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Using historical ecology to reassess the conservation status of coniferous forests in Central Europe

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Abstract

Forests cover approximately one-third of Central Europe. Oak (*Quercus*) and European beech (*Fagus sylvatica*) are considered the natural dominants at low and middle elevations, respectively. Many coniferous forests (especially of *Picea abies*) occur primarily at midelevations, but these are thought to have resulted from forestry plantations planted over the past 200 years. Nature conservation and forestry policy seek to promote broadleaved trees over conifers. However, there are discrepancies between conservation guidelines (included in Natura 2000) and historical and palaeoecological data with regard to the distribution of conifers. Our aim was to bring new evidence to the debate on the conservation of conifers versus broadleaved trees at midelevations in Central Europe. We created a vegetation and land-cover model based on pollen data for a highland area of 11,300 km^2 in the Czech Republic and assessed tree species composition in the forests before the onset of modern forestry based on 18th-century archival sources. Conifers dominated the study region throughout the entire Holocene (approximately 40–60% of the area was covered by coniferous forests) . Broadleaved trees were present in a much smaller area than envisaged by current ideas of natural vegetation. Rather than casting doubt on the principles of Central European nature conservation in general, our results highlight the necessity of detailed regional investigations and the importance of historical data in challenging established notions on the natural distribution of tree species.

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Keywords

applied historical ecology; *Fagus sylvatica*; *Picea abies*; plantation forestry; potential natural vegetation; interdisciplinarity; REVEALS

Introduction

Approximately one-third of Central Europe (here defined as Poland, the Czech Republic, Slovakia, Hungary, Germany, and Austria) is covered by woodland (Forest Europe et al. 2011). Forests are thought to have occupied almost the entire region before the appearance of settled human communities, although the structure of this vegetation has been under intense debate recently (Vera 2000; Hodder et al. 2005). The sheer amount of forests in the region and their accepted status as the natural vegetation (Bohn et al. 2000) make them the backbone of nature conservation under national and EU legislation (Evans 2006; European Commission 2013). However, not every forest is considered equally natural. Established principles of what types of forests are worth conserving or promoting have far-reaching consequences not only for protected areas but also for ordinary managed forests.

In Europe deliberate forest regeneration through planting of young trees was unusual until the 18th century (Radkau 2011). By that time, millennia of management had altered the structure and species composition of tree populations (e.g. Dufraisse 2008), but common tree species rarely spread beyond their original distribution range except in orchards and formal gardens. This changed with the advent of modern forestry. Foresters, especially in the early 19th century, were strongly engaged in experimenting with different, especially fast-growing, tree species to see which would produce the highest yields at any given location. Promising species were subsequently extensively planted, rather like an arable crop that can be freely transported. Criticism of these methods was voiced in forestry circles as they were being implemented (Gayer 1886).

Interest in what tree species could be considered native in various regions goes back at least to the 18th century (Barrington 1769). After plantation forestry became common, questions about the original range of native species also emerged. Micklitz (1857), for example, tried to determine the preplantation distribution of European larch (*Larix decidua*) in the Czech Republic. Research into past forest communities was taken to a new level by the invention and application of pollen analysis in the late 19th and early 20th centuries (von Post 1916; Manten 1967). Pollen analysis allows researchers to follow the history of tree species (or genera) over thousands rather than hundreds of years.

Roughly concurrent with the birth of palynology, phytosociology was created (Braun-Blanquet 1918). Phytosociology aims to delimit and characterize vegetation types based on floristic composition, which are combined into abstract vegetation types (Dengler et al. 2008). Perhaps the primary applied use of phytosociology is determination of potential natural vegetation (PNV), a concept which was developed in the mid-1950s (Tüxen 1956). Determination of PNV includes delineating vegetation units and mapping their distribution. Researchers studied existing pieces of what appeared to be natural vegetation and combined this information with a thorough knowledge of abiotic conditions to predict what kind of vegetation would develop “if human influence on vegetation was removed ... and the natural vegetation was imagined as switched into a new balance within a split second…” (Tüxen 1956 translated in Zerbe 1998). What was seen as natural was, among other things, determined by palynological results. Recently, the relationship between early palynology, phytosociology, and PNV has been debated intensely(e.g., Carrión & Fernández 2009; Chiarucci et al. 2010; Somodi et al. 2012).

Although it is clear that PNV was not originally intended to describe vegetation before human impact, it is also undeniable that phytosociology-based PNV maps (or the closely related maps of reconstructed natural vegetation) have been interpreted as references to the prehuman past (e.g., Györffy & Zólyomi 1994; Mikyška et al. 1968). Relative to our purpose here, the basic concepts of PNV and phytosociology have had a significant and long-lasting effect on nature conservation and forestry policy, especially in Central Europe (Chytrý 1998). Vegetation thought to be natural at any given location is often used as a baseline. Although modern nature conservation is multifaceted and concepts such as the historical range of variation complement more static views of nature (Wiens et al. 2012), baseline conditions are still widely used. Perhaps because phytosociology is one of the few branches of research to describe vegetation based on species composition over large areas in a coherent manner, it formed the basis of the NATURA 2000 network, which covers approximately 17% of the European Union (Biondi et al. 2012; European Commission 2013).

