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Landscape-scale changes in central Europe around the Pleistocene-Holocene transition and the Anthropocene

Změny na krajinné škále v období okolo přelomu pleistocén-holocén a v antropocénu ve střední Evropě

Doctoral thesis

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Abstract

This thesis investigates the dynamics of the central European landscape. Four case studies, exploring two key periods of environmental transformation: Late Glacial and the Anthropocene, are included. All case studies are connected by the spatial scale of interest: the landscape scale. This scale is targeted not only by the spatial extent of the sampling, but by the essence of the issues investigated, as broadly described in the introduction. The studies use disparate methods and different contexts, which helps to approach such a complex phenomenon - the landscape and its formation.

The included studies are dealing with the Last Glacial landscape and vegetation by (1) comparing pollen records using modern analogues (here from Yakutia) and argues that the change at the Late Glacial/Holocene transition may not have been as great as previously thought, because at least somewhere forests may had existed during the Last Glacial being supported by permafrost melting. A follow-up study (2) explores how permafrost melting, i.e., thermokarst processes, generated an entire lake landscape whose remnants unexpectedly largely persist in the Třeboň region (southern Czech Republic) to recent times. This is followed by (3) the use of a detailed palaeoenvironmental record of the discovered lakes and their contexts mainly by geochemical and sedimentological methods. The dynamics of erosion and pedogenesis during climatic fluctuations at the end of the Last Glacial revealed far-reaching landscape changes at time scales of decades to centuries. For a thought-provoking comparison, although not yet the comparison measurable in an exact way, a landscape scale case study (4) of a change in the Anthropocene is included. Biotic homogenisation of forest understory vegetation over the last half century is shown. The changes can be attributed to eutrophication of the environment and light decline under forest canopy, being partly analogized to the processes at the Late Glacial and early Holocene. But these mostly anthropogenic changes, while important from a conservation perspective, do not yet seem nearly as far-reaching as the landscape changes described by previous studies of the Late Glacial period.

Together this thesis highlights the importance of a landscape-scale perspective for understanding the dynamics of nature.

Keywords

Anthropocene, Holocene, landscape ecology, landscape scale, Late Glacial, regional spatial scale, vegetation change

Abstrakt

Práce se zabývá dynamikou středoevropské krajiny. Zahrnuty jsou čtyři případové studie zaměřené na dvě klíčová období environmentální transformace: pozdní glaciál a antropocén. Všechny případové studie spojuje krajinná škála jako prostorové měřítko zkoumaných jevů, tedy nejen jako prostorový rozsah výběru vzorků, jak je rámcově popsáno v úvodu. Případové studie využívají disparátní kontexty a metody, což napomáhá přiblížení se tak komplexnímu fenoménu – krajině.

Zahrnuté studie se zabývají krajinou a vegetací posledního glaciálu, a to (1) srovnáváním pylových záznamů napříč ČR s využitím moderních analogií (zde z Jakutska), které ukázalo, že změna na přechodu pozdního glaciálu a holocénu nemusela být tak velká, jak se dosud předpokládalo. Alespoň někde mohly již během posledního glaciálu existovat lesy podporované táním permafrostu. Navazující studie (2) zkoumá, jak tání permafrostu, tzv. termokrasové procesy vedly ke genezi celé jezerní krajiny, jejíž dědictví na Třeboňsku nečekaně přetrvalo až do současnosti. Na to navazuje studie (3) využívající podrobného paleoenvironmentálního záznamu sedimentů objevených jezer s využitím především geochemických sedimentologických metod. Dynamika eroze a pedogeneze během klimatických výkyvů v pozdním glaciálu odhalila dalekosáhlé změny krajiny v časovém měřítku desítek až stovek let. Pro možnost srovnání, i když zatím nejde o srovnání exaktně měřitelné, je zařazena případová studie (4) zaměřená na změny na krajinné škále v antropocénu. Ukazuje biotickou homogenizaci vegetace lesního podrostu za poslední půlstoletí. Změny lze přičíst eutrofizaci prostředí a postupujícímu zapojování lesů, tedy procesům částečně analogickým procesům probíhajícím v pozdním glaciálu a na počátku holocénu. Tyto převážně antropogenní změny, i když jsou z hlediska ochrany přírody důležité, se však zatím nezdají být tak dalekosáhlé jako změny krajiny popsané předchozími studiemi v období pozdního glaciálu.

Celkově práce zdůrazňuje význam krajinného měřítka pohledu pro pochopení dynamiky přírody.

Klíčová slova

antropocén, holocén, krajinná ekologie, krajinná škála, pozdní glaciál, regionální prostorové měřítko, změny vegetace

Motto:

Nature! We are surrounded and embraced by her: powerless to separate ourselves from her, and powerless to penetrate beyond her. Without asking, or warning, she snatches us up into her circling dance, and whirls us on until we are tired, and drop from her arms. She is ever shaping new forms: what is, has never yet been; what has been, comes not again. Everything is new, and yet nought but the old.

J. W. Goethe
(beginning of a text attributed to J. W. Goethe,
transcribed by T. H. Huxley, 1869, to the first article in Nature journal)

Acknowledgements:

I would like to thank my family, my supervisor, colleagues, and the creative environment within Charles University in general for all the help, tolerance, and inspiration.

Declaration / Prohlášení autora:

Prohlašuji, že jsem předloženou práci zpracoval samostatně a uvedl všechny použité informační zdroje a literaturu. Nepředložil jsem tuto práci ani její podstatnou část k získání jiného nebo stejného akademického titulu. Artificial intelligence jazykové modely byly využity pro korekce Angličtiny v úvodu práce. Podíl na výsledcích u zahrnutých teamových spoluautorských článků je uveden v prohlášení zařazeném v práci.

Jindřich Prach

Contents

Introduction

Aims and outlines of the thesis

The aim of this thesis is to contribute to the understanding of the dynamics of the central European landscape. Landscape is a complex phenomenon that is viewed through investigation of multiscale processes across space and time. A more holistic understanding can be reached through the study of many disparate issues and contexts, although measurable comparisons between them is problematic and have often not yet been achieved. Therefore, the secondary aim of the present thesis is to take a small local step towards comparing past, mostly natural, and present, mostly anthropogenic, environmental changes. This is still unanswered question in both global as well as in local contexts and each regional study focusing on a different period will contribute a little. The included case studies shaw how changes in the distant and recent past have shaped the variability of the central European landscape in selected exemplary contexts with a focus on vegetation cover.

The thesis focuses on the alterations in overall landscape dynamics, vegetation cover, and its diversity at so-called regional or landscape spatial scale. The research territory encompasses approximately the current extent of the Czech Republic. This introductory part presents the landscape scale as a distinct and important perspective, where different processes play a role compared to smaller community-level scales or larger macroecological spatial scales. A brief introduction to the main changes in the central European post-glacial landscape follows, along with a review of the problems of temporal scales, different methods, changes in biodiversity, and applications of such knowledge in nature conservation.

The thesis is not focused on a specific period but examines landscape formation processes in different key periods of environmental transformation from the Last Glacial to the present (the term "Pleistocene-Holocene transition" in the title refers to the entire period from the Last Glacial Maximum to the Holocene rather than exclusively the very transition around 11,700 cal BP). The first three case studies deal with the Last Glacial period, mainly the Late Glacial as the beginning of the Pleistocene-Holocene transition. This period, approximately 16-10 thousand years ago, experienced climate amelioration and significant changes that served as a starting point crucial for the development of vegetation patterns in central Europe. The last case study focuses on changes in the last century - the Anthropocene. Together with the Late Glacial and Pleistocene/Holocene transition, the Anthropocene is a major environmental transformation worldwide shaping spatial patterns in the distribution of biota. Some analogues between vegetation changes in these two crucial periods are suggested. The case studies cover widely different contexts, leading to the use of different research methods and data sources.

Overall, the thesis attempts to provide a landscape-scale view of environmental change. This perspective is crucial for comprehending ancient environmental transformations as well as the anthropogenic changes of the landscape in the last century and is fundamental for understanding overall vegetation dynamics. Such a view is essential as well as for conservation practice, which tries to preserve past values, especially biodiversity, in a dynamically changing and increasingly exploited world.

Spatial scales

Patterns in nature are realized at different scales. Different processes, such as changes in vegetation cover or changes in biodiversity, framed by general landscape changes, are observed at different time scales (e.g. Barnosky et al. 2011, Mottl et al. 2021a), and equally important is that processes take place at different spatial scales (McGill et al. 2015, Vellend et al. 2017, Blowes et al. 2019). On one side are small spatial scales, i.e., where direct interactions between individuals play the largest role. With increasing spatial scale, we reach the field of community ecology targeting interactions between species and the traditional vegetation science targeting processes of coenogenesis (Chytrý 2012, Chytrý et al. 2007, 2009, 2011, 2013). At such spatial scales larger than one community and larger than one study site, the scale called landscape scale, regional scale, or meta-community scale begins (McGill et al. 2015). Interactions between different ecosystems, habitats, and species across a broad area play a role. Metapopulation dynamics and the effects of historical legacies are important pattern-generated processes. A view over longer time scales is needed (e.g. Delcourt and Delcourt 1988, Svenning et al. 2008). On the larger side of the gradient from small to large spatial scales, a continent-wide and global view is increasingly common (e.g. Giesecke et al. 2019, Mottl et al. 2021a and many recent meta-analyses). Here it is useful to distinguish between studies performed as continental/global meta-analyses of rather local phenomena (e.g. plot species richness change – Dornelas et al. 2014) and the studies that target an inherently large-scale phenomena (macroecology). However, an interesting regional pattern may emerge in large-scale studies. For example, recent models of vegetation cover for Europe during the Holocene, based on pollen data (Githumbi et al. 2022), showed an important large Hercynian conifer island for the younger prehistory and medieval periods. But such regional points of interest are usually beyond the scope of large-scale studies. Global and continent-wide studies deal with scales where the pattern is mainly generated by evolution - speciation and extinction, traditionally studied by macroecology.

Clearly, phenomena at larger scales cannot be described only as the sum of phenomena at smaller scales and vice versa. Each scale of view has its own specificities, its own appropriate methods, and research questions. However, a similar disjunction does not apply to the adequate association of the spatial scale with the temporal scale - it makes sense to study one spatial scale on multiple temporal scales (as this thesis aims to do), so it would also be possible to study what happens on different spatial levels in a clearly defined temporal scale.

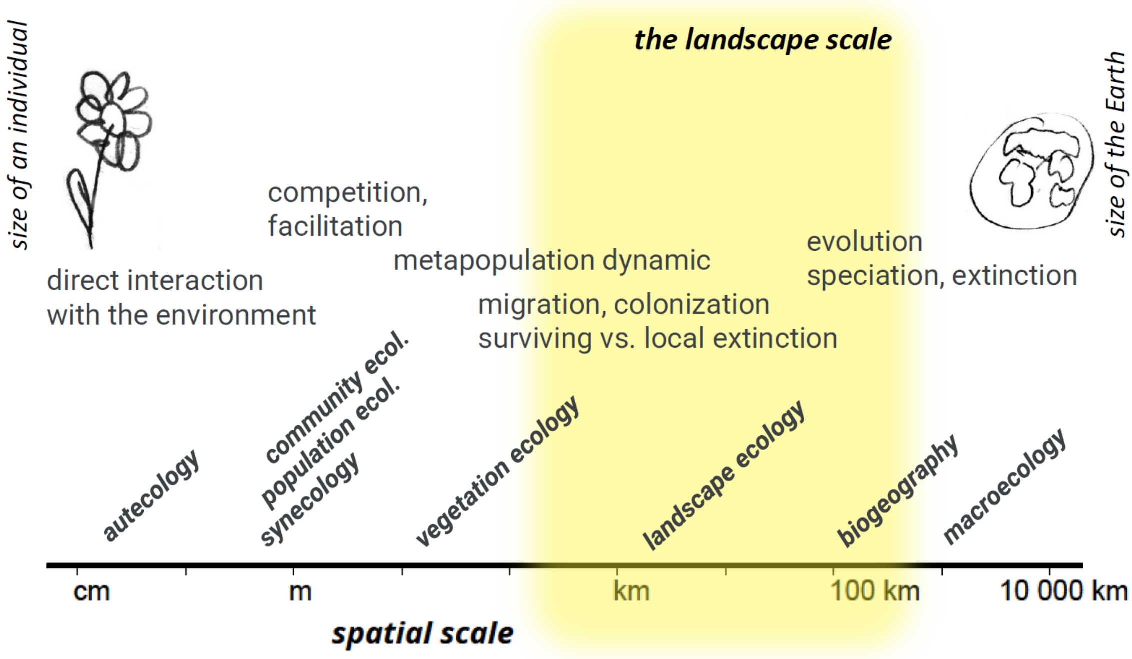


Fig. 1 - *The landscape scale specified in the scheme of logarithmic spatial scale of selected processes generating the pattern of species distribution and selected main disciplines of ecology.*

The landscape scale - the focus of this thesis

This thesis is focused on the landscape scale (fig. 1), which is understood here as a synonym of the spatial scale sometimes called the regional spatial scale or the meta-community spatial scale (McGill et al. 2015, Vellend et al. 2017). In the central European context (fig 2), this means phenomena over hundreds to tens of thousands of square kilometres. The landscape and regional scale of view were common in the classical era of geobotanical studies (see Ellenberg 1988; in our country, e.g. Domin 1904, Domin 1930, Mikyška 1968, Pišta 1982 – used as baseline data here in case study 4, Neuhäuslová ed. 2001 and many others). In recent decades, landscape scale research questions have become relatively less common in science, probably due to less exact experimental possibilities and less suitable data in common databases. Science in high-impact journals requires big, preferably global data on the one hand, or precise experimental and instrumental measurements on the other hand, and research of regional interest and practical applicability remains on the periphery of interest in relative terms.

However, the landscape-scale perspective is essential for studying the dynamics of vegetation cover. After a change (such as climate change or management change, e.g. Kolář et al. 2022), communities are formed from a species pool that is within a range of dispersal (e.g. Zobel 1997, Sádlo 2000, Roleček et al. 2015). Of course, when viewed from a geological perspective over larger time scales, species from more distant places become established over time or even speciate, but this is beyond the scope of this thesis. At a smaller and shorter scale of view, local factors play a role (when we stop mowing a meadow, dominant species selected from the already present species pool will prevail). However, the regional diversity in central Europe is largely generated by phenomena and processes at the landscape scale. Such important diversity is for example that there are remnants of fir forests in the Šumava foothills, wetland ecosystems with relict species in the Třeboň basin, extremely species-rich meadows in the White

Carpathians, or deciduous forests that are richer in the Křivoklát area than in the Brdy area in central Bohemia (and similar patterns obvious in the field; see also Divíšek and Chytrý 2018).

In palaeoecology, a landscape spatial scale is essential for understanding changes on the Quaternary time scale (Ložek 1973). In most studies, results from a single profile are often related to the surrounding landscape, but such studies could hardly be called landscape scale. However, studies directly focusing on landscape-scale questions also exist: studies that research and compare the same time interval in several sites in the landscape and interpret the context, differences, and similarities of the sites (e.g., Kuneš et al. 2008, Kuneš et al. 2009, Jamrichová et al. 2013, 2017, Abraham et al. 2016, 2023, Roleček et al. 2021, Kozáková et al. 2021; but see other regions with a long tradition of fine resolution palynology: e.g. van der Knaap et al. 2000, 2012, or Rösch 2013, Rösch et al. 2021, Theuerkauf et al. 2014).

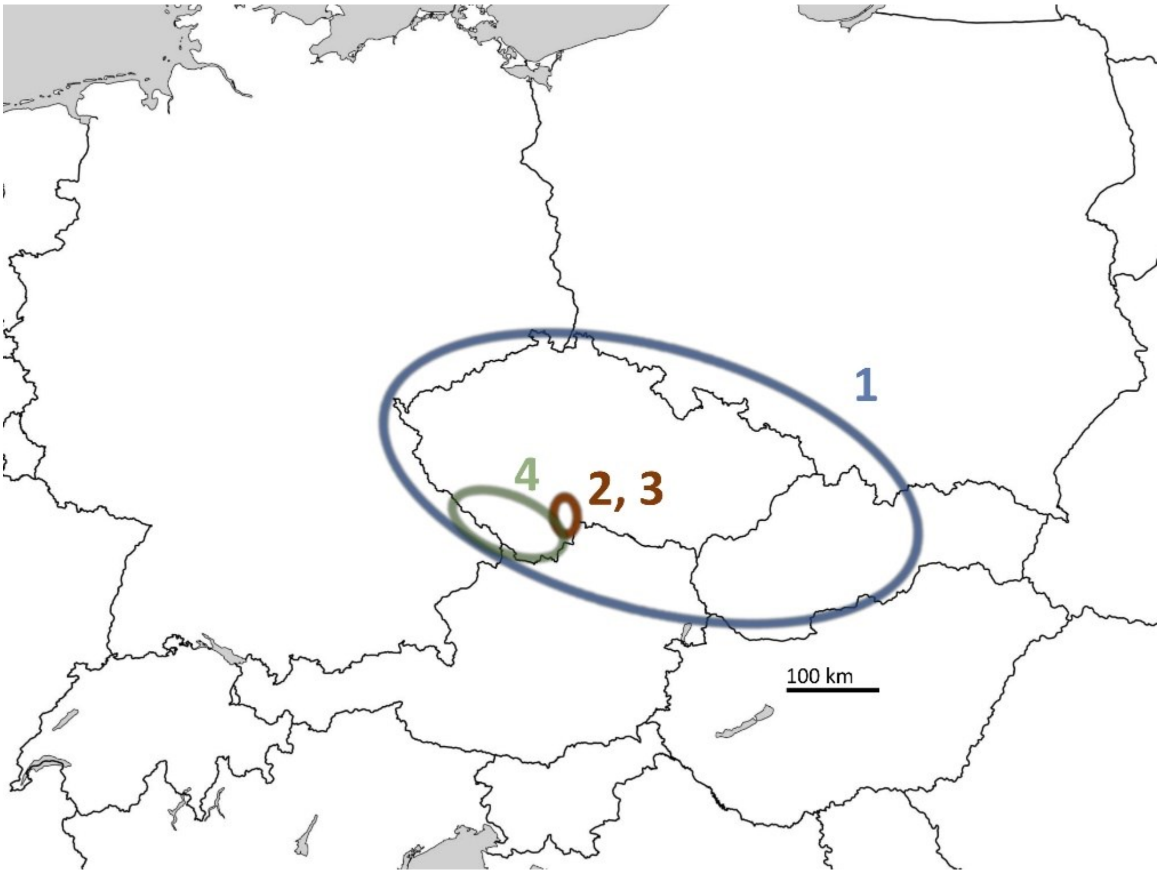


Fig. 2 *Spatial extend of source data (ellipses) used in the case studies (numbers) in this thesis on the map of Central Europe. Despite the extend of the source data differ, it illustrates that the main scale of questions targeted in this study spans tens to hundreds of kilometres in all four case studies (despite some extrapolation and generalisation are provided in the discussion of particular case studies).*

In other words, the landscape scale is related to the way of questioning, not only to the spatial extent of sampling. When a site is sampled (regardless of whether it is a palaeoecological profile for geochemical analyses, pollen etc., or a set of phytosociological relevés in one community) and even if a lot of sites are sampled/taken from a database and an average of it is presented, usually it is not addressing the landscape scale questions, but rather addressing a general pattern of local-scale phenomena. When the question is how and why one context differs from another, such as one part of the region from another, one hill or basin from another hill or basin, spruce forests from beech forests, etc., this is what could be called a question targeting landscape-scale phenomena.

Temporal scales

A similar division, as in the spatial scale, can be seen in the temporal scale. Phenomena and processes at the landscape scale need to be studied at adequate time scales (e.g. Delcourt and Delcourt 1988, Reitalu et al. 2014). Palaeoecology is both an exploration of the past per se and, through it, a significant contribution to understanding contemporary phenomena (e.g. Ložek 1973, Birks 2019). Thus, it contributes to planning contemporary applications (e.g. Willis and Birks 2006, Jackson and Hobbs 2009). Rates of change over different time windows are quantified and compared across time and space (Mottl et al. 2021b, 2021a), changes in different measures of biodiversity are obtained from both fossil data (Birks et al. 2016b, Šizling et al. 2016, Giesecke et al. 2019, Roleček et al. 2021) and, for the Anthropocene, from direct observations (e.g. Vellend et al. 2013, Jandt et al. 2022 and references therein and in the introduction in the case study 4). The comparisons quite consistently show the Late Glacial and Pleistocene-Holocene transition and the sub-recent period (Anthropocene) as the most significant periods of change. Therefore, these two periods are the focus of the case studies in this thesis. In general, studying longer time scales in the past may be useful as a reference for assessing current changes when we do not yet have observations on sufficiently long time scale for current changes.

When researching phenomena on long time scales, there are several problematic points. It should be considered that the temporal scale of a target phenomenon is not the same as the time span of a study or the time windows of observations. For a more detailed explanation in the case of palaeoecological studies: the palaeoecological record is usually sediment, which, in better cases, accumulates continuously. It is usually sampled and analysed at certain intervals (for analysing pollen, geochemical analyses, physical measurements, etc.) – Fig. 3a. A single sample (layer) from a core is, in fact, a mixture, i.e. something like an average, representing uncertain period of time (in practice, it might be tens of years). The interval at which the samples are taken determines the temporal resolution (in extreme cases, it can involve continuous sampling, usually used, for example, for quantification of microcharcoals in sediments). Thus, these represent differently wide "point" views at different time intervals (e.g. Moore et al. 1991). This inconsistent and unclear variability is partly compensated by binning samples over larger observational "time windows" in subsequent analyses (e.g. Birks et al. 2012, it could be 500 years - e.g. Abraham et al. 2016, Kuneš and Abraham 2017, Mottl et al. 2021a).

For some analyses, it is not the same whether individual samples represent a view over a year/several years or an "average" over tens or even hundreds of years. The former can be done in fine, ideally laminated lake sediments, while the latter is more common in central European contexts, for example, in the case of small peat bogs and forest hollows. Sometimes one faces attempts to make more precise interpretations than is possible from the nature of the sediment - typically in Czech local studies, where deep lakes are not present, and local peat bogs and fens are studied, including silt layers, alder hiatuses, etc., with limited funding and number of radiocarbon dates (see overview in Kuneš et al. 2009 and the PALYCZ database). Problematic contexts are difficult to distinguish in large-scale integrative studies. Such details about the sampling and the nature of the sediment are difficult or impossible to detect from databases. In common palaeoecological studies, it is not even the norm to communicate this issue regarding the temporal width of a single sample. Detailed depth-age models and sediment characteristics would need to be considered, and direct experience, along with a sampling method reflecting the characteristics of the sediment, is best. All these methodological problems complicate the consideration of phenomena on fine time scales using ordinary palaeoecological records. This is the reason why in case study 1 is interpreted the pattern in differences between sites rather than detailed changes over time. In case study 3 is used detailed and rather smoothly sedimented record for the geochemical and other analyses.

