7125	50.73889	ups_ra	178	2000	1	630	[65]
NE-Bohemia	15.7125	50.73889	up_pal	178	2004	0	258	[60]
NE-Bohemia	15.7125	50.73889	up_r_a	178	2002	0	379	[62]
NE-Bohemia	15.7125	50.73889	up_r_b	178	2002	0	243	[62]
NE-Bohemia	15.36321	50.85019	halaiz	56	2001	4	728	[66]
Polabí	14.83158	50.21639	hraban	98	2005	3	809	[67]
Polabí	14.54406	50.2603	chrast	56	1999	5	658	[68]
Polabí	14.66743	50.19793	sb_cis	56	1999	5	648	[68]
Polabí	14.53251	50.26691	tisic1	56	2004	70	987	[69]
Polabí	14.5722	50.24337	kozly1	40	2008	16	570	Petr unpubl
Polabí	14.5722	50.24337	kozly2	40	2008	10	443	[67]
Polabí	14.53251	50.26691	tisic2	56	2007	66	386	Petr unpubl
Polabí	14.54406	50.2603	kozly3	56	2008	26	320	Petr unpubl
Polabí	14.66337	50.31878	kosatk	98	2008	9	515	Kozáková unpubl
Polabí	14.66743	50.19793	sb_hra	56	2009	41	512	[70]
Polabí	14.66743	50.19793	sb_mea	56	1999	16	574	[68]
Polabí	15.17312	50.12935	libice	40	2009	20	508	[70]
Polabí	15.18186	50.06066	hradis	28	2008	35	379	[70]
S-Bohemia	14.02087	49.36006	kozli	18	2001	10	388	[71]
S-Bohemia	14.91664	48.85582	halamk	40	1996	0	1233	[72]
S-Bohemia	14.71026	48.9871	spoli	56	1977	0	677	[73]
S-Bohemia	14.81016	48.86078	c_b_a	282	1977	5	1236	[73]

Table S1

region	longitude	latitude	sigle	R (m)	year of sampling	depth (cm)	pollen sum	citation
S-Bohemia	14.81016	48.86078	c_b_aa	282	1977	0	988	[73]
S-Bohemia	14.6327	49.23277	bork_c	564	1977	0	656	[73]
S-Bohemia	14.6327	49.23277	bork_d	564	1977	0	342	Jankovská unpubl
S-Bohemia	14.83329	48.95584	barba	40	1977	0	602	[73]
S-Bohemia	14.70482	49.14562	sva_vj	399	1968	10	1434	[73]
S-Bohemia	14.77804	49.00221	mlouky	1197	1976	5	1088	[74]
S-Bohemia	14.76891	49.02481	mloukb	1197	1978	10	761	[74]
S-Bohemia	14.08968	49.25019	rezabi	138	1972	0	623	[75]
S-Bohemia	14.34901	49.07483	zbudo1	282	1964	0	706	[76]
S-Bohemia	14.34901	49.07483	zbudo2	282	1964	0	1243	[76]
S-Moravia	16.42254	48.77728	dvuran	98	1986	70	252	[77]
S-Moravia	16.3866	48.99067	olbram	252	1984	50	163	[78]
S-Moravia	17.08188	48.95432	svatob	56	1982	0	277	[79]
S-Moravia	17.2052	48.97784	vracov	246	1972	15	852	[77]
S-Moravia	17.2052	48.97784	vraco1	246	1969	22	591	[80]
S-Moravia	16.97493	48.93889	cejc	631	1989	5	600	[81]
S-Moravia	17.54092	48.83081	machov	12	2005	0	457	[82]
B-M. Highlnd	15.4243	49.23398	doupe	56	1974	0	550	[83]
B-M. Highlnd	15.96364	49.73867	kameni	40	1976	0	652	[84]
B-M. Highlnd	15.41601	49.38842	hojkov	56	1974	0	589	[83]
B-M. Highlnd	15.31478	49.21317	h_pole	56	1974	0	281	[83]
B-M. Highlnd	15.14599	49.00142	pfaff1	10	1975	0	553	[85]
B-M. Highlnd	15.14599	49.00142	pfaff2	10	1975	0	590	[85]
B-M. Highlnd	15.30071	49.02765	stalko	40	1974	0	287	[83]
B-M. Highlnd	15.24159	49.1328	suchdo	40	1974	0	328	[83]
B-M. Highlnd	15.19097	49.04174	blato1	282	1958	0	224	[86]
B-M. Highlnd	15.19097	49.04174	blato2	282	1963	0	755	[86]
B-M. Highlnd	15.36439	49.76208	chran1	98	1965	0	1428	[87]
B-M. Highlnd	15.36439	49.76208	chran2	98	1968	5	465	[87]
B-M. Highlnd	15.35538	49.75811	hrozno	98	1969	0	878	[87]
B-M. Highlnd	15.53355	49.32416	loucky	126	1958	0	499	[83]
B-M. Highlnd	15.45905	49.69159	malcin	98	1978	0	519	[88]
B-M. Highlnd	15.47796	49.68134	palasa	113	1979	0	480	[88]
B-M. Highlnd	15.47796	49.68134	palasi	113	1979	0	935	[88]
B-M. Highlnd	15.37083	49.23056	rasna	195	1959	0	221	[83]
B-M. Highlnd	15.41667	49.65	zavidk	98	1979	5	576	[88]
Šumava	13.48878	48.96231	brez_a	56	2001	0	193	Svitavská unpubl
Šumava	13.48878	48.96231	brez_b	56	2001	0	255	Svitavská unpubl
Šumava	13.32755	49.15222	hureck	445	2002	5	228	[89]
Šumava	13.66286	49.00061	chal_s	395	2001	60	367	Svitavská unpubl
Šumava	13.63503	48.96455	knizec	126	2001	0	499	[90]
Šumava	13.81606	48.91376	m_niva	455	2002	2	334	[89]
Šumava	13.88292	48.8668	m_luh	892	2001	0	377	[90]
Šumava	13.88292	48.8668	m_l_ch	892	2001	5	256	Reille unpubl
Šumava	13.28275	49.17728	n_brun	98	2001	0	303	Svitavská unpubl
Šumava	13.86571	48.77674	ple_s1	155	2001	0	145	Svitavská unpubl
Šumava	13.86571	48.77674	ple_s2	155	2001	20	388	Svitavská unpubl
Šumava	13.40531	49.05864	pr_cha	10	2001	0	445	Svitavská unpubl
Šumava	13.39069	49.11411	pr_pre	10	2001	0	264	Svitavská unpubl
Šumava	13.4122	49.0153	rokyte	798	2002	0	352	[89]
Šumava	13.46189	49.03129	rybare	319	2002	10	293	[89]
Šumava	13.74226	48.89887	straze	618	2001	0	204	[90]
Šumava	13.81857	48.92412	v_leno	691	2002	0	134	[89]
Šumava	13.81857	48.92412	v_vola	691	2001	0	295	[90]
Šumava	13.13913	48.88394	dosing	160	1984	0	527	[91]
Šumava	13.7534	48.82677	heidem	233	1983	0	553	[91]
Šumava	13.57064	48.82519	sonndo	98	1983	0	573	[91]
Šumava	13.57751	48.94813	finste	156	1983	10	561	[91]

Table S2

			Poaceae				Plantago lanceolata				Corylus			
	stand. veg. cov.(%)	seg. total	seg. pres.	seg. abun.	mean abun.	var. of abun	seg. pres.	seg. abun.	mean abun.	var. of abun	seg. pres.	seg. abun.	mean abun.	var. of abun
A1.1	77	17	17	7	69.56	6.45								
A1.2	95	192	165	144	77.67	5.39	2	2	0.00					
A2.1	50	62	60	7	2.14									
A2.2	95	189	176	53	9.38	1.53								
A3	50	9	5											
A4.1	98	313	276	96	79.19	3.73								
A4.2	95	27	20											
A4.3	95	33	28	11	6.65	8.20								
A5	55	6	5	4	45.39									
A6A	45	210	174	3	0.82									
A6B	50	70	58											
A7	50	272	199	17	20.50	6.35								
A8.2	50	6	6	1	13.46									
M1.1	100	4621	3277	2514	56.95	0.43	3	2	0.00		1			
M1.2	70	55	43	30	25.05	11.32								
M1.3	50	467	323	197	22.84	1.24	1							
M1.4	90	698	467	394	46.14	2.00	1							
M1.5	50	372	153	73	10.98	1.35								
M1.6	90	80	41	22	9.55	10.14								
M1.7	90	3043	2028	1214	33.95	0.51	3	3	0.00					
M1.8	90	2	2	2	4.12									
M2.1	60	87	48	27	12.94	6.11								
M2.2	70	6	4	1	25.93									
M2.3	60	6	4	1	11.98									
M2.4	60	1	1	1	51.72									
M3	40	24	12	6	11.38									
M4.1	10	116	34	16	2.46	0.16								
M5	40	107	23	6	1.70									
M6	90	58	35	24	4.12	0.49	1	1	0.01					
M7	20	81	12	1	11.49									
R1.1	90	10	3	2	11.47									
R1.2	80	134	76	28	14.49	5.72								
R1.3	60	78	28	11	3.74	2.20					1			
R1.4	40	1315	561	168	5.50	0.19					4			
R1.5	40	37	31											
R2.1	80	19	14	7	27.90	80.53								
R2.2	60	850	688	212	18.25	1.13	19	12	0.02	0.00	2			
R2.3	10	1593	1266	439	3.98	0.02					1			
R2.4	10	4	4	1	1.86									
R3.1	10	289	159	49	2.85	0.12								
R3.2	10	175	84	13	1.71	0.22								
R3.3	30	86	1	1	0.01									
R3.4	30	69	58	34	23.74	1.88								
S1.1	27	228	53	8	1.20		1				5	2	0.03	
S1.2	35	4853	1274	281	3.33	0.03	1				124	81	0.13	0.00
S1.3	80	78	49	17	37.83	22.71					5	3	0.11	
S1.4	50	2												
S1.5	50	76	34	5	3.68						24	15	4.05	2.17
S2A	40	31	8	1	3.40									
S2B	40	102	30	4	3.47						2	1	0.06	
S3A	40	2												
S3B	40	18												
T1.1	95	19378	14525	7151	48.34	0.09	8133	2770	4.03	0.01	24			
T1.10	50	208	109	35	9.87	1.94	2	1	0.00					
T1.2	98	2152	1648	739	55.70	0.76	394	130	0.86	0.01	2			
T1.3	85	955	646	158	32.29	1.94	391	69	4.04	0.20	1			
T1.4	95	901	636	331	40.62	1.53	199	87	0.97	0.03				
T1.5	98	10001	7411	2578	29.87	0.19	1022	347	0.69	0.00	9			
T1.6	98	3997	2448	995	16.27	0.27	24	8	0.01		3			
T1.7	95	156	92	46	23.21	5.88	38	9	0.37	0.01	1			
T1.8	98	6	6	6	57.83	65.85								
T1.9	95	1643	1418	518	46.96	1.22	307	117	1.51	0.04	6			
T2.1	95	109	66	18	54.02	18.45								

Table S2

	stand. veg. cov.(%)	seg. total	**Poaceae**				**Plantago lanceolata**				**Corylus**			
			seg. pres.	seg. abun.	mean abun.	var. of abun	seg. pres.	seg. abun.	mean abun.	var. of abun	seg. pres.	seg. abun.	mean abun.	var. of abun
T2.2	95	438	351	78	67.54	4.93	6							
T2.3A	90	69	67	17	74.26	12.15	16	6	0.51					
T2.3B	90	3176	2851	1300	60.85	0.45	514	148	0.96	0.01	12			
T3.1	45	404	359	211	18.56	0.77	4				3			
T3.2	55	79	73	52	36.09	3.82					1			
T3.3A	90	221	203	80	53.51	8.11	6				1			
T3.3B	90	62	55	30	63.18	22.91	4							
T3.3C	90	6	6	1	50.81									
T3.3D	90	664	556	380	49.63	1.59	22	6	0.25		1			
T3.4A	90	2	1											
T3.4B	90	21	20	14	65.55	38.43	1	1	0.02		2			
T3.4C	90	78	71	50	42.05	8.34	14	3	1.27					
T3.4D	90	3390	2696	1994	51.27	0.30	210	92	0.18	0.00	6			
T3.5A	90	3	3				1							
T3.5B	90	722	641	271	57.54	1.75	108	18	0.74	0.11	4			
T4.1	90	198	164	113	34.23	3.49					2			
T4.2	90	959	702	369	38.92	1.47	35	9	0.06	0.00	16			
T5.1	30	14	11	8	17.30	10.04	1							
T5.2	55	98	78	46	24.38	3.90	21	15	0.89	0.05				
T5.3	55	197	153	122	28.64	2.12	19	13	0.51	0.06				
T5.4	55	78	65	63	32.36	3.37	24							
T5.5	55	1083	944	386	27.56	0.77	216	37	0.62	0.02	8			
T6.1A	55	31	13	1	4.94									
T6.1B	55	132	48	31	6.82	1.51	6	2	0.10					
T6.2A	55	16	10											
T6.2B	55	67	24	10	6.08	2.52								
T7	80	19	15	8	46.16	75.63	5	1	0.22					
T8.1A	85	1	1	1	0.80									
T8.1B	85	170	133	66	26.69	6.45	1							
T8.2A	85	38	37	19	32.13	15.30					2			
T8.2B	85	498	362	151	28.00	2.40	5	1	0.01		5			
T8.3	85	183	67	29	7.35	2.93								
V1A	50	7	1											
V1B	50	9	4	1	0.10									
V1C	50	97	10	6	1.15									
V1E	50	1												
V1F	50	1641	163	36	1.02	0.06	1							
V1G	50	3550	209	25	1.23	0.05								
V2A	50	73	7	1	3.24									
V2B	50	32	6	3	2.32									
V2C	50	148	22	8	4.92									
V3	50	78	30	2	0.42									
V4A	50	510	32	3	0.45									
V4B	50	1787	29	4	0.61						1			
V5	50	112	5											
V6	50	1	1											
X1	10	8144	27	1	0.03		4				1			
X10	85	5455	335	53	4.01	0.08	1				11	5	0.00	
X11	85	4473	218	53	3.32	0.08					21	9	0.04	0.00
X12	95	1017									3	3	0.07	
X12A	95	10149	1536	144	8.31	0.20	20	1	0.00		959	318	1.57	0.01
X12B	95	6234	199	21	1.08	0.03	1				80	20	0.23	0.00
X13	75	5837	167	16	1.47	0.03	9	1	0.03		55	8	0.25	
X14	50	1124	27	7	0.60									
X2	75	1595	12	2	0.56									
X3	60	998	37	7	1.60		3	1	0.00					
X4	60	128					1	1	0.38					
X5	100	10586	2285	571	15.33	0.14	573	106	0.98	0.01	57	22	0.05	0.00
X6	10	1863	40	5	0.17		3							
X7	75	670	2	2	0.17									
X7A	75	5730	2052	931	21.22	0.20	46	8	0.03		44	11	0.09	0.00
X7B	75	6655	1306	511	10.34	0.10	28	5	0.02		8	1	0.02	
K1	100	3256	-	-	-	-	-	-	-	-	33	4	0.02	

Table S2

	stand. veg. cov.(%)	seg. total	**Poaceae**				**Plantago lanceolata**				**Corylus**			
			seg. pres.	seg. abun.	mean abun.	var. of abun	seg. pres.	seg. abun.	mean abun.	var. of abun	seg. pres.	seg. abun.	mean abun.	var. of abun
K2.1	100	999	-	-	-	-	-	-	-	-	11	4	0.15	
K3	100	19494	-	-	-	-	-	-	-	-	5139	3441	10.23	0.03
K4A	100	161	-	-	-	-	-	-	-	-	16	12	0.58	0.09
L1	100	790	-	-	-	-	-	-	-	-	25	11	0.04	0.00
L10.1	100	135	-	-	-	-	-	-	-	-	1	1	0.00	
L10.2	100	153	-	-	-	-	-	-	-	-	5	2	0.01	
L2.1	100	108	-	-	-	-	-	-	-	-	1	1	0.00	
L2.2	100	16784	-	-	-	-	-	-	-	-	1711	746	0.48	0.00
L2.3	100	2479	-	-	-	-	-	-	-	-	96	30	0.35	0.01
L2.3A	100	47	-	-	-	-	-	-	-	-	2	1	0.10	
L2.3B	100	457	-	-	-	-	-	-	-	-	14	8	0.10	
L2.4	100	670	-	-	-	-	-	-	-	-	9	6	0.03	
L3.1	100	15055	-	-	-	-	-	-	-	-	3311	1943	2.21	0.00
L3.3	100	2841	-	-	-	-	-	-	-	-	276	162	0.82	0.01
L3.3B	100	136	-	-	-	-	-	-	-	-	1			
L3.4	100	1238	-	-	-	-	-	-	-	-	159	46	0.90	0.03
L4	100	1442	-	-	-	-	-	-	-	-	539	297	4.17	0.09
L4A	100	604	-	-	-	-	-	-	-	-	252	133	6.94	0.47
L4B	100	55	-	-	-	-	-	-	-	-	16	14	5.17	2.12
L5.1	100	7757	-	-	-	-	-	-	-	-	719	347	0.50	0.00
L5.3	100	69	-	-	-	-	-	-	-	-	25	10	0.36	0.02
L5.4	100	14198	-	-	-	-	-	-	-	-	576	259	0.23	0.00
L6.1	100	178	-	-	-	-	-	-	-	-	51	39	3.19	0.27
L6.2	100	254	-	-	-	-	-	-	-	-	32	6	0.22	
L6.3	100	321	-	-	-	-	-	-	-	-	3			
L6.4	100	337	-	-	-	-	-	-	-	-	94	70	3.43	0.18
L6.5A	100	70	-	-	-	-	-	-	-	-	1			
L6.5B	100	1091	-	-	-	-	-	-	-	-	95	58	0.58	0.01
L7.1	100	6756	-	-	-	-	-	-	-	-	744	353	0.90	0.00
L7.2	100	1140	-	-	-	-	-	-	-	-	63	35	0.39	0.01
L7.3	100	1788	-	-	-	-	-	-	-	-	73	18	0.10	0.00
L8.1B	100	977	-	-	-	-	-	-	-	-	43	30	0.29	0.01
L8.2	100	85	-	-	-	-	-	-	-	-	32	12	3.64	1.24
L9.1	100	2764	-	-	-	-	-	-	-	-	1	1	0.00	
L9.2B	100	2519	-	-	-	-	-	-	-	-	8	3	0.02	
X8	100	1025	-	-	-	-	-	-	-	-	4			
X9A	100	28693	-	-	-	-	-	-	-	-	345	109	0.08	0.00
X9B	100	4351	-	-	-	-	-	-	-	-	30	4	0.06	
SUM		293883	60664	27042			12471	4033			16074	8715		

Table S3

		Poaceae				Plantago lanceolata					Corylus			
CLC class	**treeless seg. total**	seg. pres.	seg. abun.	mean abun.	var. of abun	seg. pres.	seg. abun.	mean abun.	var. of abun	**seg. total**	seg. pres.	seg. abun.	mean abun.	var. of abun
112	9856	2982	1545	17.72	0.12	1067	401	0.96	0.00	13035	475	258	0.38	0.00
121	878	247	131	18.34	1.43	36	11	0.36	0.03	1290	46	13	0.55	0.06
122	86	21	18	12.87	8.88					137	8	8	0.05	
123	2	1	1	35.35						2				
124	6	1	1	13.94						7				
131	192	82	40	23.53	6.79	3	1	0.26		363	30	16	1.40	0.13
132	20	5	4	16.01						28				
133	13	2	2	4.17						28				
141	276	114	83	24.78	4.85	17	5	0.84		537	27	18	0.14	0.00
142	788	256	138	19.30	1.73	49	16	0.80	0.05	1208	31	11	0.41	0.03
211	30948	12881	6744	24.79	0.05	3289	1094	0.97	0.00	57118	3848	2189	1.73	0.00
221	396	183	125	26.60	3.05	19	3	1.04		732	20	12	0.20	0.01
222	734	218	131	18.89	1.53	34	8	0.27		1265	88	53	0.68	0.01
231	35603	14689	6332	23.40	0.04	4339	1365	1.12	0.00	51487	3214	1693	1.76	0.00
242	1622	581	363	22.68	0.78	107	32	0.32	0.01	2631	106	67	0.35	0.00
243	57247	23221	11193	23.35	0.03	5888	2039	0.87	0.00	85473	5732	3116	1.67	0.00
311	12374	3271	1749	15.31	0.09	395	141	0.20	0.00	40117	2289	1403	0.48	0.00
312	37048	15462	5593	21.76	0.05	2879	660	0.77	0.00	87638	3856	1894	0.93	0.00
313	22860	6969	3118	17.49	0.06	1453	483	0.52	0.00	67312	4239	2221	0.64	0.00
321	4923	3203	781	38.37	0.77	176	17	0.10	0.00	6062	258	104	0.80	0.01
322	1009	861	260	52.12	4.74	2	2	0.00		1131				
324	10267	4923	1726	27.50	0.21	394	66	0.20	0.00	19842	739	322	0.56	0.00
332	83	9								172				
333	63	59	5	89.53						75				
411	1202	718	204	31.13	2.47	26	2	0.46		1646	2			
412	410	243	58	27.21	11.52					570				
511	590	230	187	26.77	2.32	10	6	0.09		915	20	5	0.12	
512	1792	806	460	33.82	1.22	55	4	1.04		2835	116	62	0.51	0.01
SUM	231288	92238	40992			20238	6356			4E+05	25144	13465		

Table S4

	Polabi	**N-Bohem**	**NE-Bohem**	**S-Bohem**	**S-Morav**	**Sumava**	**Boh-Mor_High**
Abies	0.17	0.06	0.16	0.69	0.33	1.29	0.37
Acer	0.39	0.91	0.62	0.22	0.54	0.40	0.27
Alnus	0.59	0.95	0.85	0.90	0.44	0.90	0.94
Betula	1.80	3.96	2.06	1.28	0.72	1.47	0.84
Carpinus	1.06	0.54	0.48	0.03	2.60	0.02	0.41
Cerealia	48.98	33.07	32.04	31.57	48.95	21.51	39.31
Corylus	0.58 (0.05)	0.69 (0.07)	0.63 (0.05)	0.67 (0.05)	0.45 (0.06)	0.81 (0.07)	0.57 (0.04)
Fagus	1.84	4.15	2.84	2.14	5.79	3.48	1.38
Fraxinus	0.77	1.38	0.66	0.13	1.86	0.21	0.27
Picea	12.53	20.21	33.01	32.55	11.69	42.97	34.85
Pinus	14.94	15.41	7.57	15.99	6.79	10.34	8.70
Pla_lanc	0.34 (0.04)	0.54 (0.05)	0.67 (0.05)	0.48 (0.05)	0.26 (0.05)	0.62 (0.06)	0.38 (0.04)
Poaceae	8.54 (0.11)	12.19 (0.16)	13.33 (0.11)	11.27 (0.11)	7.79 (0.15)	14.44 (0.17)	9.12 (0.09)
Quercus	6.82	5.35	4.71	1.74	10.28	1.26	2.15
Salix	0.04	0.04	0.04	0.02	0.14	0.02	0.03
Tilia	0.60	0.51	0.33	0.31	1.32	0.25	0.41
Ulmus	0.01	0.01	0.01	0.00	0.05	0.01	0.01

Text S1: REVEALS script manual

REVEALS algorithm is theoretically developed and described in detail by Shinya Sugita (2007). The structure of following script was adopted from his original program. Main aim of the REVEALS migration to R-project environment is possibility of further editing and batch processing.