Coniferous tree species, especially Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) were most often used in Central European forestry plantations, which created an aura of unnaturalness around them. Pollen-based biostratigraphy claimsthat the current climate (the ’Subatlantic) is the most favourable for European beech (*Fagus sylvatica*) (Firbas 1949–1952). Phytosociologists found virtually no coniferous stands they considered natural except at high elevations. At present, beech is considered the natural dominant species at most midelevation sites in Central Europe (Ellenberg 1996). This idea is supported by observations at many old-growth sites in the region, which are either dominated by beech or show succession towards beech stands (Standovár & Kenderes 2003; Mölder et al. 2008). All this is reflected in forestry policy. For example, in the Czech Republic “target forest communities” (tree species composition that should result from management and planting) from 400 to 900 metres asl are dominated by beech (Průša 2001).

The tendency to consider conifers less important than deciduous tree species was noted as a potential source of error. This is not a new claim. In 1978, Rybníček and Rybníčková pointed out discrepancies among PNV maps, pollen profiles and archival documents and suggested the possible existence of “virgin coniferous forest at middle altitudes in Czechoslovakia,” by which they meant the occurrence of Norway spruce, silver fir (*Abies alba*), and Scots pine forests between the Iron Age and the Early Middle Ages (Rybníček & Rybníčková 1978). Based on archival documents, Nožička (1972) reconstructed a much larger distribution area for spruce than documented earlier. However, this topic received little further attention and the evaluation of conifers for nature conservation and conservation-minded forestry in Central Europe have changed little since the mid-1960s.

Our aim was not to produce improved PNV maps; rather, we sought to show how the past may be relevant to the understanding of present ecosystems and their future managementt. We conducted an interdisciplinary study based on pollen data, information in archival documents, potential natural vegetation, and current vegetation. We sought to create a pollen-based vegetation and land-cover model for our study region; assess tree species composition in forests before the onset of modern forestry; and compare these results with ideas of natural vegetation as used in current nature conservation and forestry. Our approach is novel because instead of scattered point data (typical for palynology and historical research), we created a landscape model and processed large amounts of archival information from the preforestry period to provide a coherent, high-resolution picture of past vegetation for a large region.

Methods

Study area

The Bohemian-Moravian Highlands lie between the historic regions of Bohemia and Moravia in the Czech Republic (Fig. 1). To define the study area (ca. 11,300 km^2), a minimum bounding circle covering all sites where pollen was collected was generated in ArcGIS (version 10.1) , and its centroid was used to create a 60-km circle. The climate of the region is moderately warm; yearly average temperatures are 6–8 °C and precipitation is 550–700 mm (Tolasz et al. 2007). The most soils are cambisols. Generally speaking, the area is undulating; the highest point is 863 m. Human history in the region is poorly documented. Prehistoric archaeological finds are rare, at least partly because of a lack of research. Medieval colonization started in the 12th century (Hrubý et al. 2014). By the late 14th century, the settlement pattern of the region was similar to the present pattern, although settlement desertion in the Late Middle Ages was a significant factor in some areas (Nekuda 1961).

Palynological model

We used 6 pollen profiles to construct Holocene regional vegetation estimates for our study area (Fig. 1). Five sites were new and one was from a previous study (Rybníčková & Rybníček 1988), for which data were obtained from the Czech Quaternary Palynological Database (Kuneš et al. 2009). All pollen profiles were radiocarbon dated using terrestrial plant macrofossils or peat sediment if no macrofossils were available (Supporting Information). For all sites, we constructed chronologies with Bayesian age-depth modelling implemented in the Bacon program (Blaauw & Christen 2011; Supporting Information).

We aggregated pollen counts in 500-year intervals for the entire Holocene at each site and used the aggregated counts to reconstruct regional vegetation with the REVEALS model (Sugita 2007a). Previously, we validated the REVEALS model based on present-day vegetation in the Czech Republic (Abraham et al. 2014), which allowed us to correct model parameters. Validation is necessary, because parameters tend to show geographic instability due to regional climatic, edaphic or species-competition differences. Based on these simulations, we chose to reconstruct vegetation at a spatial extent of 60 km. The REVEALS model was originally developed to provide regional vegetation abundance using pollen data from large sites (>100 ha). However, REVEALS can provide reliable estimates when multiple small sites, including bogs, are used (Mazier et al. 2012). For the REVEALS runs, we used all available sites for each time window. The program then calculated the mean vegetation composition from all available sites and the corresponding mean error estimates for each taxon (Sugita 2007a). This approach, however, can result in large error estimates depending on the number of sites used and the input of taxa with low pollen counts in the calculations. In some time windows only two sites were available; thus, such results must be interpreted with caution.