The raised problem of time window and resolution in typical palaeoecological studies is similar (but not identical and transferable) to the problem of spatial scale sampling in classical vegetation ecological studies. There are relevés, their size, their distances, and the extent of the landscape section where certain questions are addressed. However, in a contemporary landscape and in questions concerning spatial scaling phenomena, the issue can be better approached, for example, by using nested relevé design. The number of meters in space that a single vegetation relevé captures is obvious; however, the number of years covered by a single centimetre of a core is unclear, especially in inhomogeneous peat sediment.

Fig. 3. *a) Traditional and still common way of subsampling a palaeoecological profile. The individual samples from which subsequent analyses (e.g., pollen, geochemical) are obtained are millimeter to centimeter sections that integrate time periods that are often difficult to estimate. b) Laminated lake sediments provide a detailed palaeoecological record with the ability to capture short environmental fluctuations on time scales of years to decades. However, such fine sediments are rare in central Europe. The image shows a yet unprocessed short bottom part (about 5 cm section, see the scale on the left) of sediment with signs of lamination from the lake near Veselí nad Lužnicí, discovered during rescue archaeological research during the construction of a highway in the southernmost part of the lake basin (the basin described in case studies 2 and 3).*

The issue of time scales in this thesis

All case studies included in this thesis have a in common certain spatial scale, which is the landscape scale, as described above. However, in contrast, the included case studies intentionally cover a variety of periods, providing examples of how different phenomena at different times have contributed to the formation of the landscape. These periods are as follows for the individual studies: Case studies 1 and 3 - Late Glacial; Case study 2 - the Late Glacial with marked consequences for the recent landscape; Case study 4 - recent and sub-recent, i.e. specifically focusing on the Anthropocene. However, the disparate placement over time in the past doesn't confuse the time scale on which the targeted phenomena themselves take place. Case studies 3 and 4 target landscape changes occurring on the scale of decades up to a few centuries. This includes climate-driven changes in landscape and vegetation cover as read through the erosional dynamics in the Late Glacial lake basins (during the Bølling and Allerød interstadials, Younger Dryas, and the transition to the Holocene) in study 3, and vegetation changes resulting from complex changes in the Anthropocene over the last half-century (in our context obviously driven by management changes and landscape legacies more than by current climate change) in study 4. Both studies allow for a detailed focus down to decadal scales. Study 3 utilizes an unprecedentedly detailed palaeoecological record of lakes discovered in the study region of Třeboň basin (described in case study 2), while study 4 relies on direct observations in the contemporary landscape. Case studies 1 and 2 address phenomena that, by their essence, do not require a precise definition of time scales; they generally involve glacial phenomena that persist and shape the landscape even in later periods. The above-mentioned problems with temporal inhomogeneity in palaeoecological studies are partially avoided here by focusing on spatial patterns without delving into the detailed temporality of the described phenomena.

Specific identification of time scales for individual case studies

Table 0.1 – time scales targeted by individual case studies:

	years	decades	centuries	millennia	tens of thousands y.
Study 1					
time scale of the targeted issue				x	
the time extent of the study				x	x
time integrated by one sample		(x)	(x)	(x)	
Study 2					
time scale of the targeted issue				x	(x)
the time extent of the study				x	
time integrated by one sample		(x)	(x)	(x)	
Study 3					
time scale of the targeted issue		x	x	x	
the time extent of the study				x	
time integrated by one sample		x			
Study 4					
time scale of the targeted issue		x	x		
the time extent of the study		x			
time integrated by one sample	x				

List of complementary methodological approaches used to uncover landscape dynamics

The thesis includes research in disparate contexts and therefore it was appropriate to choose different methods. The methods both, overlap and complement what the methods say about the issues under investigation. The list of methods used in the case studies follows. For more details and references, see the methods section of individual case studies.

- Pollen analyses of fossil samples – in case study 1, fossil pollen samples were used for the research of the glacial landscape character; in case study 2 used for palynostratigraphical indicative dating of the lake origin; in case study 3, used for comparison and discussion of sedimentological analyses.
- Pollen analyses of modern samples – in case study 1, used to investigate the representation of larch-dominated vegetation in cold conditions in lake sediments and for assessing analogues for Last Glacial fossil pollen samples.
- Multivariate comparison (PCA, DCA) of fossil and modern pollen spectra - used in case study 1 to investigate which central European fossil samples are closer to modern samples from forested parts of Siberia and which to steppe.
- Analog matching (modern analogue technique) - used for quantification and statistical testing of the association of modern analogues to the fossil samples in case study 1.
- Mapping geomorphological features in the landscape:
    - field boring and digging
    - analyses of local maps: elevation model, detailed topographic maps, historical maps, aerial photographs both historical and current - land cover and indication by vegetation, geological maps etc. – Fig. S2 and Fig 6 in case study 2

  All used in case study 2 (and partly 3) for uncovering the former permafrost-generated basis of the current landscape in the form of lakes, sand dunes containing palaeosols, permafrost-related polygons and pseudomorph of thermal-contraction crack.

- Sedimentological instrumental methods dealing with lake sediments:
    - Geochemical (XRF - X-ray fluorescence measurements) - the elemental concentration of titanium (Ti), rubidium (Rb), strontium (Sr), iron (Fe), calcium (Ca), and phosphorus (P).
    - LOI, Loss on Ignition - difference in weight between the sediment dried at 110 °C and ash produced at 550 °C quantifies the organic fraction in the sediment.
    - δ15N, stable isotopic composition of nitrogen.
    - Granulometric analyses.
    - Rock-magnetic measurements.

  All used in case study 3 (and partly used in study 2) to uncover the landscape, ecosystem, and climate dynamics in the Late Glacial in our part of central Europe while researching newly obtained cores from the Třeboň region. Namely in order to detect changes in the lithogenic influx into the lakes and chemical weathering intensity in the catchments (XRF, LOI); for better assessment of the origin of the organic matter (δ15N used in selected part of Velký Tisý core); for detecting the dynamics of the coarse-grained input to the Velký Tisý lake (granulometry); for detecting erosion, pedogenesis and influx of terrestrial organic material (different rock-magnetic parameters)

All these measurements also help lithostratigraphic dating and the relative temporal correlation of the cores, as used in case study 2 and 3.

- Micromorphology – used in case study 3 to describe of the paleosols buried under sand dunes.
- Geophysical methods - electrical resistivity tomography – used in case study 2 in connection with hand boring to obtain the cross-section of the Veselí and Lužnicí infilled lake basin.
- Radiocarbon dating and depth-age modelling – used especially in case study 3 and 2 for dating the origin of discovered lake basins and dating newly obtained cores. Mostly previously published chronologies based on radiocarbon dating were used in paper 1 for selecting Last Glacial sections of the profiles from the PALYCZ database.
- OSL dating – used in case study 2 to dating of the sedimentary infill of a pseudomorph of thermal-contraction-crack.
- Vegetation plots, phytosociological relevés – used in case study 4 to record the plant species present and subsequently to assess the vegetation change between the approx. half century old and current survey.
- Non-metric multidimensional scaling (NMDS) ordination (on the Bray-Curtis dissimilarity matrix) used in case study 4 to visually compare vegetation patterns between the old and the new survey and permutational MANOVA to detecting and testing shifts in vegetation and shifts in vegetation heterogeneity.

Presented landscape scale studies framed by the broader context of key periods of central European environmental transformation

Although a complete description of the landscape development is not the direct focus of the thesis, it is useful to provide context regarding the central European landscape and environmental changes since the Last Glacial and during the Holocene as a framework for the case studies. Therefore, a basic description follows, including regional specifics of the part of central Europe on which the thesis focuses.

Landscape and vegetation of central Europe in the Last Glacial period

We still have limited knowledge about the nature of the landscape and vegetation during the Last Glacial Maximum (around 21,000 cal BP) and Late Glacial in central Europe, therefore this is one of the focuses of this thesis – case study 1, 2 and 3. In the eastern part of our territory, in the Carpathians and surrounding basins, the presence of forests (taiga, hemiboreal forests) with probably at least a small presence of temperate tree species has been documented for the MIS 3 and MIS 2 periods (e.g. Magyari et al. 2014).

Fig. 4. *The problem of the glacial landscape visualised by possible current analogues – (a) steppe (here in the southernmost Ural Mountains in the Orenburg region), and (b) larch taiga in Yakutia. At the first sight unexpectedly, the forested region (Yakutia) is much colder and has a more continental climate, but the permafrost there significantly shapes the landcover. Steppe elements are considerably present in both cases - see Stipa spp. in the foreground.*

However, such data are still missing in the Hercynian part of central Europe. Rather open landscape with prevailing steppe and tundra is assumed to have been the predominant land cover (Kuneš and Abraham 2017). Such environment is believed to have acted as a bottleneck for today's prevailing temperate species. However, this is still rather a persistent idea since older research (Firbas 1949, 1952, Jankovská 1980, Lang 1994, and others) rather than an exact result. See fig. 4. The openness of the landscape is clearly indicated by the deposition of loess (Ložek 1973), while the presence of tree species is suggested by the presence of charcoals (Willis and Van Andel 2004) and by rapid immigration of woody plants during mild climate periods (e.g., Jamrichová et al. 2017). The recent documentation of temperate woody species in the special context of hot springs in southern Moravia also suggests their presence (J. Hošek, P. Pokorný et al. in prep.). The ongoing debate about the nature of the glacial landscape and vegetation in central Europe is unlikely to be resolved soon, despite the case study 1 focusses this topic. More information on the possible existence of tree microrefugia in central Europe and the search for possible analogues of the glacial landscape is reviewed in the introduction of case study 1.

There is still an unresolved question about the extent of larch (*Larix europea*) forests during the Last Glacial period in central Europe. Some presence of larch is undoubtedly documented by macroremains and pollen data (Jankovská and Pokorný 2008, Dudová and Szabó 2022), but in general, larch is almost invisible using conventional methods. As demonstrated in the presented case study 1, all possibilities ranging from sporadic occurrence to dense continuous larch taiga could be consistent with the existing evidence.

The fundamental transformation of entire landscapes took place during the Late Glacial and the onset of the Holocene, in the period from approximately 16,000 to 11,000 cal BP – this is the focus of case studies 2 and 3. In several waves (Bølling, Allerød, onset of the Holocene), warming, increasing moisture, permafrost melting, and other processes connected with deglaciation occurred. Some parts of the landscape were overgrown by pine and birch (in the area of present-day Czech Republic, e.g. Jankovská 1980, Pokorný 2002, Petr and Novák 2014, and others, see also case study 1). This rather dynamic period was characterized not only by alternations of vegetation cover and changes between open and overgrown landscapes (as manifested, for example, by the erosion rates captured in lake sediments - case study 3) but also by the emergence of entire landscapes, as shown in more detail in case study 2. Climate change and the associated transformation of landscapes connected with several abrupt climatic oscillations during the end of the Last Glacial are a good parallel to today's climate change. Similarly, the increasing present anthropogenic eutrophication of landscape can have some natural analogues at the end of the Last Glacial. This analogy is applicable not only at a global scale but also within specific ecosystems and particular landscapes. Moreover, there are analogues in the formation of specific landscapes. For example, the ancient processes of permafrost melting in southern Czech Republic and the associated genesis of diverse landscapes that persist today (case studies 2 and 3) are similar to what is happening now in the permafrost melting environments of Siberia and Alaska (e.g. Kokelj et Jorgenson 2013).

The beginning of the Holocene as a relatively well-investigated period

For the early Holocene and later periods, the knowledge is much better, if compared to the Last Glacial period. Forests of pine and birch expanded in central Europe, although the role of larch is still unknown (but see Pokorný 2020). There was an increase in the proportion of spruce, oak, and gradually other temperate tree species, continuing until the Holocene climatic optimum –

fig. 5 and 6. This development has been described from many sites (summarized e.g. by Kuneš et al. 2009, Kuneš et Abraham 2017).

Especially during the middle Holocene, two distinct landscape development patterns become increasingly apparent: the cooler foothills and mountains with dominant spruce and later beech on one side, and the warm lowlands with oak and later anthropogenic habitats on the other. It can be expected that during the early and middle Holocene, at least some elements of the previous diverse mosaic of vegetation persisted at the landscape scale. This is suggested by the persistence of lakes in the South Bohemian landscape, as presented in case studies 2 and 3. Similarly, other features indicate the persistence of overall central European landscape diversity: grasslands, at least in dry warm regions (Kuneš et al. 2015, Pokorný et al. 2015), as well as treeless habitats in the mountains (Jankovská 2006, Carter et al. 2018), and possibly some less extensive grasslands in all regions (Abraham et al. 2016). The landscape diversity is also indicated by the long persistence of glacial elements (Pokorný et al. 2023). Already in this period, the Mesolithic era, humans likely contributed to the diversity of the landscape (Kuneš et al. 2008, Pokorný et al. 2010). We have recently documented the same in the Pilsen Basin (Čechura et al. 2022), although the Czech written paper primarily targeting local archaeologists was not included in this thesis.

Fig. 5. *An analogy to the early Holocene landscape in central Europe can be seen in the present-day southern Ural Mountains. The forests here consist of pine, birch, oak, lime, and other tree species, with patches of steppe vegetation on the southern slopes.*

Fig. 6 *a) One of the current islands in the pond Velký Tisý on the shore of the former lake, in the Třeboň region in the southern part of the Czech Republic (see case studies 2 and 3 for details). The vegetation here, dominated by pines and oaks, looks similar to the reconstructed Middle Holocene landscape cover. b) Mesolithic artefact found directly on the marked spot during archaeological field prospection.*

Neolithization at the landscape scale - more questions than answers and subsequent prehistoric periods

The aim is not to provide a textbook description of the development of vegetation, including all periodization-determining events such as 8.2 and 4.2 ka. Instead, let's briefly touch upon another interesting landscape-scale change, namely the onset of the Neolithic (although not further included in this work, it is an important period for comparison). The neolithization during the second half of the sixth millennium BC has been presented as a major transition in lowland landscapes in conceptual syntheses (Sádlo et al. 2005, Pokorný 2011). Quantitative analyses (Abraham et al. 2016) suggest a gradual increase in the proportion of grasslands and other light-demanding species. The spread of oak, as a light-demanding tree of cultural landscapes, was shown by charcoal analyses from archaeological contexts (Novák et al. 2021, Novák in Vondrovský and Chvojka 2021). The inconsistency between landscape scale vegetation reconstructions based on pollen profiles and those based on archaeological contexts emphasizes the importance of a landscape-scale perspective. Pollen profiles and other palaeoecological proxies typically come from wetlands and bogs, which are areas outside the main interest of the first farmers. In the areas with fertile loess soils in the warm lowlands, suitable environments for sediment deposition enabling pollen and other palaeoecological analyses are almost non-existent (with a few exceptions in specific contexts - Pokorný et al. 2015, Kuneš et al. 2015).

An interesting and still almost unexplored aspect is the potential greater than expected human transformation of peripheral landscapes around the core of Neolithic settlements. Neolithic and Mesolithic subsistence strategies apparently met in closely adjacent areas (Ptáková et al. 2021a, 2021b). Recently, settlements of the Linear Pottery Culture were discovered through archaeological prospection and excavation on fertile loess soils at several sites adjacent to the northern part of the Třeboň Basin, west of Veselí nad Lužnicí (sites Horusice, Mažice, Bukovsko - Vondrovský and Chvojka 2021). These sites are within the proximity of the lake basins described in case studies 2 and 3. The temporal overlap between the lakeside settlements, detected e.g. by charcoal layers in the sediment (Pokorný 2002, Pokorný et al. 2010), and the classical settlement of Neolithic (Linear Pottery - LBK) villages with longhouses is supported by radiocarbon dates (Vondrovský and Chvojka 2021, Ptáková et al. 2021b). In contrast to earlier assumptions from classical palynological studies (Jankovská 1980, Pokorný 2002) that interpreted partial changes in pollen spectra during the Neolithic period as local natural successions, interpretation shifts are slowly occurring with archaeological findings in the region. A synthesis across regions (Abraham et al. 2016) showed yet undiscussed increase in the proportion of *Quercus* and Poaceae pollen, even in the region of southern Bohemia, exhibiting a pattern similar to that in the Polabí region, specifically during the time window of the first farmers. A closer examination of the source data suggests that *Quercus* and Poaceae pollen occurred in profiles close to the Neolithic settlements - Borkovická blata (Jankovská 1980) and Švarcenberk (Pokorný 2002). Profiles further south into the Třeboň Basin (Jankovská 1980), farther away from fertile soils, do not exhibit such an increase. A more detailed study of this locally interesting phenomenon, again incorporating a landscape scale perspective, is currently being prepared, emphasizing the importance of a landscape-scale approach.

In the following long periods of agricultural prehistory, the gradual spread of beech, fir, and later, in some regions, hornbeam, continued. It remains unclear whether the pattern of the spread of these trees was directly forced by human land use, or if both was driven by climate or if it is only a temporal correlation.

Medieval change

Another major change in the central European landscape and vegetation, both qualitatively and quantitatively, is the well-known medieval colonization. This change was primarily caused by the expansion of settlements into the foothills and the intensification of arable farming in the lowlands (Sádlo et al. 2005, Kozáková et al. 2011, 2014, 2021, van der Knaap et al. 2020, Kolář et al. 2022). Although this period is not explicitly addressed in this thesis, the influence of the medieval landscape on today's vegetation is noteworthy. The decline of light-demanding species in the forest understory over the last century (case study 4) were probably largely a consequence of pastoral use of extensive landscape even in marginal and forested areas during the Middle Ages and Early Modern Times.

In connection with the fluctuating agricultural, especially pastoral, impact, the spread of silver fir in central Europe can be expected (Kozáková et al. 2011, Szabó et al. 2017). The consequences of such a time window for the expansion of the fir could probably have been observed more recently, as previously established fir stands have experienced fir dieback (Šamonil and Vrška 2007).

Another medieval legacy in current vegetation could be the relative stability of predominantly coniferous forests. This has been newly documented in the remote part of the Brdy Mountains in central Bohemia (T. Krofta, L. Petr, P. Kočár, P. Karlík, J. Prach, in prep.), which has been surprisingly minimally influenced by humans since before the medieval and early modern period. This is consistent with the generally higher coniferous forest cover in southwestern Bohemia (Kozáková and Danielisová 2020, Novák et al. 2021), contrary to traditional assumptions (Mikyška 1968, Neuhäuslová et al. 1998) that have been incorporated into conservation goals. Similarly, a recent local study of pond sediments from the Late Medieval and Early Modern periods indicated a consistently high proportion of pine in local forests on poor sandy soils on the border of central and western Bohemia (Prach et al. 2022; research report for the Nature Conservation Agency, not yet published as a standard article, and therefore not included in the thesis). This is contrary to the widespread idea that such pine stands are solely a result of modern forestry plantations replacing former "natural" oak and beech forests. Both of these examples represent important local issues similar to relict pine forests in northern Czech Republic (Novák et al. 2012; phenomenon locally called "tajga bezdězskaя" by J. Sádlo). Further research on these topics is underway.

Overall, the legacy of the medieval landscape may have a more significant presence in today's landscape than expected after several hundred years of forestry. This heritage is gradually disappearing due to ongoing management unification, which is probably one of the reasons of the heterogeneity change demonstrated in case study 4.

Anthropocene

Fig. 7. *Illustrative photo of the Anthropocene. The photo depicts the anthropogenic but still relatively diversified Czech landscape (Brdy foothills) and the intensive agricultural landscape after anthropocene intensification (southern Moravia). See also Fig. 5 in case study 4 and Fig S2 in case study 2 for an illustration of the same phenomena.*

The Anthropocene is a period in which humans have become significant agents of planetary change (Crutzen 2002). There is considerable debate about the start dates of the Anthropocene, ranging from prehistory (Ellis et al. 2008, 2013) to the 1960s. For the purposes of this thesis, let aside wide debates regarding whether to include the Industrial Revolution of the 18th and 19th centuries or even prehistory with the beginnings of agriculture in the concept of the Anthropocene. For simplicity, let consider the Anthropocene in the present context of this thesis to be approximately the period since the so-called Great Acceleration after the Second World War (fig 7).

When comparing changes on Holocene time scales, it can be summarized that overall change in the Anthropocene, in general, compared to, for example, the early Holocene, is still relatively small (Birks et al. 2016a, 2016b). However, the rate of change is high (Mottl et al. 2021a), fig. 8. Significant reconfigurations of biota at all spatial scales are occurring (e.g. Barnosky et al. 2011, Dornales et al. 2014, McGill et al. 2015, Blowes et al. 2019), resulting in the creation of novel ecosystems (Hobbs et al. 2009). Plant communities are good models for describing these changes (e.g. Vellend et al. 2013, 2017, Staude et al. 2020, Jandt et al. 2022). These changes are often referred to as unprecedented, but direct comparisons between very recent times uncovered by fossil sequences and the past are still lacking. Even less is known about changes in heterogeneity and beta-diversity (but see Šizling et al. 2016 using fossil data and Blowes et al. 2022 for recent meta-analyses). The changes in heterogeneity over the last half-century are explicitly addressed in case study 4 (see fig. 3 in case study 4 - p. 146). See also figure 11.

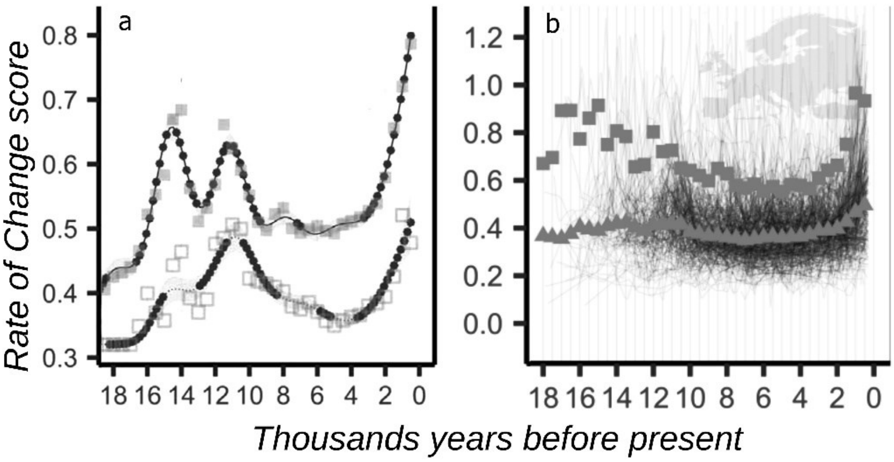


Fig. 8. *Graph from Mottl et al. 2021a (Science 372, p. 861). The graph illustrates the rate of change during the Late Glacial and Holocene, obtained from multiple pollen profiles, here for Europe (calculated over 500-year time bins; for the meaning of units and details, see Mottl et al. 2021a, 2021b). The graph serves to illustrate two aspects: a) The rate of change during the Anthropocene, i.e., the last millennium (no resolution available in the source data for the last century), is comparable to or even higher than the rate of change during the last deglaciation. b) Behind the nice wide-scale pattern, there is huge site-to-site variability – the similar measure of rate of change as on left but individual sequences are shown as lines in the background (behind the median and 95th quantile of the rate of change; Mottl et al. 2021a, Science 372 – Suppl. mat.). This highlights the need to use a similar approach in regional landscape scale studies, as also the author of this Science study suggests.*

Changes in diversity

Changes in diversity are one aspect of changes in communities and in the environment in general. In recent methodologically tractable research, biodiversity changes serve as a good proxy for overall change. Most often, changes in the number of species (alpha-diversity) at local scales are described. Both declines and increases in biodiversity are reported. Global meta-analyses of numerous local studies often show balanced average trends (Vellend et al. 2013, Dornelas et al. 2014). However, it is important to exercise caution in making overall judgments, as it often appears that locally important species of conservation importance are being replaced by more widespread invasive and expansive species (Jandt et al. 2022).