Input data:

The script requires a set of input files as follows:

1) **list of pollen sites**, i.e. list of names of the files from (2), e.g.:
   ```
   site1.csv
   site2.csv
   ...
   ```

2) **pollen data from sites** included in (1) as separated files. First row of this file is a header. It contains names of the time windows. If any site has no record in some time window, column must be included anyway and pollen counts are filled with zeros. Second row contains radiuses of sedimentation basin. Third row lists codes of the deposition model. If pollen was deposited in a bog, use Prentice model (Prentice, 1985) by writing: 1. Any other option, e.g.:2, will process lake model (Sugita, 1993). Fourth and next rows are different taxa and their pollen counts, e.g.:
   ```
   taxa,0-500BP,500-1000BP,...
   Radius,100,100,...
   Model,1,2,...
   taxon1,0,100,...
   taxon2,0,254 ,...
   ...
   ```

3) **pollen productivity estimates and fall speed of pollen**. First row of this file is a header, then follows list of taxa with pollen productivity estimate (first value) and fall speed of pollen (second value). Order of taxa must correspond to ordering in pollen data (2).
   ```
   taxa,alpha,vg
   taxon1,4.2,0.021
   taxon2,2.31,0.022
   ...
   ```

All these data files have to be placed in the working directory of R. All these data files must be in formatted as Comma Separated Values (*.csv).

When files are prepared, you start R, select working directory with your files, copy distance weighting function and reveals function into a console. Reveals function has following syntax:

```
> reveals(file_name_list,file_name_avg,u,Zmax,r)
```

parameters:

a) **file_name_list** - name of the file with the list of pollen sites (1)
b) **file_name_avg** - name of the file with pollen productivity estimates and fall speed of pollen (3)
c) **u** - wind speed (m/s)
d) **Zmax** - radius of the area of background component (km)
e) **r** - radius of the sedimentation basin (m)

Example, create three files from the example (below), copy a REVELAS script code (below) into the R and call by following :

```
> reveals("my_site_list.csv", "alpha.csv", 3, 60, 100)
```

Output is a table of REVEALS estimates (proportions) for all time window (columns) and all taxa (rows). Output is returned on the screen and also written to the working directory as "results_my_site_list.csv".

Text S1: REVEALS script code

```
library(zipfR)

### DEFINE Sugita's KP
KPf <- function(vg,u,Zmax,radius,model)
{
        b<-75.2*vg/u
        if(model=="Prentice")

                #Prentice bog model
                {
                KP<-(exp(-1*b*radius^0.125)-exp(-1*b*(Zmax*1000)^0.125))
                }
        else
                #Sugita lake model
                {
                xa<-b*(Zmax*1000-radius)^(1/8)
                xb<-b*(Zmax*1000+radius)^(1/8)
                xc<-b*(radius+radius)^(1/8)
                KP<-(4*pi*radius/(b^8))*(Igamma(8,xa)-Igamma(8,xb)+Igamma(8,xc))
                }
return(KP)
}
##############################################
```

```
reveals <- function(file_name_list,file_name_avg,u,Zmax,r)
{
avg <- read.table(file_name_avg, row.names=1, header=T, sep=",")
lst <- read.table(file_name_list)
paldatasample <- read.table(as.character(lst[1,]),sep=",", row.names=1, header=T)
          veg <- matrix(nrow=length(row.names(paldatasample))-2,ncol=length(paldatasample))
rownames(veg) <- rownames(paldatasample)[3:length(rownames(paldatasample))]
colnames(veg) <- colnames(paldatasample)

## LOOP FOR TIMELAYERS
for (w in 1:(length(paldatasample)))
        {
        ## LOOP FOR ALL SITES
        allsites <- matrix(nrow=nrow(avg), ncol=length(rownames(lst)))
        allsitesprop <- matrix(nrow=nrow(avg), ncol=length(rownames(lst)))
        for (m in 1:(length(rownames(lst))))
                {
                polcount <- read.table(as.character(lst[m,]),sep=",", row.names=1,header=T)
                polcount[is.na(polcount)]<-0

                ## pollen sum
                sumv<-0
                for (j in 1:(length(rownames(polcount))-2))
                        {
                                               vg <- avg[j,2]
                                             radius <- r
                        if(polcount[2,w]==1){model<-"Prentice"     }else{
                                               model<- "Sugita"}

                        v<-polcount[j+1,w]/(avg[j,1]*KPf(vg,u,Zmax,radius,model))
                        sumv <- sumv+v
                        }
                ## vegetation proportion for 1 species
                for (i in 1:(length(rownames(polcount))-2))
                        {
                                                 vg <- avg[i,2]
                                             radius <- r
                        if(polcount[2,w]==1){model <-"Prentice"      }else{
                                              model  <-"Sugita"}
                        v1 <- polcount[i+2,w]/(avg[i,1]*KPf(vg,u, Zmax,radius,model))
                        allsitesprop[i,m] <- v1/sumv
                        allsites[i,m]     <- v1
                        }
        } ## END OF ALL SITES LOOP
veg[,w] <- rowSums(allsites)/sum(rowSums(allsites))

} ## END OF TIMELAYERS LOOP
write.table(veg, paste("result_from_",file_name_list, ".csv", sep=""), sep=",", quote=F)
return(veg)

}
```

Text S1: Example files

Copy text into a empty notepad file with following name. (Do not forget to put one empty line after last line.)

file "my_site_list.csv":

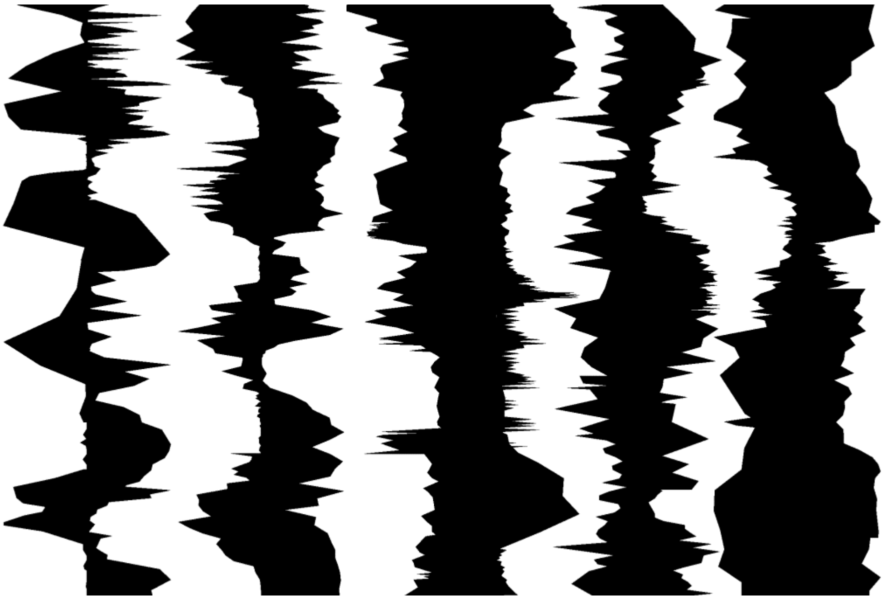
```
example.csv
```

file "example.csv":

```
plants,0
Radius(m),18
Model(Prent_is1Sugit_is2),1
Alnus,100
Salix,100
Fraxinus,100
Betula,100
Corylus,100
Pla_lanc,100
Pinus,100
Ulmus,100
Tilia,100
Quercus,100
Poaceae,100
Carpinus,100
Picea,100
Acer,100
Fagus,100
Cerealia,100
Abies,100
```

file "alpha.csv":

```
,alpha,vg
Alnus,4.2000000,0.021
Salix,2.31,0.022
Fraxinus,0.6700000,0.022
Betula,2.4200000,0.024
Corylus,1.4000000,0.025
Pla_lanc,0.9000000,0.029
Pinus,1.3500000,0.031
Ulmus,1.2700000,0.0320000
Tilia,0.8,0.032
Quercus,1.76,0.035
Poaceae,1.0000000,0.035
Carpinus,2.1,0.042
Picea,0.5700000,0.056
Acer,0.3200000,0.056
Fagus,1.2000000,0.057
Cerealia,0.0462000,0.06
Abies,9.92,0.12
```



Chapter 5: reconstructed Holocene vegetation

Abraham, V., Kuneš, P., Petr, L., Svitavská-Svobodová, H., Kozáková, R., Jamrichová, E., Švarcová, M.G. & Pokorný, P. (*manuscript*). A pollen-based quantitative land-cover reconstruction in stages of the Holocene explains the naturalness of today's vegetation.

A pollen-based quantitative land-cover reconstruction in stages of the Holocene explains the naturalness of today's vegetation

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Abstract

Questions: What is the pollen-based quantitative vegetation reconstruction for the entire Holocene in the Czech and Slovak Republics? Which time window in the past best fits the results of Potential Natural Vegetation (PNV) mapping?

Location: 87 sites in nine regions of 60 km radius in the Czech and Slovak Republics.

Methods: We calculated regional vegetation estimates using a REVEALS model - Regional VEgetation Algorithm from Large Sites. Compared to traditional methods, the REVEALS approach takes into consideration the following biases as its parameters: taxon-specific pollen productivity and dispersal, and the effect of the size and type of the sedimentation basin on the taphonomy of pollen assemblage. We sought for natural vegetation in the Holocene past by measuring the dissimilarity among all time windows (500 years) of the pollen-based vegetation reconstruction and the composition of Potential Natural Vegetation (PNV).

Results: Post-glacial vegetation development can be clustered into three general phases: Early, Middle and Late Holocene. Pine was the most abundant during the Early Holocene. In the Middle Holocene, lowlands were dominated by oak. Spruce was the most prevalent taxon (>32%) in all regions from medium to high altitudes. In the Late Holocene, vegetation with beech, fir and spruce, and/or vegetation with variable intensity of cereal cultivation is revealed. In some lowland regions, we identified the continuous presence of an open landscape (Poaceae >9%) and/or continuous persistence of pine (>6%). The most similar vegetation composition to PNV is in the 750 AD time window. Inter-regional vegetation gradients of individual taxa are roughly similar for both the REVEALS estimates around 750 AD and the PNV data, but the quantities of individual taxa differ substantially. PNV overestimates broadleaved taxa at the expense of *Picea* and trees of early successional stages (*Pinus, Betula*).

Conclusions: The Mid-Holocene spruce phase contrasts with most previous interpretations, which describe it as being characterized by mixed oak woodlands. We explain the mismatch between the pollen-based vegetation reconstruction and PNV by methodological and conceptual differences. PNV mapping is based on preferential sampling of modern vegetation with the maximum floristic richness, so it is not representative of real vegetation in the past or in the future. The continuity of landscape openness and occurrence of pioneer trees indicate an important role of possible natural drivers allowing their permanent abundance, be it herbivores, a dry climate or fire activity.

Introduction

The long-term perspective is crucial for understanding present-day vegetation patterns affected by species invasions or various kinds of disturbances. It may reveal valuable information about past biodiversity changes and thresholds within natural variability and thus facilitate pertinent decisions in conservation management policies (Willis and Birks, 2006). Some of the fundamental questions asked by vegetation scientists (including palynologists) revolve around reconstructing natural vegetation composition. In general, palynologists aim to interpret pollen spectra as past vegetation originating before humans started to have a considerable impact. The outputs represent past states denoted as “reconstructed vegetation”.

Vegetation ecology seeks in space for samples of natural and semi-natural fragments of vegetation existing within the actual landscape mosaic. Subsequent classification of vegetation relevés produces mapping units, which are based on abiotic conditions (e.g. the climate, soils or the relief) extrapolated to sites of similar habitat types where natural vegetation no longer exists due to anthropogenic pressure. Each combination of abiotic conditions is assigned a mapping unit, which makes potential natural vegetation (PNV) a hypothetical concept.

A recent attempt to link palaeoecological data with PNV (Carrión and Fernández, 2009) prompted a hot debate about the sense of such comparisons and also about the basic concept of PNV itself (Chiarucci et al., 2010). PNV, which should represent merely a hypothetical future state (Loidi et al., 2010), cannot be compared with palaeoecological data, because environmental conditions possibly differed in the past. However, large variation exists among the diverse definitions of PNV that can be found in the literature (Mucina, 2010). The principal objective of all PNV maps is the removal of human impact in order to obtain an abstraction of the “natural state”. Differences among PNV definitions are always attached to human-induced changes (soils, climate, etc.) and their reversibility. One example from former Czechoslovakia puts the hypothetical state of natural vegetation in the past before its deterioration or even destruction by humans (Mikyška, 1968); this concept is referred to as Reconstructed Natural Vegetation (RNV). A step further is the imaginary map scenario (Neuhäuslová, 2001), derived from RNV, which predicts how vegetation would develop after the cessation of all human activities. These two maps are, however, closely similar, because they differ only in small areas that have been irreversibly altered by human activities (drained areas, opencast mines, etc.). If we disregard such areas, we can consider these two land-cover maps as the best expression of current site conditions and species pools. The similarity between RNV and PNV makes PNV applicable also to the past.

Notwithstanding catastrophic, cyclic, or abrupt events, present-day (natural) vegetation in Central Europe bears the legacy of long-term continuous dynamics. Nevertheless, most vegetation has been influenced by human activity. Humans were present during the prehistory in both lowlands and highlands (Dreslerová, 2011). Forests were influenced by cattle grazing, burning, cropping, sort cutting or complete forest removal. Thus, the seek for the youngest period of natural vegetation development without any human impact may easily take us back to the Early Neolithic or even earlier. However, practical reasons for drawing maps of PNV, which are useful in forest management and nature conservation, require that maps of PNV are drawn with some connection to the present. We therefore compared PNV composition with results of pollen analyses.

Phytosociological and palynological results were considered together throughout the long history of research into natural vegetation (Firbas, 1949). The importance of vegetation history is highlighted in the construction of PNV (Neuhäuslová, 2001). Results of palynological investigations were gradually integrated into the concept of PNV (Pokorný, 2002a), but many taxa in previous palynological studies focusing on comparisons with PNV show mismatches such as overrepresentation of oak and hornbeam in historically reconstructed coniferous forests (Peichlová, 1979; Rybníček and Rybníčková, 1978; Rybníčková, 1973). In spite of the multitude of palynological evidence of a spruce forest at medium altitudes, the natural altitude limit of spruce is still claimed to be lying above 800 m a.s.l. except for wet depressions in lowlands (Chytrý, 2012).

When comparing PNV and results of pollen analyses, it is reasonable to criticize pollen analyses for their lack of spatial reference (Loidi and Fernández-González, 2012) and bias given by taxon-specific pollen production and dispersal (Loidi et al., 2010). This problem stems from traditional palynological reconstructions, which are mostly based on interpreting pollen proportions. The Landscape Reconstruction Algorithm (LRA) (Sugita, 2007a, 2007b) has one great advantage in that it overcomes these biases by using pollen productivity, pollen dispersal, and the size and type of the sedimentation basin to estimate past vegetation abundances in a given space. In our study, we focus on the first step of the LRA – the REVEALS model

(Sugita, 2007a), which estimates vegetation from the pollen record of many small sites or a few large sites across an area of 10^6 km^2.

Our main aim was to produce a pollen-based quantitative vegetation reconstruction for the entire Holocene in selected regions of the Czech and Slovak Republics using a previously tested REVEALS model (Abraham et al., 2014). The formalized interpretation of this tool transforms pollen percentages into vegetation history more transparently. Based on that, we aimed to use PNV to identify the most similar time window of the REVEALS-reconstructed vegetation, which we refer to as pollen-based reconstructed natural vegetation (pRNV). By comparing PNV, pRNV and actual vegetation, we attempted to determine the approach which best describes natural vegetation. We then discuss the implications of our results for conservation management policies.

Vegetation development according to the traditional interpretation

Vegetation development in the Czech and Slovak Republics was described already during the first decades of pollen-analytical investigations (Rudolph, 1931). Comparisons of pollen curves of tree taxa from different sites allowed to distinguish maxima for each taxon and to delimit phases based on these maxima. Sequences of phases at several sites per region were subsequently generalized as types of forest succession during the Holocene. Rudolph (1931) described several succession types for Central Europe. The most general succession type (birch-pine, hazel, mixed oak forest and beech) is, however, valid only in lowlands and westwards of our target regions. From the west to the east, pollen maxima of deciduous temperate trees (*Corylus*, *Quercus*, *Fagus*) generally decrease whereas *Picea* increases along the same longitudinal gradient. Numerous sites allowed the recognition of an altitudinal gradient based on the lack of *Picea* in lowlands. In mountainous regions surrounding the Bohemian Massif (the Sudetes), a succession type with an additional spruce phase between beech and mixed oak woodlands has been proposed (Rudolph, 1931). Further east, in forest succession in the Tatra region of the Carpathians, the spruce phase appears much earlier before the hazel phase. This pattern is reflected also by the relatively early arrival of spruce around 8500–7500 BP in the Bohemian Massif and earlier than 12000 BP in the Carpathians (Lang, 1994). All knowledge from the pioneer period was summarized by Firbas (1949). He distinguished seven phases of the Holocene, numbered as IV.-X.

Methods

Fossil pollen data

We extracted 87 sequences from the Czech Quaternary pollen (PALYCZ) database (Kuneš et al., 2009). Pollen types denoted by names of genera, except for *Pinus*, refer to all species within the given genera. The name *Pinus* refers only to species belonging to the subgenus *Diploxylon*. *Plantago lanceolata* is the only pollen taxon defined at the species level. Poaceae encompass all wild grasses, except *Phragmites australis* if determined. The genera *Triticum*, *Hordeum* and *Avena* were pooled into the group taxon Cerealia; if distinguished, pollen of *Secale* and *Zea* was excluded. The data contain some Cerealia pollen from the Early Holocene; we assumed that this is incorrectly determined pollen of certain large grasses (*Glyceria maxima*), so we exclude all occurrences of Cerealia before 5.5 kyr BC from the analysis (their list is presented in Table S2).

Chronologies were established by classical depth-age modelling (Blaauw, 2010), mainly by linear interpolation of radiocarbon dates. Exceptionally, some chronologies in South and North-West Bohemia were improved by palynostratigraphical dating extrapolated from the closest dated profiles within the same region. Since all sites where palynostratigraphical correlation was applied are relatively large, it was assumed that they reflect the same regional vegetation changes and that all pollen events are synchronous. Uncertainties of these pollen control points were set to 250 years (Giesecke et al., 2014). Depth-age modelling methods for each sequence in detail and all dating points including new radiocarbon dates which were not previously published are summarized in Table S2.

The Prentice-Sugita dispersal function assumes that the most pollen is transported by the canopy component. Pollen deposited in the sedimentation basin by different ways represents a possible source of biases. Unusually high proportion of *Tilia* appears at the bottom of many profiles, e.g. Jelení Louže (Pokorný and Kuneš, 2005), Zahájí2 (Pokorný unpubl.). As this pollen type is among the most resistant, (Havinga, 1967), we interpreted it as an indication of the initial stage of the peatbog, when dry conditions allowed microbial processes to decompose the rest of the pollen grains. Additionally, at Zahájí between 381 and 461 cm, a high proportion of Ceralia pollen occurred. A *Panicum* seed discovered by macrofossil analysis in the same layer proved direct transport of material from a close settlement (Albert and Pokorný, 2012; Pokorný, 2005), probably by water. We excluded samples influenced by post-taphonomic processes before aggregating them into time windows.

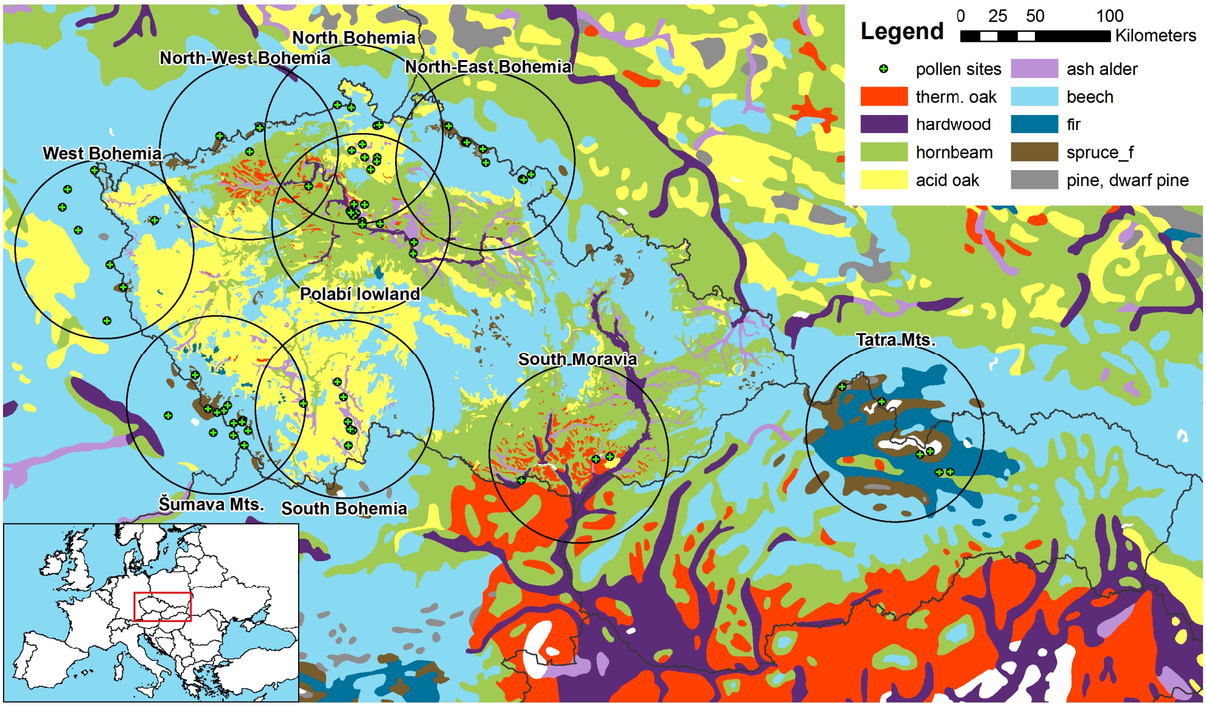


Figure 1: Map of PNV adopted from Neuhäuslová (2001) and Bohn et al. (2004) the in Czech and the Slovak Republic indicating circular regions of REVEALS reconstruction and pollen sites. Units of PNV correspond to Table S1. See Table S2 for the allocation of sites to regions in cases when sites are situated in two or three overlapping regions. White areas represent bare land (alpine zone, lakes, steppe and bogs).