Altogether 29 pollen-equivalent taxa were used for which relative pollen productivities, one of the most important model input parameters, were available and tested for the region (Abraham & Kozáková 2012; Abraham et al. 2014). Other parameters included the fall speed of pollen (Supporting Information) and wind speed, which was set to 4 m/s according to average measured values. The Prentice dispersal-depositional bog model (Prentice 1985) was used to calculate regional vegetation composition (Sugita 2007b). We made calculations in R (R Core Team 2014) and used the R function to calculate mean vegetation abundances and their error estimates based on the bootstrap method (https://github.com/petrkunes/LRA).

Vegetation reconstruction based on archival data

We gathered information on tree species composition for the late 18th century. In this period, forests were affected by traditional management (such as coppicing or litter raking) but not by conifer plantations (Nožička 1957). Our basic source was the so-called Josephian cadastre. Cadastral surveys in the Czech Lands were carried out from the 17th century onwards to establish the value of each piece of land for taxation purposes. Compiled from 1787 to 1789, the Josephian cadastre was an ambitious undertaking of Emperor Joseph II of Austria (Roubík 1954). This survey took the parish (usually a single village and the surrounding area) as the basic survey unit. Part of this cadastre was the *Waldfassion*, a detailed survey of forests that included the name, topographic description, size, dominant tree species composition, and management (coppice or high forest). The Josephian cadastre thus described the entire study region (rather than random points) in sufficiently high resolution immediately before the onset of plantation forestry. This survey was compiled separately for Bohemia and Moravia. Processing the Josephian cadastre was extremely time consuming: a single *Waldfassion* often comprises dozens of folios in which data have to be aggregated manually. Furthermore, Czech archival regulations restrict the number of documents that can be accessed daily. Therefore, we had to limit ourselves to the Moravian part of the cadastre (57% of the area covered by REVEALS), which is kept at the Moravian Archives under shelfmark MZA D 6. Not providing complete coverage for the area described by the pollen-based model is a disadvantage. Nonetheless, vegetation in the Bohemian and Moravian parts of the Highlands is reasonably similar. Analysing only Moravian data did not compromise the relevance of our conclusions in the sense that we did not intend to compare pollen results with archival documents in a straightforward and spatially explicit manner but rather aimed to point out similarities in these independent datasets. All historical information was connected to current parishes because these – as in other parts of Europe – have been relatively stable since the Middle Ages. Data were

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processed in ArcGIS 10.1. Current parish boundaries were obtained from the Czech Office for Surveying, Mapping and Cadastres.

PNV and current vegetation

Potential natural vegetation was available as a GIS layer of the latest PNV map of the Czech Republic (Neuhäuslová et al. 2001). In the study area, the PNV map shows the dominance of oak-hornbeam forests (37%, mainly at 250–500 m), acidophilous beech forest (37%, mainly at 450–700 m), and herb-rich beech forests (19%, mainly at 450–650 m). Conifer-dominated vegetation was negligible. Current vegetation was derived from CORINE 2006 land-cover mapping based on satellite imagery; forests were classified as broadleaved, coniferous, or mixed (Heymann et al. 1994; European Environment Agency 2007). At present, forests cover almost 29% of the area; the lowest elevations (150–250 m) are largely deforested. Forests are mostly coniferous (63%) or mixed (30%). These data refer to the part of the study area covered by archival sources.

Results

Palynological model

The REVEALS model for the region (Fig. 2) showed the continuous dominance of spruce (as much as 60–70% of the area covered by spruce forests in some periods) from approximately 7000 BC onwards, when spruce replaced the earlier dominant pine. The spruce cover in the REVEALS model could be three times higher than values shown by mere pollen percentages (Fig. 2). Spruce was less overwhelming in the landscape after 2000 BC, and during this period an increase in *Quercus* occurred. *Fagus*, *Abies* and *Carpinus* also increased albeit to a much smaller degree. Approximately 2500 years ago oak forests declined and *Cerealia* (arable fields) significantly increased. It would be logical to assume (even though the REVEALS model says nothing about spatial distribution) that arable fields replaced oak forests. Nonetheless, spruce remained dominant throughout. Beech stands apparently never covered more than 10% of the landscape. The effects of large-scale spruce plantations, which were supposed to completely alter tree species composition in the region, were invisible in the model and in individual profiles (Supporting Information).

The model produced large error estimates especially in the middle period (ca. 3500-500 BC) because the time slices were modelled based on different numbers of sites (Fig. 2). However, the overall image of vegetation development was consistent and the dominance of spruce forests was such that it remained evident even for lower values within the range.

Archival sources

The study area included 1183 parishes in Moravia. We did not find archival records for 41 parishes, and 126 parishes were completely deforested. We found species-level data for 761 parishes. For the remaining parishes, we used data differentiating only between hardwood and softwood forests. With few and relatively unimportant exceptions (such as willow), softwood species in the region equal conifers (pine, spruce, fir) and hardwood species equal broadleaved trees (oak, beech, hornbeam); therefore, even this basic classification provided the same detail as CORINE land-cover mapping. In the majority of cases, the forested areas in each parish were described and a list of dominant tree species was provided; there was no information on the proportion of each species. Thus, we used the presence or absence of species in individual parishes rather than area coverage by species.