Once again, there is a spatial scaling problem (e.g., Blowes et al. 2019). Understandably, most studies have focused on local and at macroecological scales due to data availability. Much less is known about changes at landscape scales. Cumulative alpha-diversity, which expresses overall diversity at regional (landscape) scales, often increases because of the spread of non-native species (Vellend et al. 2017) - fig. 9a. However, when considering species identity and abundance in greater detail, it usually becomes apparent that local species decline and are replaced by more widely distributed species. Recent analyses of European vegetation plots have shown this pattern (Staude et al. 2020, Jandt et al. 2022).

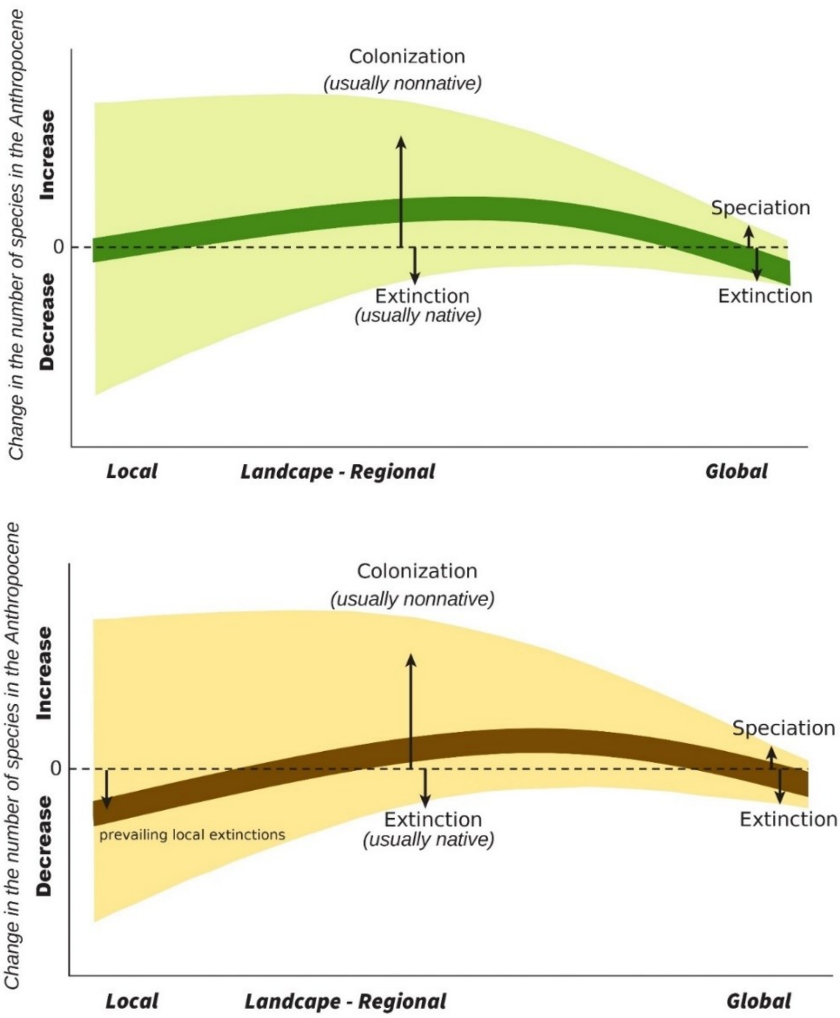


Fig. 9. *a) Conceptual scheme after Vellend et al. 2016 (Annu. Rev. Plant Biol. 2017, p. 578, Fig. 5), modified and simplified. The figure illustrates biodiversity trends in the Anthropocene, represented by the number of species in a given area at different spatial scales. The light green background shows the range of possibilities, while the dark region represents the average trend based on multiple individual studies. It should be noted that this representation seems to be influenced by the American context, as more recent European studies have shown significant species loss (see case study 4 and the papers cited there and Jandt et al. 2022).*

b) The same concept as above, which I have modified according to observations in central Europe (Anthropocene = the time period approximately since the 1960s).

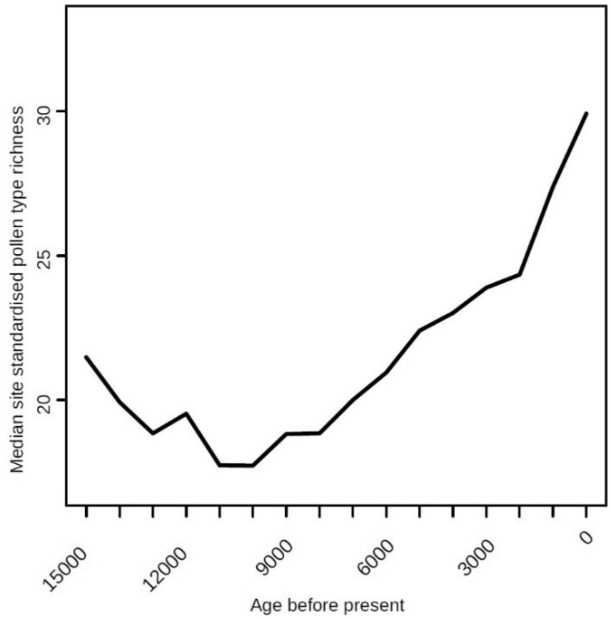
Given the primary landscape scale of interest in this thesis, beta diversity (heterogeneity) may be more important than species richness alone. Several studies in different landscape contexts have highlighted a decline in heterogeneity, case study 4 is one of them (see Introduction and Discussion in case study 4 for more references). The loss of heterogeneity appears to be a potential universal trend in the Anthropocene from a central European perspective (Prach 2020 in Pokorný et Storch eds.). However, the most recent comparison (yet in preprint, Blowes et al. 2022) suggests that even changes in heterogeneity (temporal trends in changes in spatial beta diversity) vary greatly across different contexts, with approximately equal evidence for homogenization and differentiation. Generalization is still unclear, as changes are context-dependent, emphasizing the need for further regional case studies.

Past diversity changes seen through palaeoecological data – a challenge

Interesting attempts have been made to uncover changes in diversity in the past through the examination of fossil sequences in paleoecology (van der Knaap 2009, Birks et al. 2016a, Giesecke et al. 2019). In the central European area, changes in both local diversity from individual profiles (Roleček et al. 2021) and heterogeneity between profiles (Šizling et al. 2016) have been demonstrated. These observed shifts appear to correspond to the major changes in land use practices in the central European landscape described above – fig 10.

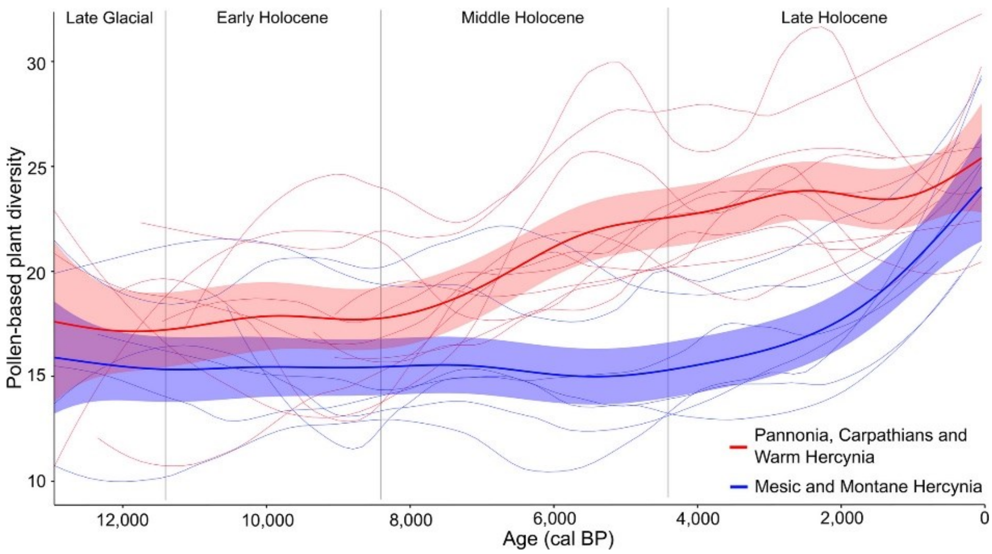
Despite this diverse literature emerged, in my personal opinion there are still serious methodological constraints when attempting to detect past diversity changes from fossil pollen data. To describe it simply, there is a challenge in distinguishing between 1) possible changes in the taphonomic context and 2) real changes in plant diversity in the landscape. Models will hardly solve the "two equations with two unknowns" when both the real diversity (and heterogeneity) of communities change over time, and the source area of pollen for a given profile is also likely to change. (The vegetation structure changed as follows: open glacial landscape – Late Glacial steppe patches – forested landscape of the Holocene climatic optimum - human-driven open cultural landscape - overgrown landscape after the decline of extensive farming/unified modern agricultural landscape). However, attempts have been made to address this issue as much as possible, such as by considering the proportion of tree pollen and demonstrating that it does not explain the observed shifts in diversity and heterogeneity (Šizling et al. 2016, Fig. S9), or by recalculating tree pollen based on pollen productivity values of the trees (Roleček et al. 2021, especially supporting information 6 there). Recently, methodological studies have emerged that address in detail the problem of the relationship between different levels of real vegetation and pollen diversity, using recent data (Abraham et al. 2022). Among other findings, they indicate that the pollen spectra somewhat reflect diversity, although the relationship appears to differ in forested and treeless landscapes. Attempts to compare past and present changes in diversity in specific landscapes could be the next step, but they are not explicitly addressed in the presented case studies.

a)



Giesecke et al. 2019, *Nat. Comm.*, *simplified*

b)



Roleček et al. 2021, *Journal of Biogeography*

Fig. 10. *a) The general pattern in the diversity of pollen types during the Late Glacial and Holocene in fossil sequences from Central and Eastern Europe after Giesecke et al. A gradual increase, which temporarily corresponds to anthropogenic landscape openness, is evident during the Holocene. While these general patterns make sense, but when simplified by looking integrated over large spatial scales, the fundamental differences that generate regional variability vanish. b) A similar trend investigated at the landscape scale by J. Roleček, V. Abraham, and colleagues (Roleček et al. 2021). Crucial insights for understanding the pattern of central European vegetation and its biodiversity emerge only when viewed at a proportionately smaller scale, the landscape scale. The diversity and its changes over time show very different patterns from place to place (lines in the background), with different patterns observed in mountain areas in the Hercynian part of central Europe (blue, where most diversity increases with medieval settlement) compared to lowland areas and Pannonia (red, where diversity increases with prehistoric agriculture).*

Methodological problems of comparison between past and present

Addressing the comparison of the extend and the rate of environmental change in the past and present is complicated by the different scales of traditionally disparate disciplines - palaeoecology and modern ecology, as discussed earlier in this thesis. In palaeoecological studies, the issue of which time window one sample unit covers is only indirectly and uncertainly estimated (e.g., Moore et al. 1991, Birks et al. 2015). Studies of recent contexts can be designed to target specific spatial scales. However, for sub-recent studies that examine changes over the past decades to centuries, research is once again constrained by methodological limitations, such as the availability of historical data. In vegetation ecology, a common approach is to compare old and contemporary vegetation relevés (as done in case study 4). It is also possible to infer more generalized changes from records of past occurrences of important species (e.g., herbarium records) and the disappearance of their localities, as is done in conservation applications. At the landscape scale, without distinguishing individual species, changes in recent centuries can be inferred by comparing historical maps (see case study 4 fig. 5 and case study 2 fig S2). However, all these contemporary methods are significantly different from paleoecology, which relies on a view through sediments.

One of the key methodological differences that complicates the direct comparison of paleoecological data and vegetation surveys is the nature of absences. In a vegetation relevé, the absence of a species implies its real absence (except for seasonal species and those present in subterranean organs but only occasionally visible, such as some orchids). In contrast, the absence of a species in a pollen (and macrofossil) sample does not indicate its absence in a community. Instead, the likelihood of detection is determined by factors such as its abundance, pollen productivity, the abundance and pollen productivity of other species, and taphonomy (or other complicating factors such as pollen durability, similarly applicable to macrofossils). At this level, a single fossil sample should be understood as a set of phytocenological relevés of a community that also randomly misses some present but rare species. To address this, rarefaction methods and various standardizations based on pollen productivity are used in practice (Roleček et al. 2021, Abraham et al. 2022, Birks et al. 2016b). Another possibility is to consider a larger level of organization, such as the landscape, although it may be challenging to describe precisely.

Thus, the case studies in this thesis primarily deal with diversity at the landscape level rather than focusing on individual species or their communities. This includes studying the forested vs. treeless character in case study 1, the proxies for erosion rates in the landscape in case study 3 (see fig. 11 and fig 3, 4 and 5 within case study 3). Despite the methodological challenges discussed earlier, the landscape emerges as the lowest possible level where statements from different time periods, contexts, and methods (including geological and sedimentological) can be integrated to some extent.

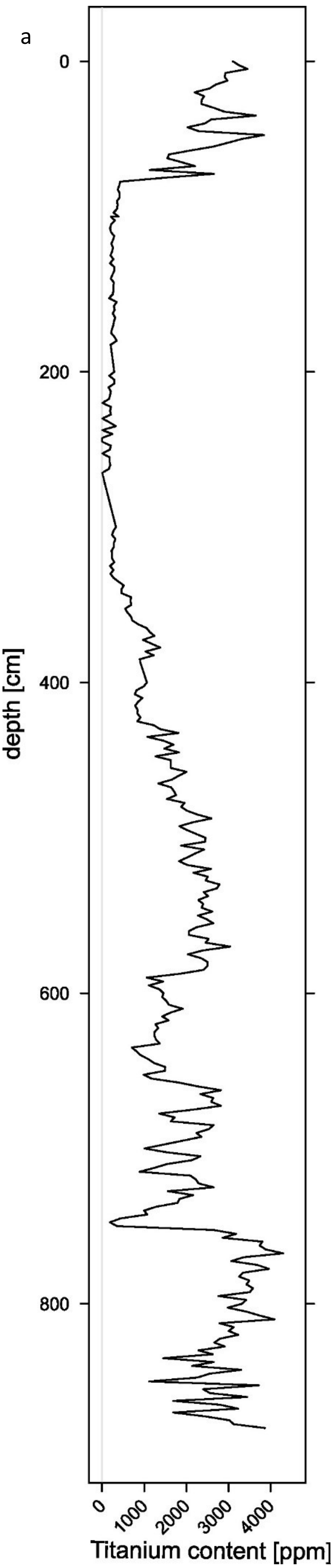
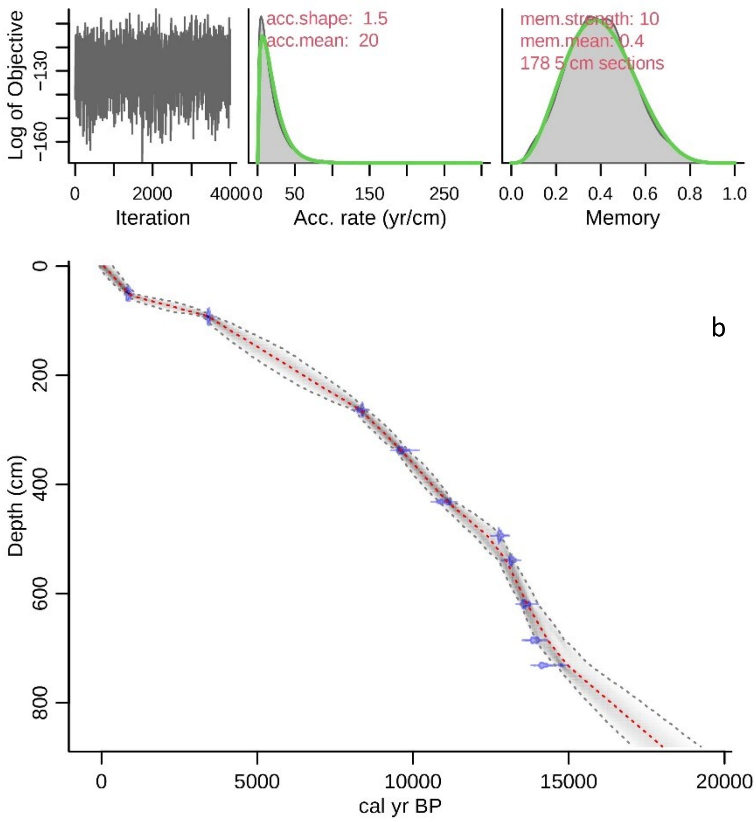


Fig. 11. a) *The titanium content in lake sediments measured by XRF spectrometry as a proxy for erosion rates at the Velký Tisý locality (core VTC in case study 2 and 3; the bottom part, the Late Glacial section at a depth of 400-880 cm, is published - case study 3, for the depths 0 - 400 cm unpublished data) and b) dept-age model (bacon) for the core.*

The figure suggests comparable rates of erosion, i.e. disturbance of the surface not stabilised by vegetation cover, during the climatically unstable periods of the Late Glacial (as discussed in case study 3) and in the Anthropocene, at about the uppermost 70 cm, roughly corresponding to the last millennium. Similar pattern can be seen in the data in other proxies, e.g. rock-magnetic measurements.

For methodological details, references, and a discussion of this proxy, see case study 3, for the description of lithology see fig 3 and fig 5 within case study 2, dates in Table 1 within case study 2 (see p. 80).

Interpretation must be made with caution. It cannot be argued that high erosion rates in the Anthropocene reflect the same extent of landscape change as during the times of the natural lake. There is an obvious uncertainty in dating, and the current pond differs from the past lake, resulting in different sediment deposition patterns - including larger surface area, different catchment due to artificial channels, water level fluctuations due to management practices (such as fish harvesting), and intensive fishing and connected bioturbation in recent decades, among other factors.



Remaining knowledge gaps and emerging directions of future research

Regional and local questions

Further local studies, both based on the study of sedimentary contexts and based on direct records of vegetation, are still needed. Local changes are highly dependent on specific contexts. These individual studies are valuable for both large-scale meta-analyses, where additional data points contribute to revealing general trends, and for regional interpretations and local applications, such as in nature conservation.

Palaeoecological studies directly investigating the vegetation change in the past should also focus on other important periods of landscape transformation (Kolář et al. 2022, Sádlo et al. 2005, in the central European context) such as, for example, on the neolithization of peripheral areas mentioned above. And, on the exploitation and possibly resilience of the marginal landscape during settlement expansion in the Bronze and Iron Age, which is so far rather understood as local and unique from anecdotic evidence (e.g., Dreslerová et al. 2020, Kozáková et al. 2021). Interesting questions about landscape and vegetation dynamics also remain in connection with medieval colonization. Written sources documented landscapes where medieval villages were established in previously uninhabited forest (e.g., on Tepelská plošina plateau in western Czech Republic and in the eastern České Středohoří Highlands - P. Meduna pers. comm.). For further research remains a question as how this sudden change impacted local vegetation and diversity, what is the origin of nowadays valued heritage of a diverse traditional cultural landscape (such as species-rich meadows), if such elements were present somewhere in the landscape context before colonisati7on or how slowly they took place in the new landscape. The results of such research would be applicable to today's dynamically changing landscape.

Comparison of the changes in the past and in the present

One of the biggest challenges for future research is to address the comparison of the extend and the rate of changes in the past and in the present. This could be possible only by bringing time scales of traditionally methodologically different palaeoecology and contemporary ecology studies closer to each other. This is not easy, e.g. recent global analyses (Mottl et al. 2021a) address the present only as a recent approx. 500 year time window and do not use any methods and data for the last century, when the changes are clearly highest in both aspects, rate and extend (e.g. Crutzen 2002). This gap could be bridged by applying:

a/ Palaeoecological studies with a temporal resolution of at least decades. This was shown possible e.g., in the Alps (van der Knaap et al. 2012). It seems possible in the contexts described in the case studies 2 and 3, dealing with the South Bohemian lakes. The fine record sedimented here at a rate of circa 20 years on average per 1 cm, which, when sampled in 2 mm slices (minimum technically possible), seems to indicate meaningful vegetation development on a decadal scale. I have tried this as a pilot study using the example context of the onset of the Younger Dryas, i.e., sudden cooling, in the lake sediment at Veselí nad Lužnicí. This was partly done together with attempts to find Laacher-see tephra (G. Kletetschka, D. Vondrák), but lack of capacity and grant funding to complete independent dating of the profile section did not led to presentable results yet.

b/Another direction of possible methodological convergence is to focus palaeoecological studies on (sub)-recent contexts. Preferably to the contexts already independently described by time series of vegetation relevés. This could be e.g., post mining sites like ponds on coal mining spoil heaps, ponds in abandoned villages in the borderlands, etc. This would make it possible to reveal what real vegetation change is reflected in the classical palaeoecological records. A pilot study in the context of the pond already reconstructed by the National Nature Conservation Agency (therefore, small founding was available) showed that it is possible to trace sediments where the last hundred years are covered by more than a meter of fine sediment with good preservation and readability of all useful proxy data (Prach et al. 2022). Some comparison could be done using sedimentological, geochemical proxies, used in case study 3 also for the subrecent part of the sediment from the same locality, former lake, and nowadays artificial pond – see fig 11. The titanium content in the sediment, a proxy for the erosion (see discussion of case study 3 for more details) shows similar increased values in recent centuries like during highest erosion events during lake formation in Late glacial and like never in the Holocene. But the dating there for modern age is unclear and there are other methodological uncertainties.