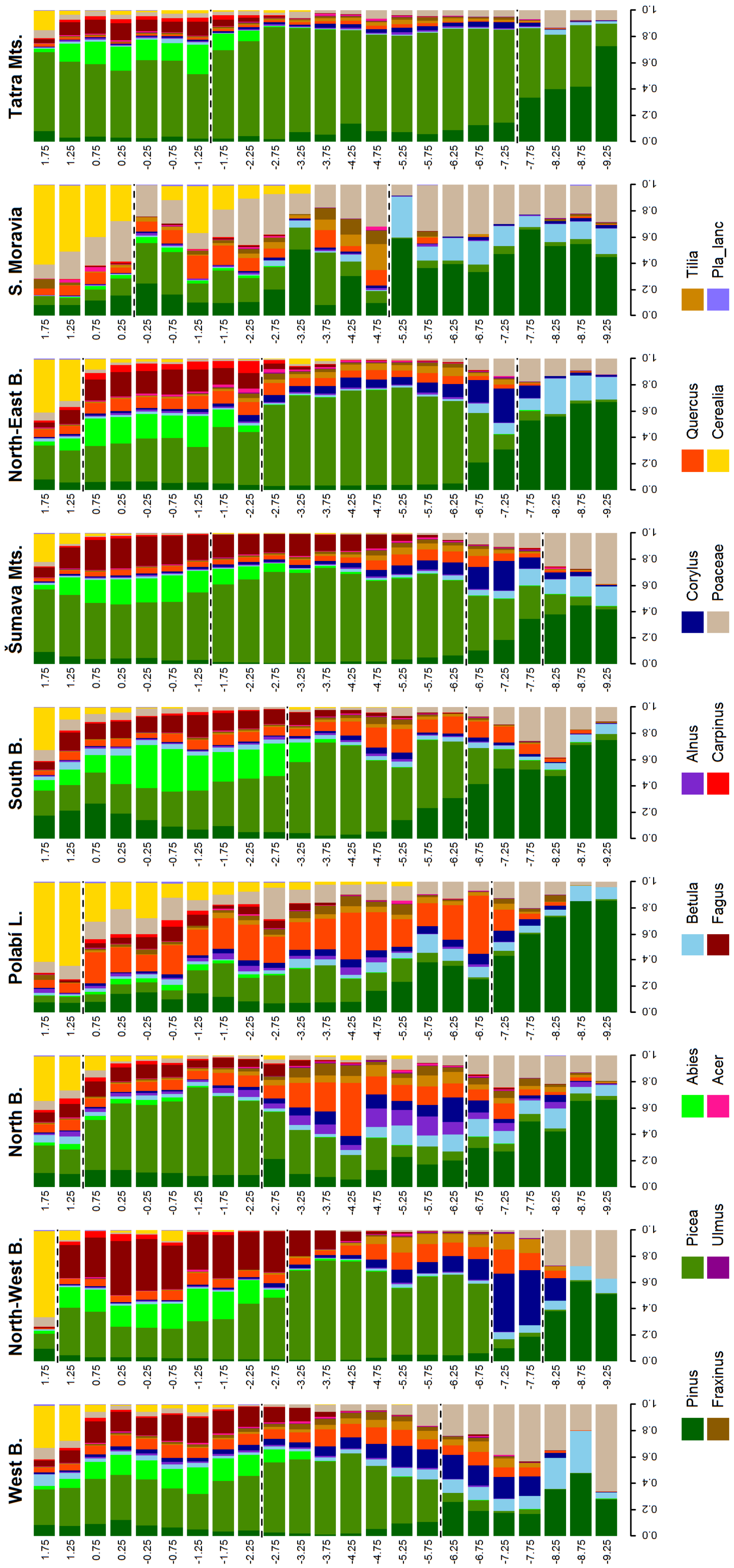
The second source of biases is pollen transported by the gravity component from taxa growing within the sedimentation basin. By overlapping pollen curves of all target taxa (Figure S2), we identified sites in three regions (South Bohemia, South Moravia and West Bohemia) where the proportion of *Alnus* was much higher than in the other profiles. We thus interpreted it as present locally for a certain period. The pollen proportion of *Alnus* in all other profiles was very similar, so we calculated the average from these profiles and used it to calculate of pollen counts in profiles with local presence of *Alnus*. Samples and profiles where we applied this replacement are listed in Table S2. The threshold for local presence of *Alnus* varied around 20% depending on region. The pollen signal of *Alnus* in the Polabí lowland and in North Bohemia exceeds this threshold at most of the 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 as a regional signal.

Model setting

We chose the best set of parameters (Pollen Productivity Estimates, wind speed) tested on present-day vegetation in the same regions as used here (Abraham et al., 2014), using the original basin sizes adopted from the PALYCZ database. We assumed the wind speed to be 4 m/s, which corresponds best to the wind conditions in the study area (Czech Hydrometeorological Institute, 2005). We adopted also the equivalent set of pollen productivity estimates compiled from various studies and adjusted to actual regional vegetation (Abraham et al., 2014). 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 by the script “reveals.v1.1.R” (Abraham et al., 2014).

Potential Natural Vegetation

The area of PNV was calculated according to (Neuhäuslová, 2001) in the Czech Republic and according to (Bohn et al., 2004) in adjacent countries (Figure 1). Proportions of tree taxa within each mapping unit were calculated from typical vegetation relevés (Neuhäuslová, 2001) or as their mean 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 (cover of canopy layer) and also about the abundance of herbs inside the forest, but we selected only trees (including *Corylus* recorded in the shrub layer) and set them to cover the entire surface of the given relevé (=100%). This decision follows from the assumptions of the Prentice-Sugita model that the



prevailing source of pollen loading is the canopy component, so non-arboreal taxa are considered only outside forests. Moreover, almost all PNV units in the selected area are forests; only the tops of the Tatras and the Krkonoše mountains are covered by alpine treeless vegetation, here considered as bare land.

A few relevés were excluded, for example, *Brachypodio pinnati-Quercetum* (unit 30), (Neuhäuslová, 2001) because the tree layer did not correspond to natural composition. Mapping units from both sources were assigned to common 11 classes defined according to the syntaxon and their tree dominant. Within these classes, the composition of mapping units was again averaged in order to obtain a tree proportion also outside the Czech Republic. The assignation and averaging is summarized in Table S1.

Cluster analysis

Several multivariate techniques were employed in R (R Development Core Team, 2013) to analyse the variability of obtained estimates. Zones in each region were calculated based on the squared chord-distance matrix by 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 sought by Ward´s hierarchical clustering. Its exact input was

Figure 2: REVEALS estimates for nine regions and 23 time windows of half kyr (BC/AD). Dashed lines mark the position of significant vegetation zones.

a dissimilarity matrix of squared chord distances calculated from the mean composition of each significant zone. Clusters were cut at the height of 0.33. This threshold was sufficiently low to have zones from one region in different hierarchical clusters, but at same time sufficiently high to obtain reasonable vegetation groups. Vegetation estimates within vegetation classes were plotted as boxplots using the R Graphics package (R Development Core Team, 2013). The same function provided values of both quartiles, which were used for the description of general patterns.

Reconstructed vegetation and its comparison with PNV.

The most optimal period for extracting pRNV was sought by comparing REVEALS estimates with proportions in PNV. For each comparison between REVEALS estimates (i.e. for each region in each time window) and PNV composition, we calculated the dissimilarity on a squared chord-distance matrix using the Analogue R package (Simpson and Oksanen, 2011). Subsequently, we averaged results from all regions and sought the lowest mean dissimilarity representing reconstructed natural vegetation.

We compared average dissimilarities for three slightly different datasets. In all of them, *Plantago lanceolata* and Poaceae were excluded from the comparison because neither of them has a counterpart in PNV. Firstly, to test the hypothesis that *Carpinion* vegetation developed under human influence, we added the proportion of Cerealia to the proportion of *Carpinus*, further referenced as *Carpinus*+Cerealia and compared the result with the proportion of *Carpinus* in PNV. Secondly, we excluded Cerealia from the REVEALS estimates. Thirdly, we compared average pollen proportions also with excluded *Plantago lanceolata,* Poaceae Cerealia in order to see the advantage of pollen modelling over the traditional approach.

Finally, we included data on actual vegetation – only six out of nine of regions from (Abraham et al., 2014) – to compare reconstructed vegetation and PNV with real-world vegetation. We produced scatter plots where we plotted for each taxon i) pRNV against PNV and ii) pRNV against actual vegetation.

Results

Dominants of vegetation classes

The development of the vegetation cover during the Holocene in selected regions of Central Europe (Figure 2) can be clustered into eight different groups and three general phases: Early, Middle and Late Holocene. Figure 3 shows that the first group of clusters on the left side (a-d) emerges during the Early Holocene in all regions and during the Mid Holocene in lowlands. The second group of clusters on the right side (e-h) appears in the Middle Holocene in highlands and in the Late Holocene in

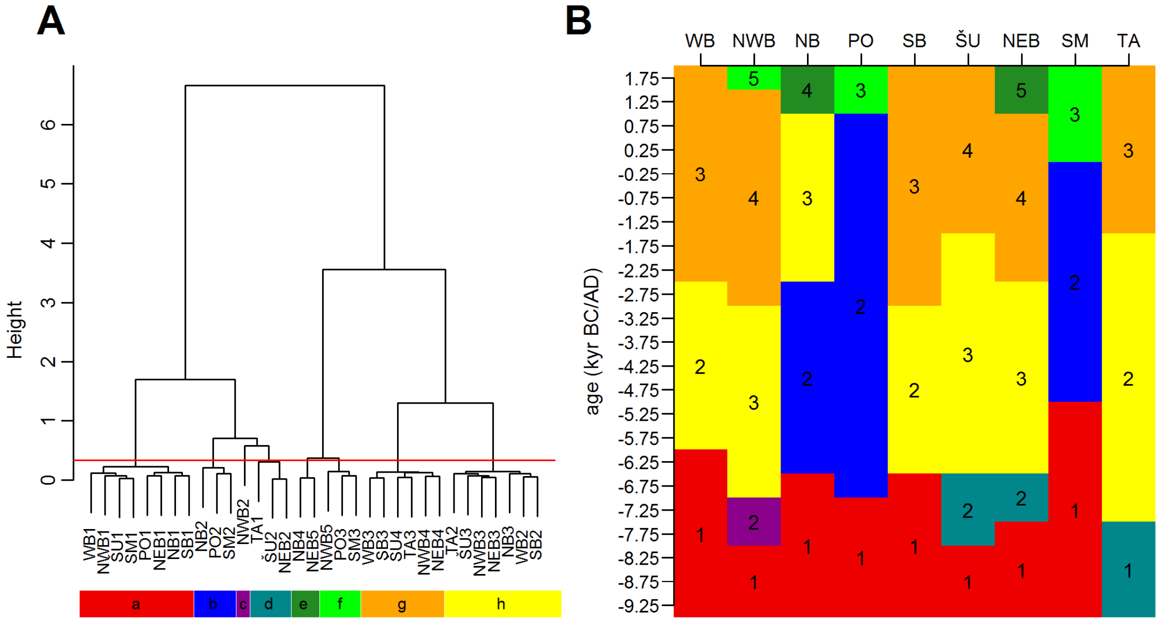


Figure 3: A) Ward's hierarchical clustering of average composition from each vegetation zone, description of clusters indicated by different colours: a) semi-open pine forests; b) mixed oak woodlands; c) hazel woodlands; d) semi-open coniferous forests; e) vegetation under low human influence; f) vegetation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

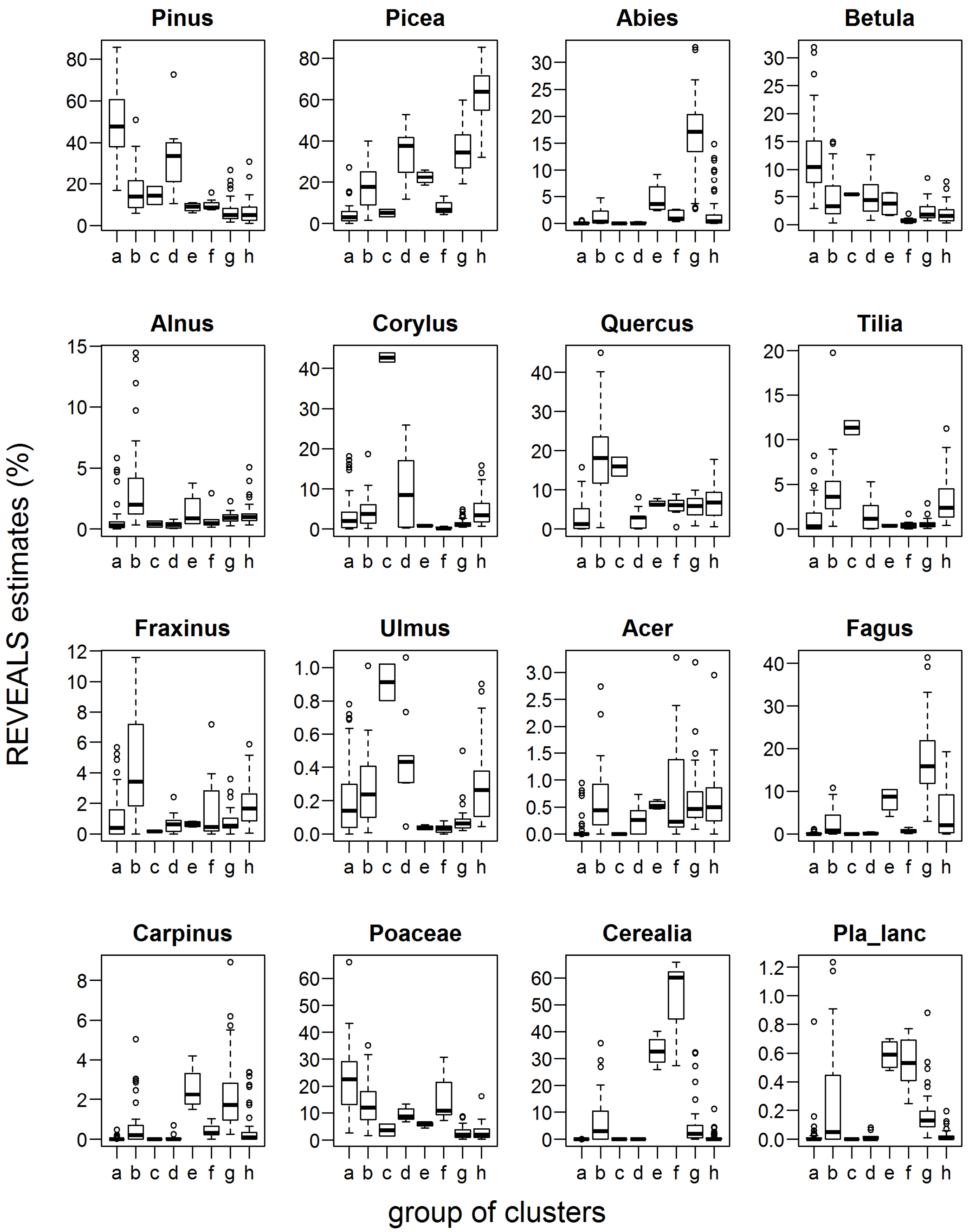


Figure 4: Boxplots of taxa abundances in each vegetation cluster description of clusters corresponds to Figure 3

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).

Semi-open pine forests (a) are the initial vegetation after the end of the Pleistocene in all regions except for the Tatras. Figure 4 shows that they were dominated by *Pinus* (38-61%), Poaceae (13-29%) and *Betula* (8-15%). Their spruce variant (d) occurs in two regions: in the Šumava Mts and NE Bohemia as a short transition to spruce-dominated forests, and in the Tatras as an initial formation. Semi-open coniferous forests (d) host a high admixture of *Picea* (25-42%). The rest of the Early-

Holocene dominants hold high proportion of *Pinus* (21-40%), Poaceae (8-11%) and *Betula* (3-7%).

Mixed oak woodlands (b) can be inferred based on the dominance of *Quercus* (12-24%), *Picea* (9-25%) and *Pinus* (9-21%). They are a continuation of semi-open pine forests in North Bohemia, South Moravia and the Polabí lowland, but *Quercus*, *Picea* and other subdominant taxa, namely *Acer, Fraxinus* and *Tilia*, newly appear in this vegetation stage or even gain their maximum in it.

The proportion of Poaceae in three latter formations remains relatively high (>8%), so they can be regarded as a semi open landscape. Very similar to mixed oak woodlands, however, with lower Poaceae proportion (1-6%), are hazel woodlands (c) - a vegetation class appearing only in two time windows of Northwest Bohemia as a millennial transition from semi-open pine forests to spruce forests. It is characterized by dominance of *Corylus* (42-44%), *Quercus* (14-18%), *Tilia* (11-12%) and *Pinus* (10-19%).

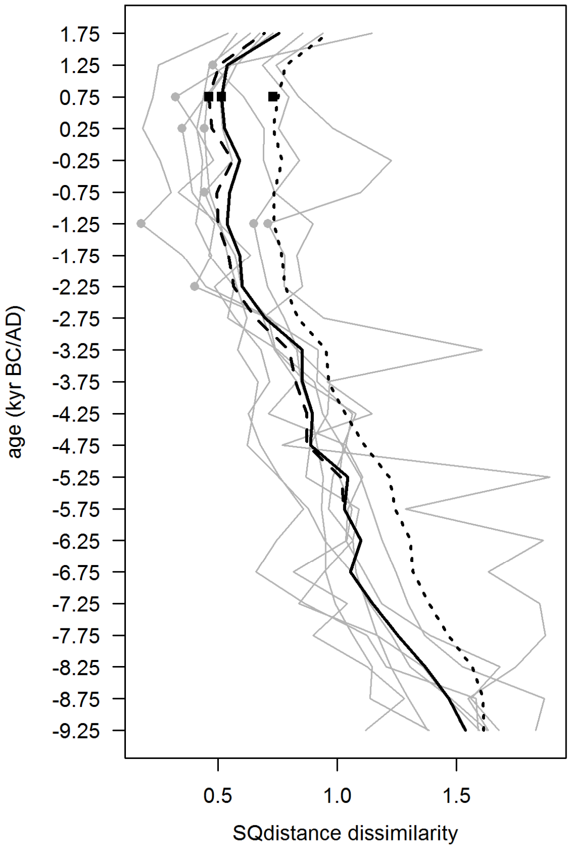


Figure 5: Changes of dissimilarity coefficients in time calculated: between PNV and REVEALS estimates for each region (gray lines) and their average (full black line); the average dissimilarity between PNV and REVEALS, when Cerealia were merged with *Carpinus* (black dashed line); the average dissimilarity between PNV and pollen percentages (black dotted line). Squares mark the lowest average dissimilarity.

Spruce forests (h) were dominated by *Picea* (55-71%). *Pinus* (3-9%), *Quercus* (4-9%), *Corylus* (2-6%) and *Tilia* (1-5%) emerge as an admixture. The variable range of their representation is due to the appearance of this formation in the Middle Holocene and in the Late Holocene (N Bohemia). Fir-beech forests (g) are dominated by *Picea* (27-43%), *Abies* (14-20%) and *Fagus* (12-22%). Admixed are new elements typical for the Late Holocene, *Carpinus* (1-3 %) and Cerealia (1-5%). Taxa from earlier periods, *Pinus* (3-8%) and *Quercus* (4-8%), retain the same proportion as in spruce forests, from which fir-beech forests evolved.

Poaceae attain the lowest proportion in the last two formations. This, together with the dominance of shadow-tolerant taxa (*Picea*, *Fagus* and *Abies*), can be interpreted as forest with closed canopy.

Vegetation under low human influence (e) is dominated by Cerealia (29-37%). Subdominants are *Fagus* (6-10%), *Quercus* (6-7%), *Picea* (20-25%) and *Pinus* (7-11%). *Carpinus* (2-3%) and *Plantago lanceolata* (1%) achieve their maxima. This vegetation class developed only in two regions - North Bohemia and Northeast Bohemia. Vegetation under high human influence (f) appears in Polabí lowland, South Moravia and NW Bohemia. Main dominants are Cerealia (45-62%), *Pinus* (8-11%), *Picea* (5-10%) and *Quercus* (5-7%). Poaceae, again, increased in the last two formations to such a high level (5-6% and 9-21%) that we can interpret this, together with the high proportion of Cerealia, as an indication of an open landscape.

Pollen-based reconstructed natural vegetation

Figure 5 shows that REVEALS estimates match better with PNV than pollen proportions during the whole Holocene, and if we assume that the area of cereal fields in the reconstructed vegetation belongs to the area of *Carpinus*, the match with PNV improves even more. However, all curves of average dissimilarities have a similar shape with minimum in the same time window.

The lowest average dissimilarity between REVEALS estimates and PNV appears at 0.75 kyr AD. This time window was selected as pollen-based reconstructed natural vegetation (pRNV). However, if we consider dissimilarities of each region separately, the dating of reconstructed natural vegetation ranges from 2.25 kyr BC to 1.25 kyr AD.

Figure 6 shows that in terms of interregional gradients of abundances of different taxa, pRNV better matches PNV than actual vegetation (linear alignment of full circles), but that absolute quantities of pRNV are closer to actual vegetation than abundances from PNV (triangles are closer to the line of optimal fit). *Quercus, Fraxinus, Fagus,* *Ulmus* and *Carpinus* are overestimated in the PNV at the expense of *Pinus, Picea, Abies, Betula* and *Alnus,* which are more abundant in pRNV.

Discussion

Limits of REVEALS reconstructions

Although the REVEALS results show the composition of the target taxa, the coarse temporal resolution of REVEALS does not allow us to check the synchronicity of their expansion. The percentage character of REVEALS estimates does not consider bare land or areas taken up by other taxa (e.g. *Larix, Juniperus*) even though the extent of these areas can be significant. In the actual landscape, they constitute from 20 % in forested areas to 40 % in agricultural land (Abraham et al., 2014). Similarly, we obtained estimates for three herb taxa, by which we quantify the minimal degree of landscape openness (see below); however, the real openness of the landscape will remain unclear until absolute palynological methods are employed (Seppä et al., 2009).

The present reconstruction was calculated using the simplest dispersal deposition function in the Prentice-Sugita model (Prentice, 1985; Sugita, 1993). It assumes zero injection height and a flat landscape, but the actual dispersal conditions, especially in our mountains, are far from these optimal conditions. An effect of high mountains was suggested for the Tatras (Rybníčková and Rybníček, 2006). The sites Popradské pleso and Štrbské pleso above 1300 m a.s.l. (Rybníčková and Rybníček, 2006) contain much more *Fagus* and *Quercus* pollen originating from long-distance transport than sites in the Poprad basin - Spišská Teplica and at Hozelec above ca 650 m a.s.l (Jankovská, 1988). Bog sites in summit parts of the Giant Mountains in North-East Bohemia may suffer from the same bias because pollen rises to higher layers of the atmosphere, being dispersed by faster winds from farther distances. If we assume an elevated deposits of pollen, the source area would enlarge even more.