Conifers dominated in terms of both the number of parishes with the occurrence of individual species and the area of forests in which different species occurred. Out of the 1016 parishes with forests, only 22 had no conifers in them (Table 1). The elevation distribution of species showed a characteristic pattern (Fig. 3 a, b, c). Broadleaved trees were the most frequent at elevations between 300 and 350 m. In this zone, beech, oak and hornbeam often occurred in the same forests. As expected, beech also grew at higher elevations up to 800 m but far less frequently than supposed by PNV maps. Beech was less common from 400 to 600 m (the elevation at which according to forestry zones it should be absolutely dominant), which created a bimodal distribution pattern. Conifers were more widely distributed than broadleaved trees already at low elevations (300–350 m). Above about 400 m, conifers were present virtually everywhere. Furthermore, forests in 58% of the parishes were made up of only conifers (Fig. 4). This was particularly striking from 450 to 600 m, where broadleaved trees occurred only in about 15% of the study area.

Spatial distribution patterns were also pronounced (Fig. 4, Supporting Information). When not in the oak-hornbeam phytogeographical zone, beech tended to occur in the herb-rich beech and spruce-beech woodland zones and was mostly absent from the acidophilous beech zone (which is approximately between the oak- hornbeam and acidophilous beech zones, hence the bimodal elevation distribution). Forest stands of only beech did not exist.

Comparison of preforestry vegetation with PNV and current vegetation cover

There was a striking difference between vegetation in the late 18th century and PNV (Fig. 3 c, d, e; Table 2). According to the PNV maps, broadleaved trees occupied almost the entire region up to 700 m; historically they occurred in a much smaller part of the area. According to PNV maps, conifers are in about 30–40% of all parishes from 450 to 700 m and their proportion increases only above 700 m. By contrast, in the preforestry period, conifers were more frequent than broadleaved trees (already between 300 and 350 m, and the majority of forests at 450-600 m consisted only of conifers. Current vegetation based on the CORINE land-cover map showed a picture similar to the late 18th century in the sense that conifers were more frequent already at low elevations (although they did not necessarily occupy a larger territory). However, the low proportion of broadleaved trees at midelevations in the pre-forestry period was not observed in current vegetation cover.

Discussion

Both the pollen-based landscape model and preforestry archival evidence showed the long-term dominance of coniferous trees in the study region. The two types of sources were complementary. The landscape model provided data on the proportion of individual taxa, and written sources added spatial detail. Furthermore, pollen data offered a long-term perspective. A recent palaeoanthracological study from the same region also demonstrated the prevalence of conifers. At three sites from 463 to 646 m, spruce and fir usually dominated in the past millennium and beech rarely reached >20% in the overall charcoal or

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wooden macroremains composition (Hrubý et al. 2014). Older palynological literature envisaged a more dynamic vegetation over the Holocene. In approximately 1000 BC, fir and beech were supposed to have expanded at the expense of spruce and beech was thought to be gaining dominance over most of the region (Rybníčková 1974; Rybníčková & Rybníček 1985, 1988; Břízová 2009).

Spruce stands would have survived only at climatically and edaphically suitable sites in inversion valleys and in the close vicinity of peat bogs. The continuous dominance of spruce over the entire Holocene would have been restricted to a few scattered sites (Rybníčková 1974; Peichlová 1977; Rybníčková & Rybníček 1988). However, profiles in these studies were not dated by absolute methods and were based on simple pollen percentages with intuitive modifications to compensate for varying pollen production among species and other factors influencing the pollen rain. This procedure was criticized many times in older and more recent literature (e.g. Davis 1963). By contrast, we used radiocarbon-dated profiles in a transparent and tested landscape model. Numerous modern approaches allow for quantitative or semiquantitative vegetation reconstruction. For example, pollen accumulation rates provide taxon-independent values of abundance and can be directly linked to plant (tree) biomass (e.g., Seppä et al. 2009; Matthias & Giesecke 2014). Unfortunately, due to discontinuous sedimentation in some of our bog records, we lacked high-quality pollen-accumulation rates essential for such approaches. The REVEALS and other models may suffer from parameter instability over millennia (Kuneš et al. 2011; Trondman et al. 2015). Even though quantitative vegetation reconstruction (such as REVEALS) may yield variable results when considering different pollen-dispersal models (e.g., Jackson & Lyford 1999; Sjögren et al. 2010; Theuerkauf et al. 2013, 2016), we believe REVEALS provided us with a reasonably reliable picture of past vegetation, especially thanks to validation and testing in our region (Abraham et al. 2014; Mazier et al. 2012).