Another area of investigation, but an even more complex challenge, is to compare the biodiversity change in the present and in the past. This would be useful because lot of recent studies quantifies the biodiversity. Further rather methodological studies revealing the reflection of current diversity in pollen in a variety of contexts and regional settings are needed (Abraham et al. 2022). In this topic, I was partly involved in processing samples from moss pollsters collected on a transect (sampled for macroecological questions, A. Šizling, L. Juřičková, P. Pokorný and others in prep.) from Scandinavian tundra to taiga and temperate forest. Initial results comparing pollen spectra with the alpha diversity of vegetation relevés at the site and with the beta diversity of the landscape captured by the three vegetation relevés in the surroundings of each sampling point suggest that pollen diversity more reflects the absence of large pollen-producers at the sampling site rather than the real diversity or the landscape heterogeneity, but more data and further research about possible recalculation is needed.

Science for practice – landscape scale perspective mostly missing in nature conservation

The studies of landscape scale changes, both in past and present, are essential for practice. It is a basis for informed and meaningful nature conservation planning, defining restoration targets and setting thresholds for future sustainable management (e.g. Birks 1996, Willis Birks 2006, Jackson et Hobbs 2009, Socolar et al. 2016, Whitlock et al. 2018).

In the Czech Republic, the idea of reconstructed "natural" or "potential" vegetation (Mikyška 1968, Neuhäuslová et al. 1998) or forestry typology (e.g., Plíva 1991) is often adopted by practical applied disciplines - nature conservation, landscape planning, etc. as a target for individual areas. These are useful but problematic concepts (Boublík et al. 2007, Abraham et al. 2016). The second thing is that in practice it is often applied the assessment of naturalness vs. non-naturalness of habitats (Chytrý et al. 2010, Lustyk ed. 2023) and resulting priorities and objectives of natural protected areas (Ministry of the Environment of the Czech Republic 2019). For example, disturbances associated with, for example, soil erosion (as, although in the distant past, case study 3 has shown) are not taken into account. Indeed, in most cases, the concept adopted in this way probably somehow corresponds to the vegetation of a given site before intensification of management (a question that we leave aside for now is the meaning of term "natural" in a central European environment influenced by humans deeply since prehistoric times, i.e., earlier before spreading of some major tree species).

However, a generalised application could hide possible interesting local and regional variations. For example, meadows are commonly regarded as 'natural' and target vegetation (which is useful, even though it's obviously a human-maintained habitat). Whereas, for example, pastoral pine forests, which are in many places probably an older cultural habitat than meadows, and no less important for biodiversity, fall into the non-natural category (as pines planted by forestry in place of beech or oak stands). Similar problem is also occurrence spruce at lower altitudes, which is probably natural to some extent at least in wetlands, but in the zone of oak and beech forests usually all spruce stands are considered as unnatural plantations. The aforementioned coniferous forests (spruce, pine, silver fir) already before artificial planting in western, south-western and southern Bohemia (e.g., Brdy, Třeboňsko) or in the Bohemian-Moravian Uplands (Szabó et al. 2017) are similar problem. Only focussed local palaeoecological (especially stand-scale palynology) and historical-ecological research can reveal these and similar interesting local features in conservation plans and strategies. Palaeoecological outputs directly targeting conservation goals are emerging for the territory of the Czech Republic (e.g., Jamrichová et al. 2013, Szabó et al. 2017, Carter et al. 2018, van der Knaap et al. 2020, Roleček et al. 2020, Marešová et al. 2022, Prach et al. 2022) but often still miss the spatial and temporal scale necessary for local decision making. There is still a long way to proper application in practice. Better communication even of what has already been researched from palaeoecologists to decision-makers is needed.

Biodiversity conservation is relatively well established in the Czech nature conservation system. Protected species (by law) correspond at least to some extent to red lists that are corroborated by scientific approaches. Most occurrences of rare and protected species are protected as protected areas of various categories. The situation is worse with respect to heterogeneity, variability at the landscape scale (beta-diversity), although this aspect is no less important for successful conservation (Socolar et al. 2016, Blowes et al. 2022). This is what the case study 4 tries to contribute. In the environment of the Šumava and foothills, traditionally most efforts have been devoted to forest conservation, where the target is non-interventional natural forests. Active protection of meadows and pastures with the species-pools belonging to them is implemented only in spatially limited protected areas. The case study has shown that a significant part of the diversity of the understory of the forests consisted of species today considered as mostly grassland species pool, while half a century ago were relatively common in the forests probably as the legacy of former traditionally managed light-canopy forests. If we want to maintain biodiversity even at the landscape scale in the form of heterogeneity, it is not enough to protect the best forests patches as nature reserve, but it would be useful to restore traditional uses forest management such as grazing, collecting firewood and so on.

Similarly, the geomorphological landscape diversity uncovered by case studies 2 and 3 is only slowly becoming one of the explicitly defined conservation goals of the Třeboňsko Protected Landscape Area (Anonym 2017). Although both, the landscape mosaic where today's structures (ponds, peat bogs) unexpectedly relate to a 15,000-year-old landscape, and the relevant sediments as archives for future research, should be considered as one of subjects protected by the Protected Landscape Area.

Key results, general conclusions, and interpretations

Individual key results of presented case studies

- The first study shows that the prevailing general idea of a mainly treeless glacial landscape in central Europe may not be as certain as it had seemed. The study compares fossil pollen spectra from the central European Last Glacial period (up to the Pleistocene/Holocene transition) with recent pollen spectra from Siberia. The fossil records and contemporary analogues point to the possibility of existence of larch taiga forests in central Europe, which are almost invisible using usual palaeoecological methods but were likely present at least during the Late Glacial period in basins formed by unconsolidated bedrock and water-saturated permafrost. The glacial landscape of central Europe may, therefore had been spatially very diverse, including forested areas like those in current Siberia. Thus, the starting point for the formation of Holocene patterns in the distribution of biota may not have been just steppe-tundra, steppe, or forest-steppe, as the persistent 'textbook' idea still expects, but also an extensive larch taiga forest.

- The second study discovered tens of paleo-lake basins formed around the Late Pleniglacial – Late Glacial transition during permafrost degradation. It shows the significant impact of the Last Glacial period on the evolution of the landscape in at least some regions of central Europe. The former lake landscape was apparently diverse and dynamic both in space and time. The discovery of the long-term existence of a mosaic of natural aquatic and wetland habitats has far-reaching implications in the field of phytogeography and coenogenesis; the rich wetland vegetation of the Třeboň region is therefore not a new phenomenon since the time of the establishment of current artificial ponds in the Middle and Early Modern Ages, but a continuation of a similar landscape that has existed here for about 15,000 years. So, there was not only the unique Švarcenberk lake, known for decades, but dozens of similar lakes in the Třeboň Basin, and the glacial processes which generated the basis of today's landscape.

- Sediments of the aforementioned lakes and their context (third case study) provide an opportunity to explore the landscape evolution during the Late Glacial period of prominent climatic change. Fluctuations of the erosion processes and other proxies of vegetation cover during the Bølling and Allerød interstadials, Younger Dryas and the onset of the Holocene are shown at a rather fine scale of centuries to even decades. Observed changes have been correlated with the Older Dryas and the Intra-Allerød Cold Period which is probably the first detection of a rather strong impact of these rapid climate fluctuations on the ecosystems in the wider central-eastern European region.

- The fourth study deals with vegetation and landscape changes in the Anthropocene. As large-scale studies have repeatedly shown, the Anthropocene and the Pleistocene/Holocene transition are the two periods with the greatest vegetation turnover. Therefore, case studies from both periods are included in this thesis. Changes in landscape, vegetation and its diversity are described here in more detail - the study focuses on the changes in vegetation heterogeneity, i.e., beta-diversity. It shows that the fundamental change is the homogenization of vegetation - the loss of beta-diversity at the landscape scale. The study deals with the landscape mosaic of the central European cultural landscape, studied by repeated vegetation relevés after about half a century, using the example of the forest understory. The overall change here is still relatively small, obviously smaller than the changes observed by previous studies in the Late Glacial but increasing nutrient loads and mesophytization can have some analogues in the past.

General interpretations and factual context of the studies

- In all the studies non-trivial, mostly previously unexplored, and newly discovered insights into landscape changes were demonstrated. This was studied for both far-reaching environmental transformations: the end of the Last Glacial period and the Anthropocene, i.e. both two periods repeatedly show as the most significant periods of change within the current Quaternary climatic cycle by global analyses. These discovered insights are the erosion changes in the Oder Dryas and Allerød, the formation of the "lake landscape", possible smaller-than-expected changes around Pleistocene-Holocene transition because of forest present before, and the significant homogenisation in the Anthropocene.

- The effects of permafrost and its melting on the landscape and vegetation is one of the important and unexpected results of the thesis. This was shown in the first and second, and partly in the third study as well. Permafrost has probably altered the character of the periglacial landscape, not towards harsh tundra as assumed in earlier studies, but towards patchy taiga, by mitigating drought. The processes of permafrost melting also created landscape structures that still exist today and provide key natural archives which were previously unknown.

- The case studies are complementary in time scales. The first study covered a broad area and pooled data over a large time window, which allowed studying a difference between dozens of sites of different landscape and biogeographic contexts. However, it did not allow capturing finer temporal scales. The changes on the time scale of millennia, centuries or even decades were studied in detail in studies 2 and especially 3. The third and fourth studies both focus on the dynamics of exemplar landscapes during key environmental transformations on decadal to centennial time scales.

- The thesis does not provide an exact and measurable comparison between current and past changes in the studied landscape contexts. However, partial insights in this direction are suggested. The changes even at the decadal scales associated with climatic fluctuations in the Late Glacial period were substantial and reflected in the landscape at least through the erosion intensity. Measures of geochemical proxy data for erosion became increasing again in the Anthropocene. Changes in the Anthropocene, using the forest understory as an example, are relatively small and multidirectional despite increased eutrophication, acidification, and other influences. However, far-reaching impacts of anthropogenic environmental changes on ecosystems are known from other studies and other landscape contexts, thus further research is needed to make relevant generalisations.

- Implication for application in nature conservation - current local protection of the most valuable areas and species does not seem to be sufficient. Landscape structures with glacial origins and the lake sediments themselves should be included as objects of protection in the

Třeboňsko Protected Landscape Area. In the adjacent area, it has been shown that the observed heterogeneity loss in the Anthropocene is probably to a great extent caused by management unification. Together, it can be recommended to consider the heterogeneity of a landscape, the landscape history, and the heterogeneity of past management practices as conservation goals.

- Overall, the thesis demonstrated that an essential approach to understanding central European environmental transformations across time is emerging through the targeting of landscape-scale phenomena. This approach complements previous local studies on the one hand and macroecological studies on the other. The variation of different landscapes within the central European area, specifically regarding glacial vegetation, was exemplified in case study 1. Case studies 2 and 3 focused on the Třeboň region, revealing variations within multiple sites and contexts across the landscape, providing insights into the genesis and dynamics of the landscape. Finally, case study 4 compared multiple sites and contexts (here multiple vegetation types) across the landscape and revealed a phenomenon that is undetectable at the local scale - biotic homogenization in the Anthropocene.

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Author contribution statement

Well-hidden forests? Modern pollen spectra from central Yakutia (E Siberia) contribute to the interpretation of the Last Glacial vegetation in central Europe

Jindřich Prach, Jan Hošek, Adéla Pokorná, Kristýna Hošková, Petr Pokorný

(after revision in Folia Geobotanica)

JP (~80%) had the initial idea, planned the study, analysed and interpreted the data, and wrote the manuscript, PP analysed the recent pollen, all authors contributed to the presented ideas and editing of the manuscript.

Buried Late Weichselian thermokarst landscape discovered in the Czech Republic, central Europe

Jan Hošek, Jindřich Prach, Marek Křížek, Petr Šída, Piotr Moska, Petr Pokorný

2019, *Boreas*, *48*(4), 988-1005.

JP (~25%) leaded most of the field work and discovered the scattering of most of the lake basins across the landscape, cooperated on laboratory work and some geochemical proxy measurement, commented the manuscript. JH leaded the research, the writing, performed and interpreted most of the geochemical analyses, prepared the figures, PP and PŠ had the original idea and cooperated on all stages of the work. All authors contributed to the editing of the manuscript.

Late Glacial erosion and pedogenesis dynamics: Evidence from high-resolution lacustrine archives and paleosols in south Bohemia (Czech Republic)

Jan Hošek, Petr Pokorný, Jindřich Prach, Lenka Lisá, Tomáš Matys Grygar, Ilja Knésl, Jakub Trubač

2017, *Catena* 150, 1, 261-278.

JP (~15%) leaded most of the field work and discovered some of the lake basins, cooperated on laboratory processing of some geochemical measurement, JH leaded the writing, performed and interpreted most of the geochemical analyses, prepared the figures. All authors contributed to the editing of the manuscript.

Landscape-scale vegetation homogenization in Central European sub-montane forests over the past 50 years

Jindřich Prach, Martin Kopecký

2018, *Applied Vegetation Science*, *21*(3), 373-384.

JP (~80%) designed the study, resampled in the field all plots, wrote the manuscript. MK advised the study design, coordinated the statistical analyses and cooperated on manuscript writing.

Supervisor: Petr Pokorný

case studies

Last Glacial as a still unclear "starting-point" for central European communities

Yakutia, from expedition to the Glacial period.

case study 1

Well-hidden forests? Modern pollen spectra from central Yakutia (E Siberia) contribute to the interpretation of the Last Glacial vegetation in central Europe

(after revision in Folia Geobotanica)

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Abstract

The landscape of central Europe is considered to be dominated by steppe, forest-steppe, or tundra during the Last Glacial. This classical view is mostly based on the pollen records. However, as the pollen production and taphonomy during the cold periods are largely unknown, modern analogies of past landscapes need to be involved to provide more plausible vegetation reconstructions. Here we performed pollen analyses of recent samples from small lakes in Yakutia, eastern Siberia, a cold region where larch taiga forest is maintained by water from cyclically melting permafrost. We compared the pollen samples using multivariate (PCA) and Analogue Matching technique with 842 fossil pollen samples from central Europe dated to MIS3-MIS1 (ca 35-11.7 ky BP). We have shown that the non-arboreal pollen proportion is around 50% in the lakes within Yakutian forested landscape, while such proportions have been interpreted as an indication of forest-free landscape in European fossil records. Some Central European fossil samples are more similar to samples from present-day Yakutia than to the South Siberian steppes so far considered as an analogy, this is especially true for samples from areas on unconsolidated bedrock with water-saturated permafrost from the Late Glacial, Bølling–Allerød interstadials. Together, we advocate the idea of extending the so-far interpretations of past landscapes; the fossil pollen might not only reflect steppe-tundra vegetation, but, in addition to that, at least the Late Glacial pollen samples from central Europe may reflect landscape forested by "invisible" larch with spatially limited steppe patches like the one found in modern Yakutia.

Keywords: pollen analysis, modern analogues, *Larix*, Late Glacial, vegetation history

Introduction

A nearly treeless steppe, or a steppe-tundra, has been the long-established reconstruction based on the fossil pollen records of the Last Glacial Maximum (hereafter LGM) and Late Glacial in central Europe (Firbas 1949, 1959, Frenzel 1968, Lang 1994). Although different interpretations have emerged along with further pollen evidence (e.g. Rybníčková and Rybníček 1991, Pokorný 2002, Jankovská and Pokorný 2008), the traditional "textbook" steppe-tundra concept still circulates among academics. This concept is mainly based on the proportion of arboreal vs. non-arboreal pollen in central European LGM and Late Glacial samples. Such proportion is usually between 1:1 and 5:1, respectively, but varies considerably through time and between sites.

Various summarising but contradictory hypotheses on LGM and Late Glacial vegetation cover in central Europe have been proposed in the last decades (e.g. Willis and Van Andel 2004, Birks and Willis 2008, Svenning et al. 2008, Tzedakis et al. 2013). The most recent summary of the vegetation history of the Czech Republic (Kuneš and Abraham 2017) supposes coniferous taiga forests in the Western Carpathians and a hypothesized steppe, steppe-tundra, or forest-steppe in the current Czech Republic in the LGM and Late Glacial. Nevertheless, such interpretation of the pollen evidence is still problematic, mainly due to the fact that the pollen spectra composition is not a straightforward reflection of the regional vegetation; pollen taphonomy may play a crucial role.

There are still at least three problematic points hypothesising the nature of the central European glacial landscape and vegetation: the search for a possible modern analogy, the study of the pollen taphonomy, and the more specific problem concerning the probable occurrence but apparent 'invisibility' of larch (*Larix* spp. div.) in pollen samples. A considerable number of studies have shown the potential of modern vegetation analogues to partially overcome the problems connected with the interpretation of the fossil record. Up to now, the dry and cold areas of southern Siberia were considered to be the best analogy for the central European LGM and Late Glacial periods (Frenzel 1968, Kuneš et al. 2008, Magyari et al. 2014, Chytrý et al. 2018). The climate, species pool and vegetation are all features that have been found at least partly analogical (e.g. Horsák et al. 2015, Janská et al. 2017, Chytrý et al. 2018). But in terms of such analogues, some issues still remain questionable. These include differences in the physical parameters of the compared regions - the landscape of southern Siberia has mostly a high-mountain character, whereas a noticeable part of central Europe includes flat plains and basins formed in unconsolidated, water-saturated, clayey bedrock. In central Europe, permafrost was widely present during the LGM (Žák et al 2012, Vandenberghe et al 2014). This permanently frozen ground extensively shaped the local geomorphology and hydrogeological settings (Křížek et al 2018, Hošek et al. 2019) - and, consequently, also shaped the vegetation. One further aspect complicating the possible analogy is the long-term anthropogenic pastoral impact and connected landscape transformation in some southern Siberian areas. We therefore added to this study a Yakutian modern pollen dataset for the comparison.

The taphonomy, which differs through time and space, is another huge problem connected with the interpretation of a fossil pollen records (e.g., Birks et al. 2016). Therefore, when considering analogues to the Last Glacial, the need arises for studies that include modern pollen spectra from similar taphonomy, i.e., areas under a continental climate, and samples from lakes and wetlands. Commonly used models dealing with pollen dispersion (Sugita 2007) are parameterized using recent climate-vegetation systems (e.g. windy NW Europe, Trondman et al. 2016). These methods consider a relatively spatially extended area from where the pollen enters the sedimentation basin. This is probably the best solution for a Holocene vegetation reconstruction (e.g. Abraham et al. 2016) in a situation much similar to current natural conditions, but they could hardly be sufficient in the case of the more continental Last Glacial climates. Previous studies that have focussed on modern pollen–vegetation relationships from southern Siberian continental mountain regions (Pelánková et al. 2008, Pelánková and Chytrý 2009) have used moss pollsters and topsoil samples for extracting pollen, while fossil samples from European sites have come from lacustrine sediments or peat. Here, we present a study of modern pollen spectra from small lakes within the continental region – an approach that was still missing.

One particular problem is the question of the larch tree and its peculiar pollen-vegetation relationship. The larch *Larix spp. div.* (including related species *L. decidua, L. sibirica,* and *L. gmelinii)* is usually considered a tree which formed glacial forest patches in central Europe (Willis and Van Andel 2004, Jankovská and Pokorný 2008) and which now form vast larch taiga forests in far east Siberia (Troeva et al. 2010, Schulte et al. 2022). However, it produces much lower quantities of pollen than other arboreal species and has been rarely detected in the European pollen records (Jankovská and Pokorný 2015, Šolcová et al. 2020, Dudová et Szabo 2022). Also, concerning macrofossils, the situation is not much better. Research on fossil wood and charcoals does not usually provide a solution of this problem, since larch and spruce wood anatomy is similar, which has resulted in the use of a *'Larix/Picea'* compound category (e.g. Opravil 1980, Willis and Van Andel 2004, Nerudová et al. 2016). Findings of plant macrofossils from the Last Glacial period in central Europe are rare in general, but importantly where there are preserved macrofossil spectra in some such old peat, these often include larch cones and twigs – for example, on the locality in the current city of Prague, Praha–Podbaba, or sites in the Western Carpatians (Jankovská and Pokorný 2008). To summarize this point, the cover of larch in central European LGM and Late Glacial periods remains largely unknown and all possibilities - between sporadic trees and dense larch forests - can be consistent with the evidence obtained so far.

These three problematic points (i.e., a modern analogue, pollen taphonomy, and larch 'invisibility') have led us in this study to focus on central Yakutia as a potential analogue of some characteristics of the LGM and Late Glacial periods in central Europe. We propose that this region could be relevant as an alternative to those analogies previously suggested in southern Siberia (Kuneš et al. 2008, Chytrý et al. 2018). Central Yakutia is very cold, dry, and climatically continental, but widely forested. The main vegetation types that were previously suggested as analogous to the central European LGM and Late Glacial in southern Siberia are also represented here. However, these vegetation types in central Yakutia occur here in very different proportions and in a different kind of mosaic – the larch taiga is a matrix of a vast flat landscape and patches contained within it, like 'islands', containing lakes, wetlands, steppes, and meadow-steppes (Mirkin et al. 1985, Troeva et al. 2010).

We consider central Yakutia to be a relevant analogy for several reasons. First, the occurrence of the small lakes and wetlands enable a comparison with the sites providing a fossil record in Europe. We therefore consider this analogy to be especially strong in terms of pollen dispersal and pollen taphonomy. Nevertheless, this analogy is considerably weaker in the case of colder climate (Janská et al. 2017), as well as the overall poorer species pool (Horsák et al. 2013) and details in vegetation composition (Chytrý et al. 2018). Secondly, the presence of permafrost shaping the landscape is also an advantage for the analogy. Previously, permafrost was considered to be a limitation to tree vegetation (Willis and Van Andel 2004, with further literature) but in a continental climate, where drought is the limiting factor, the case is just the opposite: in summer, the upper-permafrost active layer melts, making the water available and thus supporting tree vegetation (Schulte et al. 2022). This is the situation in central Yakutia nowadays. Here, the flat regions on the deep permafrost (called the Yedoma complex, Iijima and Fedorov 2019, Ulrich et al. 2019) are densely forested, while slopes and regions more to the south are more open in character (Troeva et al. 2010). Thus, we propose that central Yakutia is an ideal model landscape for testing the relationship between forest cover and its representation in pollen spectra in small lakes under a continental climate and permafrost conditions.