We learned from a detailed examination of 87 sequences in nine different regions that REVEALS functionality may vary among regions. The most questionable remains its use in heterogeneous

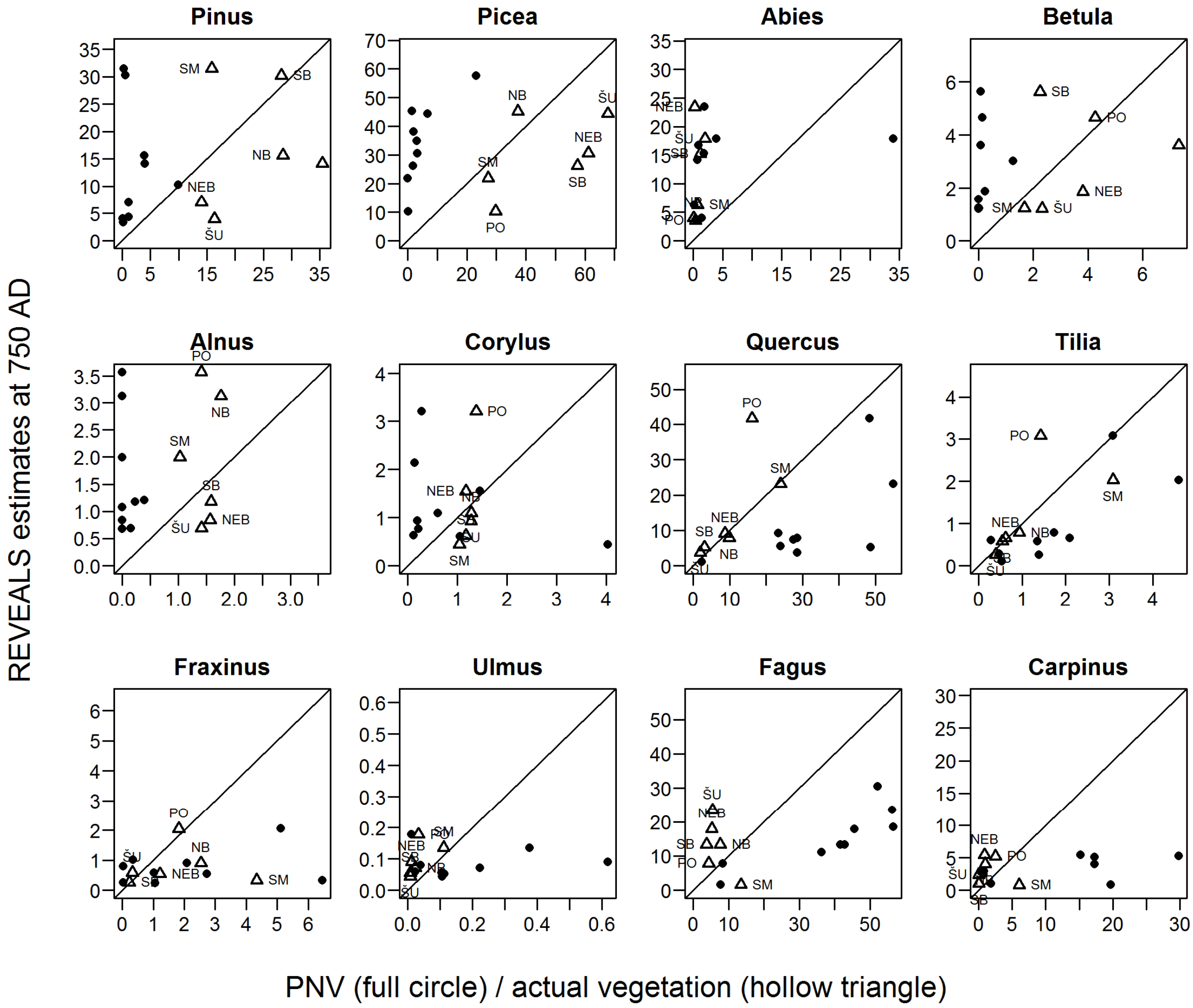


Figure 6: Scatter plots comparing of REVEALS around 0.75 kyr AD (pRNV) with PNV and actual vegetation.

landscapes with small sites. Theoretically, such a scenario should cause higher variability in pollen spectra, but also a certain degree of similarity given by the common background component. Taxa with heavy pollen grains (*Abies, Fagus*) vary much more in lowland pollen spectra. For example (Figure S2 - Polabí), there is strong signal of *Fagus* at the site Košátky (gain 10-20%), but no *Fagus* pollen is present at sites within the distance of 5-10 km. If the signal at the site Košátky originates from the background component, why do we not have it at other sites? The distance of those sites is conspicuously similar to the size of the "characteristic radius 70" of those taxa (Abraham et al., 2014), so it seems that heavy pollen grains disperse over shorter distances than our Zmax distance of 60 km. Our simulation showed that the setting of Zmax in the REVEALS model does not affect the result significantly (Abraham et al., 2014); therefore, evenly distributed small sites within the heterogeneous region may produce representative REVEALS estimates.

After comparing pollen curves for all regions, we are aware that the results from North Bohemia, the Polabí lowland and South Moravia are potentially affected by scarce sampling in the heterogeneous landscape. Pollen curves from sites in the rest of regions exhibit high mutual similarity, partly caused by the larger size of these sites and partly by higher homogeneity of the landscape around them.

Pollen productivity represents another source of possible biases. It is assumed that pollen productivity was constant during our focal periods. However, pollen productivity might have varied in the past as consequence of the changing environment and taxa within pollen types. Apart from the climate, vegetation structure might play an important role. Solitary trees are better illuminated by sun, so they produce more pollen than the similar individuals in closed forests. Taxonomical problems arise with pollen taxa of many plant species, especially the Poaceae and Cerealia. Different species than those used for PPEs measurements possibly occurred in the past. The largest difference may come up during the High Medieval period, when autogamous cereals (*Triticum*) were replaced by anemogamous (*Secale*), which some pollen analysts cannot distinguish. This is also the reason why the last time window contains more Cerealia than estimated in the shallowest depths (Abraham et al., 2014).

Vegetation development

REVEALS reconstructions provide different numbers of vegetation phases than classical pollen biostratigraphy (Firbas, 1949). In REVEALS we lack typical pollen zones because of wide time windows. Secondly, modelled vegetation is dominated by other species than pollen spectra due to differences in pollen productivity and dispersal. The main difference in dominants between the traditional and the quantitative interpretation might reside in the presence of spruce in the Middle Holocene in all except lowland regions. Regardless of the different numbers of zones, the traditional interpretation also supports the dominance of spruce in the Czech Republic (Firbas, 1949), but not by all studies and most recent ones. In these more recent studies, high pollen proportions of spruce are interpreted as individuals locally growing in waterlogged areas, and general vegetation during the Atlantic is described as consisting of mixed-oak woodlands, for example (Jankovská, 1980; Rybníčková and Rybníček, 1996).

Early Holocene in all regions

The initial stage of Holocene vegetation development was characterized by semi-open pine forests. In the Tatra Mountains, similar vegetation emerges as a class of semi-open pine forests, but with spruce. Today, there is no doubt about the survival of spruce during the Last Glacial Maximum in the Western Carpathians (Tzedakis et al., 2013). The proximity of LGM spruce refugia increases its occurrences in Bohemia during the Late Glacial. Macrofossil evidence of spruce (needles or charcoals) was found in the Polabí lowland (Petr et al., 2014), North Bohemia (Pokorný, 2003) and North-East Bohemia (Nováková, 2000). Besides spruce, a significant proportion of temperate taxa appear in both vegetation classes. Early occurrence of *Corylus* pollen was reported from Northaestern Bohemia (Peichlová, 1979). The whole set of temperate deciduous taxa *Corylus*, *Quercus*, *Ulmus* and *Tilia* was recorded by continuous pollen curves in during the Late Glacial only 80 km south of our sites in South Moravia (Petr et al., 2013). *Corylus* expanded to the whole northern part of Central Europe around 8650 BC (Giesecke et al., 2011). Such a synchronous expansion could be triggered by abrupt warming of North Atlantic ocean water around 10.3 kyr BP, known as the end of Bond event 7 (Bond et al., 1997). Similar timing and magnitude of *Corylus* changes can be found only in North-West Bohemia, where its strong pollen signal resulted in a *Corylus* zone (estimates exceed by 40 %). This probably happened due to the geographical proximity of this region to the Atlantic. The hazel expansion in the rest of the regions in this study is less pronounced and does not have the same timing.

Mountain and highland regions

The transition from the Early Holocene to the Mid Holocene vegetation stages occurred between 8 and 5 kyr BC, depending on the region. The *Corylus* zone, a short transitional vegetation stage in North-West Bohemia, was controlled by temperature (Giesecke et al., 2011). On the other hand, *Picea*, creating the Mid Holocene vegetation stage in mountain and highland regions, was generally controlled by humidity. This can be illustrated by the accumulation rate of calcareous tufa in the village of Svatý Ján pod Skálou, which is a unique proxy record of climate humidity. The accumulation started roughly around 7550 BC, and maximal growth was reached between 6450 and 4550 BC (Žák et al., 2002), which matches the time passed from the spruce expansion until its maximal abundance. This supports the hypothesis that spruce dynamics during the Holocene were generally controlled by soil moisture (Henne et al., 2011).

We can even distinguish millennial differences between the easternmost and the westernmost region, which agrees with the timing inferred on the continental scale (Latałowa and van der Knaap, 2006), on which spruce spread in three millennial steps: 1) area spanning from Slovakia (Tatras) to the south-eastern Czech Republic, 2) the rest of Bohemia and 3) western Bohemia. Here, we do not find the typical response to a climatic trigger, that is, a synchronous increase in a large geographic area. The character of the expansion could evoke the moving front from the east to the west; however, phylogeography indicates possible refugia in the southern Bohemian Massif, including its southern foreland (Tollefsrud et al., 2008). The delayed expansion in the Šumava Mts compared to the Western Carpathians could be explained by smaller size of the initial population.

In highland and mountainous regions, the transition from Middle Holocene to the Late Holocene vegetation was connected with the expansion of *Fagus* and *Abies*. Depending on the abundance and arrival time of each taxon, the Late Holocene vegetation phase started between 3 and 1.5 kyr BC. In West Bohemia, Nothaestern Bohemia and the Tatra region, both taxa spread at the same time, but in the Šumava Mts, North-West Bohemia and South Bohemia, *Fagus* expanded earlier than *Abies*. Lowlands host less than 10% of *Fagus* and less than 5% of *Abies*.

Lowlands

The lowlands of the Czech Republic exhibit different development than the country's mountain ranges. Instead of the spruce stage, we find an oak stage in North Bohemia, the Polabí lowland and South Moravia. The earliest appearance of oak is found around 9 kyr BC in South Bohemia. Its general spread in most of our regions occurred within the following millennium, except for South Moravia where the oak zone starts around 5 kyr BC. The climate of South Moravia is the driest of all regions under study, so the later transition from semi-open pine to oak forests could have been triggered climatically by higher precipitation. On the other hand, the synchronicity of the spread with the beginning of the Early Neolithic period also offers some connection with human activity.

In South Moravia and the Polabí lowland, the oak phase lasted until the first human impact phase, whereas in North Bohemia, the vegetation changed around 2.5 kyr BC to a spruce forest. The Late Holocene expansion of spruce in the study region is not anomalous from a wider, Central European perspective. It was reported from south-eastern Poland, the Harz mountains and other small areas on the periphery of the main distribution range (Latałowa and van der Knaap, 2006). The late spread of spruce in North Bohemia could be also related to the process of Holocene acidification described in this area (Pokorný and Kuneš, 2005). Sandstone bedrock in this region was covered by loess after the Pleistocene. The spread of lime woodlands allowed the persistence of basic soil, but long-lasting humidity caused its gradual degradation, and only acidic sandstone remained. Different human prehistory might also have played a role in the vegetation succession of North Bohemia. In contrast to the Polabí lowland and South Moravia, human occupation in North Bohemia was scarce and oscillating. Stable colonization dates back to the Late Iron Age (Dreslerová et al., 2013) whereas South Moravia and the Polabí lowland were settled by farmers since the Early Neolithic.

Relating human impact to REVEALS estimates of Cerealia and *Plantago lanceolata* must be done with much caution, because of mismatch of time windows and archaeological periods and also some further biases discussed above. The most significant event is the appearance of *Plantago lanceolata* around 3.5 kyr BC. Its arrival at this time coincides with the areas occupied already during the Late Neolithic. By contrast, the rise of *Plantago lanceolata* around 2.5 kyr BC in the Šumava Mts and South Bohemia is connected with the colonization of southern Bohemia in the Early Bronze Age (Dreslerová, 2011). The human impact increased in the Late Bronze age, when the area occupied by humans doubled for a short time, and can be related with the peaks of *Plantago lanceolata* around 1 and 1.5 kyr BC in several regions.

Besides indicators of continuous human occupation in South Moravia and the Polabí lowland, these regions also host certain disjunctive floristic elements of continental steppes, such as *Helictotrichon desertorum* or selected species from the genera *Astragalus* and *Stipa*. The survival of these taxa before the Neolithic, during the Holocene climatic optimum, became a popular object of many geobotanical investigations (Slavíková, 1983). The strongest proof of continuous forest-free patches are fossil assemblages of snails living strictly in open landscapes (Juřičková et al., 2013). The widespread presence of chernozem soils in both regions may indicate landscape openness as well, because pedogenesis of chernozems is dependent on a dry climate restricting the expansion of forests (Antoine et al., 2013). However, detailed analysis showed that local chernozems are resistant to colonization by trees and that their stability against degradation enables them to keep the ancient aspect (Vysloužilová et al., 2014). We can contribute a little to answering this hot biogeographical question by quantifying the minimal degree of landscape openness. In South Moravia and the Polabí lowland, we obtained regional estimates of Poaceae exceeding 9 % throughout the Holocene. The proportion of Poaceae remained stable under different intensities of human activity, suggesting two possible natural mechanisms maintaining landscape openness – a dry climate with fires and grazing pressure by large herbivores (Vera, 2000). One justified objection to our results is that Poaceae pollen can originate from local grasses such as *Phragmites australis*, which often cover lowland peatbogs as well as shores of shallow lakes. It is difficult to filter out local pollen; however, peatbogs in North Bohemia are also overgrown by local grasses, yet strong evidence of continuous openness is lacking.

Carpinus reached its maximal vegetation cover (around 5%) in North-East Bohemia from 2.25 kyr BC to 0.25 kyr AD. The lowest vegetation cover of *Carpinus* (<2%) was reached in the Šumava Mts, South Moravia, and West and South Bohemia. The pattern of high abundances and rapid spread in the north-eastern regions contrasting with low abundances and gradual increase in south-western regions confirms the old hypothesis that *Carpinus* expanded to the Czech Republic from the northeast (Rybníčková and Rybníček, 1996); however, evidence from neighbouring regions such as the Pannonian Basin shows that the expansion of hornbeam was not a simple case of a "moving front" (Magyari, 2002).

When was vegetation natural?

The best fit for pRNV was reached in Early Medieval times. The transition from the Early to the High Medieval period represents a dramatic change in human impact. A considerable increase in human population lead to the colonization of highlands and ensuing deforestation (Kozáková et al., 2014). On the background of this quantitative change, the relationship of people with the landscape inevitably led to social and economic transformations. Firstly, in the common history of man and nature, shifts occurred in the exploitation of natural resources, which since the High Medieval period consisted of central planning and assignment of landscape functions (Sádlo, 2005). Our results are in agreement with original the assumption of RNV, which places the hypothetical state of natural vegetation in this period.

That *Betula* and *Pinus* are underestimated in PNV is relatively expected. Formations of these two pioneer trees were considered by the PNV methodology as temporal succession phases, which will turn to some stable community, so they were not recorded. Our results show that *Betula* has had a stable proportion since its decrease around 6.5 to 5 kyr BC. Similarly, a high stable cover of *Pinus* is documented in the Polabí lowland, South Moravia and North Bohemia, whereas in the rest of the regions, *Pinus* shows a decrease during the Holocene forest optimum during the time windows of 4.25 and 3.75 kyr BC. Its stable occurrence in those three regions is connected with sandy soils, on which spruce can suffer from periodic droughts. Various sandstone landscapes in North Bohemia are some of the most suitable habitats for pine vegetation; high and stable occurrence of pine was recorded by charcoal (Novák et al., 2014). Decreasing pine in other regions indicates lower ecological competitiveness of pine during the maximum spread of spruce. This equilibrium given by soil conditions and ecological competitiveness can be destroyed by fire and higher level of disturbance. Regular fire regimes favour pine over spruce in the boreal zone (Engelmark, 1987; Gromtsev, 2002), fire was recently considered as a natural driver also in the temperate zone (Adámek et al., 2015; Bobek, 2013; Novák et al., 2012). Moreover, half-millennial fluctuations of pine in South Bohemia correlate with the intensity of human occupation; noticeable peaks of pine vegetation estimates around 1.75 kyr BC and 0.25 kyr BC belong to the Older Bronze Age and Late Iron Age. The increase of *Pinus* in the last time window was caused by plantations during the 18th and 19th century.

Together with pine, spruce was the most popular timber wood since the beginning of artificial reforestation (Nožička, 1957); however, substitution of natural spruce forests by cultural stands is almost unnoticeable in the REVEALS results. Moreover, on the local scale, only two pollen diagrams show an increase of spruce in the last centuries: Pryskyřičný důl in North Bohemia (Abraham and Pokorný, 2008) and, to a lesser extent, Černá hora in Northeast Bohemia (Speranza et al., 2000a). Instead of the abundance of spruce in the vegetation, forest structure might have changed - most today's spruce forests are evenly aged. This strong indication of cultural origin caused spruce in PNV to be severely underestimated. Beside our high frequency of spruce in pRNV, there is ample evidence of spruce presence at middle altitudes before forest management – charcoal (Kozáková et al., 2011), toponyms (Rybníček and Rybníčková, 1978) and historical sources (Nožička, 1972; Pokorný, 1955). The original distribution of natural spruce and spruce-fir forests is placed between the fir-beech and oak or oak-hornbeam vegetation belt. Such forests remain as negligible fragments considerably affected by forest management (Rybníček and Rybníčková, 1978).

This unexpected result is emphasized by even higher frequency of spruce in the Mid Holocene. Such long persistence of dark spruce forest introduces many questions regarding herb diversity and also geochemical conditions. The chemical composition of spruce litter leads to acidification and even subsequent podzolization (Emmer et al., 1998); however, most of the soils in the study area belong to cambisols, which have supposedly evolved under deciduous forests.

Abies is the only case where the conceptual difference between PNV and RNV really matters. Fir was relatively abundant in the past, but it declined a couple of centuries ago for uncertain reasons. In the case of the Czech Republic, its entire dynamics seem to be connected with some kind of human impact (Kozáková et al., 2011). Nowadays, reintroductions of *Abies* are not successful, and the low expectations of its spread are expressed by its low abundance in PNV. Regions with high *Abies* in pRNV (13-25% North-East Bohemia, Šumava Mts and South Bohemia) overlap with areas of fir forests (*Galio rotundifolii-Abietetum albae, Luzulo-Abietetum albae* and *Vaccinio myrtilli-Abietetum albae*), and no relevés linkable with fir forests were found in regions with low *Abies* in pRNV (Chytrý, 2013).

Similarly to the previous taxa, *Alnus* is underestimated by PNV whereas the current state matches pRNV. Its higher presence in pRNV in the Polabí lowland and North Bohemia is caused by local presence at most sites (See Methods).

pRNVs of *Quercus, Tilia* and *Fagus* exhibit a roughly similar gradient of individual taxa between regions as PNV. However, PNV tends to largely overestimate them together with *Fraxinus, Ulmus* and *Carpinus*. The actual state of those taxa fits relatively better or is slightly lower than in pRNV. Additionally, the trend of *Carpinus, Quercus* and *Fagus* in reconstructed vegetation is markedly decreasing from the Early Middle Ages towards the present (Figure S3). According to our results, they receded to arable land, which is indicated by increasing Cerealia. Interestingly, *Carpinus, Quercus* and *Fagus* are also the most abundant taxa in PNV. The assumption of PNV that *Carpinion* vegetation would dominate most of the present arable land is in accordance to our results, suggesting that *Carpinus* was replaced by Cerealia in the past. If we assume that Cerealia fields were once covered by *Carpinus*, we get even closer to PNV composition.

Source of similarities and differences between PNV and pRNV

The similarity of interregional gradients of abundances of different taxa inferred from pRNV and PNV underlines the potential of both methodologies to successfully seek for natural vegetation. Information about the variety of different environmental conditions aggregated into recent plant assemblages from natural sites can be used for extrapolation to anthropogenic landscapes. The results can be subsequently crossvalidated using plant communities formed prior to the human impact. However, beside common trends, there are huge quantitative differences. Palaeoecological data suggest more coniferous and less temperate broadleaved taxa than PNV. Similar results were found also in the Iberian Peninsula (Carrión and Fernández, 2009). The reasons reside partly in the PNV methodology and partly in conceptual particularities. In contrast to all previous comparisons, REVEALS estimates are spatially explicit vegetation proportions, and PNV does not meet the same dimensions.

The four methodical steps of PNV construction – sampling, classification, extrapolation and description – may be subject to the following biases related with representativeness of the results. Biases of the first two steps are common with any phytosociological system, and have already been pointed out by other authors (Blažková, 2005; Chytrý, 2000; Hédl, 2005). Usually non-random sampling is preceded by interpretation of vegetation in the field, so placing 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 in the result. Classification depends on the number of taxa and combination of specific taxa. Broadleaved forests host more specific taxa, while spruce forests are poor and inhabited by vegetation generalists.

In comparison to the first two methodical problems, the two following biases are technical in character and are easy to address. The exact method of extrapolation of the vegetation units to PNV is somewhat hidden from the user. We are aware that the use of expert knowledge could shift current PNV towards broadleaved taxa because too many coniferous stands were interpreted as plantations.

Finally, typical phytosociological relevés might not optimally represent abundances of taxa in PNV. The few relevés we used to fill the whole unit cannot capture the variability of the extended plant community.

The substantial mismatch between abundances projected by PNV and pRNV arises also from differences on the conceptual level. The hypothetical state of PNV in the future apparently matters only in the case of *Abies*. Additionally, it might produce some differences in recently expanding (e.g. *Fraxinus*) or generally declining taxa (e.g. *Ulmus*), but its impact is probably too small, so this temporal aspect does not prevent us from approximating past natural vegetation by PNV. Secondly, the PNV concept assumes that they would develop into ecologically stable communities. Current vegetation formations are considered successionally very young because permanent human influence blocks this natural development. Following these assumptions, stands of pioneer vegetation get replaced by mature forests. However, this consideration in PNV neglects the role of certain natural factors of vegetation formation. The importance of wild fires has been intensively revisited in the last years (Adámek et al., 2015; Bobek, 2013; Chytrý, 2012). The high and stable presence of *Pinus* in South Moravia, the Polabí lowland and North Bohemia is overlooked by PNV. On the other hand, findings from South Bohemia, where the fluctuations of pine match the intensity of human occupation, point out the role of man in the development of natural vegetation. In this case, it would be understandable why PNV maps do not consider a higher proportion of *Pinus*.

The reasons of beech and oak dominance in PNV composition probably stem from presumed ecological characteristics, usually plotted as Ellenberg's ecograms (Ellenberg, 1988). Hornbeam is the strongest competitor in the lowland and the supracoline belt of the Czech Republic whereas oak preferably occupies drier sites (Chytrý, 2012). Beech is described as the most competitive tree from the submontane to the montane belt; north-westwards of the Czech Republic, beech would dominate even at lower altitudes whereas in the Carpathians it would remain only at higher altitudes (Bohn et al., 2004). This model generally underestimates the potential of spruce, but on the other hand, all assumptions adopted from Ellenberg (1988) are based on field observations in Germany, which might differ from the conditions in the Czech Republic, at least in the past (Firbas, 1949; Latałowa and van der Knaap, 2006; Rudolph, 1931).