Earlier forestry literature included remarkable insights into the past occurrence of conifers in the region. Based partly on the results of Málek (1958, 1961), Nožička (1972) attempted to reconstruct the original distribution of spruce in the Czech Republic, and his results were not unlike ours although we pushed the limit of spruce distribution even farther towards the lowlands. However, he argued that even though spruce was present in many regions, it was only an admixture species in broadleaved stands. Earlier authors usually argued that the occurrence of conifers at midelevations resulted from human management, which suppressed the otherwise dominant beech (Nožička 1972; Ellenberg 1996). Our results suggest that the past presence of conifers in the region was not necessarily the consequence of preforestry management, such as selective felling for industrial purposes. In fact, we observed surprisingly long-term stability in vegetation: spruce has been the dominant species for approximately 9,000 years. A similar pattern, albeit with the dominance of pine, was recorded in a sandstone region in northern Bohemia by Novák et al. (2012). These authors concluded that “the general concept of cultural replacement of broadleaved forests by pine forests is not necessarily inappropriate. However, our results imply that in extremely nutrient-poor habitats another scenario can exist, at least at a local scale.”

Unexpectedly high proportions of Scots pine at many Neolithic mid- and low-elevation sites in the Czech Republic were discovered in a recent anthracological study, whose authors remarked that earlier researchers had been reluctant to reconstruct coniferous forests for the Neolithic partly because of a “certain ideological struggle” against recent Scots pine monocultures (Kočár et al. 2014). Although it was not our explicit aim to establish the reasons behind long-term vegetation stability in our study region, we hypothesize that edaphic conditions are an important factor here as well (cf. Samek 1959). In particular, hard siliceous bedrock and the resulting acidic, nutrient-poor soils may have impeded succession toward broadleaved forests since the early Holocene. Spruce, a species less demanding in terms of soil fertility, started to occupy such sites around 7,000 BC. The usual Central European scenario of vegetation succession was diverted, which resulted in the long-term stability of spruce-dominated vegetation. Along similar lines, several recent studies point to previously unsuspected continuity of various vegetation types in Central Europe (Kuneš et al. 2015; Hájková et al. 2011; Magyari et al. 2010).

The picture emerging from our study has far-reaching consequences for nature conservation and forestry policy in the study region and beyond, especially in midelevation forests in Central Europe. Although we do not doubt the results of successional studies in beech-dominated reserves, such places apparently represent local cases rather than the rule. If the region was dominated by conifers to the extent that even large-scale modern spruce plantations are invisible in the pollen record, it is perhaps time to reconsider conservation preferences and targets. Currently 2% of the study area is protected under NATURA 2000. Most protected sites are situated at middle elevations (300–450 m) and are over 63% beech, oak, and hornbeam woodlands. Coniferous forests (excluding plantations) cover <1% of protected sites (NCA CR 2011). We do not suggest that planting spruce monocultures is a sustainable solution for the region, but encouraging the conversion of coniferous stands to beech forests in all conditions (cf. Emmer et al. 1998; Souček & Tesař 2008) may not be suitableeither.