In this study, by focusing on central Yakutia, we fill the knowledge gap between studies of modern analogues that have been developed in the steppe regions of southern Siberia (e.g. Pelánková et al. 2008, Pelánková and Chytrý 2009) or in northern Siberia, where northern taiga and tundra vegetation lack steppe elements (see e.g. Clayden et al. 1996, Tarasov et al. 2007, de Klerk et al. 2009, Klemm et al. 2013, but see Katamura et al. 2006 and Müller et al. 2010). Specifically, our aims are the following:

1) To obtain modern pollen spectra from small lakes within the larch taiga forest with steppe and meadow patches to find out the arboreal pollen / non arboreal pollen ratio and to compare this ratio with the site characteristics, especially the proportion of forest / non-forest vegetation within a radius of 1 km around the sampling points.
2) To compare the data from the Czech Quaternary Palynological Database (PALYCZ) and the data from central Yakutia in order to found out which sites from central Europe provided fossil pollen that appear to be comparable to modern pollen spectra from central Yakutia; and to compare this with published surface pollen samples data from southern Siberia that have been used as an analogy to glacial central Europe in a series of previous studies.
3) To compare Siberian modern pollen spectra with a newly obtained pollen record in the Czech Republic (site Dračí díra), covering the time period 9600 – 17000 years BP, in order to identify the time when the central European fossil pollen spectra are most similar to central Yakutian modern ones.
4) To uncover the consequences of all these comparisons for the interpretation of central European Last Glacial vegetation.

Material and Methods

Modern pollen spectra from central Yakutia

We chose a territory in central-eastern Siberia, central Yakutia (see map on Fig. 1a). This flat (ca 100 x 200 km) area lies by the Lena River east of the city of Yakutsk. Central Yakutia is today a unique area on Earth, located only at 62° latitude and about 150-250 m asl, but where the landscape is determined by the presence of a deep and continuous permafrost (Iijima and Fedorov 2019). In addition to this, it is the most northern occurrence of a landscape covered by dense taiga forest as the prevailing vegetation type, but with patches of dry steppes and meadows (Troeva et al. 2010).

The occurrence of lakes is a crucial feature for testing questions concerning pollen taphonomy. On a spatial scale of hundreds of kilometres, central Yakutia is a relatively homogeneous and largely forested landscape. But within the forest, there are basins that were originally generated by a selective melting of the permafrost (e.g. Ulrich et al. 2019) – a geomorphological structure called an *alas*, a word from the indigenous Yakutian language that has come to be an international geomorphological term; – see photo on Fig. 1c. Thousands of these basins, usually containing small lakes, are scattered across the landscape. These patches contain vegetation of great variability on spatial scales of tens to hundreds of metres: each basin usually contains a lake and wetlands on the bottom and a meadow and steppe belt around the lake. Steppes dominated by *Artemisia* and *Stipa* usually occur here on south-facing slopes only a few meters high (for details about the vegetation, see Mirkin et al. 1985, Troeva et al. 2010; for details about the origin of alases, see e.g., Katamura et al. 2006, Ulrich et al. 2019 and references).

Together, 12 such basins containing a small lake were chosen for our study (Table 1). The field sampling was carried out during august 2016. In each of the lakes we sampled a few upper centimetres of the lake sediment. These samples were then treated by a standard pollen preparation using 10% KOH, HCL, HF and acetolysis (Erdtman 1943, Moore et al. 1991). Pollen analysis was performed using a light microscope 400x and standard pollen identification literature (Moore et al. 1991, Beug 2004). At least 500 pollen grains (total terrestrial sum) were counted for each sample.

We measured the extent of the lake and the proportion of forest vs. grassland vegetation in the 1 km surroundings (i.e., 1 km radius) of the sampling point using visually-interpreted aerial photographs available at the website https://yandex.com/maps. In the field we obtained a species list of all vascular plants near the lake banks up to its approx. 100 m surroundings to quantify the local plant diversity. More detailed field vegetation mapping of the surrounding of each site was impossible due to technical reasons.

Table 1. Localities of the lakes in central Yakutia, Siberia, where the modern pollen samples were collected.

Locality field number (order in Fig. 2)	Latitude	Longitude	Lake water surface area [ha]
1	62.0700	130.5740	2.72
2	61.8823	130.8377	2.92
3	61.8829	130.8263	2.53
4	61.8810	130.8279	1.91
5	61.8499	130.6770	0.07
6	61.8507	130.6734	0.04
7	61.8385	130.6056	7.24
8	61.8436	130.5702	0.28
9	61.8210	130.3560	0.04
10	61.8167	130.3370	3.27
11	61.8102	130.2627	0.08
12	61.8077	130.2453	0.5

Fossil dataset from central Europe

We selected data from the PALYCZ pollen database (Kuneš et al. 2009). For our comparison, we took layers considered to be older than the Pleistocene/Holocene boundary (11700 BP) according to published chronologies. Together, we used 842 individual pollen assemblages from 47 sites (Fig. 1c).

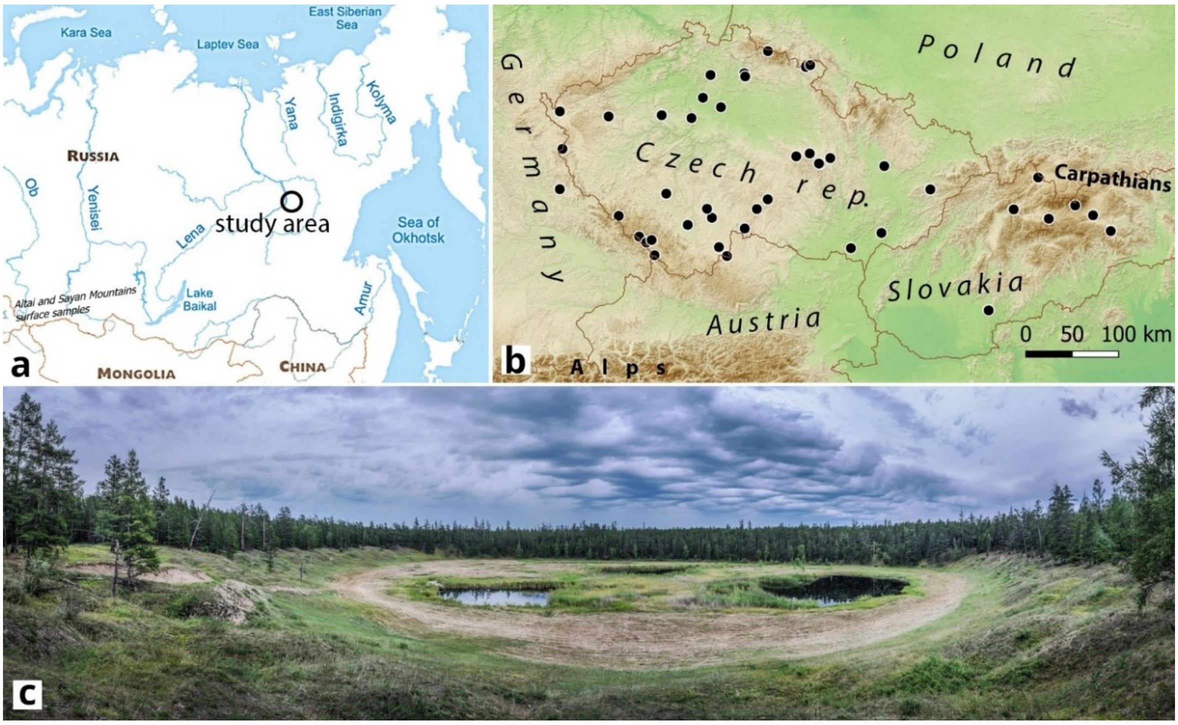

Fig. 1. – *The area under study: (a) - schematic map of the position of central Yakutia, Siberia, where pollen samples from recent lake sediments were taken. (b) - the positions of central European localities from the Czech pollen database where fossil pollen spectra were available for comparison with the modern Yakutian ones. (c) – a typical lake basin in central Yakutia surrounded by a narrow belt of meadow and steppe vegetation in a matrix of larch taiga forest.*

The Late Glacial pollen assemblages used in this study are, in most cases, found at the lowermost layers, just below the Holocene sequences. We decided not to use modelled chronologies from PALYCZ as linear time scale. For such old phases the chronologies are too unreliable and hypothetical because of unknown sedimentation rates, probable hiatuses, etc. while dealing with the bottom layers of Holocene peat profiles, dated only as a prolongation of the Holocene depth-age models (perhaps with the exception of Švarcenberk lake, here separately discussed locality Dračí díra and Santovka in Carpathian-Pannonian boundary). Therefore, we used the chronologies only to set up the threshold Pleistocene-Holocene boundary to select a batch of glacial layers. In general, as a matter of principle, we refuse to use an already imprecise model as an input to another model and pretend that it gives us accurate results. A few older but poorly dated sequences were used as well – namely pollen assemblages from the LGM (MIS2) and MIS3 periods from the sites Šafárka and Jablůnka (Jankovská et al. 2002, Jankovská and Pokorný 2008) and Bulhary (Rybníčková and Rybníček 1991, 2014).

The altitude over all used sites ranged from 150 to 1500 m asl. The Late Glacial time period (14 – 11.7 ka), containing 340 fossil pollen assemblages from 43 sites, was the best covered by the available data. The 29 -14 ka time period (LGM; MIS2) was covered by 447 assemblages from 22 sites. The 57-29 ka time period (MIS3) was covered by 43 assemblages from 4 sites. For further details to the sites, see PALYCZ database - https://botany.natur.cuni.cz/palycz/ (Kuneš et al. 2009) and references therein.

Besides the database, we used our original pollen data from a recently analysed key site continuously covering the end of the LGM and the entire Late Glacial. This site, Dračí díra, is a small infilled lake of an area approximately 0.2 ha located in a sandstone area Český Ráj in the northern part of the Czech Republic (50.5486N 15.1903E, 333 m asl). The lake, created by a landslide, has provided a 2.5 m long core and is the only known site in the Czech Republic covering continually the period 9600 – 17000 years BP according to radiocarbon dating (for full pollen diagram and site details see Šída and Pokorný 2020; data again available at PALYCZ database). This profile was sampled in 5 cm intervals and the pollen analyses were performed in a similar way and by the same author (P. Pokorný) as were the analyses of the Yakutian modern samples.

Data analysis

We used multivariate analysis to determine the main patterns across the recent and fossil pollen spectra. Square root transformed pollen percentages were used as input in further analyses. All analyses were performed using R software (R Core Team 2015). R packages Vegan (Oksanen et al. 2015) and Analogue (Simpson 2007) were used.

To analyse main variability across the modern pollen spectra from the lakes in central Yakutia, we used Principal Component Analysis (PCA). For better interpretation, we additionally fitted available environmental variables to the PCA using the *envfit* command. As additionally-fitted environmental variables, we used: lake size; latitude; longitude; number of plant taxa in the proximal lake surroundings; and the proportion of forest in a 1 km radius around the sampling point.

To compare fossil European data with modern ones from Siberia (incl. central Yakutia), we again used PCA. Prior to the analysis, we performed the following steps: we grouped several pollen types which were distinguished only on some localities (or by some authors, respectively) into wider taxa – (e.g., Apiaceae, Caryophyllaceae, Ericaceae). We excluded the pollen of aquatic taxa present on several lake sites but absent on mire environments. We also excluded wetland species supposed to grow locally (e.g. Cyperaceae). If present, reworked Tertiary pollen was also excluded from fossil pollen assemblages. All PCA analyses were performed using the *rda* command in the default setting in the Vegan R package.

Considering previously published comparisons of fossil central European pollen samples to modern ones from southern Siberia (Kuneš et al. 2008, Magyari et al. 2014), we also used the dataset (145 pollen samples, Pelánková et al. 2008, Pelánková and Chytrý 2009) available as a part of the surface samples dataset at http://www.europeanpollendatabase.net (Davis et al. 2013). The same steps and PCA analyses as described above were used while comparing our new central Yakutian samples with the fossil central European ones and including the previously published surface samples that originated from southern Siberia. For visualisation in PCA (shown in Fig. 4c) we used 95% dispersion ellipses based on the SE and SD of plot coordinates of the pollen spectra. The ellipses "taiga forest" are based on grouped all taiga forest types and ellipses "steppe" contain grouped dry steppe, fen meadow, meadow steppe, mesic grassland, saline grassland, and steppic scrub categories, as used in the original dataset (Pelánková et al. 2008, Pelánková and Chytrý 2009). Pollen spectra that originated in alpine grasslands, tundra and hemiboreal forest were shown only as points, and not included in the ellipses.

For a quantification and statistical testing of the association of modern analogues to the fossil samples, we used analogue matching (Simpson 2012) implemented in R package Analogue (Simpson 2007). As an input, we used proportions of pollen types of both the fossil (PALYCZ) and modern (Yakutian and southern Siberian) datasets. The same exclusions of aquatic and wetland taxa and grouped pollen types into wider taxa, as used in PCA, was used also here. Chord distance was used as a dissimilarity measure. Threshold dissimilarity value distinguishing between modern pollen samples considered as analogy and non-analogy, respectively, to each fossil one was calculated using ROC, receiver operating characteristic, using defined groups according to an environment of the origin of the modern pollen samples (steppe and grassland, tundra, hemiboreal woodland, taiga, alas from Yakutia). Together, we used the same approach as Magyari et al. (2014) while analysing Pannonian and Carpathian fossil data, but we added new Yakutian samples to the modern pollen dataset and added several fossil localities originated from the Hercynian part of the Central Europe.

Additionally, we compared the modern pollen samples from central Yakutia with the new 17000 – 9000 cal. yr BP record (site Dračí díra) separately. This was performed to answer a specific question: To what time period of the Late Glacial in central Europe are the new central Yakutian pollen spectra most similar? It was not necessary to group the taxa in such a wide way as described above and we also did not exclude the aquatic species (the taxonomical approach while pollen counting was the same, and there was a comparable small lake environment on this fossil locality as in modern central Yakutia). In this case, we used DCA analyses of pollen percentages, because a unimodal species response to the time gradient could be expected considering one locality during a relatively long time period. DCA was performed using the *decorana* command as the default setting in the Vegan R package.

Results

Variability of modern pollen spectra in central Yakutia reflects local site characteristics

Results of the pollen analyses of the recent sediments from lakes in central Yakutia are summarised in Fig. 2. *Pinus* pollen prevailed in almost every site (15–68% of the total pollen sum in a site, median 29%), followed by *Betula* pollen (4%-35%, med. 15%). *Larix* pollen reached only 2-8% (med. 3.5%) despite larch being the dominant tree forming forests over the whole region. Other tree species, such as *Picea* and *Populus,* were represented only marginally in the pollen spectra, even though spruce and aspen are abundant in some patches in the region. In summary, the arboreal pollen proportion varied between 27% and 86%, with the median over 12 sites being 54% (Fig. 2b).

Concerning non-arboreal pollen, the Poaceae were represented the most (5% - 49%, med. 18%), followed by Cyperaceae (differing highly among sites by 1% - 25%, med. 4%) and *Artemisia* (1% - 8%, med. 4%). Several other pollen types were found occasionally in the pollen spectra – see Fig. 2c.

The studied lakes in central Yakutia differed in the proportion of forest vs. steppe/meadow vegetation in their proximal surroundings (up to 1 km, Fig. 2a), which was reflected in the arboreal pollen/non arboreal pollen ratio (hereafter AP/NAP) in the pollen spectra of the modern samples from the lakes (Fig. 2b). The pollen spectra were relatively variable (Fig. 2c), differing highly from site to site. The pattern in the variability was mainly driven by the pollen of *Pinus* and *Betula* on the one hand and by pollen types of plant species growing in the steppes and meadows - mainly Poaceae*, Artemisia* and other forb pollen types, on the other, as shown by the PCA (Fig. 3). This separated lakes nos. 2, 10 and 11 (on the right side of the diagram in Fig. 3), being characterized mostly by the forested surroundings and high AP/NAP ratio (Figs. 2a and 2b). On the other side of the gradient (Fig. 3) are the lakes nos. 6 and 7 characterized by a high proportion of Poaceae pollen (Fig. 2c) and by prevailing grasslands in their surroundings (Fig. 2a). The first PCA axis explained 35% of the data variability. Obviously, there remained variability unexplained by the main PCA gradient, which is hard to interpret, especially regarding the number of replicates (12 sites). Other studied 'environmental variables', namely geographical position (latitude, longitude), number of plant species recorded near the lake banks, and the lake size, did not show any connection with the main gradients of the variability shown by the PCA.

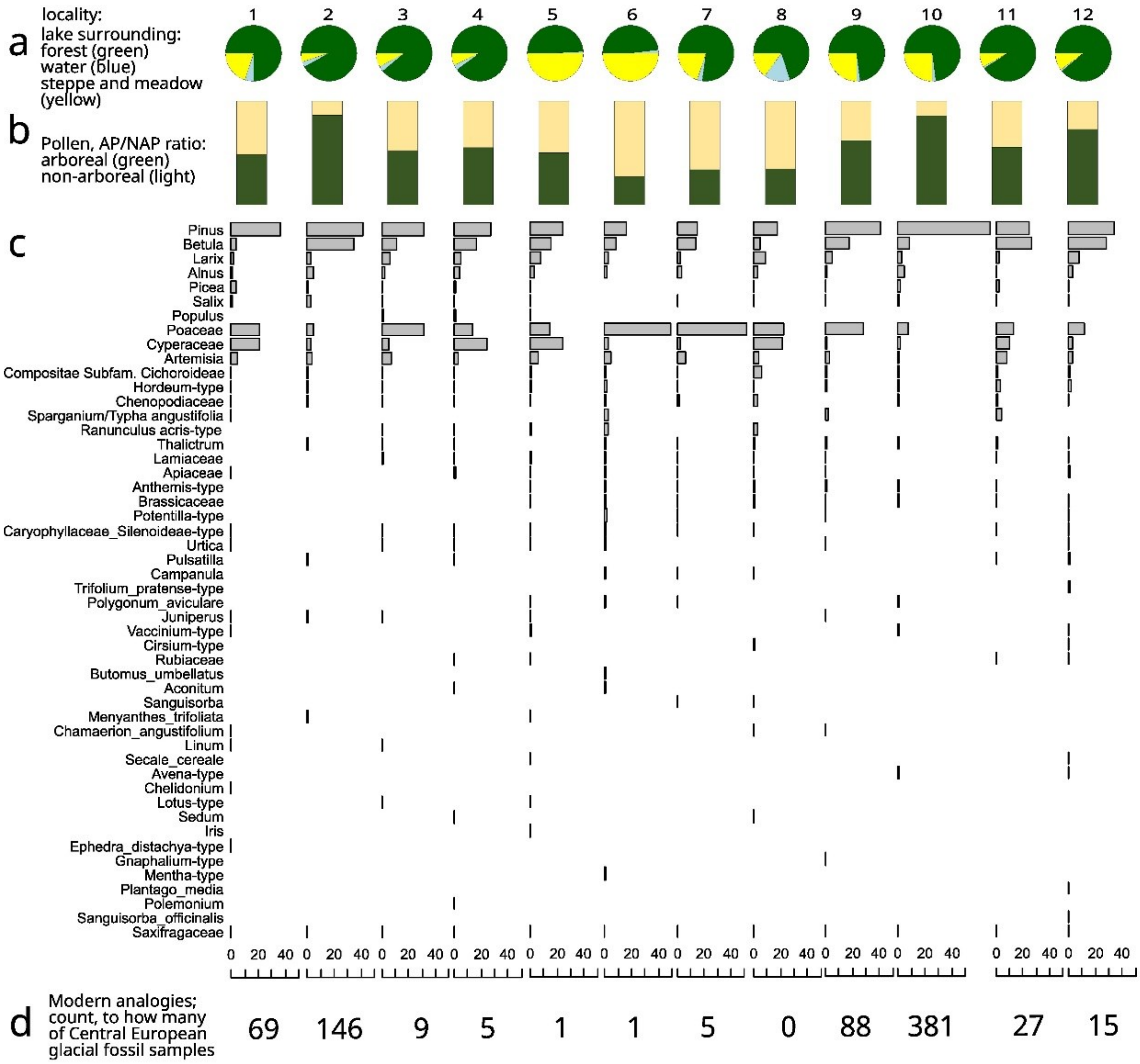

Fig. 2. – *(a) Basic characteristics of the landscape near each of the sampled lakes (the same order of localities as in Table 1, determined by their geographical position), the proportion of forest (taiga, mostly larch, dark green), grassland (steppe and meadows, yellow) and water bodies (blue) in the 1 km surroundings of each sampling point. This is compared with (b) the ratio of arboreal pollen (dark green) and non-arboreal pollen (light brown) in the pollen assemblage in the recent lake sediment on each site. (c) Pollen assemblages of the recent lake sediments from 12 studied lakes in central Yakutia. Note that the Larix pollen (third row) is represented only as 2-8% of the total pollen sum, despite this taxon forming the prevailing vegetation in the region. (d) Number of central European glacial fossil pollen samples (from 842 in total) to which the individual alas pollen spectra is a significant modern analogue according to analogue matching and ROC threshold dissimilarity.*

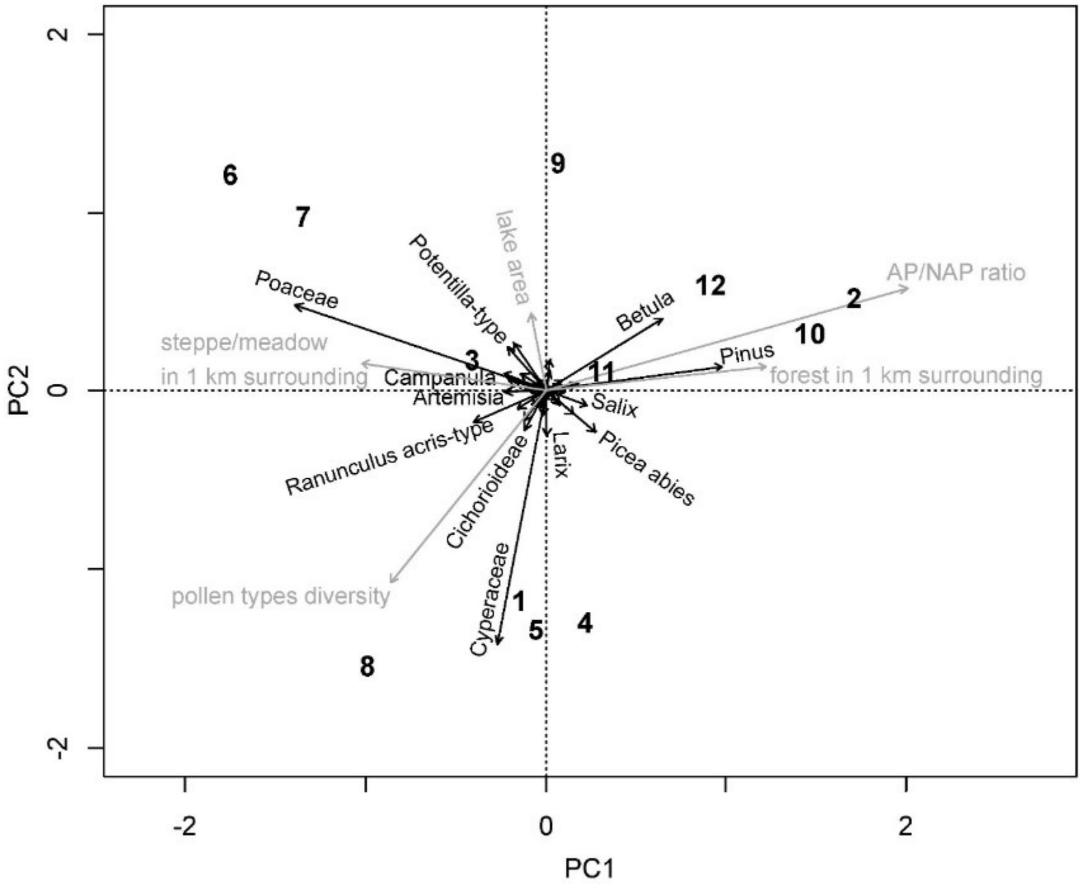

Fig. 3. – *PCA biplot based on square-root transformed data of pollen type percentages in recent samples from 12 lakes in central Yakutia. The first two axes shown in the diagram explain 59% variability of the total variation in pollen type composition. Selected pollen types are indicated, the sites are shown as numbers (identical to that used in Table 1 and Fig. 2), and passively projected characteristics (in grey).*

Central European fossil pollen spectra compared to central Yakutian modern ones

We compared two aspects: (i) the overall variability among the group of pollen spectra and the positions and (ii) relationships in the results of the multivariate analyses. This comparison showed that the variability among the pollen spectra from the 12 lakes within one central Yakutian landscape is huge. The variability is comparable to that observed among fossil samples that originated from sites in different central European regions and layers formed in different ages (Fig. 4a).