Practical consequences of present comparison

Palynological reconstructions and PNV are largely understood as target composition in forest management and nature conservation. If the aim behind a management policy is natural vegetation, we must consider the utility of both concepts. Reintroductions based on reconstructed vegetation composition will create artefacts. The past is irretrievably gone and cannot be fully restored pollen findings, even if we obtain vegetation composition by quantitative methods. PNV overcomes this trouble, but its practical use remains problematic because its current state is far from real vegetation. Moreover, similarly to reconstructed vegetation, it is represented by static composition.

The importance of palaeoecological results lies in the insight they bring into long-term dynamics and stability of species. Abundances of selected taxa roughly outline processes that might be the object of protection rather than static percentages. Processes that can be supported or simulated by nature protection (herbivores, fire regimes, disturbances) are relatively dynamic. Whereas factors controlling most tree vegetation are relatively slow and stable (e.g. the climate or soil development), they probably cannot be influenced directly. Tree vegetation dominants changed three times during the Holocene. Thus, from the decadal perspective, each of those phases can be denoted as a climax that does not need any management. Although we propose that natural processes maintained the openness of the landscape during the Holocene, unforested areas are the most primeval and at the same time the most vulnerable to disappearance, so some intervention to stop the spread of forests is needed time to time. Any concrete strategy from the gradient of classical conservation to non-intervention management should be designed in accordance with landscape history and the degree of human impact. Lowland landscapes developed as a result of long-lasting co-evolution between man and nature. The construction of natural vegetation in cultural landscapes is possible; however, it is practically useless because human drivers are dominant and inseparable from natural ones. The protection of such landscape requires the identification of spontaneous human-induced processes in order to integrate and support primeval components in the context of the modern landscape (Sádlo, 2010).

Conclusions

We obtained REVEALS estimates for nine regions of the Czech and Slovak Republics. Within the Holocene 500-year time windows, we have distinguished three general vegetation phases: Early, Middle and Late Holocene. Clustering of interregional variability clearly divided lowlands from highlands and mountains. In the Middle

Holocene, lowlands were dominated by oak. Spruce was the most prevailing taxon (>32%) in all highland and mountainous regions. The proportion of spruce also remained high (>19%) in the subsequent fir-beech phase lasting in some regions until today. The rest of the regions and lowlands developed into landscapes dominated by cereal fields. The finding of spruce in the Middle Holocene provided by the formal and quantitative method contrasts with most previous studies because they interpret the Atlantic period at middle altitudes of the Czech Republic as characterized by mixed oak woodlands.

REVEALS vegetation estimates for the 750 AD time window resulted in the most similar vegetation to PNV composition. This period falls into the Early Middle Ages, which agrees with the hypothetical period of RNV, the original map for current PNV. By quantifying the dynamics of Holocene vegetation, we discovered higher proportions of certain taxa (*Picea, Pinus, Betula, Alnus* and Poaceae representing an open landscape) in the reconstructed natural vegetation and stressed the importance of possible drivers that maintained their abundances during the Holocene (herbivores, a dry climate or wild fires). These factors, which lacking in current PNV, should be the object of further investigations, for example, the second step of LRA refining the vegetation reconstruction on the local scale (Sugita, 2007b). We and many other authors see the combination of palynological evidence with some phytoindication system as the best way to construct maps of natural vegetation. This preliminary comparison identifies methodological barriers to such an approach, rather than invalidation of PNV. The construction of maps of natural vegetation may lead to the identification of processes that keep the climax dynamic. Such maps may be assembled from processes, their factors, frequencies and intensities. Static percentages of taxa per area unit, provided by pRNV and PNV vegetation, represent a potential danger in their direct practical application in nature conservation or forest management (Jackson, 2013).

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Appendix

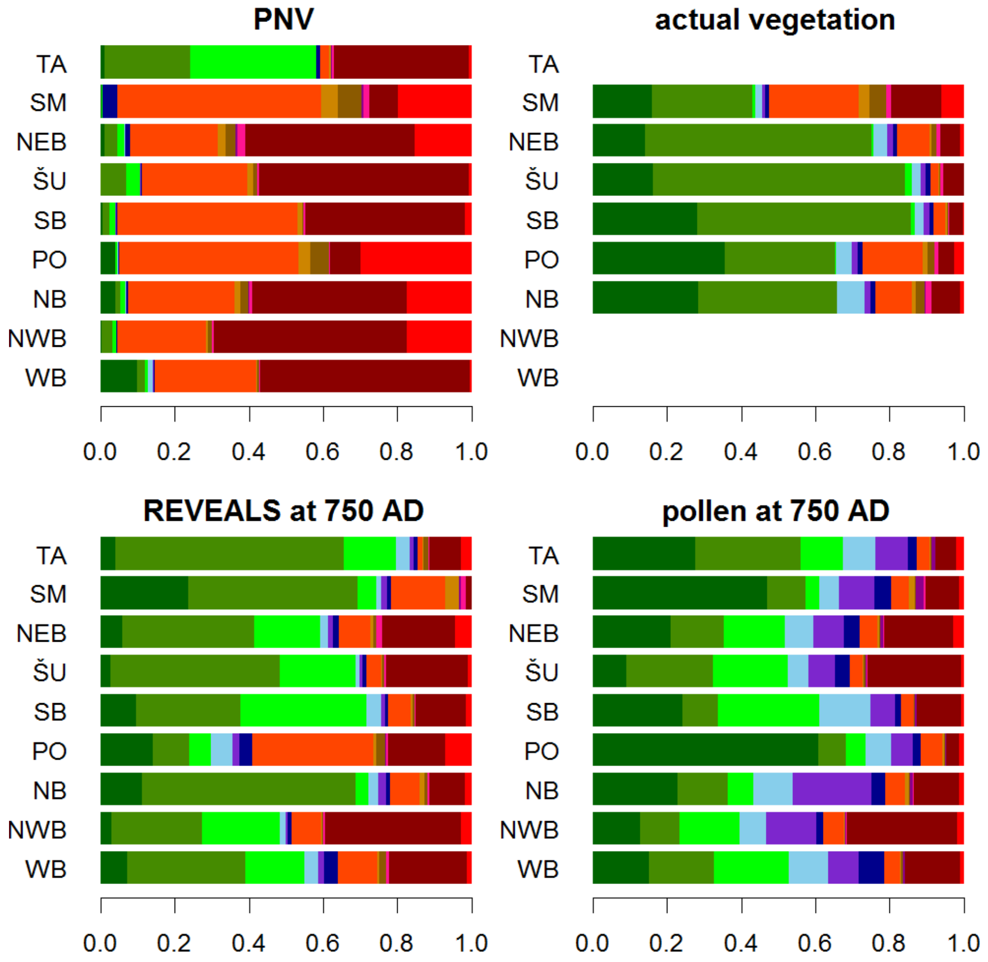
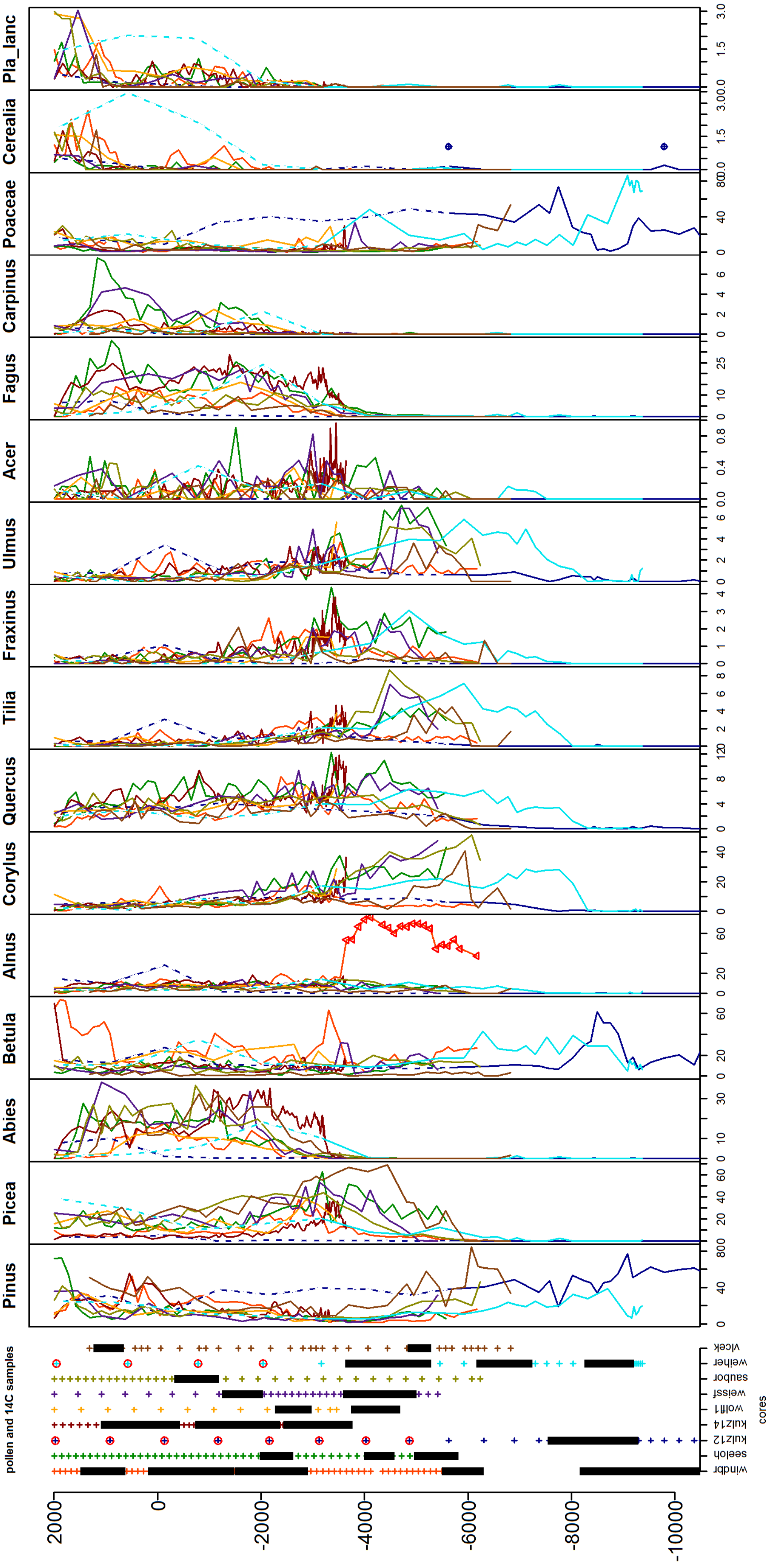
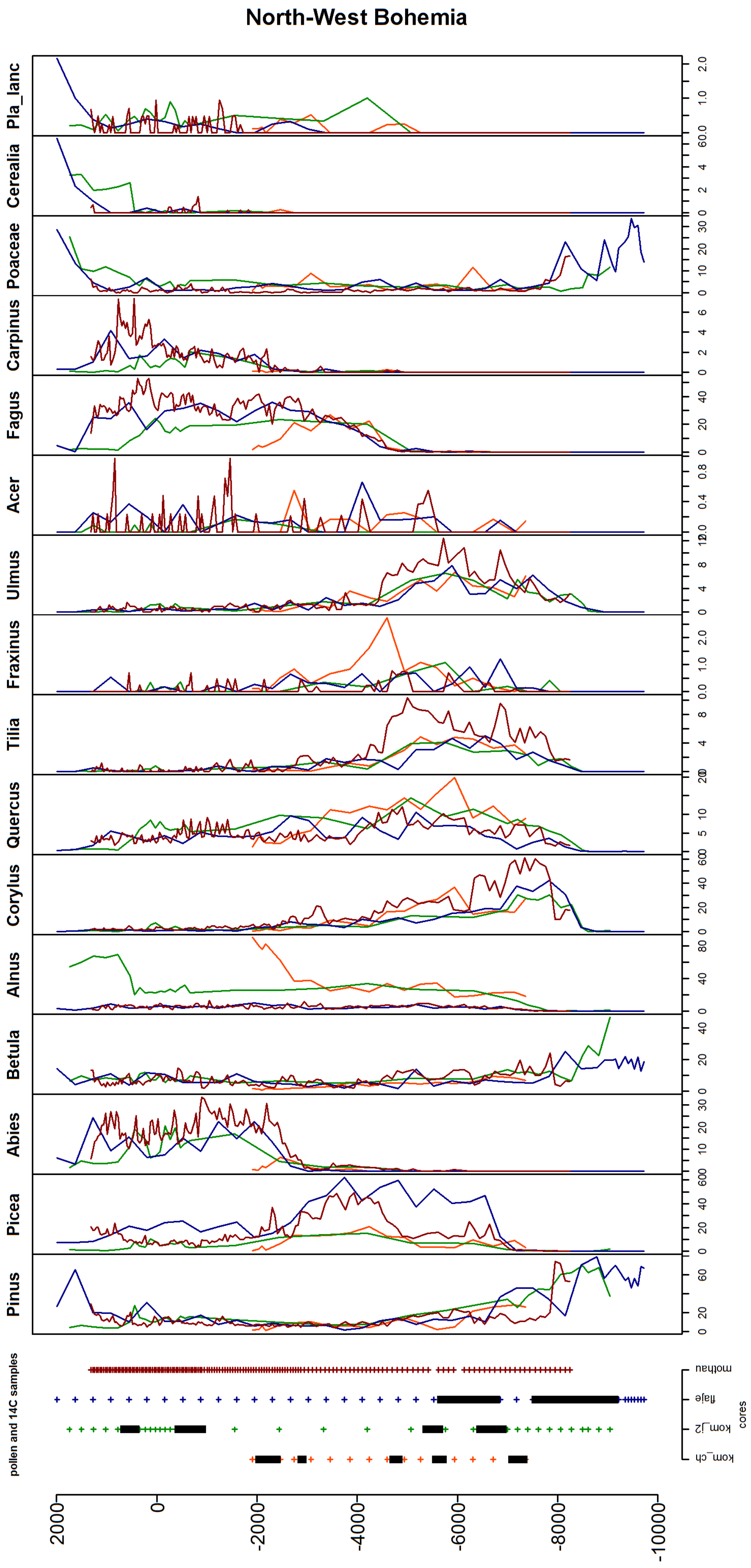


Figure S1: Bar plots comparing of REVEALS around 0.75 kyr AD (pRNV), PNV actual vegetation and pollen proportion.

Figures S2 (next colour pages): Input data for each region. The field labelled as "pollen and 14C samples" illustrates the density of pollen samples in the profiles (plus sign) and the density of datings; most of them are calibrated ^{14}C dates at the 95% confidence level (black rectangles). The colours of the profiles correspond to the colours used for all taxa. Excluded samples due to: 1) a weak depth-age model or 2) strange taphonomy are marked by red circles. Corrected pollen counts in the samples are marked: 3) by dots in the field of Cerealia before 5.5 kyr BC, where the pollen counts were set to zero, and by triangles on the pollen curves of *Alnus*, where the pollen counts were set to the regional average due to the species' obvious local presence →.