Considering the wider Central European context, it is apparent that the lack of phytosociological interest in coniferous stands (cf. Chytrý 2013), the legacy of which resurfaced in current nature conservation, leaves many questions unanswered. Regional differences in what is considered the beech region are of paramount importance. For example, a comparable study in northeastern Germany showed that current vegetation (mostly pine plantations) was very different from vegetation in the 1780s. However, the latter was not composed of the beech stands of the PNV maps but rather of various oak communities (Wulf & Rujner 2011). Future conservation and forestry policy decisions must involve a detailed evaluation of local conditions. By providing information about the past, interdisciplinary historical ecology can contribute to a better understanding of long-term vegetation stability and change. Historical ecology can challenge “modern assumptions about species’ natural distribution, providing opportunities for new hypotheses to be tested with additional data” (McClenachan et al. 2015). Coniferous forests at midelevations appear to have been part of the Central European landscape for millennia. They should be decoupled from the associations created by their less-than-glorious recent past, allowing them to find their way back into carefully planned nature conservation and forestry policy.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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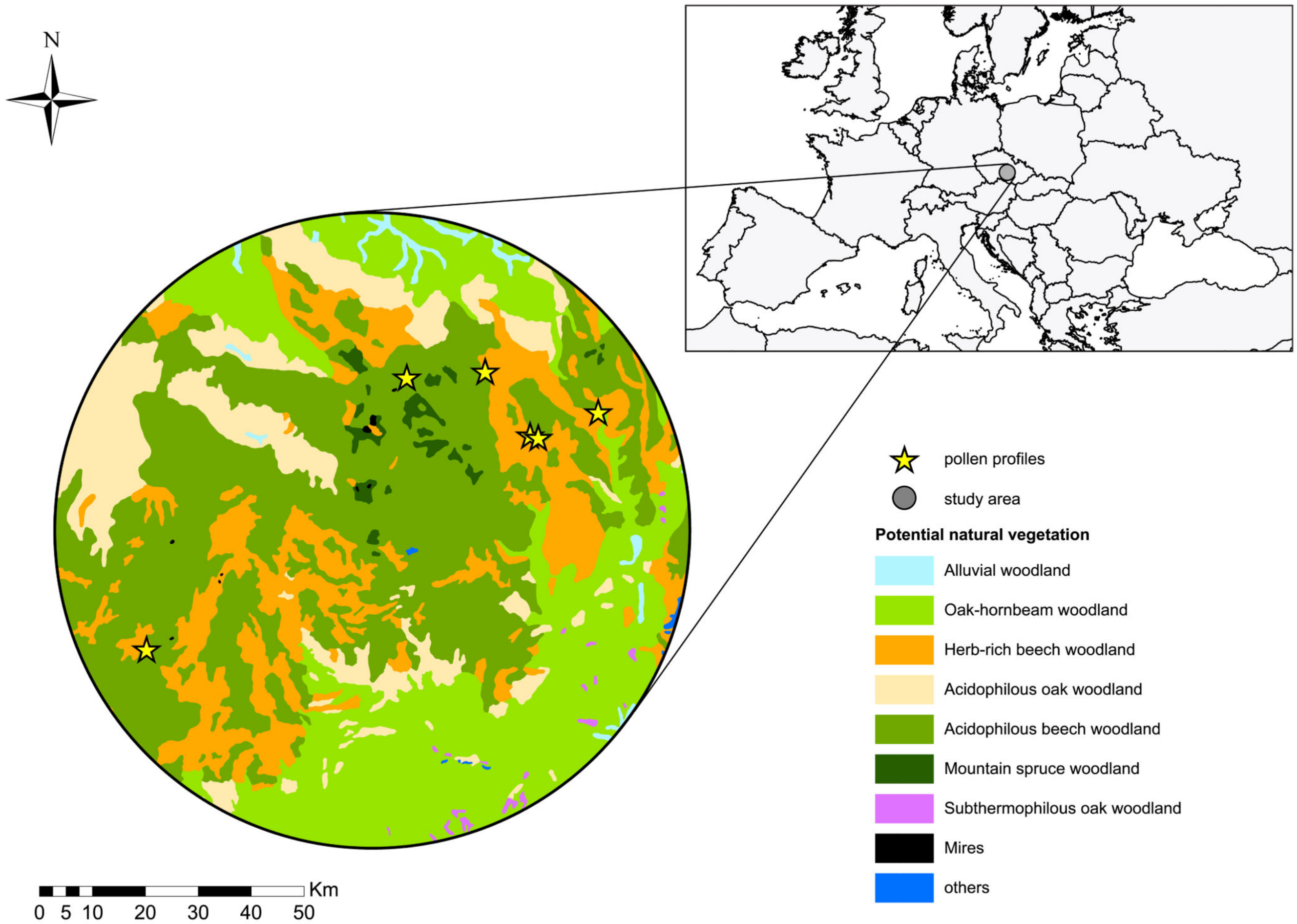
N
pollen profiles
study area
Potential natural vegetation
Alluvial woodland
Oak-hornbeam woodland
Herb-rich beech woodland
Acidophilous oak woodland
Acidophilous beech woodland
Mountain spruce woodland
Subthermophilous oak woodland
Mires
others
Km
0 5 10 20 30 40 50

Fig. 1.

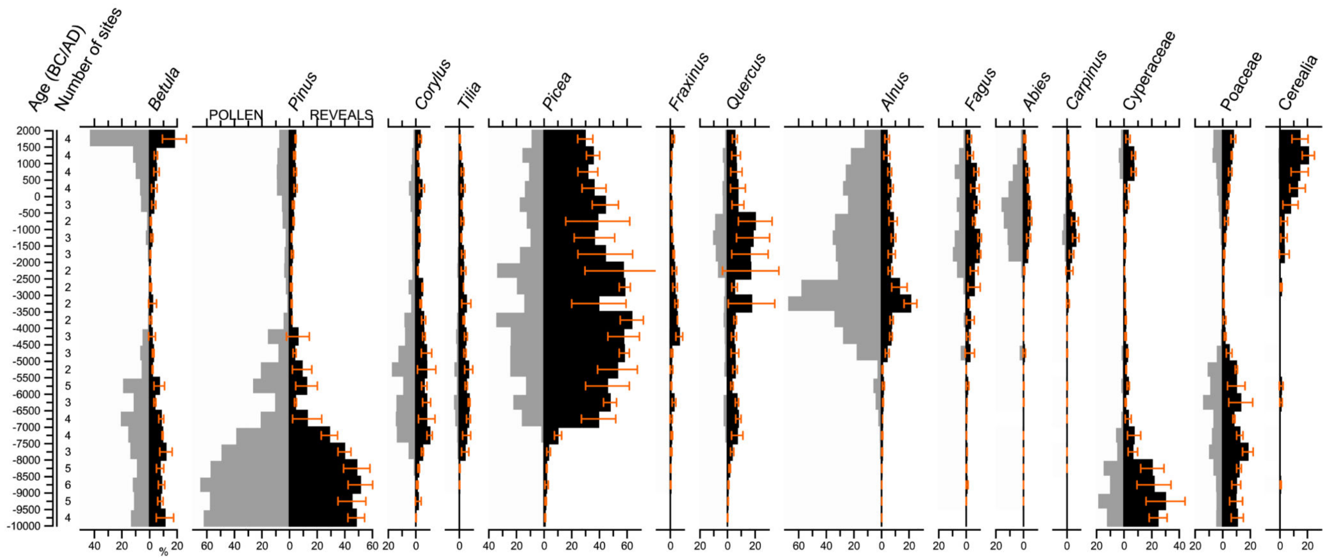

Fig. 2.