The comparison of central European pollen spectra and our pollen spectra from central Yakutia using PCA analysis are summarised in Fig. 4a, 4b and Fig. 5. Similarly as in the case of the PCA of the new central Yakutian dataset as such (Fig. 3), while also analysing this together with the 776 fossil pollen spectra, the main axes clearly expressed the gradient between steppe and forest elements (Fig. 4b): pollen spectra dominated by pine are on one side and pollen spectra with considerable amounts of Poaceae and other non-arboreal pollen, such as *Artemisia*, *Helianthemum*, *Thalictrum,* are on the other. Most of our pollen spectra from central Yakutian lakes are shifted towards non-arboreal pollen, compared to the average of samples from the central European Last Glacial period. The DCA comparison of Dračí díra, the single pollen record spanning 17 000 to 9 600 BP and 12 modern samples from Yakutia is shown on Fig. 6.

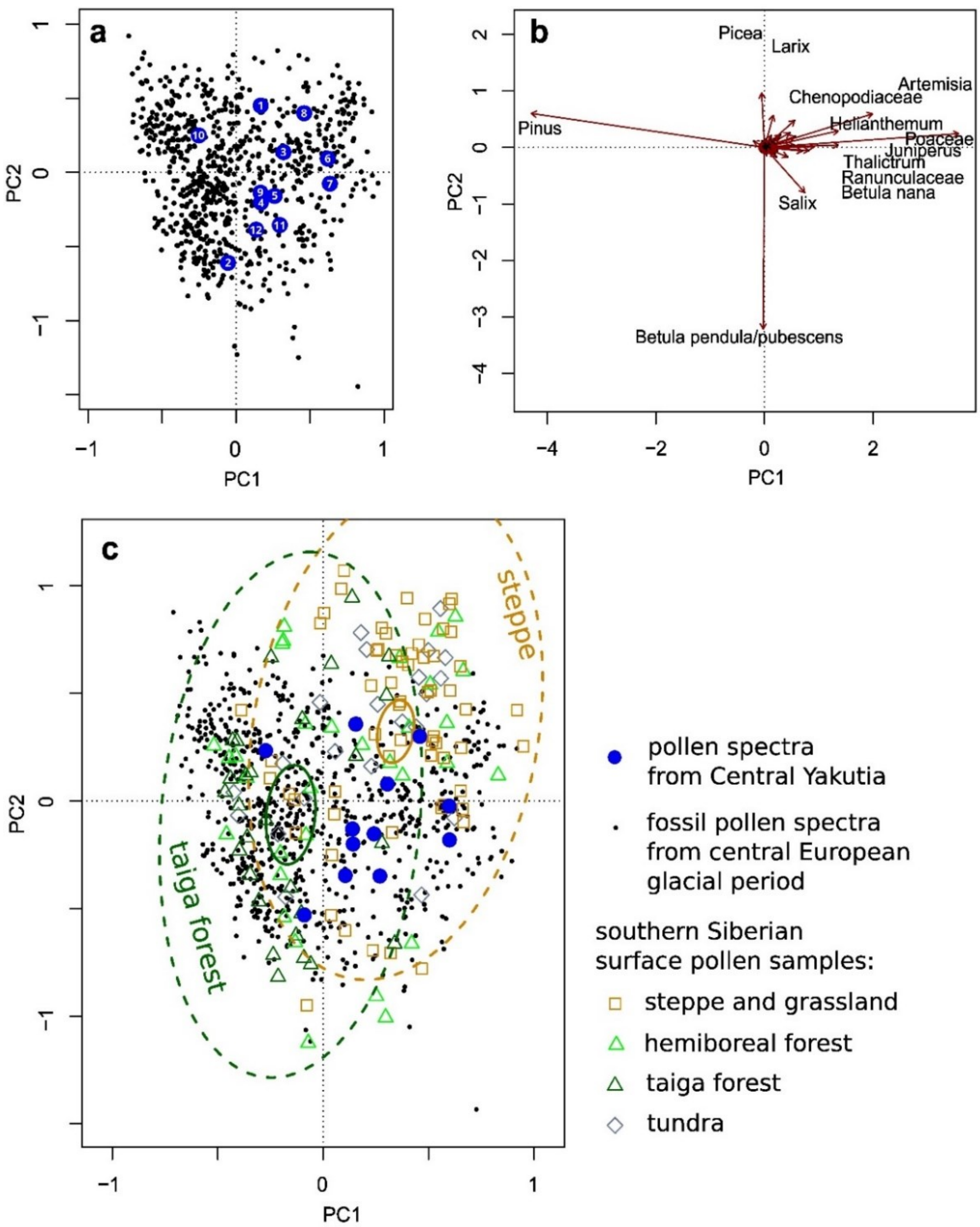

Fig. 4. – *(a) - Principal Component Analysis of the central European pollen spectra from the last glacial period (black dots, 776 fossil layers from 42 sites) together with modern pollen spectra from 12 small lakes in central Yakutia (full blue circles, numbers same as in Table 1 and Fig. 2). Note that the pollen spectra from Yakutia are scattered across almost the whole space, thus showing that the variability among the sites of one region at one given time is surprisingly high, compared to the variability among the fossil pollen spectra (black dots) that originated over hundreds of kilometres and a timespan of thousands of years in central Europe. Based on square-root transformed pollen-type percentages. (b) – the same analyses, showing selected main pollen types. The first two axes shown in the diagram explain 47% variability of the total variation in pollen type composition. (c) – a similar analysis to that of a and a, but including the southern Siberian surface pollen samples from Pelánková et al. (2008), Pelánková & Chytrý (2009), used afterwards by Kuneš et al. (2008), and Magyari et al. (2014), showing that the modern samples from 12 lakes in Central Yakutia (blue dots) are more similar to most of the fossil central*

European pollen spectra than the surface samples from the south-Siberian steppes and grasslands. The first two axes explain 43% variability of the total variation in pollen type composition. Here, the pattern of main pollen types shaping the ordination results remains very similar to the pattern in Figure 3B, even after adding the 145 pollen spectra from southern Siberia to the analysis. The 95% dispersion ellipses shown are based on the SE and SD of plot coordinates of the pollen spectra; for further details, see methods.

Including southern Siberian surface samples from a set of previous studies to the comparison

If we add 145 modern pollen spectra from southern Siberia's surface samples to the PCA analysis (Fig. 4c), the overall pattern remains the same. In the direction of the main ordination axis, spectra with forest-free components and forested spectra, corresponding with southern Siberian steppes versus forests of different types, were clearly separated. Samples from central Yakutia appear scattered somewhere in between but shifted more in the direction of the southern Siberian steppes. The gradient along the second ordination axis seems to further divide the pollen spectra into birch versus spruce, but the interpretation is unclear.

It should be noted that most of the pollen spectra from the southern Siberian steppes appeared outside the main clump of samples. These steppe surface pollen samples obviously differ from central European fossil pollen spectra as well as from the new central Yakutian pollen spectra. In general, most Last Glacial central European pollen spectra are more similar to pollen spectra from central Yakutia and to spectra from different types of forests in southern Siberia than to steppes from southern Siberia as shown by the PCA in Fig. 4c.

The use of analogue matching approach showed in general similar results as the PCA. Threshold dissimilarity value calculated by ROC was 0.45 (AUC = 0.801, p-value: < 2.22e-16). This resulted in 585 fossil samples with at least one significant modern analogy and 245 without any modern analogy (full analogue matrix not shown here, localities and ages of the fossil samples with more significant analogies are discussed later).

Considering the groups of modern pollen samples, 11 from 12 Yakutian alases were significant analogies for at least one fossil pollen sample (Fig. 2d), while alas number 10 was even a modern analogy for the largest number of fossil samples in the entire modern dataset. From southern Siberian modern pollen samples, 14 from 63 steppe and grassland samples were a significant analogy, 12 from 22 tundra samples, 19 from 32 hemiboreal woodland samples and 23 from 28 taiga woodland samples, respectively, were a significant analogies to at least one fossil pollen sample. In other words, slightly more than half (77 from 145) southern Siberian pollen samples are not an analogy to any central European Last Glacial pollen sample. While in central Yakutia 1 from 12 our modern pollen sample resulted as non-analogical to Last Glacial European samples.

Discussion

Pollen spectra under continental conditions are highly variable and underrepresent forest

Unexpectedly, the tree cover is highly underrepresented in the central Yakutian pollen spectra, as was shown by the approximate 1:1 AP/NAP ratio. This took place despite the total spatial prevalence of forests in this area of Yakutia (Troeva et al. 2010). In this context, the previous concepts of the Last Glacial - prevailing treeless habitats based on traditional European interpretations of fossil pollen - seem to be problematic. A well-known review by Willis and Van Andel (2004) stated, discussing lake sites, that: "…the pollen diagram indicates an open-forested vegetation during the LGM, with tree pollen accounting for over 60% of the total pollen." While they considered the landscape to be 'open', we found that in a cold continental climate even around 50% of tree pollen is a representation of a densely-forested landscape in general, and definitely not an 'open' landscape. We have shown here that a small steppe 'island' on a slope near a sedimentation basin is enough to produce such a high amount of NAP component in the pollen spectra, despite the sampling locality being entirely surrounded by dense forest.

Not only the low average AP/NAP ratio, but also the variability of the pollen spectra over the studied sites is important. The flat Siberian landscape in central Yakutia is relatively homogenous at a spatial scale of tens to hundreds of kilometres (Troeva et al. 2010). But contrary to that, the studied pollen assemblages from the small lakes are highly variable. The high site-to-site variability of the modern pollen spectra shows that the proportion of main pollen types in such sediments of small lakes is not a straight response to the regional vegetation dominated by taiga forest. Instead, the pollen assemblage reflects the proximal surrounding of each site (Fig. 2, Fig. 3a) and the vast forest prevailing in the landscape is underrepresented. This is generally consistent with previous studies from similar Siberian landscapes, considering the very local scale (Katamura et al. 2006, de Klerk et al. 2009). But this point was not obvious from previous studies when considering large spatial scales (e.g. Tarasov et al. 2007, that compared pollen data with vegetation characteristics around the lake, but integrated over a 10 km grid; see also Müller et al. 2010, Klemm et al. 2013). This dispersal and taphonomy issue, taking place on a local landscape scale, is a crucial one when interpreting the central European pollen record, where there are no large lakes, the localities providing fossil pollen records are small lakes or mires, and where relatively large landscape heterogeneity is suspected over a range of kilometres (Kuneš and Abraham 2017).

There may be two explanations why the pollen spectra reflect the mostly proximal surroundings of the lakes and not the regional vegetation. First, the matrix of the landscape, the taiga forest, is comprised of poor pollen producers, mostly larch (see Clayden et al. 1996, Jankovská and Pokorný 2015, Schulte et al. 2022). Vacciniaceae are also much under-represented in the modern pollen spectra, despite these plants dominating the forest understory. Most pollen-producing plants are growing in the treeless belt near the lake (for details about the vegetation, see Mirkin et al. 1985) and generate the NAP pollen component which showed similar pattern as the proportion of steppe and meadow vegetation in the site surrounding. The second possible explanation is the specific pollen production and pollen taphonomy caused by the local climatic conditions. The trees growing in the region are on or close to their physiological limit, the growing season is short (Troeva et al. 2010), and the permafrost restricts the rhizosphere. The tree taxa involved (*Larix*, but also *Pinus*, *Betula*, *Populus*) could therefore hypothetically produce an unusual low amount of pollen (see also van der Knaap et al. 2010, Nielsen et al. 2010, Niemeyer et al. 2015, Abraham et al. 2021). Moreover, the short summer is characterised by rather stable weather, with mild winds, and, hypothetically, quite limited pollen dispersal. This is in obvious contrast with current north-western Europe or North America, the regions where pollen taphonomy has been traditionally studied. From this viewpoint, traditional pollen transport and deposition models (Sugita 2007, Prentice 1985) hardly seem to be extrapolated to such situations under a strongly continental climate, such that exists in current central Yakutia, or have likely existed in the Last Glacial in central Europe. However, exploration of a proper model of vegetation representation in the pollen spectra in lake sediments and detailed pollen dispersal research under a continental climate is beyond the scope of this study, which is limited to only the simple mapping of the vegetation surrounding the pollen sampling sites.

Which features of the central Yakutian landscape can be analogous to European Last Glacial ones and which can hardly be so?

As shown by the similarity of the pollen spectra, we consider the landscape in central Yakutia to be a good model area for comparison to landscapes in central Europe during the Last Glacial period. Previously, southern Siberian, mostly treeless landscapes in the Altay high mountain region were postulated as an analogy (Kuneš et al. 2008, Magyari et al. 2014, Chytrý et al. 2018). Our aim, however, is not to reject this previous point of view, but rather to add some new insights into the search for possible analogies. Obviously, at a large biogeographical spatial scale, there are regions where the analogy to central European Last Glacial vegetation is better seen than in central Yakutia. One of the larger scale issues is the climate (Janská et al. 2017): on average the climate in central Yakutia is too cold compared to the reconstructed Last Glacial climate in central Europe. Another issue is the species pool: there are several species which are missing in central Yakutia, being limited by extremely cold winters (Horsák et al. 2013, Chytrý et al. 2018).

Our results have shown that at a smaller landscape spatial scale, some features in central Yakutia could be more analogous to some Last Glacial landscapes in central Europe than were the previous analogues seen in the southern Siberian mountains and basins. These features include: (1) the overall shaping of the landscape by permafrost; (2) the resulting structure and proportion of vegetation types; and (3) the representation of the vegetation in the pollen record in the sediments of small lakes and wetlands. The landscape shaped by permafrost aggradation-degradation processes includes not only the geomorphological features (thermokarst; Ulrich et al. 2019, Iijima and Fedorov 2019, recently found in fossil form in central Europe, Hošek et al. 2019), but additionally the vegetation saturated by water in the dry summer period (Schulte et al. 2022). In contrast, southern Siberia is characterised by a discontinuous permafrost that has a rather low effect on the regional geomorphology and vegetation variability (Chytrý et al. 2018).

The current landscape in central Yakutia contains all the main genera producing pollen types typical for central European Last Glacial pollen spectra – *Pinus, Betula, Picea, Larix, Artemisia,* Chenopodiaceae*,* Poaceae - and its pollen also prevailed in our modern pollen samples presented here. And what is most important, unlike previous studies performed in southern Siberia (Kuneš et al. 2008, Pelánková et al. 2008, Pelánková and Chytrý 2009, Magyari et al. 2014), our study uses pollen spectra from small and shallow lakes. We believe that such a sampling design is necessary when addressing taphonomical processes. Taking into account their physical characteristics, the studied lake sites are comparable to the sites providing the fossil pollen record in central Europe (e.g. Pokorný 2002, Kuneš et al. 2015, Hošek et al. 2017).

We hypothesize that the high proportion of non-arboreal pollen in the central European fossil samples, at least at some localities, could also be a reflection of small patches of steppe vegetation on the slopes near the sedimentation basin, possibly surrounded by larch forest – and not just a reflection of steppe vegetation covering the whole landscape. The larch taiga forest cover can be hypothesized in particular to the central European lowlands and sandy flatlands in the Late Glacial period after climate amelioration in about 15 ka BP and before the onset of the Holocene warming around 11.7 ka BP.

Key central European fossil pollen sites in a brief comparison to modern central Yakutia

Sites providing reliable pollen records of the Last Glacial period are relatively sparse in the territory of central Europe (Kuneš et al. 2009, Kuneš and Abraham 2017), and the concept of vegetation and landscape reconstruction has been based on only a few sites. Hence a discussion concerning these individual key sites follows.

The Late Glacial layers from the very base of the Švarcenberk lake in the southern part of the Czech Republic (Jankovská 1980, Pokorný and Jankovská 2000) were previously interpreted as the following: "high NAP values, suggesting open herbaceous vegetation" (Pokorný 2002). Nevertheless, open herbaceous vegetation is not the only possibility: as these pollen assemblages show high similarity to the central Yakutian modern ones. Layers originated within the approximately 14-13,5 ky BP timespan showed relatively highest number of significant modern analogies among aur modern samples from Yakutia using analogue matching. Other layers, especially younger layers are shifted more to the forested landscape according to the PCA diagram (for the overall pattern see Fig. 5a). Either way, this is probably one of the landscapes in central Europe where the analogy to current central Yakutia is also at its best in terms of its vegetation and landscape structure (Hošek et al. 2019). Unfortunately, *Larix* pollen was not regularly distinguished in the older pollen analyses in the region, but this was because of limited technical skills rather than because of the absence of larch.

The Vracov site (Kuneš et al. 2015), a lowland lake on the northern edge of the Pannonian Basin, is another case where the fossil pollen assemblages have a similar composition to the current central Yakutian ones (Fig. 5b). This shown by PCA is especially true for the basal layers dated to 15-16.5 ky BP, while the younger part of the record tends to be more forested. Layers dated to 14,5-13 ky BP showed high number of significant modern analogies among Yakutin alases (up to 6 out of 12 Yakutian samples are significant analogies while only 2 out of 36 southern Siberian steppe modern samples are analogical for Vracov layers dated to 13,9-13.2 BP). Moreover, the surrounding flatland landscape has recently been discovered to have also been shifted by Pleistocene permafrost degradation processes (Hošek et al. 2020).

More variable is the fossil pollen record on another key lowland site, Hrabanovská Černava (Fig. 5c), in the central part of the Czech Republic (Petr and Novák 2014). This site, dated to reaching cca 16.5 ky BP, lies in a landscape of sand dunes and neighbours with the Labe/Elbe River floodplain. While some fossil samples there seem to be similar to that of current central Yakutia, others, especially the oldest ones, show more arboreal pollen.

The fossil samples from one period of the southern Moravian site Bulhary (Rybníčková and Rybníček 1991, 2014) also showed an obvious similarity to our central Yakutian samples. This is the case for the layers slightly above the depth dated to around 25000 BP (Rybníčková and Rybníček 2014). Here, the AP/NAP ratio reached almost 1:1 and these layers came out to have modern analogues among our samples from Yakutia also using analogue matching. But only one dating and strange taphonomy of the site makes it uncertain and the most part of this profile was shifted to much treeless vegetation (Fig. 5d). Overall, this comparison pointed out that the northern Pannonia at least part of the MIS3 period was characterised by more open steppe landscape (see also Šolcová et al. 2020).

In conclusion, all the above-described sites lie in areas of generally flat terrain with fine-grained bedrock sediment. Generally, the fine-grained sediments and the low topographic gradient both have contributed to poor surface hydrological drainage across the area and could have promoted the development of an ice-rich permafrost under glacial conditions (Hošek et al. 2019, Hošek et al. 2020). These landscapes were probably shaped by permafrost degradation (thermokarst processes) during Late Glacial, quite similar to the condition known from the current central Yakutia (Ulrich et al. 2019). Furthermore, thawing seasonal ground ice was probably an important water source for trees – the mechanism well known from the "yedoma" complexes of recent Yakutian or Alaskan permafrost regions (Schulte et all. 2022).

In contrast to the lowland Late Glacial sites (and oldest samples like on Fig. 5e), Late Glacial pollen spectra from the mountains show a much more treeless pattern. This is the case of the pollen spectra from Plešné lake (Jankovská 2006; Fig. 5f), a site located at 1100 m asl in the

Šumava/Böhmerwald mountains near the Czech–Austria–German border. The pollen spectra here indicate a tundra or steppe-tundra vegetation. This open landscape character seems to be present in the mountains on the solid bedrock at least up to the Pleistocene/Holocene transition (or later; Carter et al. 2018), and the pollen spectra are obviously different from the lowland sites, as well as from modern central Yakutia.

MIS3 sites in the Western Carpathians are analogical to current central Yakutia into some extent. These pollen records show a landscape that was much more forested in comparison to our modern samples from central Yakutia (Fig. 5e). Fossil pollen assemblages from the site Šafárka (Jankovská et al. 2002, Jankovská and Pokorný 2008) are from sediments providing the dates 30,186 ± 1,935 BP and 18,287 ± 1,512 BP, but unfortunately a precise dating of the whole pollen sequence is not available. The dates come directly from larch macroremains, so that it is proof that the larch forest occurred in proximity of this small peatbog. This pattern may reflect the vegetation in the more favourable climate over MIS3 or could reflect the forested Western Carpathians in general (Magyari et al. 2014). A similar pattern shifted towards forest is shown by pollen assemblages from the site Jablůnka in the western foothills of the Carpathians (Jankovská and Pokorný 2008) from around 40 ka BC and earlier.

The only site providing a well-dated LGM to Late Glacial pollen record in the studied Hercynian part of the central Europe up to now is the site Dračí díra. This has enabled a direct comparison using the DCA analyses (Fig. 6). This clearly shows that the modern pollen spectra from central Yakutian alases are most similar to the 12 – 14 ka BP time period around this central European small lake. The older, 16-15 ka BP, pollen spectra show a much more steppe-like vegetation, containing less arboreal pollen, and are more similar to the southern Siberian surface samples (not directly shown; some of the black ‘dots’ in the upper-right corner in Fig. 3c are the basal layers from the Dračí díra site). Subsequently, the pollen spectra that originated around the Late Glacial-Holocene boundary are dominated by arboreal pollen, showing much less open land indicators than the spectra from central Yakutia.