West Bohemia




North-West Bohemia
Pla_lanc
Cerealia
Poaceae
Carpinus
Fagus
Acer
Ulmus
Fraxinus
Tilia
Quercus
Corylus
Alnus
Betula
Abies
Picea
Pinus
0.0 1.0 2.0
0 2 4 6
0 10 20 30
0 2 4 6
0 20 40
0.0 0.4 0.8
0 4 8 12
0.0 1.0 2.0
0 4 8
0 5 10 20
0 20 40 60
0 40 80
0 20 40
0 10 20 30
0 20 40 60
0 20 60
pollen and 14C samples
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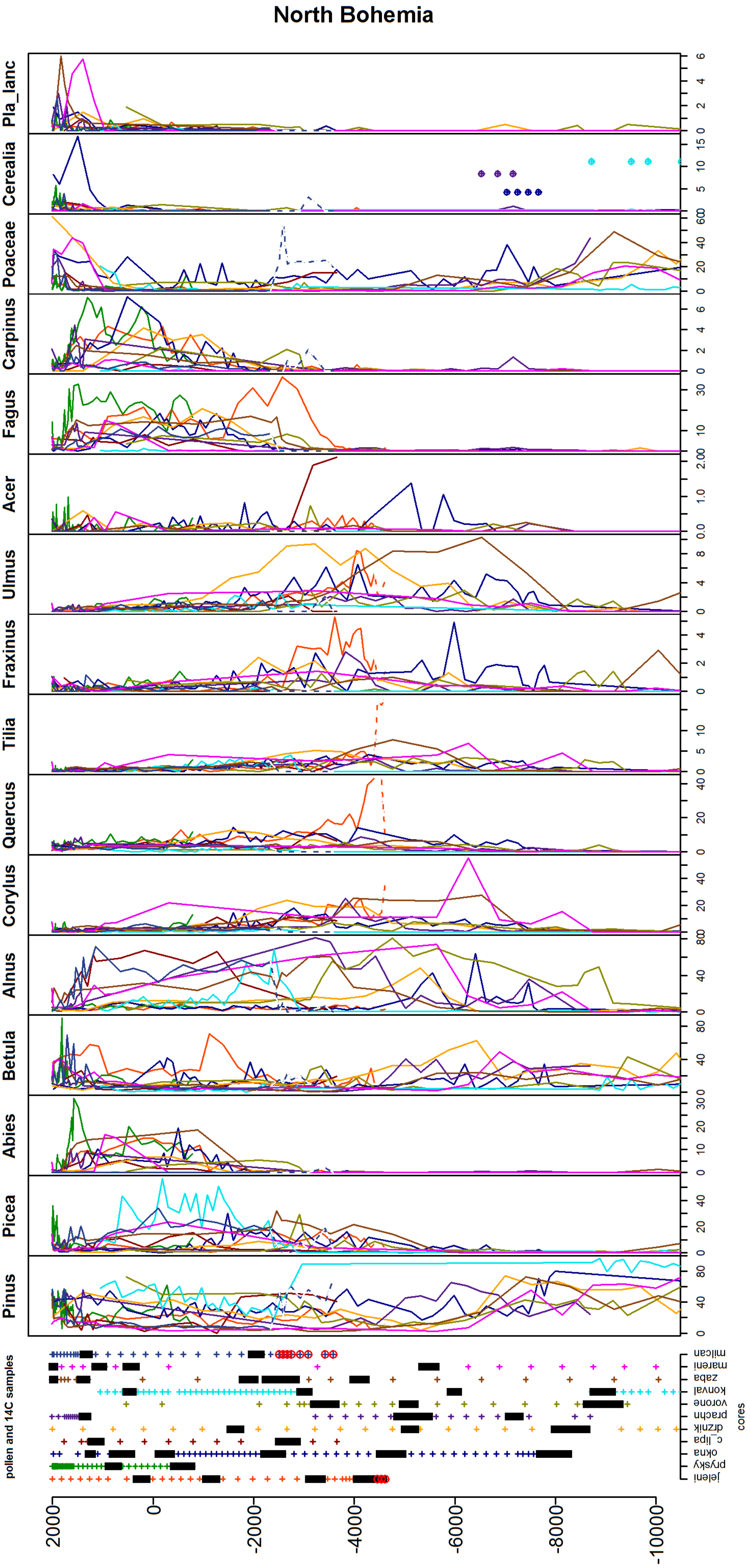
North Bohemia
Pla_lanc
Cerealia
Poaceae
Carpinus
Fagus
Acer
Ulmus
Fraxinus
Tilia
Quercus
Corylus
Alnus
Betula
Abies
Picea
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pollen and 14C samples
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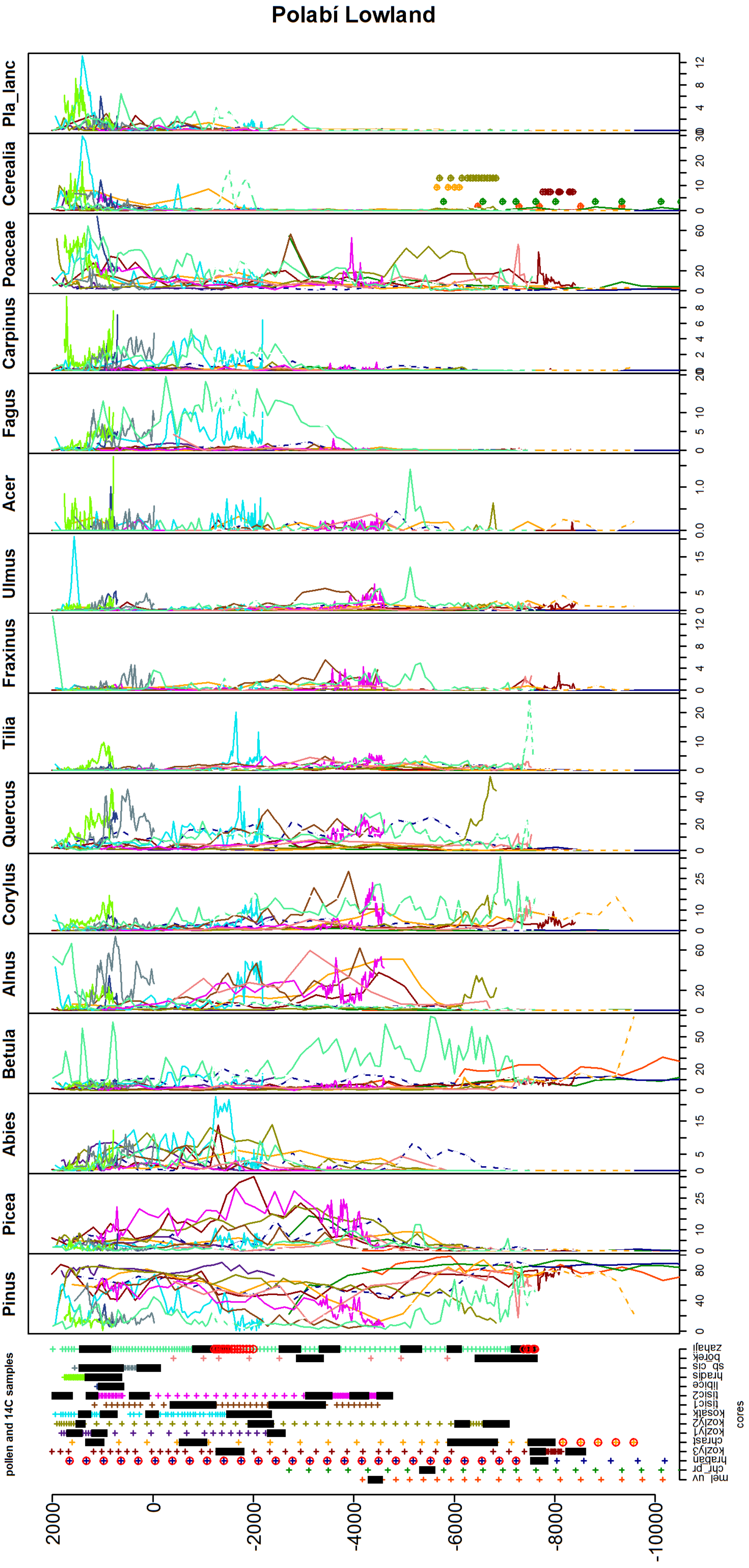
Polabí Lowland
Pla_lanc
Cerealia
Poaceae
Carpinus
Fagus
Acer
Ulmus
Fraxinus
Tilia
Quercus
Corylus
Alnus
Betula
Abies
Picea
Pinus
pollen and 14C samples
cores
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sb_cis
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tisic2
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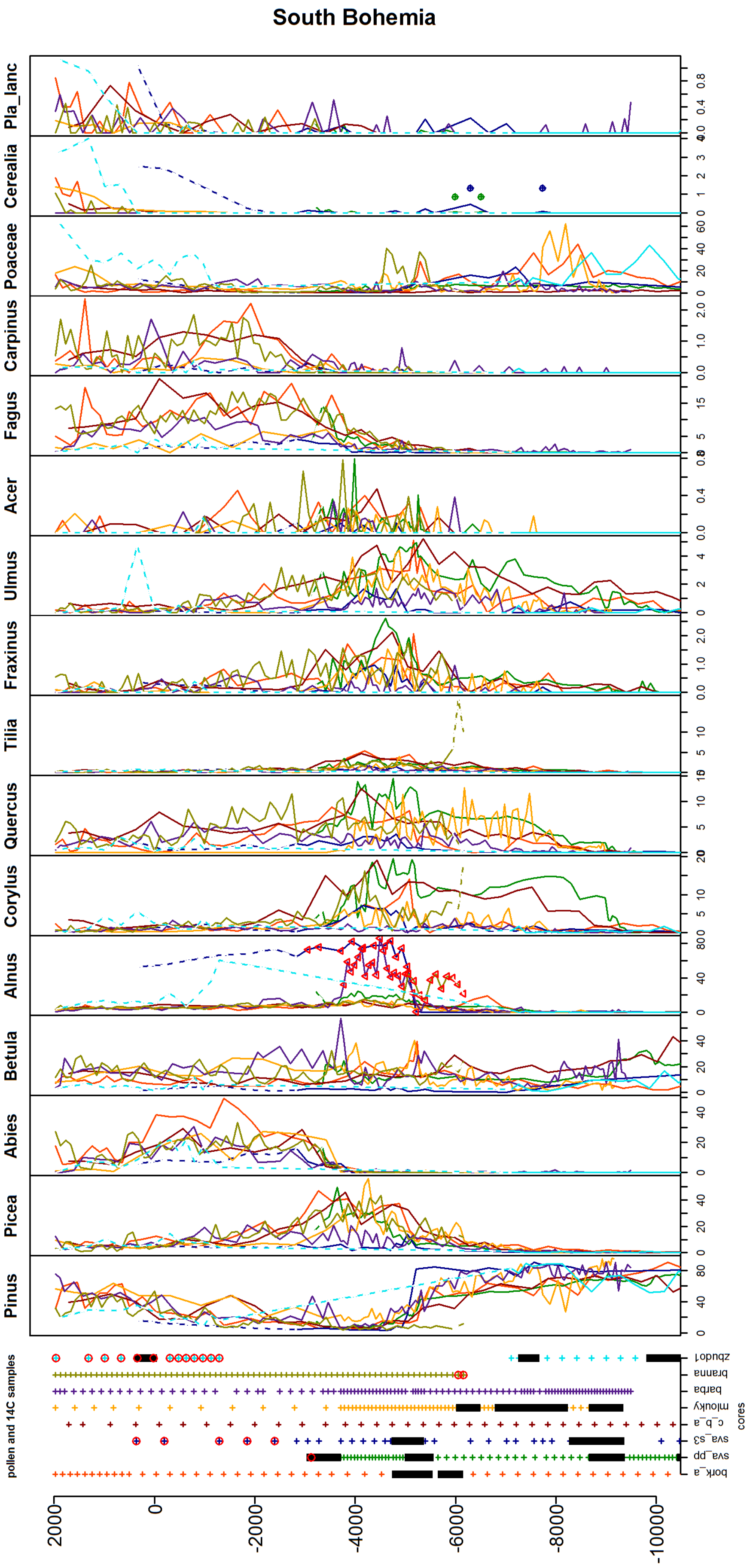
South Bohemia
Pla_lanc
Cerealia
Poaceae
Carpinus
Fagus
Acer
Ulmus
Fraxinus
Tilia
Quercus
Corylus
Alnus
Betula
Abies
Picea
Pinus
pollen and 14C samples
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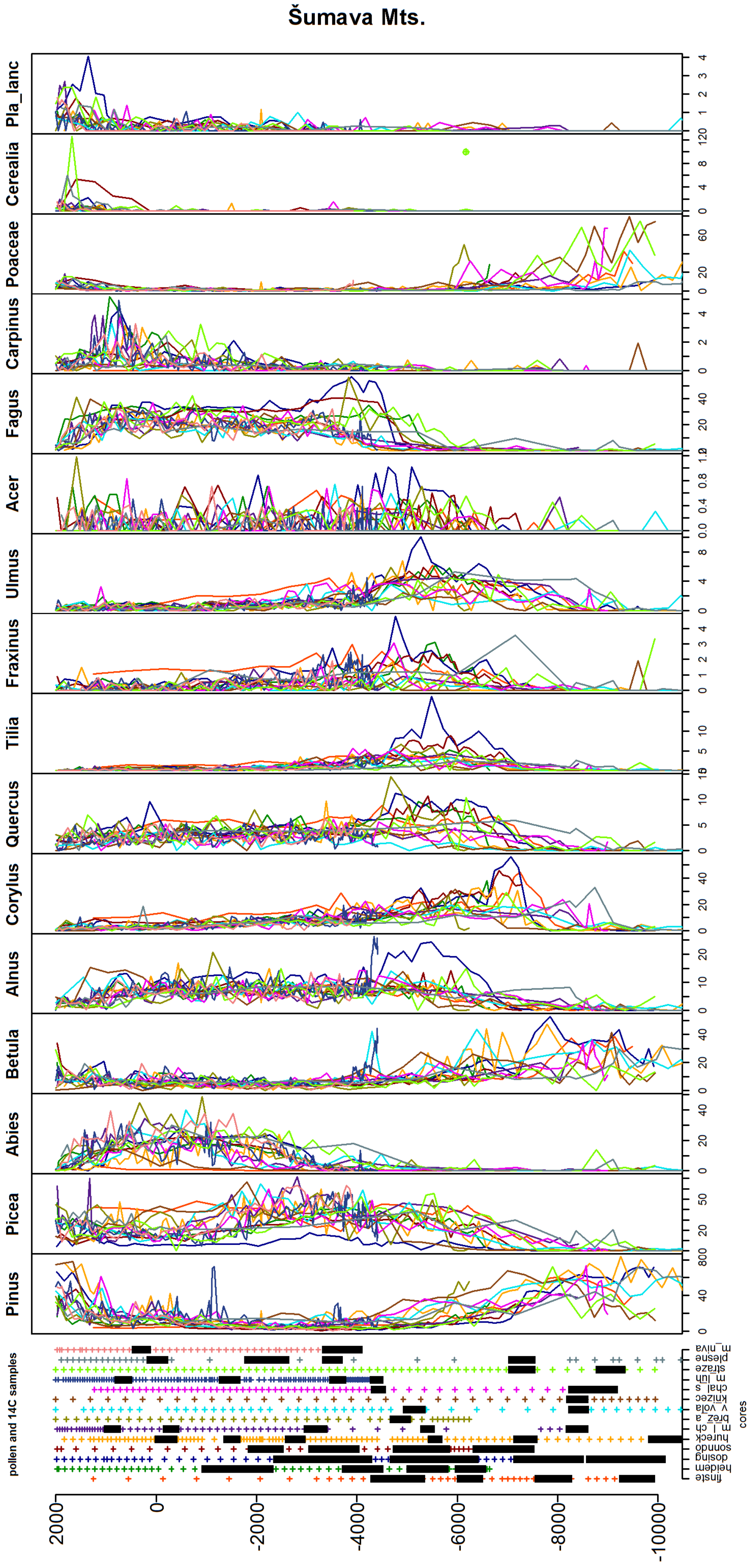
Šumava Mts.
Pla_lanc
Cerealia
Poaceae
Carpinus
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Acer
Ulmus
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Betula
Abies
Picea
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pollen and 14C samples
cores
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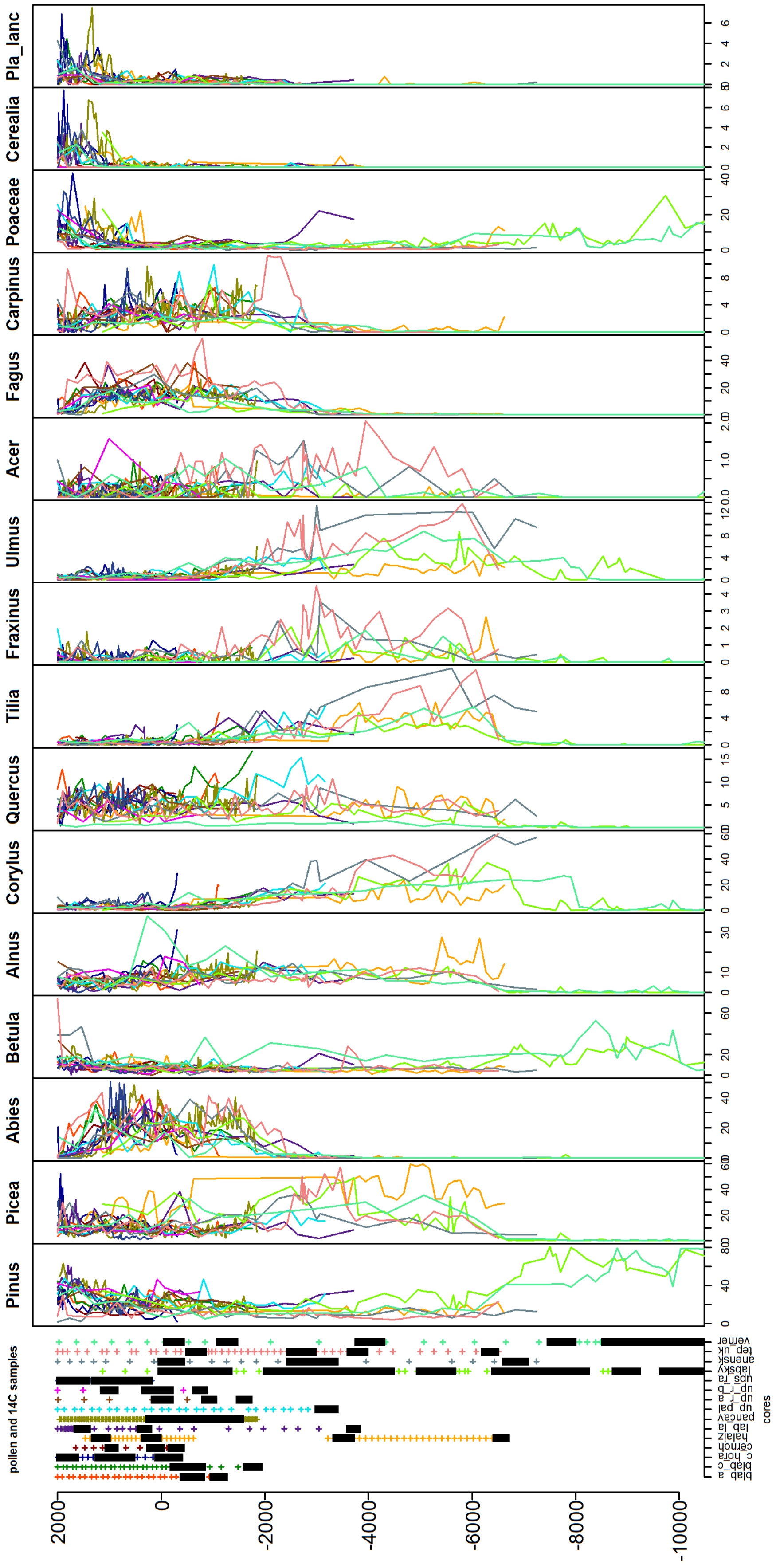
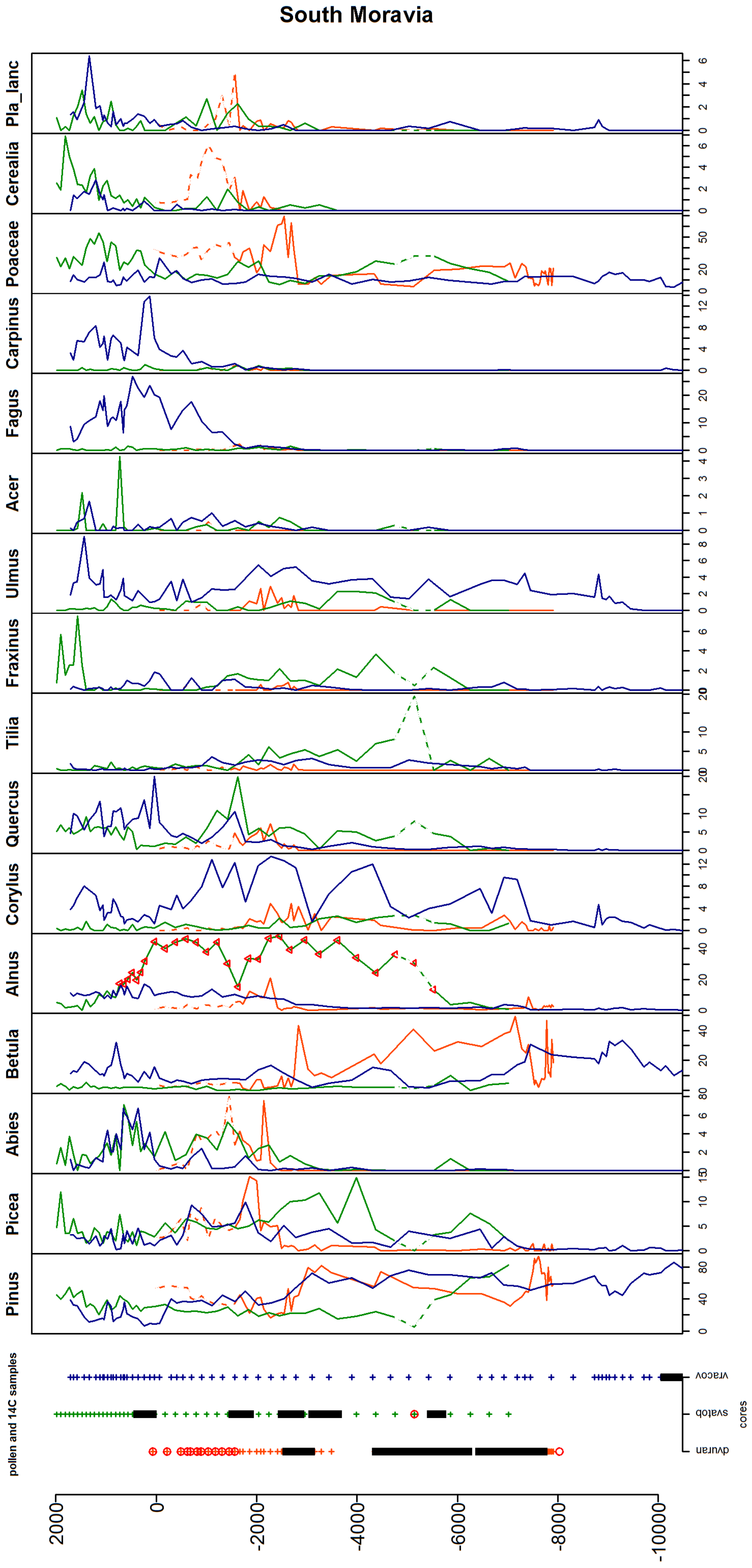
North-East Bohemia




South Moravia
Pla_lanc
Cerealia
Poaceae
Carpinus
Fagus
Acer
Ulmus
Fraxinus
Tilia
Quercus
Corylus
Alnus
Betula
Abies
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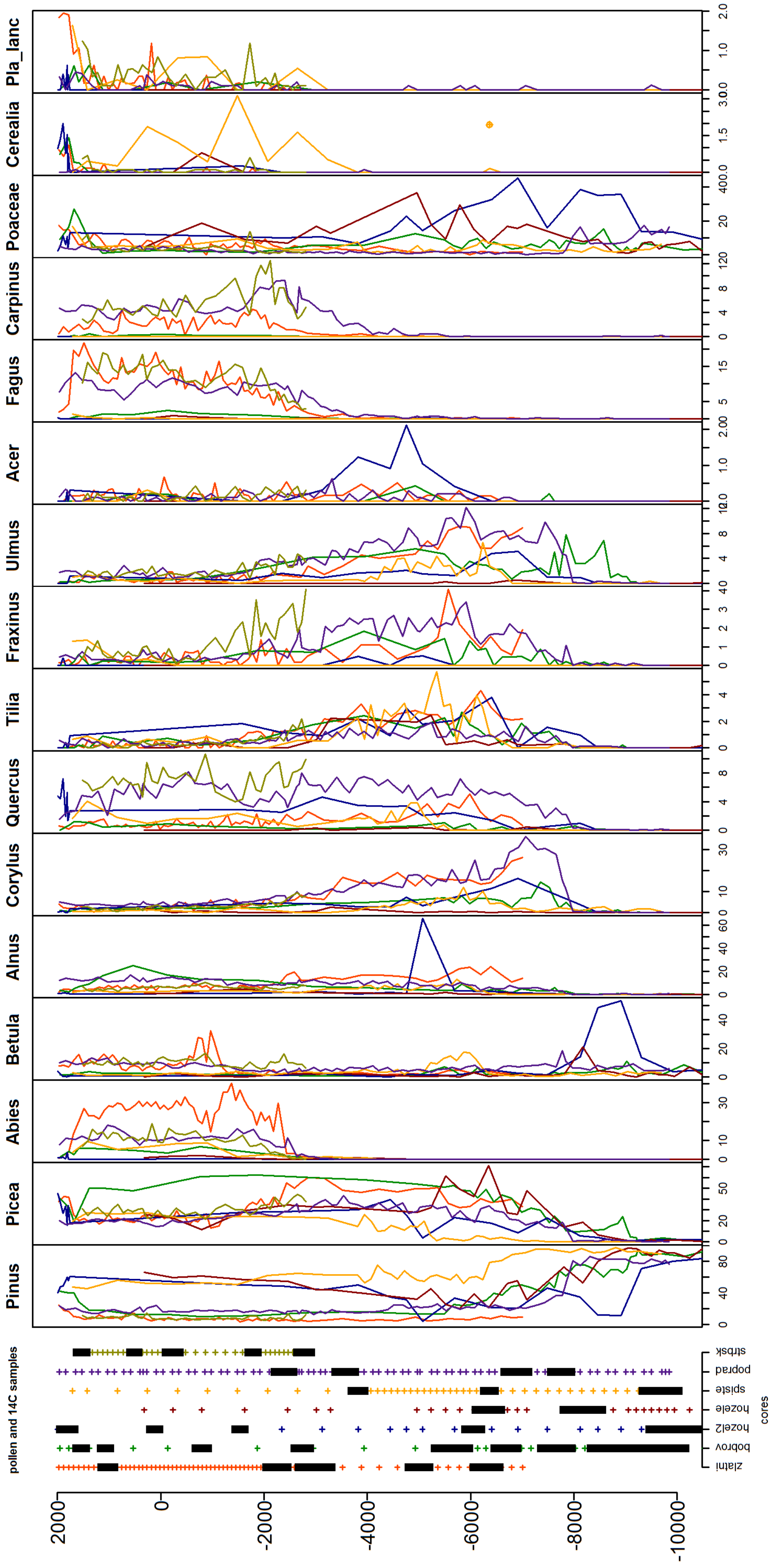
Tatra Mts.


Pla_lanc
Cerealia
Poaceae
Carpinus
Fagus
Acer
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Quercus
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Picea
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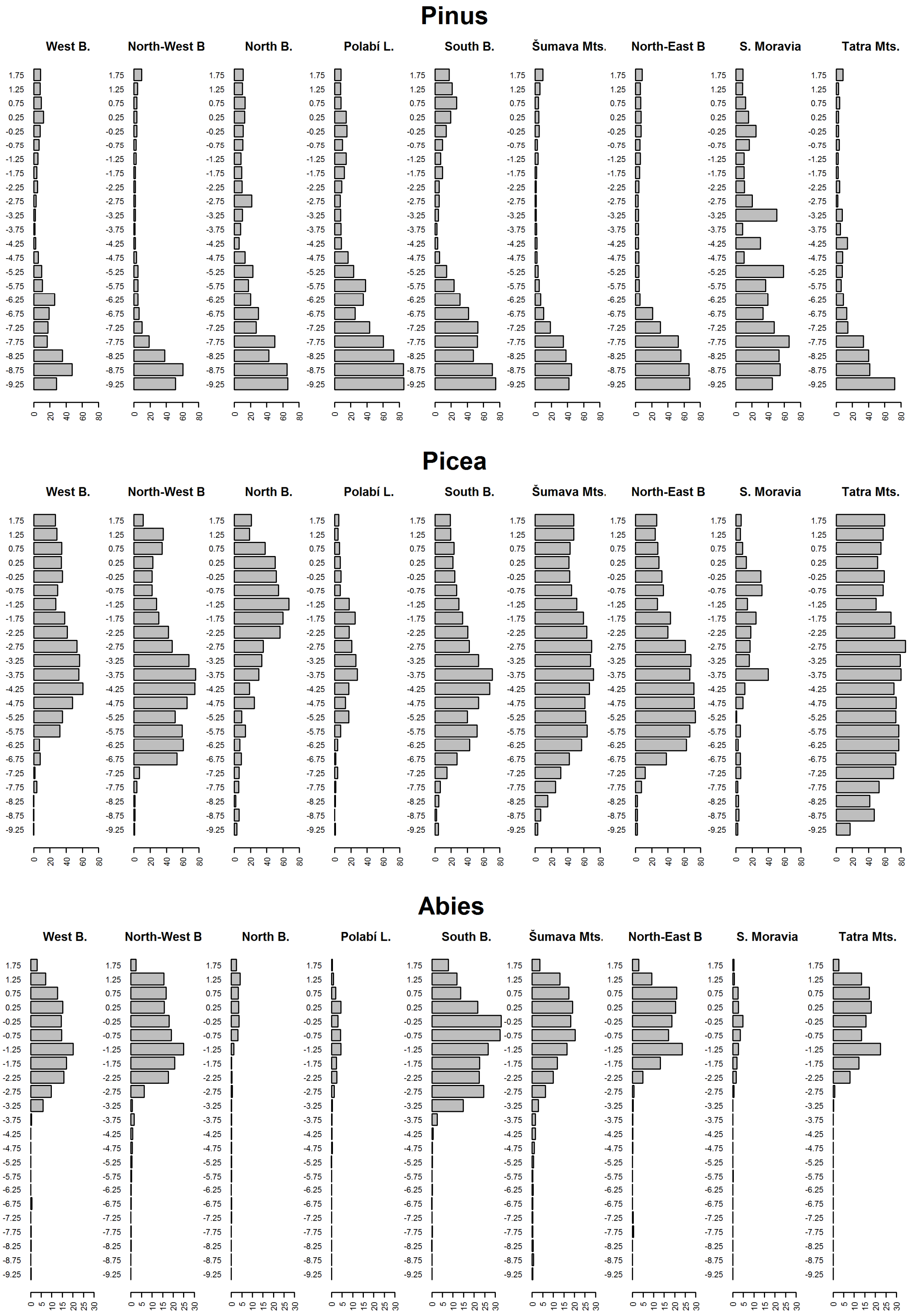


Figure S3 (cont.): REVEALS estimates for each taxon.