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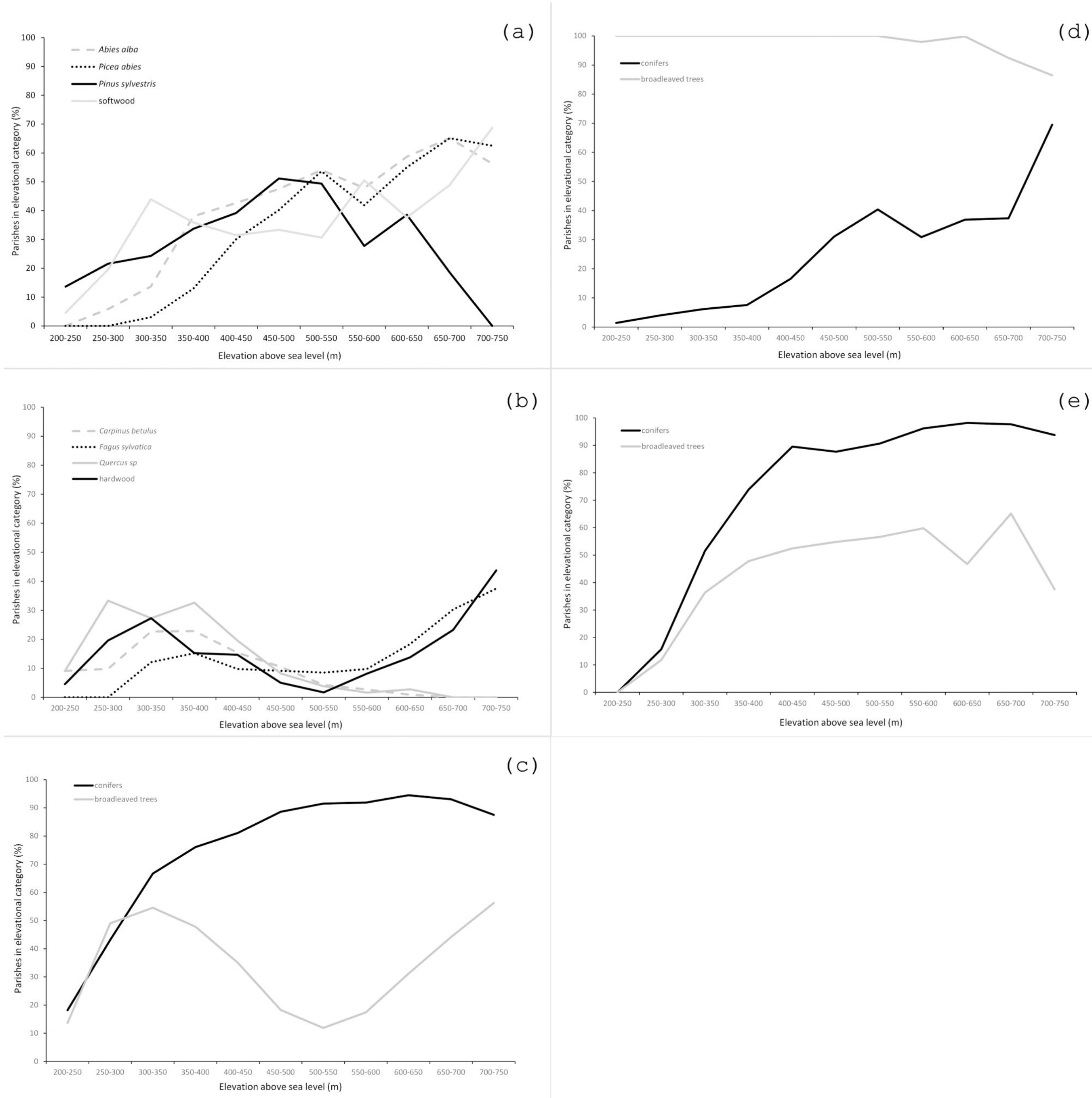
(a)
Abies alba
Picea abies
Pinus sylvestris
softwood
Parishes in elevational category (%)
Elevation above sea level (m)
200-250
250-300
300-350
350-400
400-450
450-500
500-550
550-600
600-650
650-700
700-750
(b)
Carpinus betulus
Fagus sylvatica
Quercus sp
hardwood
(c)
conifers
broadleaved trees
(d)
(e)

Fig. 3.