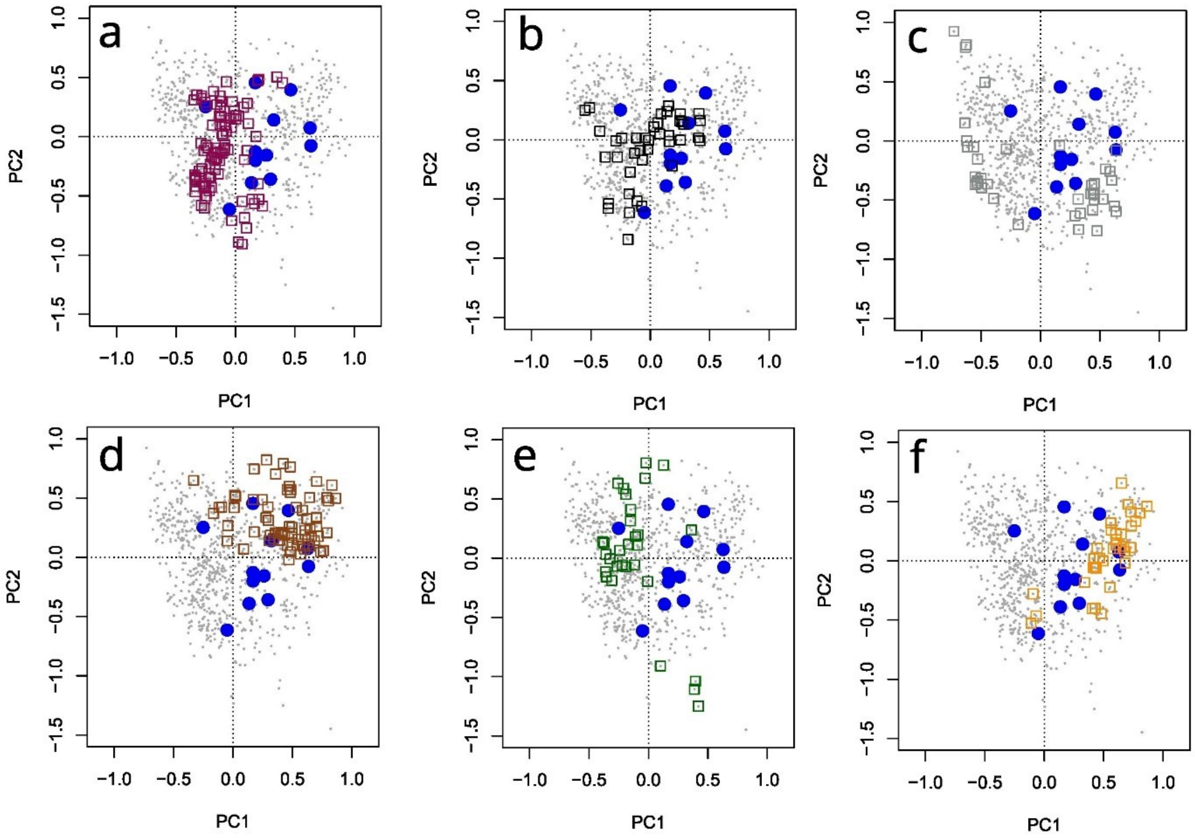

Fig. 5 – *Central European last glacial fossil pollen spectra (taken from the PALYCZ database, grey dots) in comparison with the modern pollen spectra from 12 lakes in Yakutia (blue full circles). The same analysis as in Fig. 4 is used (i.e. on the left is the forested pattern in the pollen spectra, on the right is the steppe pattern, see Figs. 4a and 4b). The positions of pollen spectra from the well-known, previously-studied and discussed central European sites are highlighted as squares: (a) Švarcenberk; (b) Vracov; (c) Hrabanovská černava; (d) Bulhary; (e) Šafárka; and (f) Plešné jezero.*

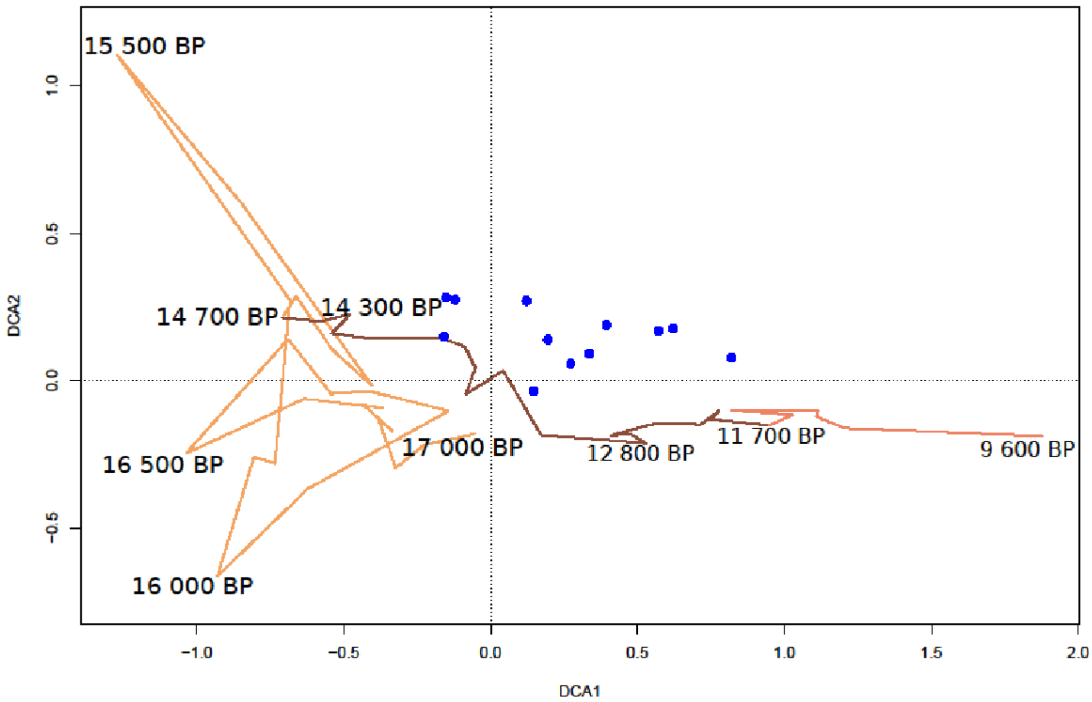

Fig. 6 – *A comparison of modern pollen spectra from 12 small lakes in central Yakutia (blue dots) to a single central European pollen record spanning 17 000 to 9 600 BP (line, site Dračí díra, for pollen diagram see Šída and Pokorný 2020). The time period around 12 – 14 ka BP (dark-brown part of line) is the most similar to modern central Yakutia, while the older fossil layers (to the left side, light-brown) show a much more steppe-like vegetation, and the pollen spectra originating from around the Late Glacial-Holocene boundary on the right (orange-brown) show much less open-land indicators than the pollen spectra from central Yakutia. Detrended correspondence analysis (DCA) based on pollen percentages.*

Conclusions: How the glacial landscapes of central Europe could have looked like?

Our study has added the following insight into the long-lasting discussion about forest cover during the Last Glacial in central Europe: The fossil pollen evidence does not necessarily imply only steppe/tundra or a sparse parkland landscape structure. The fossil evidence is also commensurate with the possible existence of taiga forests dominated by larch – a vegetation type that is almost invisible using pollen analyses. During climatically-favourable interstadials of the MIS3 and the Late Glacial, a larch-type taiga could have existed in flat areas maintained by water released from a thawing permafrost. Obviously, we cannot directly prove this hypothesis, but we have shown that this hypothesis is consistent with the fossil pollen evidence. And it is consistent with environmental dynamics and pollen record of modern analogies from Siberia.

On other site, during the LGM, the landscape was probably indeed quite open, containing mostly loess steppe and tundra as indicated by the higher proportion of steppe elements in some fossil samples, compared to the modern samples from central Yakutia, as well as by the large-scale sedimentation of loess itself. However, for this period there is still a lack of data from Hercynian part of Central Europe; the available fossil records of forest tree taxa within the territory of the current Czech Republic pre-date or post-date the LGM period (Kuneš and Abraham 2017), and ideas concerning the question of taiga vs. steppe land cover remain rather speculative.

Our results such as the strong dependence of the pollen spectra on the proximal surroundings of the site and the 'invisibility' of larch also stress some methodological limitations of pollen analysis when considering the vegetation in cold continental conditions.

Future research focussed on differences in the environment of micro-regions around fossil pollen sites and the finding of new sites in central Europe where the fossil record reaches the LGM could only help solve the problems concerning the Last Glacial landscape and vegetation reconstruction. For now, both hypotheses, i.e. one of a prevailing Last Glacial treeless landscape, as well as one of a prevailing larch-dominated taiga forest, should be considered in central Europe.

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Supplementary Information: Spreadsheet that contains (1) list of all sites and depths of fossil samples used in the analyses (for further details, see palycz database), (2) list of all Siberian samples used (codes of surface samples from http://www.europeanpollendatabase.net), (3) a complete analogue matrix in both forms - full numbers of similarity and analogue/non-analogue based on the threshold value (because of the size not printed in the thesis).

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Czech “lake landscape” – formation and former vegetation–erosion dynamic of one specific region

Field research of former glacial lakes in the Třeboň region.

case study 2

Buried Late Weichselian thermokarst landscape discovered in the Czech Republic, central Europe

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Abstract

Pronounced climatic warming associated with the Late Weichselian Pleniglacial–to–Lateglacial transition caused considerable environmental changes throughout the former periglacial zones (in Europe ~53°–46°N). During permafrost degradation and subsequent ground subsidence (i.e. thermokarst processes), the landscape changed rapidly. In this study we investigated a flat mid-altitude area in south Bohemia, Czech Republic, lying close to the southern limit of the Weichselian permafrost. We discovered palaeo-lake basins with sedimentary infillings up to 11 m in depth. According to radiocarbon and palynostratigraphic dating, these basins were formed at the onset of the Late Pleniglacial–to–Lateglacial transition, whereas the smaller depressions were formed later. We suggest a hypothesis that the basins resulted from thermal and fluvio-thermal erosion of the former permafrost and represent remnants of discontinuous gullies and possibly collapsed frost mounds (pingo/lithalsa scars). The formation of such a fossil thermokarst landscape was climatically driven and multiple phased, with the major phase during the climatic warming and wetting at the onset of GI-1e (Bølling) and the minor phase during GI-1c (Allerød). This study enhances knowledge on the palaeogeography of the former European periglacial zone by showing that Late Pleistocene thermokarst activity could have had a significant impact on the evolution of the landscape of at least some regions of central Europe along the southern limit of the continuous permafrost zone. The research also points to a similar history for the physical transformation of the landscape of the former European periglacial zone and current thermokarst landscapes and could be a valuable source of information with respect to the future transformation of the Artic under conditions of ongoing global warming.

Introduction

In recent permafrost environments, thermokarst encompasses the whole range of geomorphological landforms affecting the landscapes of the Arctic and the Antarctic (Jorgenson 2013; Kokelj & Jorgenson 2013; Farquharson *et al*. 2016). Thermokarst is understood in terms of processes associated with the thawing of ice-rich permafrost that lead to local or widespread ground collapse, erosion, and surface instability. Resulting landscapes are characterized by pits, basins, and irregular depressions that lack surrounding ramparts (French 2017). Thermokarst (thaw) lakes are the most ubiquitous of these landforms (Jones *et al*. 2011; Morgenstern *et al*. 2011, 2013; Farquharson *et al*. 2016), usually initiated by complete subsurface ice degradation, ground collapse, and the subsequent accumulation of water in the closed depression (Van Everdingen 1988; French 2017). The sizes, shapes and morphologies of thermokarst lakes and depressions can vary enormously among and even within various regions (Grosse *et al*. 2013), depending mostly on the local relief resulting from geological structure (e.g. fault lines), the topography associated with fluvial patterns (e.g. basins related to beaded streams; Short & Wright 1974; Merck *et al*. 2012; Jorgenson 2013), or the post-formation history of erosion and deposition. Widespread thermokarst initiation appears to have coincided with the onset of the Holocene as a result of warmer and wetter conditions relative to the Pleistocene (Czudek & Demek 1970; Rampton 1988; Walter *et al*. 2007; Morgenstern *et al*. 2011; Biskaborn *et al*. 2013; Lenz *et al*. 2016). Observations indicate that over the past several decades, geomorphic processes in permafrost regions have been intensifying (Biskaborn *et al*. 2019), affecting ecological and biological systems, and destabilizing arctic infrastructure (e.g. Rowland *et al*. 2010). Some projections indicate accelerated modifications to permafrost in the near future as a system-wide response to ongoing global warming (Hinzman *et al*. 2005). Studying relict landforms of past periglacial landscapes may provide useful information on how modern periglacial landscapes will respond to ongoing warming at high latitudes.

Along the Weichselian Pleniglacial–Lateglacial transition (~18–15 ka BP), rapid and pronounced climatic oscillations caused distinct environmental changes (Roberts 2014) and induced large-scale physical landscape transformation throughout the former European periglacial zone (Isarin 1997; Huizer & Vandenberghe 1998). Some structures such as gullies, pits, or involutions have been interpreted as relict thermokarst features resulting from the decay of former Pleistocene permafrost (Vandenberghe & Pissart 1993). Of various types of thermokarst depressions distinguished within recent thermokarst landforms (Jorgenson 2013), collapsed open-system pingos and lithalsas are the most frequent kind, documented from numerous sites throughout the lowlands of north, northwestern, and western Europe (Svennson 1964; Hoek 1997; Pissart 2000). Both types of depressions are typically circular or elongated and rimmed by a distinct rampart, which formed by the action of mass wasting down the sides of a former mound that enclosed a central depression where the ice core had melted (French 2017; Harris *et al.* 2018). These depressions are usually filled by colluvial sediments, peat, and sometimes lacustrine sediments. In contrast to pingo and lithalsa scars, evidence of landforms representing Pleistocene non-ramparted thermokarst lakes is very limited. This could be due to their low potential for preservation in fossil record (French 2017) once the permafrost had thawed, such thawing reducing the terrain to the level of former depression floor (Ballantyne 2018). In Europe, non-ramparted thermokarst depressions filled by lacustrine deposits have so far been described from several sites in the Netherlands and eastern Germany (Bohncke *et al*. 1993; Van Huissteden & Kasse 2001), northern Poland (Dylik 1963), southern England (Berry 1979; Banks *et al*. 2014), and northern France (Van Vliet-Lanoë *et al*. 2017; Bertran *et al*. 2018). In contrast to N and NW Europe, knowledge on thermokarst processes and their importance in the genesis of the Late

Pleistocene landscapes of central Europe remains poor (Czudek 1986, 2005; Vandenberghe 2001; Žák *et al*. 2012).

In light of these considerations, the Třeboň region in south Bohemia (Czech Republic) could be a key area with respect to reconstructing the Late Pleistocene environment of central Europe. Even though this landscape has been extensively remodeled by the Early Modern Age (~AD 1500 - 1600) construction of fishponds, large non-ramparted palaeo-lake basins have been discovered in recent years by drilling (Šída & Pokorný 2011; Hošek *et al*. 2013, 2016). High-resolution, up-to-eleven-meter-thick lacustrine sequences of the largest palaeo-lake basins have provided detailed information on supra-regional environmental transformation and dynamics along the Late Pleistocene-Holocene transition (Pokorný & Jankovská 2000; Pokorný 2002; Pokorný *et al*. 2010; Hošek *et al*. 2014, 2017b). However, the origin of these palaeo-lakes and depressions is so far unknown. Here, we describe these particular and rare landforms in their geological and palaeoenvironmental setting and examine their mechanisms of formation in the context of the Late Pleistocene landscape transformation of the former periglacial zone. Knowledge of past landscape and environmental dynamics could provide a valuable information on the interaction between permafrost and climate during the last deglaciation (e.g. Köhler *et al*. 2014), as well as insight into current permafrost deformation, mechanisms behind which are still not sufficiently understood.

Regional settings

Geology and geomorphology

The study area is situated in South Bohemia, Czech Republic (49.1°N, 14.7°E; 400–430 m a.s.l.; Fig. 1), in the northern part of the Třeboň Basin, which consists of an area of generally flat terrain, with elevations only 25–30 m in height. The Třeboň Basin is filled by Cretaceous clastic sediments consisting of sandstones, conglomerates, and mudstones. These Cretaceous sediments are partially covered by a layer of Miocene fluvio-lacustrine sediments up to 60 m in thickness (Malecha *et al*. 1991). All the studied thermokarst depressions are situated on the upper part of the Miocene sequence (Fig. 2), which consists of layers of fine-sandy clays, sandy gravel, diatomite, and lignite. Miocene sediments fill the NNW-SSE graben, which is a dominant tectonic and geomorphologic structure in the area. The boundary between Cretaceous and Miocene sediments is characterized by a system of faults perpendicular to the main tectonic structure. The graben constitutes the shallow depression, up to 2 km in width, in the generally flat terrain. The surface of this zone is characterized by undulating terrain formed by isolated elevations up to several meters in height and depressions between them. The predominant orientation of these features is NE-SW, i.e. in concordance with the zone's current surface drainage system.

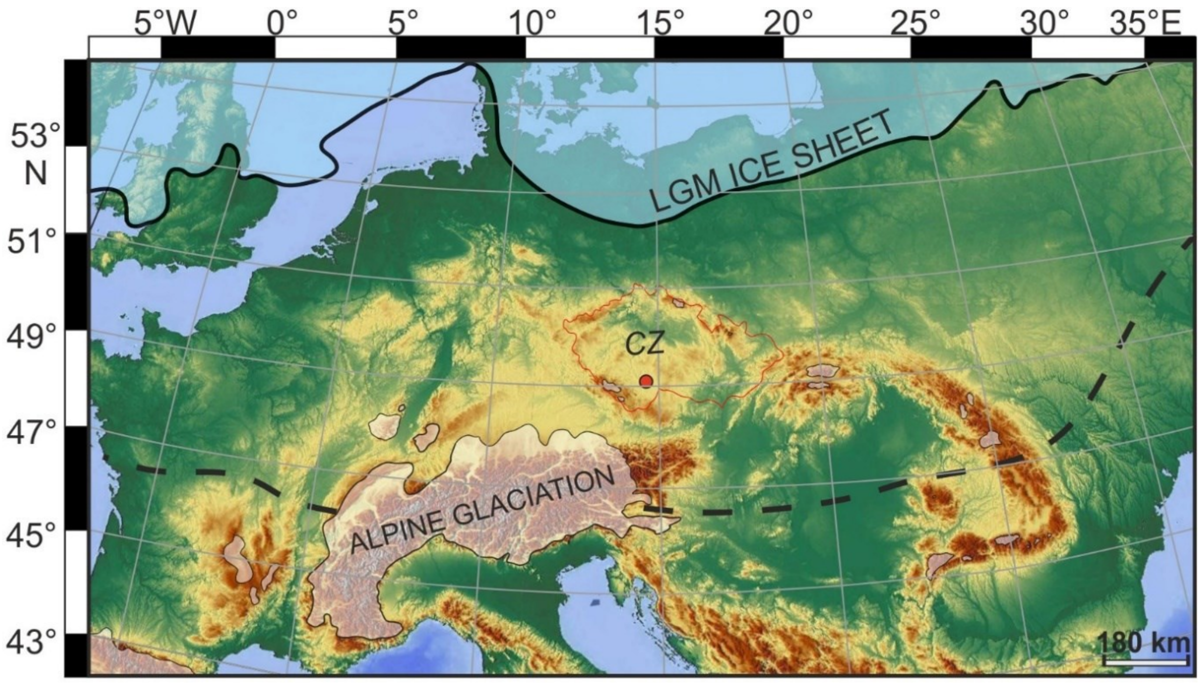

Fig. 1. *Map showing the location of the study area (red dot) within the Czech Repuplic (CZ) together with the maximal extent of the continuous permafrost (dashed line), Scandinavian Ice Sheet and Alpine glaciation during the Last Glacial Maximum, ~20 ka ago (after Vandenbergh et al. 2014 and Ehlers & Gibbard 2004).*

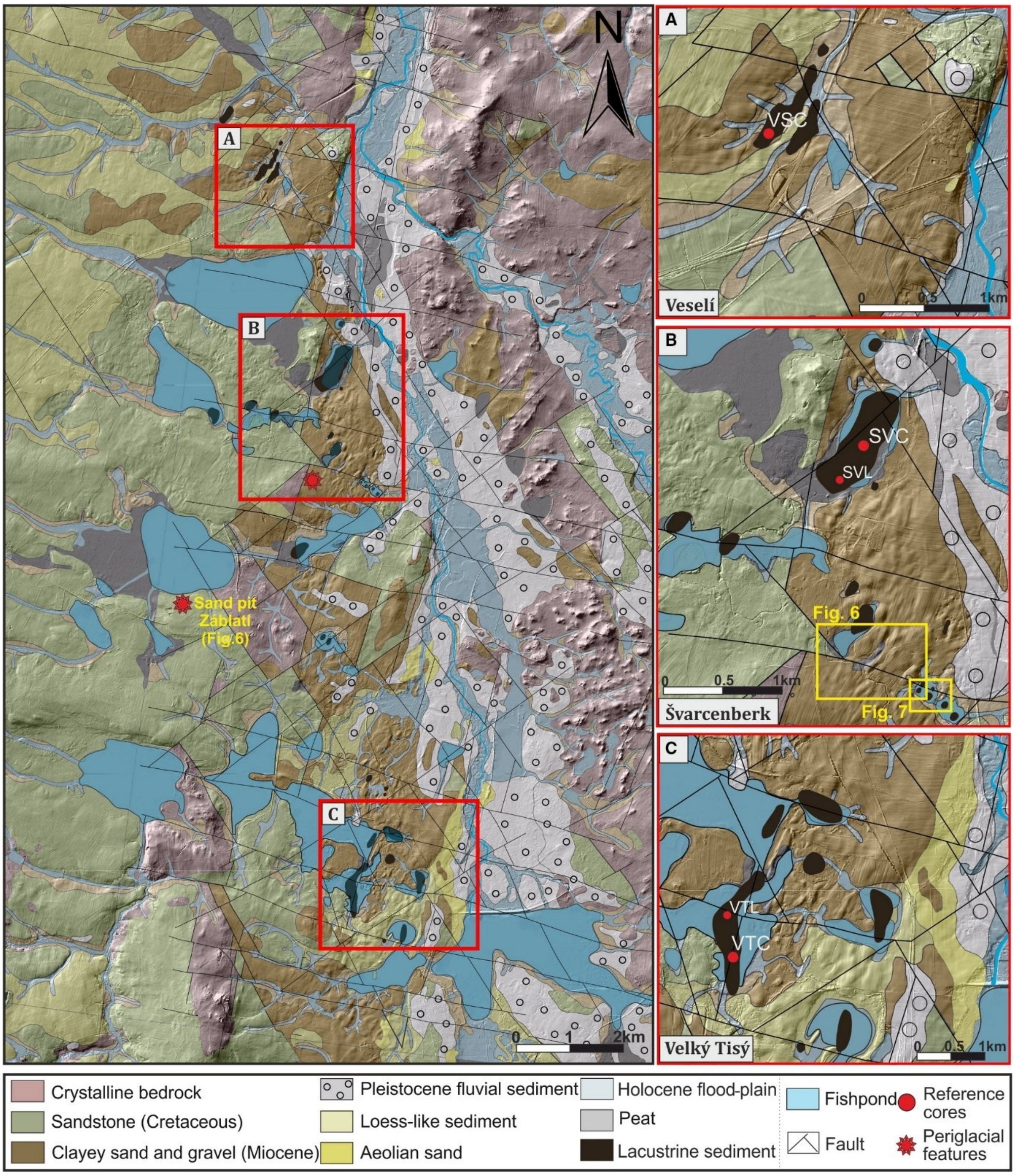

Fig. 2. *Geological map of the study area (based on Dornič et al. 1977) and the spatial distribution of Late Pleistocene lacustrine sediments. The most investigated areas in the surroundings of the, Veselí (A), Švarcenberk fishpond (B), and Velký Tisý (C) fishpond are shown in detail together with locations of sampling cores SVC (Švarcenberk Central Core), SVL (Švarcenberk Littoral Core), VTC (Velký Tisý Central), VTL (Velký Tisý Littoral) and VSC (Veselí Central).*

Periglacial deposits include loess-like sediments and stratified slope deposits. The area of loess deposits is nowadays restricted to the NW part of the study area. These deposits are 1–6 m thick, slightly sandy, and completely decalcified. Within the low-lying water-saturated terrain along the Lužnice River, loess-like sediments were preserved only in isolated islands, due to intensive decalcification and consequent erosion during the Early Holocene (Hošek *et al*. 2017b). Middle and Upper Pleistocene fluvial sandy gravels are preserved discontinuously along the Lužnice River as alluvial terraces with surfaces 5 and 8 m, respectively, above the Holocene floodplain (Chábera & Vojtěch 1972). Pleistocene fluvial sediments are partially covered by numerous aeolian sand dunes formed here during the Younger Dryas (Pokorný & Růžičková 2000).