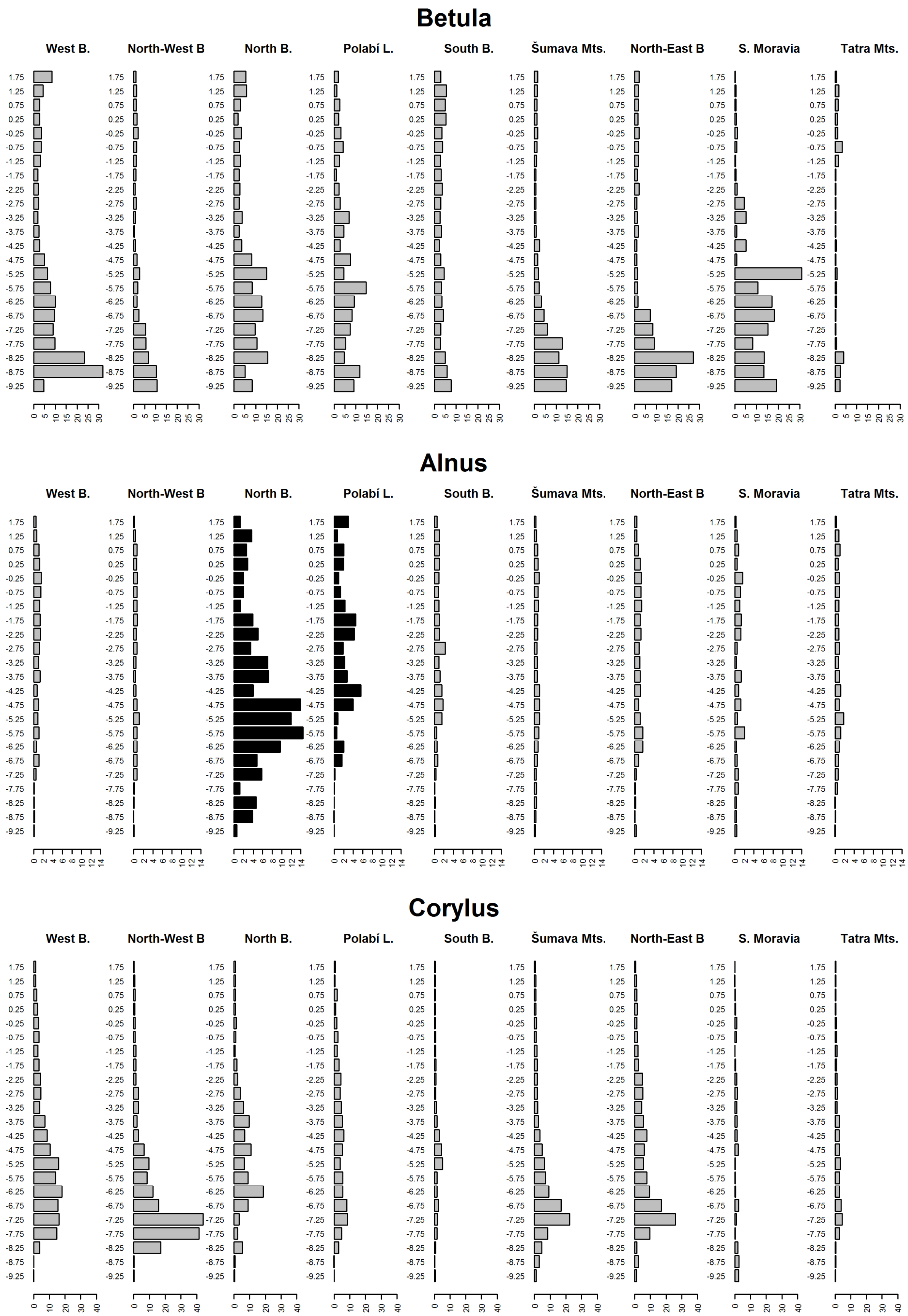


Figure S3 (cont.): REVEALS estimates for each taxon. Black bars indicate regions where input pollen counts of *Alnus* remained unchanged and where it was impossible to obtain a reliable average as regional signal.

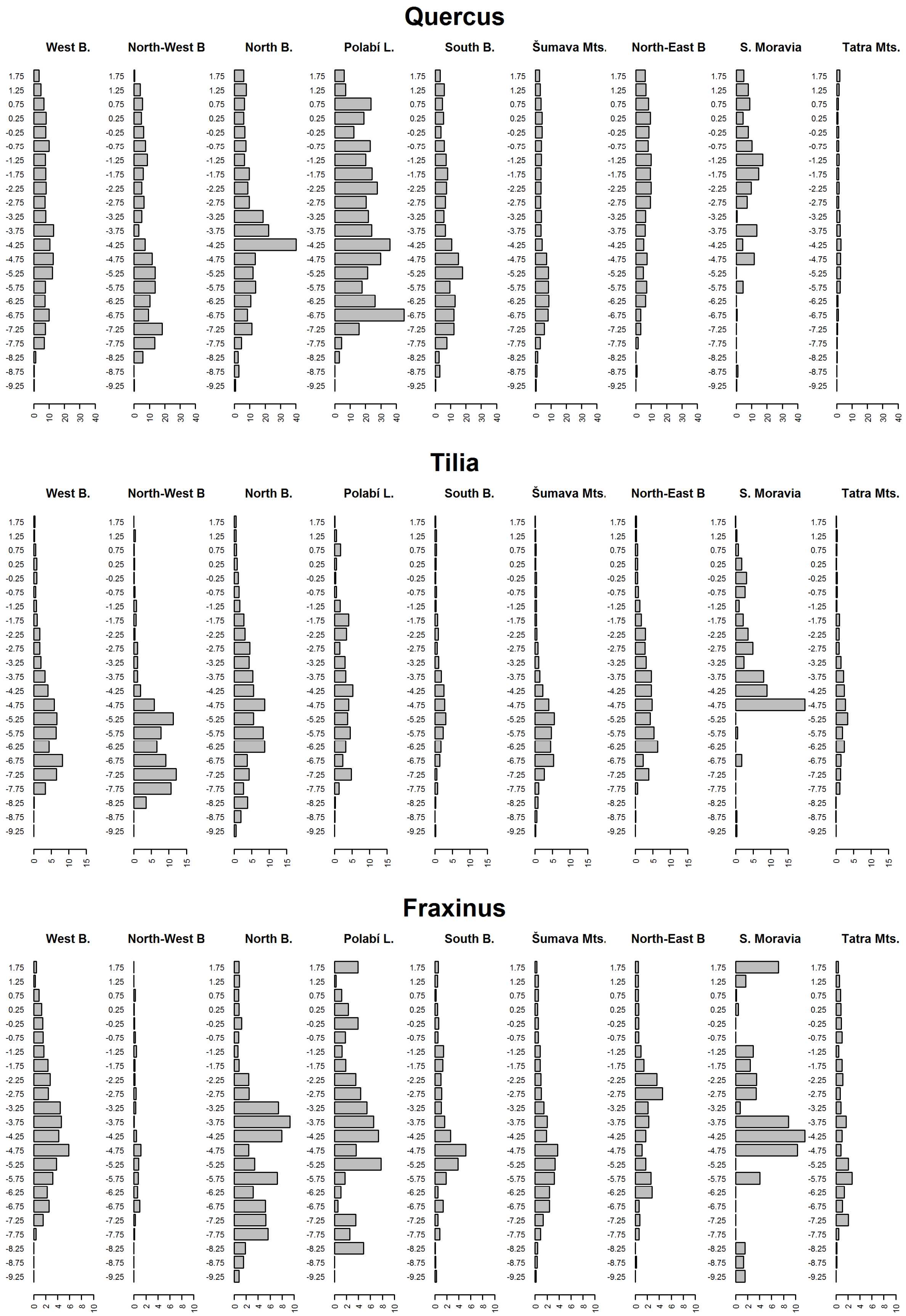
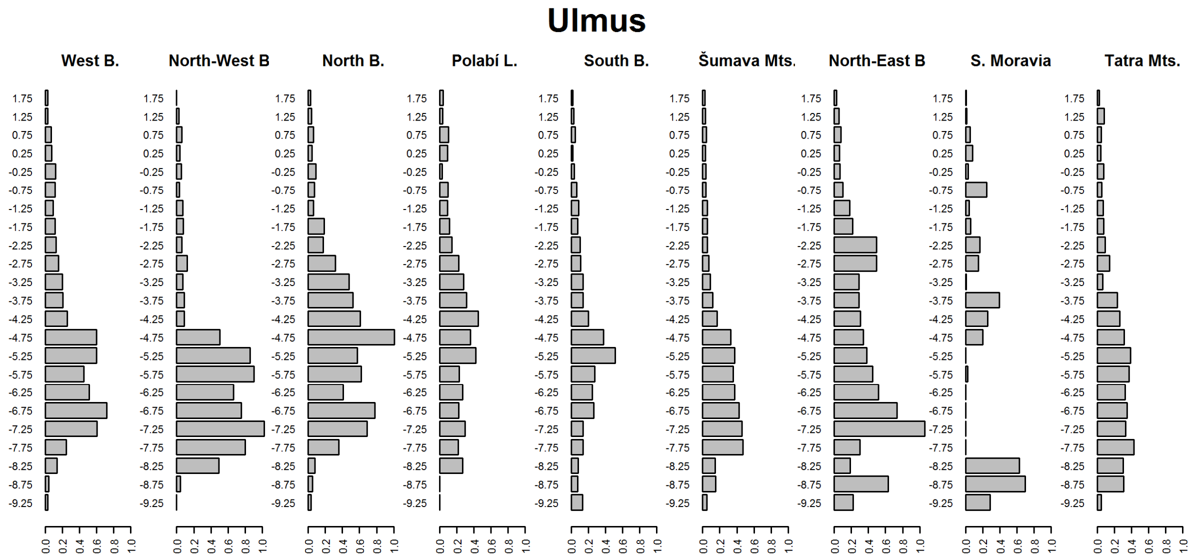
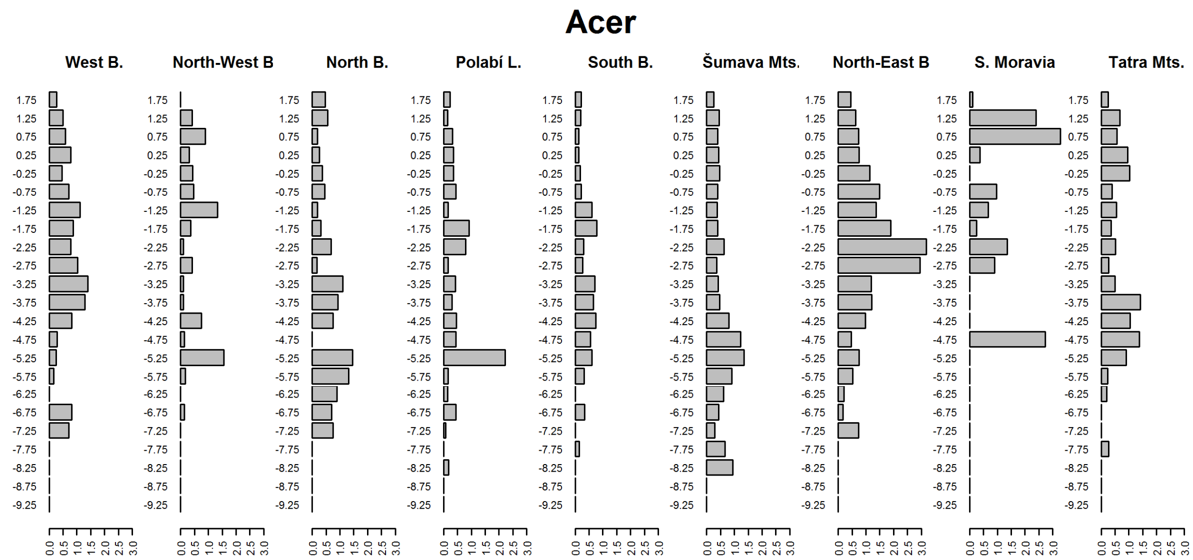


Figure S3 (cont.): REVEALS estimates for each taxon.





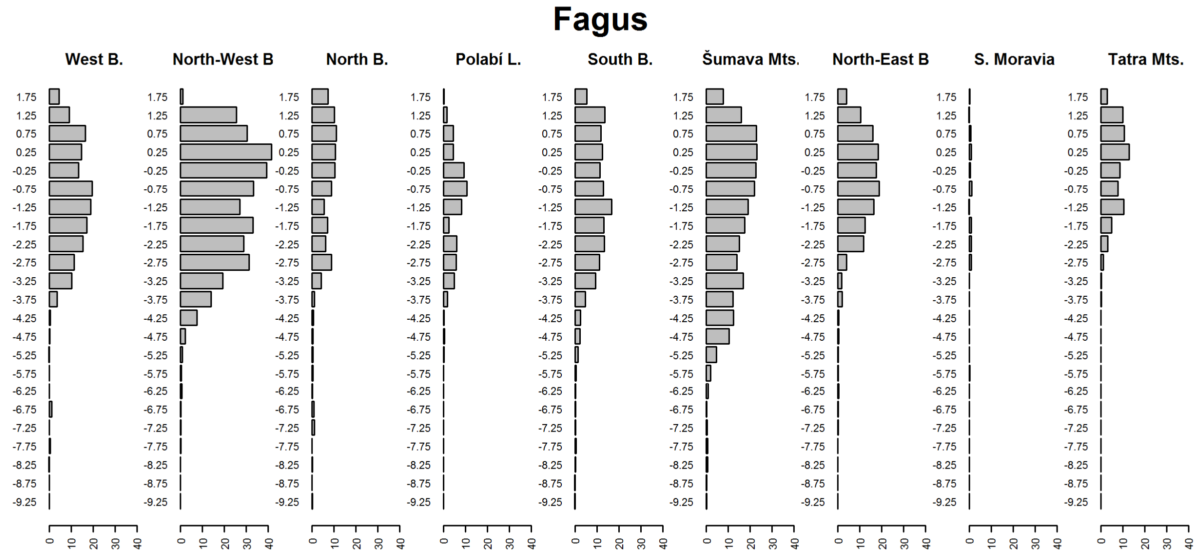


Figure S3 (cont.): REVEALS estimates for each taxon.

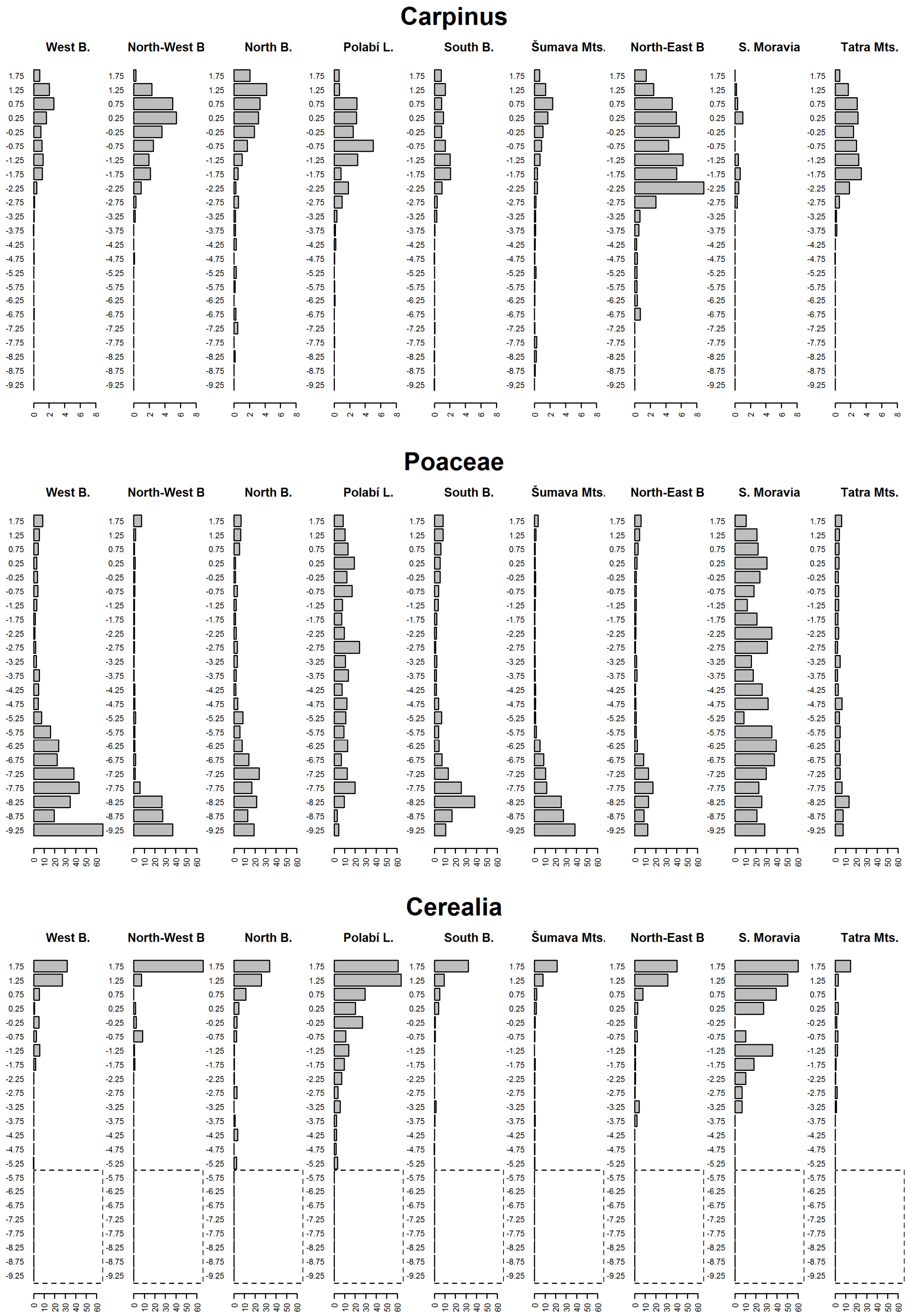


Figure S3 (cont.): REVEALS estimates for each taxon. Dashed fields indicate periods in which all occurrences of Cerealia were excluded due to incorrectly determined large grasses.

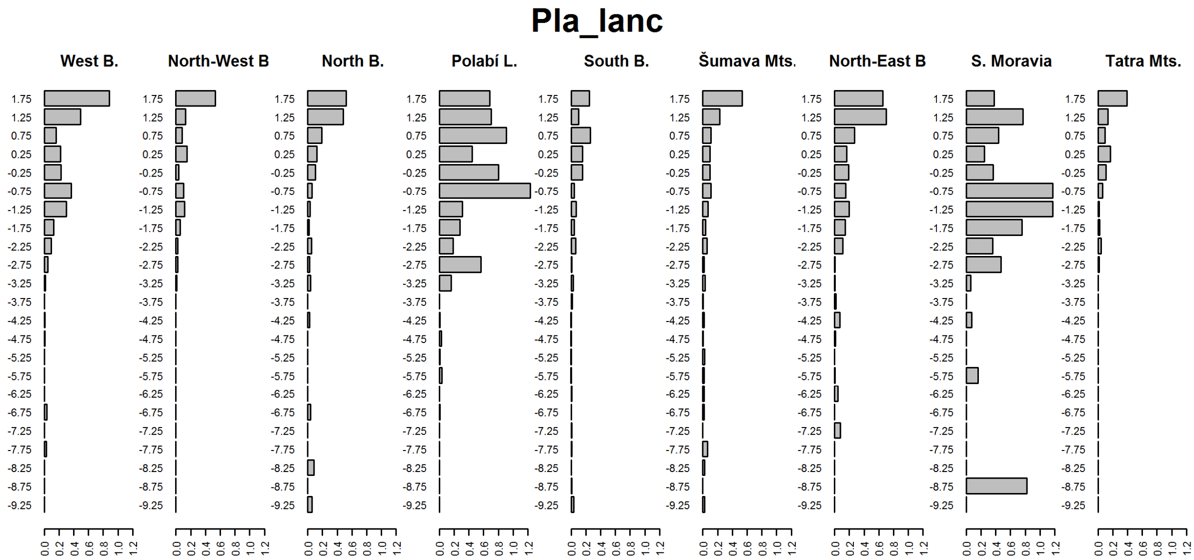


Figure S3 (cont.): REVEALS estimates for each taxon.

Tables

Table S1: Mean tree composition within PNV units in the Czech Republic, calculated from typical vegetation relevés (Neuhäuslová, 2001). Tree composition outside of the Czech Republic was averaged for units of European PNV map (Bohn et al., 2004)(EU_PNV). Missing units (e.g. 11) are situated outside of target regions.

(Neuhäuslová 2001) class	*Pinus*	*Picea*	*Abies*	*Betula*	*Alnus*	*Corylus*	*Quercus*	*Tilia*	*Fraxinus*	*Ulmus*	*Acer*	*Fagus*	*Carpinus*	EU_PVN	syntax
1						3.7	18.5		77.1	0.1	0.6			ash_ald	*Alnion-incanae*
2					5.1		64.1	25.6			5.1			ash_ald	*Alnion-incanae*
3	0.1	0.5			95.2				3.3					ash_ald	*Alnion-incanae*
4							10							hardwood	*Alnion-incanae*
5							5.4	67	26.8	0.2				hardwood	*Alnion-incanae*
6							49.7	0.7	49.7					hardwood	*Alnion-incanae*
7							37.5						62.5	hornbeam	*Carpinion*
8							80.6	19.4						hornbeam	*Carpinion*
9						17.5	73	3.5					0.6	hornbeam	*Carpinion*
10							47.3	0.6					47.3	hornbeam	*Carpinion*
12			0.8			8.9	10.2	10.5	4	12.6	41.9	0.2	9.7	hornbeam	*Carpinion*
13						3.8		3.8	47.2	18.9	0.6	18.9		ravine_f	*Tilio-Acerion*
14								3.3			0.5	96		beech _f	*Eu-Fagenion*
15							0.5	0.5				91		beech _f	*Eu-Fagenion*
16												83.9		beech _f	*Eu-Fagenion*
17							0.6					99.4		beech _f	*Eu-Fagenion*
18		0.5	14.2									83.1		beech _f	*Eu-Fagenion*
21											3.2	92.6		beech _f	*Eu-Fagenion*
22											0.6	99.4		beech _f	*Cephalanthero-Fagenion*
23		4.6	94.9									0.2		fir	*Galio-Abietenion*
24												98.7		beech _f	*Luzulo-Fagion*
25		18.5	0.6									77.1		beech _f	*Luzulo-Fagion*
27	0.6	0.6	70.2			3.4								fir	*Deschampsio flexulosae-Abietetum*
28							78.5				21.4			thermoak	*Quercion pubescenti pertae*
29						3.8	48.1						48.1	thermoak	*Quercion pubescenti pertae*
30						1.9	63.3				10.7		24	thermoak	*Quercion pubescenti pertae*
31							10							thermoak	*Aceri tatarici Quercion*
32							89.1							thermoak	*Aceri tatarici Quercion*
33						3.3	96.7							thermoak	*Quecion petrae*
34							70.7						25	thermoak	*Quecion petrae*
35							5						5	thermoak	*Quecion petrae*
36		0.5					83.5						0.5	acid_oak	*Genisto germanicea Quercion*
37	5.4			26.8		0.9	67							acid_oak	*Genisto germanicea Quercion*
38	5						5							acid_oak	*Genisto germanicea Quercion*
39	33						54.9							acid_oak	*Genisto germanicea Quercion*
40	73.7													pine_f	*Erico-Pinion*
41	38.2	32.9		27.4										pine_f	*Dicrano Pinion*
42	97.2			1.3										pine_f	*Dicrano Pinion*
43		45.5												spruce_f	*Piceion excelsae*
44		98.3												spruce_f	*Piceion excelsae*
45		94.3												spruce_f	*Athyrio alpestris Piceion*
46	98.1	0.1												dwarf_pine	*Pinion mughi*

Table S2 (next pages): List of sites with excluded samples or corrected pollen counts, the depth-age model, previously unpublished datings and palynostratigraphical time control points (in brackets: dated profile of reference). Samples (depths) were excluded because of: 1) a weak depth-age model or 2) strange taphonomy (high pollen counts of *Tilia*). Corrected pollen counts in samples were obtained as follows: 3) pollen counts of Cerealia were set to zero or 4) pollen counts of *Alnus* were set to the regional average. The table contains the following abbreviations: sam.usd. - samples used, publ. - published s. - seed, r. - remain, char. - charcoal., (L) - lake sediment.