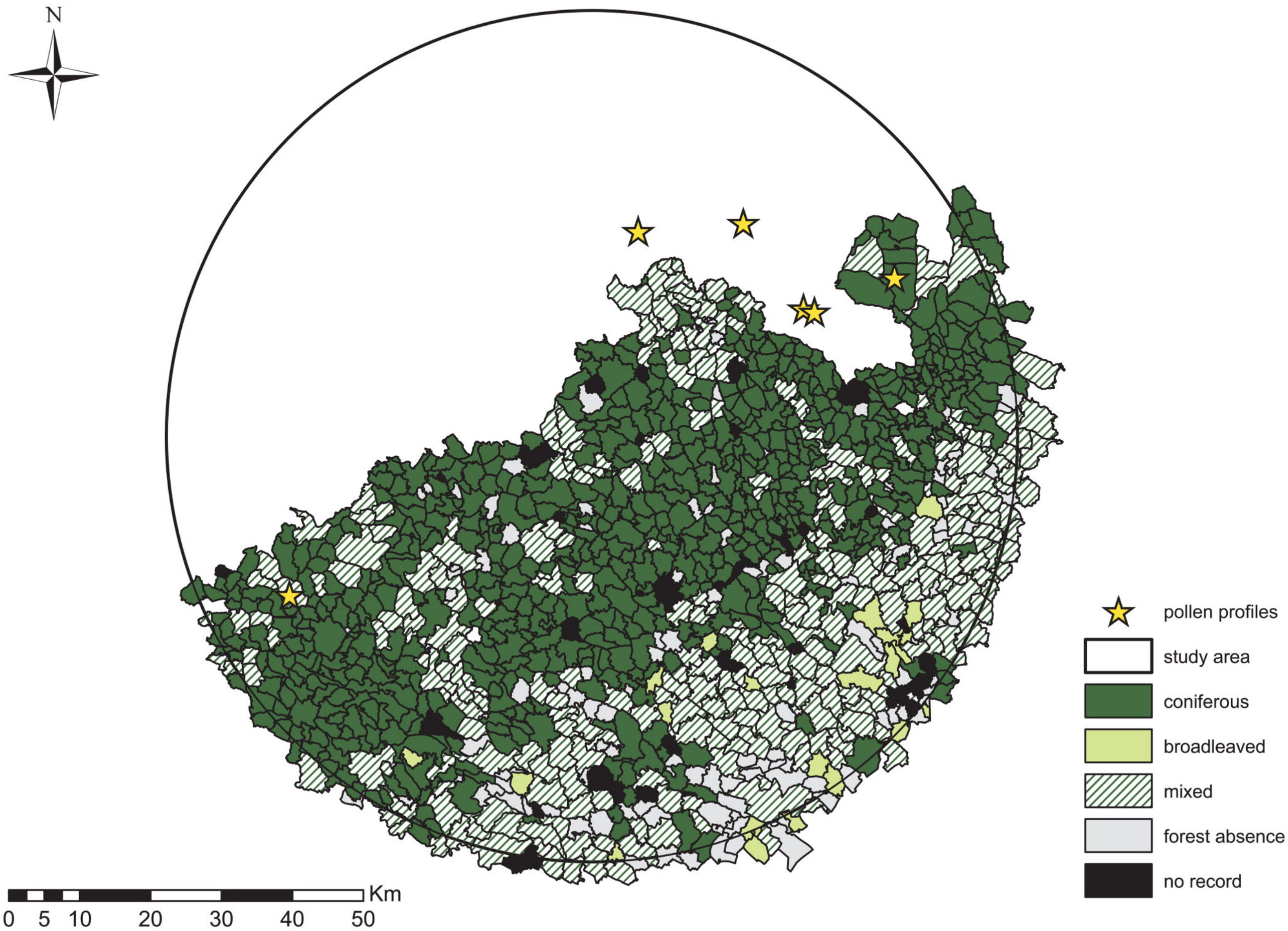
N
pollen profiles
study area
coniferous
broadleaved
mixed
forest absence
no record
Km
0
5
10
20
30
40
50

Fig. 4.

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Table 1

Occurrence of conifers and broadleaved trees in parishes and the area of forests in which individual species occurred at the end of the 18th century.

	Conifers				Broadleaved trees			
	Picea	***Abies***	***Pinus***	**“softwood”**	**Fagus**	***Quercus***	***Carpinus***	**“hardwood”**
No. of parishes with occurrence of species (*n*=1183)	449	531	446	432	136	129	105	129
Area of forests in which species occurred (ha) *	53 510	79 157	29 126	58 054	27 496	20 650	21 001	28 631

* Usually more species occurred in the same forest; therefore, the area for each species does not imply the species was the most abundant over the entire area.

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Table 2

Overlap in forest types between the Josephian cadastre (1780s) and a) current land cover (CORINE) and b) potential natural vegetation (PNV). Parishes are categorized as containing broadleaved (BL), coniferous (CF), mixed (M), and no forests (NF).

a)				
1780s	**CORINE**			
	BL (n=0)	CF (n=378)	M (n=586)	NF (n=178)
BL (n=22)	0	1	7	14
CF (n=692)	0	259	369	64
M (n=302)	0	99	164	39
NF (n=126)	0	19	46	61

b)			
1780s	**PNV**		
	BL (n=382)	CF (n=0)	M (n=780)
BL (n=22)	8	0	14
CF (n=692)	236	0	456
M (n=302)	99	0	203
NF (n=126)	39	0	87