REGION	profile	area (m)	sam.usd.	reference for the pollen core and for the 14C samples (depths) excluded or corrected, for kind of intervention (1,2,3,4) see the caption	14C publ.	14C new	depth-age model palynostratigraphical time control points	details, exclusion of dates and differences from default setting of the depth-age model lab. no., depth, material, age (uncal. BP. or BC/AD)			
West Bohemia	**kulz12**	195	17	(Knipping, 1997, 1989)	6		smooth spline				
			1) 0, 10, 20, 30, 40, 50, 60, 70 cm								
			3) 80 cm								
	kulz14	195	112	(Knipping, 1997, 1989)	9		linear	excl:Hv-16628, Hv-16332			
	saubor	40	37	(Hahne, 1992)	2		linear				
	seeloh	40	51	(Hahne, 1992)	3		smooth spline				
	vlcek	98	37	(Švarcová, 2012)	2		linear	excl.: present			
	weiher	56	24	(Knipping, 1997, 1989)	4		smooth spline				
			1) 0, 10, 20, 30 cm								
	weissf	40	34	(Hahne, 1992)	3		linear				
	windbr	252	65	(Knipping, 1997, 1989)	7		linear				
			4) 90, 92, 94, 96, 98, 102, 104, 106, 108, 110, 112, 114, 116, 118, 120, 122, 124, 126, 128, 130 cm								
	wolfl1	56	14	(Hahne, 1992)	2		linear				
North-West Bohemia	**flaje**	282	43	(Jankovská et al., 2007)	3		linear	excl.: CU-1293			
	kom_ch (L)	2523	19	(Jankovská and Pokorný, 2013)	6		smooth spline	smooth=0.24			
	kom_j2 (L)	2523	36	(Jankovská, 1984, 1983)	4		pollen based linear				
							POLLEN event Corylus increase (flaje)		*137.5*		*-8600±250 BC*
	mothau	399	155	(Lange et al., 2005)			pollen based linear				
							POLLEN event Abies increase (kom_ch)		*502.5*		*-2900±250 BC*
							POLLEN event Fagus increase (flaje)		*605*		*-4600±250 BC*
							POLLEN event Picea increase (flaje)		*722.5*		*-7000±250 BC*
North Bohemia	**c_lipa**	113	14	Kuneš unpubl.		2	linear	Poz-8118	75	*Pinus syl.* wood	885±30 uncal. BP
								Poz-8117	115	*Pinus syl.* wood	4100±35 uncal. BP
	drznik	56	22	Svitavská unpubl.		5	smooth spline	Poz-27472 and Poz-27473 has swiched depths			
								UGAMS-5633	30	peat	3360±30 uncal. BP
								UGAMS-4715	65	peat	6150±40 uncal. BP
								UGAMS-5634	90	peat	9270±30 uncal. BP
								Poz-27472	95	peat	10700±60 uncal. BP
								Poz-27473	125	peat	9010±50 uncal. BP
	jeleni	25	36	(Pokorný and Kuneš, 2005)	5		linear				
			2) 280, 285, 290 cm								
	konval	1262	44	Petr unpubl.		5	linear	hiatus=112 cm, excl: present, UGAMS-4716			
			3) 113 cm					UGAMS-5635	17.5	wood	1610±25 uncal. BP
								UGAMS-5636	111.5	wood	4390±30 uncal. BP
								UGAMS-12278	117.5	seed	9520±30 uncal. BP
								UGAMS-4716	137	peat	7120±40 uncal. BP
								UGAMS-5637	149	seeds	10660±30 uncal. BP

North Bohemia	**mareni**	18	19	Kozáková unpubl.		8	linear	Poz-43836	2.5		-803±25 uncal. BP
								Poz-43837	11		995±30 uncal. BP
								Poz-43895	17		1640±30 uncal. BP
								Poz-48936	25		6530±80 uncal. BP
								Poz-48937	60.5		11110±80 uncal. BP
								Poz-48938	67.5		11350±90 uncal. BP
								Poz-43838	82		11580±70 uncal. BP
								Poz-43839	178.5		12390±60 uncal. BP
	milcan	98	28	Petr unpubl.		4	linear	UGAMS-12909	101.5	needles	680±30 uncal. BP
				1) 194, 196, 198, 200, 204, 208, 216, 220 cm			excl: UGAMS-5891, UGAMS-12911	UGAMS-12910	183	needles	3670±30 uncal. BP
								UGAMS-12911	224	plant fragments	12650±80 uncal. BP
								UGAMS-5891	229	charcoal	45940±320 uncal. BP
	okna	113	56	Abraham unpubl.		7	linear	Poz-33652	62	entomo, plant r.	770±35 uncal. BP
				3) 266, 270, 274, 278 cm				Poz-33653	78	charcoal	1390±80 uncal. BP
								UGAMS-3538	100.5	charcoal	2150±25 uncal. BP
								Poz-33654	178	char.,ent. and plant r.	3900±60 uncal. BP
								Crl-7070	222.5	Alnus wood	5869±92 uncal. BP
								Poz-33655	284	char. and plant r.	8860±90 uncal. BP
								UGAMS-3539	360.5	charcoal	11010±40 uncal. BP
	prachn	98	30	Svitavská unpubl.		4	linear	UGAMS-5631	80	peat	590±20 uncal. BP
				3) 140, 145, 150 cm			hiatus=82.5 cm, excl: Poz-27471	UGAMS-4714	115	peat	6080±40 uncal. BP
								UGAMS-5632	150	peat	8150±25 uncal. BP
								Poz-27471	160	peat	6450±40 uncal. BP
	prysky	25	52	(Abraham and Pokorný, 2008)	8		linear				
	vorone	98	25	(Novák et al., 2012)	2*	5	smooth spline	UGAMS-4711	80	charcoal	4730±30 uncal. BP
				*dates published in Novák et al 2012 belong to another profile, thus they were not considered				UGAMS-5629	90	peat	4610±30 uncal. BP
								UGAMS-5630	125	peat	6120±30 uncal. BP
								UGAMS-4712	140	peat	9710±40 uncal. BP
								UGAMS-4713	150	peat	9460±50 uncal. BP
	zaba	18	23	(Peša and Kozáková, 2012)	?	9	linear	Poz-43840	6.5		-1266±25 uncal. BP
							excl.: Poz-48939	Poz-43841	29.5		505±35 uncal. BP
								Poz-48939	37.5		-1859±24 uncal. BP
								Poz-43843	47.5		3565±35 uncal. BP
								Poz-48940	53.5		3895±35 uncal. BP
								Poz-43844	73		4060±30 uncal. BP
								Poz-48942	92.5		5255±35 uncal. BP
								Poz-43845	151		12530±110 uncal. BP
								Poz-43846	245		13190±70 uncal. BP
Polabí lowland |	**borek**	40	24	Kuneš unpubl.	4		linear	Poz-33648	68	charcoal	4420±40 uncal. BP
								Poz-35353	91		7790±50 uncal. BP
								Poz-33650	128.5	carex seeds	8140±80 uncal. BP
								Poz-33651	162	*Carex, Lysimachia, Filipendula, Lycopus* seeds	8380±70 uncal. BP

Polabí lowland	**hraban**	98	28	(Petr and Novák, 2014)	4	linear				
				1) 3, 6, 9, 12, 15, 18, 21, 24, 27, 30, 33, 36, 39, 42, 45, 48, 51, 54, 57, 60, 63, 66, 69, 72, 75, 78, 81 cm						
	hradis	28	70	(Kozáková et al., 2014)	4	linear				
	chr_pr	40	27	(Petr et al., 2014)	5	linear	excl.: Crl-6199B, present			
				3) 110, 116, 119, 121, 124, 127, 133, 137 cm						
	chrast	56	18	(Břízová, 1999; Dreslerová and Pokorný, 2004)	6	smooth spline				
				1) 140, 145, 150, 155, 160 cm						
				3) 75, 80, 85, 90 cm						
	kosatk	98	81	Kozáková unpubl.	6	linear	Poz-24239	87.5		585±30 uncal. BP
							Poz-24241	162.5		1145±30 uncal. BP
							Poz-24242	232.5		1975±30 uncal. BP
							Poz-24243	456		3345±35 uncal. BP
							Crl-7026	530		3628±86 uncal. BP
							Poz-24244	660		3770±35 uncal. BP
	kozly1	40	29	Petr unpubl.	3	linear	Poz-31125	37.5		320±35 uncal. BP
							Poz-31126	72.5		1010±30 uncal. BP
							Poz-31127	112.5		3960±35 uncal. BP
	kozly2	40	58	(Petr and Pokorný, 2008)	4	linear	Poz-29402	59.5		460±30 uncal. BP
				3) 120, 122, 124, 128, 130, 132, 134, 136, 138, 140, 142, 144, 146, 148 cm			Poz-31128	88		3740±60 uncal. BP
							Poz-29401	124		7310±40 uncal. BP
							Poz-22834	148		7900±50 uncal. BP
	kozly3	56	66	Petr unpubl.	4	linear	Poz-32690	90.5		3260±90 uncal. BP
				3) 168, 177, 189, 195, 222, 228, 256, 259, 268 cm		excl.: Poz-31129	Poz-32689	148.5		8620±50 uncal. BP
							Poz-31129	214.5		9200±50 uncal. BP
							Poz-31130	273		9150±50 uncal. BP
	libice	40	17	(Kozáková et al., 2014)	3	linear	excl.: present			
	mel_uv	564	16	(Petr and Novák, 2014)	2	linear				
				3) 40, 46, 49, 55, 61 cm						
	sb_cis	56	49	(Břízová, 1999; Dreslerová and Pokorný, 2004)	4	linear				
	tisic1	56	42	(Dreslerová et al., 2004)	2	linear	excl.: present			
	tisic2	56	97	Petr unpubl.	6	linear	Poz-27209	60		830±30 uncal. BP
						excl.: Poz-27210	Poz-27174	112		1750±50 uncal. BP
							Poz-27239	149		4570±40 uncal. BP
							Poz-27210	180		140±25 uncal. BP
							Poz-27211	214		5270±40 uncal. BP
							Poz-27212	274		5755±35 uncal. BP
	zahaji	98	81	(Albert and Pokorný, 2012; Pokorný, 2005)	6	smooth spline together with zahaj2	smooth=0.25			
				2) 385, 390, 395, 400, 405, 410, 415, 420, 425, 430, 435, 440, 445, 450, 455, 460 cm						
	zahaji2	98	46	Pokorný unpubl.	4	see zahaji	Poz-51054	648	*Betula* s., mosses	6180±40 uncal. BP
				2) 805, 810 cm			Poz-51054	648	*Betula* s., mosses	Poz-51055
							Poz-51057	784	*Betula* seeds	8340±50 uncal. BP
							Poz-51058	826	*Betula* bark	8360±50 uncal. BP

South Bohemia	**barba**	40	103	(Jankovská, 1980)		linear				
				4) 290, 300, 310, 320, 330, 340, 350, 360, 370, 380, 390, 400, 410, 420, 430, 440, 450, 460, 480 cm		*POLLEN event Abies decrease*		*75*		*600±250 AD*
						POLLEN event Abies increase (sva_pp)		*275*		*-3660±250 BC*
						POLLEN event Pinus decrease (sva_pp)		*482*		*-5150±250 BC*
						POLLEN event Quercus increase (sva_pp)		*717*		*-8000±250 BC*
	bork_a	564	82	(Jankovská, 1980)	2	smooth spline				
				* Both 14C dates were reported in the original publication as 4234±125 BC and 7040±100 BC. The first date, however, was reported in the EPD as 6184±125 uncal. BP. We added 1950 years to 7040 BC and dealt with the second date similarly, however measured ^{14}C age remains uncertain.		*POLLEN event Abies decrease*		*47.5*		*600±250 AD*
						POLLEN event Abies increase (sva_pp)		*205*		*-3660±250 BC*
						C14 strange reporting*		245		6184±125 uncal. BP*
						POLLEN event Pinus decrease (sva_pp)		*285*		*-5150±250 BC*
						POLLEN event Quercus increase (sva_pp)		*375*		*-8000±250 BC*
						C14 strange reporting*		430		8990±100 uncal. BP*
	branna	40	74	(Jankovská, 1980)		linear				
				2) 370, 375 cm		POLLEN event *Abies* decrease		67		600±250 AD
				4) 325, 330, 335, 340, 345, 350, 355, 360, 365 cm		POLLEN event *Abies* increase (sva_pp)		262		-3660±250 BC
	c_b_a	282	31	(Jankovská, 1980)		linear				
						POLLEN event Abies decrease		*25*		*600±250 AD*
						POLLEN event Abies increase (sva_pp)		*115*		*-3660±250 BC*
						POLLEN event Quercus increase (sva_pp)		*255*		*-8000±250 BC*
	mlouky	1197	82	(Jankovská, 1987)	5	linear	excl: WIS-1415			
						POLLEN event Abies decrease		*22.5*		*600±250 AD*
						POLLEN event Abies increase (sva_pp)		*57*		*-3660±250 BC*
	sva_pp (L)	399	61	(Hošek et al., 2014; Pokorný, 2002b) **1)** 130 cm **3)** 338, 347 cm	6	linear				
	sva_s3	399	29	(Pokorný et al., 2010, 2008) **1)** 15, 20, 30, 35, 40 cm **3)** 71, 79 cm **4)** 46, 48, 52, 54, 56, 58, 60, 61, 62, 63, 64, 65 cm	4	linear	excl: Poz-16752, Poz-16753			
	zbudo1	282	10	(Rybníčková, 1982; Rybníčková et al., 1975) **1)** 0, 20, 30, 40, 50, 60, 70, 75, 80, 85, 90, 95, 100 cm	3	linear	hiatus=103 cm			
Šumava Mts.	**brez_a**	56	43	Svitavská unpubl.	1	linear	Poz-33658	330	ent. and plant r.	5990±50 uncal. BP
	dosing	160	64	(Stalling, 1987)	7	smooth spline				
	finste	156	40	(Stalling, 1987)	5	smooth spline				
	heidem	233	55	(Stalling, 1987)	6	smooth spline				
	hureck	445	100	(Svobodová et al., 2002)	6	linear				
	chal_s	395	67	Svitavská unpubl.	3	linear	Poz-33666	500	peat	5600±40 uncal. BP
							Poz-33656	630	peat	9160±60 uncal. BP
							Poz-33657	670	peat	9470±60 uncal. BP
	knizec	126	38	(Svobodová et al., 2001)	1	linear	UtC-7653	300		9120±60 uncal. BP

Šumava Mts.	**m_l_ch**		892	58	Svitavská unpubl.		6	linear	excl.: UGAMS-3530			
									UGAMS-3529	100	peat	2245±30 uncal. BP
									UGAMS-3530	215	peat	1155±30 uncal. BP
									UGAMS-3531	495	peat	4455±30 uncal. BP
									UGAMS-3532	540	peat	6430±35 uncal. BP
									UGAMS-3533	620	peat	9190±40 uncal. BP
									UGAMS-3534	640	sediment	9070±40 uncal. BP
	m_luh		892	136	(Svobodová et al., 2001)	4		linear				
	m_niva		455	53	(Svobodová et al., 2002)	3		linear				
	plesne	**(L)**	155	33	(Jankovská, 2006)	5		linear				
	sonndo		98	50	(Stalling, 1987)	6		smooth spline				
	straze		618	67	(Svobodová et al., 2001)	2		linear				
				3) 510 cm								
	v_vola		691	44	(Svobodová et al., 2001)		2	linear	Poz-33820	385	peat	6170±50 uncal. BP
									Poz-33660	450	peat	9180±60 uncal. BP
North-East Bohemia	**anensk**		18	26	(Pokorný and Kuneš, 2005)	4		linear				
	blab_a		178	30	(Svobodová, 2004)	1	2	linear	UGAMS-3543	60	peat	2485±25 uncal. BP
									Poz-4005	67.5		2900±30 uncal. BP
	blab_c		178	34	(Svobodová, 2004)	1	2	linear	excl.: UGAMS-3545			
									UGAMS-3544	72.5	peat	2515±25 uncal. BP
									UGAMS-3545	92.5	sediment	2280±25 uncal. BP
	c_hora		437	37	(Speranza et al., 2000a)	5		linear				
	cernoh		437	14	{Svobodová, 2002}		4	linear	Poz-1087	60		1080±30 uncal. BP
									Poz-1092	90		1890±30 uncal. BP
									Poz-1098	130		1910±40 uncal. BP
									Poz-1111	150		2210±30 uncal. BP
	halaiz		56	55	(Skrzypek et al., 2009)	4		linear	hiatus=105.5			
	lab_la		160	49	Svitavská unpubl.		5	linear	excl.: UGAMS-3540			
									UGAMS-3540	55	peat	-6±25 uncal. BP
									UGAMS-3541	77.5	peat	405±25 uncal. BP
									UGAMS-3542	100	peat	1715±25 uncal. BP
									Poz-4008	120		1715±30 uncal. BP
									Poz-4054	150		4920±40 uncal. BP
	labsky		40	54	(Engel et al., 2010)	17		linear				
	pancav		299	130	(Speranza et al., 2000b)	29		Bacon default and linear extrapolation				
	tep_uk		56	54	(Kuneš and Jankovská, 2000)	5		linear				
	up_pal		178	31	(Svobodová, 2004)	1		linear				
	up_r_a		178	8	(Svobodová, 2004, 2002)	4		smooth spline				
	up_r_b		178	8	(Svobodová, 2004, 2002)	4		linear				
	ups_ra		178	50	(Speranza, 2000)	7		smooth spline				
	verner		69	30	(Peichlová, 1979; Rybníčková and Rybníček, 1996)	9		linear				

South Moravia	**dvuran**	98	57	(Svobodová, 1997, 1992)	4		linear				
			1) 70, 80, 90, 95, 97, 102, 105, 110, 115, 120, 125, 129, 275 cm								
	svatob	56	47	(Svobodová, 1997, 1989)	5		linear				
			2) 210 cm								
			4) 75, 80, 85, 90, 95, 100, 105, 110, 115, 120, 125, 130, 135, 140, 145, 150, 155, 160, 165, 170, 175, 180, 185, 190, 195, 200, 205, 215 cm								
	vracov	**(L)** 271	87	(Svobodová, 1997, 1992)	1	10	Bacon default setting				
								Poz-51951	40	seeds of *Carex*	670±30 uncal. BP
								Poz-51947	125	plant remains	1870±50 uncal. BP
								Poz-51948	185	plant remains	4715±35 uncal. BP
								Beta377320	252	pollen extract	9410±40 uncal. BP
								Poz-51949	280	seed *Najas marina*	9830±60 uncal. BP
								Beta377321	362.5	pollen extract	12390±50 uncal. BP
								HV-1868	372	sediment	12260±372 uncal. BP
								Poz-51952	417	plant remains	12890±90 uncal. BP
								Poz-51954	452	plant remains	3410±120 uncal. BP
								Beta364949	480	pollen extract	10880±50 uncal. BP
Tatry Mts.	**bobrov**	149	41	(Rybníček and Rybníčková, 2002, 1985)	13		linear				
	hozele	149	23	(Jankovská, 1988)	3		linear				
	hozel2	149	23	Jamrichová unpubl., (Hájková et al., 2012)	4	5	linear	hiatus=60 cm, excl.: UG-11625, UG-11626			
								UG-11623	26.5	seeds	130±25
								UG-11624	52	mosses	150±25
								UG-11625	146.5	tissue	1890±25
								UG-11626	186.5	tissue	1920±25
								UG-11627	199	seeds	11780±40
	poprad	**(L)** 144	81	(Rybníčková and Rybníček, 2006)	4		linear				
	spiste	56	45	Jamrichová unpubl.		3	linear				
			3) 60 cm					Poz-33662	20	*Isoëtes* spore, char., *Carex* seed	5000±40 uncal. BP
								Poz-33665	60	*Isoëtes* spore, char., *Carex* seed	7540±50 uncal. BP
								Poz-33661	90	plant remains	10060±90 uncal. BP
	strbsk	**(L)** 239	39	(Rybníčková and Rybníček, 2006)	5		linear				
	zlatni	138	71	(Rybníček and Rybníčková, 2002, 1985)	5		linear				

Conclusions

In line with the aims outlined at the beginning of the Introduction, the following wrap-up is divided into conclusions regarding the quantitative way of interpretation and synthetic information from gathered fossil data.

The most important parameters of the relationship between pollen and vegetation are pollen productivity, size of the sedimentation basin and wind speed. PPE values are influenced above all by imperfect approximation of pollen dispersal by the Prentice-Sugita model. This method of distance weighting underestimates the dispersal of heavy pollen grains. On the other hand, the simplicity of this function makes it possible to apply various ad hoc correction settings, which can be done by adjusting only one of a few parameters (**Chapter 4**).

Validation of PPEs appeared necessary due to the 100-fold difference between the area of the PPE study (**Chapter 3**) and the extent of their application in the REVEALS model. Theoretically, compilation of the PPEs from adjacent studies within the same region after such validation can substitute new PPE studies, since the resulting set of PPEs indicates the role of regional similarity (PPEs of dominant taxa originate from studies in Central Europe, i.e. Switzerland, Germany – **Chapter 4**).

Reconstructed vegetation for the Early Holocene are semi-open pine forests, which was only gradually enriched by temperate taxa (**Chapter 5**). Among the first migrants was *Lonicera nigra* (or alternatively *L. xylosteum*) (**Chapter 2**), which found refuge in this biotope until mesic deciduous broad-leaved woodlands appeared.

Mid-Holocene vegetation at middle altitudes calculated by the quantitative method partly agrees and partly differs from expert interpretations (**Chapter 5**). The results do not represent a completely new story, but their benefit lies in their quantitative character and the more controlled way of achieving them. Even if the present results are found to be incorrect in the future, it will be possible to efficiently search for the source of error (**Chapter 3, 4 and 5**).

Reconstructed vegetation can influence policy makers in the field of nature conservation. If their aim is “natural vegetation”, understanding the time window of 750 AD as the target composition is at least problematic. From the palaeoecological perspective, the apparent stability of prevailing vegetation is just a phase of long-term tree succession. On the other hand, **Chapter 5** proposes some processes whose frequencies and intensities allowed the continuous presence of pioneer trees and open-land vegetation. Maps of natural vegetation as a basis for nature management may be assembled beside static composition also from factors which maintain their dynamics or stability.

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