Hydrogeology

Groundwater in the northern part of the Třeboň Basin currently flows through Cretaceous sediments from the highlands lying southeastern of this area (Krásný *et al*. 2012). Along the contact between Miocene sediments and crystalline bedrock, the groundwater flows upward to the surface along faults. Artesian springs are localized in these zones if the uppermost part of the Miocene sequence consists of sufficiently thick clayey sediment (aquitard; Kadlecová *et al*. 2016). Generally, these fine-grained sediments and a low topographic gradient both contribute to poor surface hydrological drainage across the area and promote the existence of extensive and thick Holocene peat bogs (Pokorný *et al*. 2010). These periodically or permanently waterlogged depressions were also used for the construction of large fishponds during the Early Modern Age – today, artificial ponds are an omnipresent feature of the local landscape.

Periglacial features

During the Last Glacial Maximum (LGM; ~23–19 ka, Mix *et al*. 2001) the study area was located ~110 km north of the Alpine piedmont glaciers and ~400 km from the southern edge of the North European continental ice sheet (Fig. 1). It was also deep below the LGM-equilibrium line altitude of the glaciation of the Bohemian Forest, which was about 1050–1150 m a.s.l. (Křížek *et al*. 2012; Vočadlová *et al*. 2015). Pseudomorphs of thermal-contraction-cracking features clustered into polygonal nets previously documented in the south of the Czech Republic (Kunský 1946; Chábera & Mach 1977) suggest that this region underwent permafrost evolution long enough to allow the growth of thick ground ice bodies. Thermokarst features include soft-sediment deformations (thermokarst involution), abundantly present in the poorly consolidated Cretaceous and Miocene clayey sand as well as in the Upper Pleistocene alluvial sediment. Thermokarst sediments accumulated mostly along the foothills of asymmetrical valleys with steeper slopes (Chábera & Mach 1977).

Methods

Fieldwork and imagery

The presence of lacustrine deposits at selected sites was detected using more than 500 individual boreholes performed within terrain depressions, almost all of which are currently flooded by artificial fishpond bodies. On non-flooded sites we also used Electrical Resistivity Tomography for detailed investigation of subsurface geology (for technical details, see Hošek *et al*. 2016). The extent of lacustrine deposits and the morphology of basins were mapped using hand-operated corers (25 mm in diameter) in several transects with 20 to 100 m grids across the basins. Lake sediments covered by fishponds were cored from a boat in summer and from ice during winter seasons. Due to their potential with respect to high-resolution palaeoenvironmental reconstruction, the largest lake basins – Velký Tisý, Švarcenberk, and Veselí – were studied in greater detail (220 boreholes in 42 transects) and, thus, a substantial part of the findings relating to morphology and lithostragraphy discussed below arises from observations made at these sites. Reference cores VTC, SVC, and VSC were taken from the central parts of these lakes using a pneumatic hammer-operated piston corer (tube 50 mm in diameter) and the subsampled material (bulk gyttja and plant macro-remains) was used for radiocarbon dating.

Our field interpretations were consolidated by the analysis of aerial photographs (www.mapy.cz), and the use of a high-resolution digital elevation model (DEM; the Czech State Administration of Land Surveying and Cadastre – CUZK, 1 m grid), which allowed the identification of inherited periglacial patterns at the scale of the region. As the study area has been influenced significantly by modern agricultural management and fishpond building over the last 50 years, we also used historical topographic maps and aerial photographs from the 1950s (provided by the Office of Military Geography and Hydrometeorology of the Ministry of Defence of the Czech Republic), which were produced before agriculture and fishpond management intensified and in which the shapes of several former shallow depressions in the landscape were evident. For expression of the shape of lake basins (elongated, semi-circular, circular) elongation index was calculated. The elongation index (major axis/minor axis) refers to the axes of a best-approximated ellipse with an area equal to that of the object being analyzed (Morgenstern *et al*. 2011).

Radiocarbon and OSL dating

The radiocarbon dating of plant remains and bulk lacustrine sediment was performed in order to obtain detailed stratigraphic information on the initiation and evolution of palaeo-lakes. Sediment was sampled from the profundal parts of palaeo-lakes to eliminate the effect of possible redeposition. Overall, 21 radiocarbon ages are presented in this study, some of them already published (Pokorný 2002; Hošek *et al*. 2014, 2017b; Table 1). Samples were prepared for ^{14}C accelerated mass spectrometry (AMS) and dated at the Poznań Radiocarbon Laboratory in Poland (abrr. Poz-), at the Center for Applied Isotope Studies, University of Georgia, USA (abrr. UGAMS-), and at the Radiocarbon Dating Laboratory, Department of Quaternary Geology, Lund, Sweden (abrr. LuA-; Table 1). All radiocarbon dates are presented as calibrated (ka BP) against the IntCal13 curve using OxCal version 4.2 (Reimer *et al.* 2013).

Two samples for OSL dating were taken from the sedimentary infill of a pseudomorph of thermal-contraction-crack exposed in the wall at the Záblatí sandpit (Zablati_1 and Zablati_2) and processed at the OSL laboratory at the University of Gliwice (Poland). Details on the method of pre-treatment and the measurements of samples are provided in Data S1 and Fig. S1 in Supporting Information.

Comparison of studied sections with modern thermokarst forms – criteria selection

The interpretive syllogism of the study is based substantially on comparison of our observations with known recent thermokarst landforms and structures. Nevertheless, the studied structures represent past (palaeo) features in the recent temperate region, and hence the diagnostic criteria for periglacial processes were blurred by Holocene surface re-shaping. Furthermore, almost all the studied palaeo-lakes are buried by recent fishponds, which make them unavailable for the detailed evaluation of some characteristic features and structures linked with thermokarst processes. Consequently, comparison of the studied palaeo-lakes with modern ones is based on characteristics which could be obtained by borehole investigations. These characteristics include i) basin morphology and morphometry, ii) lithostratigraphy, and iii) the palaeoenvironmental context derived from the sedimentary record.

Table 1. Results of radiocarbon dating from the Velký Tisý, Švarcenbek and Veselí palaeo-lakes:

Lab. code	Profile, depth (cm)	Type of material	^{14}C age (a BP)	Calibrated age range (cal. a BP)	Reference
LuA-4590	SVC, 390-393	Woody stem fragment	9640±115	10 801–11 147 (68%)	Pokorný (2002)
LuA-4591	SVC, 520-523	Bulk gyttja sample	10 780±115	12 654–12 877 (68%)	Pokorný (2002)
LuA-4738	SVC, 680-683	Bulk gyttja sample	11 750±120	13 464–13 813 (68%)	Pokorný (2002)
LuA-4737	SVC, 985-995	*Salix* twigs	12 800±120	14 943–15 617(68%)	Hošek *et al.* (2014)
Poz-71857	VTC, 50-52	Terrestrial plant seeds	960±30	796–886 (64.8%) 891–929 (30%)	This study
Poz-72025	VTC, 92.5	Bulk gyttja sample	3230±35	3380–3512 (84.2%) 3527–3558 (10.8%)	This study
Poz-71858	VTC, 240-242	Bulk gyttja sample	7550±50	8209–8261 (7.8%) 8294–8428 (87.1%)	This study
Poz-71859	VTC, 330-335	Bulk gyttja sample	8630±70	9487–9788 (94.1%) 9850–9861 (0.6%) 9878–9883 (0.3%)	This study
Poz-72027	VTC, 422-423	Bulk gyttja sample	9670±60	11 061–11 214 (50.7%) 10 786–10 981(39.2%) 10 986–11 033 (5.1%)	Hošek *et al.* (2017)
Poz-72212	VTC, 487-488	Bulk gyttja sample	10 840±60	12 672–12 823 (95%)	Hošek *et al.* (2017)
Poz-72071	VTC, 536-537	Bulk gyttja sample	11 250±60	13 019–13 249 (95%)	Hošek *et al.* (2017)
UGAMS-25537	VTC, 590	Bulk gyttja sample	11 400±30	13 152–13 306 (95%)	Hošek *et al.* (2017)
Poz-72028	VTC, 617-618	Bulk gyttja sample	11 730±70	13 448–13 717 (95%)	Hošek *et al.* (2017)
Poz-71860	VTC, 678-679	*Betula* (seeds)	12 000±60	13 729–14 037 (95%)	Hošek *et al.* (2017)
Poz-71861	VTC, 730-735	Woody fragment	12 240±60	13 960–14 449 (95%)	Hošek *et al.* (2017)
UGAMS-17379	VTL, 66	Plant frag.	4400±30	4867–5046 (94.1%) 5205–5210 (0.8%)	This study
UGAMS-17380	VTL, 430	Plant frag.	13 090±35	15 496–15 909 (95%)	This study
UGAMS-25536	VSC, 282.5	Bulk gyttja sample	11 890±35	13 580–13 776 (95%)	Hošek *et al.* (2017)
UGAMS-23611	VSC, 355-360	Bulk gyttja sample	11 830±70	13 534–13 772 (89.8%) 13 483–13 527 (5.2%)	Hošek *et al.* (2017)
UGAMS-23612	VSC, 420-422	*Salix/Populus* (wood fragment)	12 140±30	13 905–14 152 (94.7%) 13 880–13 884 (0.3%)	Hošek *et al.* (2017)
UGAMS-30901	VS, lake bottom	Wood	11 640±30	13 401–13 658 (95%)	This study

Table 2. Morphometric characteristics and ages of basal deposits of Velký Tisý, Švarcenbek and Veselí palaeolakes:

Site	Number of cores	Width×length×maximum depth (m)	Surface of lake sediment (km^2)	Perimeter of former shoreline (km)	Radiocarbon age of basal deposits (cal. ka BP)
Velký Tisý_1	31	970×370×12	0.2	0.23	14.3; 15.8
Velký Tisý_2	5	142×562×6.8	0.1	1.3	–
Švarcenberk	149	450×1280×10	0.44	3.1	15.3; 13.7
Veselí_1	45	130×640×6	0.061	1.6	14.1
Veselí_2	35	154×420×6	0.049	1.02	13.5

Table 3. Dose rate, equivalent dose data and OSL ages of the ice-wedge pseudomorph infill exposed at former sand pit Záblatí. H_2O % = measured water content (water mass over dry sediment mass); U = Uranium; Th = Thorium; K = Potassium:

Lab. code	Sample ID	Sampling depth (cm)	H_2O (%)	U (Bq kg^{-1})	Th (Bq kg^{-1})	K (Bq kg^{-1})	Dose rate (Gy ka^{-1})	OSL age (ka)
GdTL-3531	Zablati_1	110	15±5	30.1±0.5	53.2±0.8	384±10	2.54±0.1	58.3±2.5
GdTL-3532	Zablati_2	130	15±5	30.1±0.5	53.2±0.8	384±10	2.51±0.1	53.3±2.8

Results and interpretation

Spatial distribution and morphology of palaeo-lakes

Overall, 31 sedimentary basins were documented in the study area (Fig. 2). They were found solely on Miocene bedrock (sand/clayey sand) within poorly-drained (waterlogged) low-lying areas determined mostly by bedrock faults (Fig. 2). All of the basins are enclosed and non-ramparted.

The shapes of most basins are rather irregular, elongated, or trough-shaped (n = 16). Nevertheless semi-circular (n = 9) or circular (n = 6) shapes were also mapped. The length of the longer axis of the lake basins ranged from several meters to several hundred meters. The predominant orientation of the longer axis of most of the basins is SW-NE, in concordance with the tectonic fault system as well as with the current surface drainage system (Fig. 2). The minimum lake depth was found to be 1 m, and the maximum, 11 m, while the surface area of the current sediment of the former lakes ranged from 0.01 to 0.44 km^2.

On the basis of size and morphometric/morphologic characterization, the studied lake basins can be divided into two groups. The first group is represented by basins with an obvious elongated or trough shape, a longer axis greater than 120 m, and a depth of between 6 and 11 m (Table 3). All of these basins were found within short shallow valley-form depressions with low gradients going from slightly elevated areas of SW slopes toward the erosion base of the area, i.e. Lužnice River floodplain (Fig. 2). The orientation of the longer axes of the basins are usually parallel to the axes of the short valleys. In addition, a system of elongated elevations of Miocene bedrock and depressions parallel to the basin axes directions is typical for surfaces in the vicinity of the palaeo-lakes and denotes past fluvial activity in these zones (Fig. 2B, C).

The typical morphology and bottom bathymetry of these basins is shown in Fig. 3 and 4, on the example of the Švarcenberk (SV), Velký Tisý (VT) and Veselí (VS) palaeo-lakes. The basins are characterized by an asymmetric profile with steep slopes and a cone-like shaped bottom (see the longitudinal profiles through SV and VT palaeo-lakes). The basins can be partially divided by internal ridges into semi-separate individual depressions. This is most striking in the case of the Švarcenberk palaeo-lake, where ridges up to 3.5 m in height were found. Cross sections reveal V-shaped slopes with an internal valley in the central part running parallel with the longer axis and making a step-like profile (Fig. 3). Taking into account the location of the palaeo-lakes within short shallow valleys-form depressions, these basins could be remnants of past tributaries of the Lužnice River. However, all basins were found to be entirely enclosed and, consequently, no connection between the sedimentary sequences of the palaeo-lakes and the Lužnice River valley was found. Therefore, this possibility can be rejected (see also discussion below).

The second group of palaeo-lake basins is characterized by a generally circular or semi-circular shape with a diameter of less than 120 m and a maximum depth of 6 m. In comparison with basins of the first group, these are located farther from the down-valley axis. Cross sections revealed rather gentler slopes and a pan-like shaped bottoms (Fig. 7B).

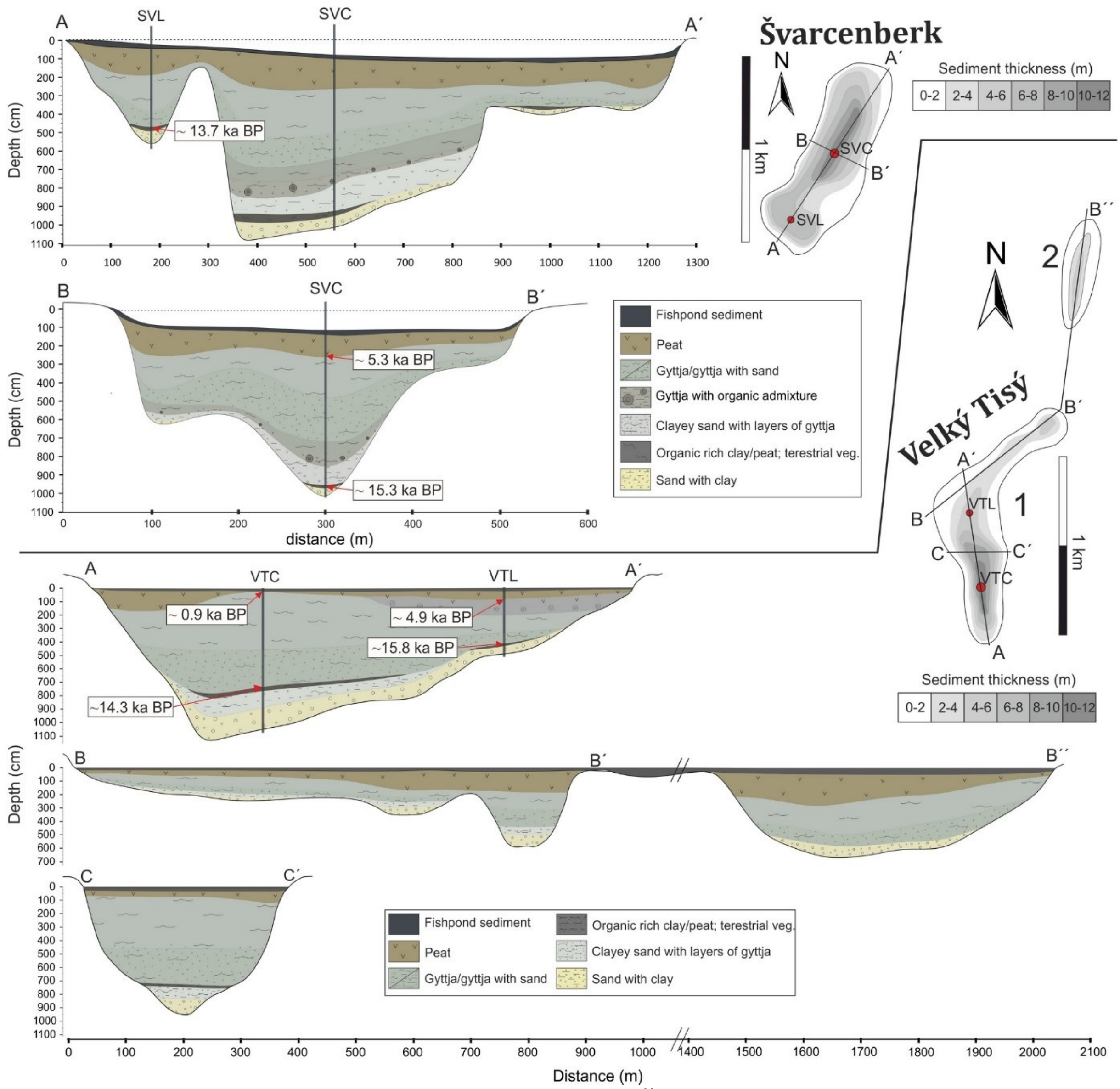

Fig. 3. *Bathymetry and stratigraphic cross-sections of the Švarcenberk and Velký Tisý palaeo-lake basins together with the locations of sampling cores and the calibrated radiocarbon ages.*

Lithostratigraphy of lacustrine sediments

Although the dating of thermokarst lake sediments has been repeatedly reported as problematic (e.g. Gaglioti *et al*. 2014), several sites from the circumpolar Arctic/Subarctic were shown to provide useful palaeoenvironmental archives (Bouchard *et al*. 2017). In our study the radiocarbon ages obtained from the plant macro-remains and bulk gyttja sediment of the largest and deepest palaeo-lakes (Table 1, Fig. 5) are in stratigraphic order and reveal continuous sedimentation throughout the Lateglacial and the Holocene. On the basis of these data and lithological characterizations, sedimentary records of the largest palaeo-lakes can be divided into three main zones (A-B-C), corresponding to major environmental changes in the study area (Fig. 5).

Zone A consists of two units: 1) minerogenic sediments (clayed sand/gravel and calcareous silt) and 2) clayey sand with layers of minero-organic sediment (gyttja). Both units have a massive structure and rather low contents of organic matter. The maximum thicknesses (up to 3 m) of these strata were found in the central parts of basins, while the thickness was reduced or even null toward the littoral zones (Fig. 3). A distinct layer of clayey peat with the remains of terrestrial vegetation was often found in impure sand within or at the surface of this sequence. It contained the remains of herbs, twigs of arctic dwarf shrubs (*Salix*, *Betula nana* in the case of the Švarcenberk palaeo-lake), and pine trunks (Veselí palaeo-lake). The radiocarbon dates of these remains of the terrestrial vegetation (Table 1) together with palynostratigraphical investigations (Pokorný 2002) revealed that zone A accumulated along the late Pleniglacial/Lateglacial transition (~16-15 cal. ka BP). Zone A represents the initial phase of the lake infill. Diamict sediments were relocated into the lake basin by surface erosion and slope processes. They also could originate from retrogressive slumps of the thawing sides of the lake and can be considered as thermokarst sediments which are colluvial in nature and consist of a range of locally redeposited and heterogeneous materials, or diamictons, which often incorporate clumps of organic material (see also Murton 1996). The source of allogenic components consisted primarily of exposed Miocene and Cretaceous sediments in the catchment. An additional source was likely loess washed from watersheds, as indicated by the high concentration of medium/coarse silt and the substantially-elevated concentration of calcium in these sedimentary strata (Hošek *et al*. 2017b).

Zone B consists of a sequence of organo-mineral deposits (fine-detritus gyttja), up to 8 m in thickness. In the lower part of this zone, an increased input of allochthonous material (fine-grained sand and silt) mixed with the remains of terrestrial vegetation was usually found (subzone B_1), whereas in the upper part the strata are characterized by quiet lacustrine sedimentation (subzone B_2). On the basis of radiocarbon dates obtained from plant macro-remains and bulk gyttja sediment, zone B corresponds to the Lateglacial.

The above lying zone C corresponds to the Holocene. The lithology of this zone is characterized by the presence of coarse-detritus gyttja with high contents of organic matter and low allochtonous input. In most cases, the lacustrine sediments are overlain by a layer of ligno-herbaceous peat 1-3 m in thickness (Fig. 5). This lithological switch points to a change in depositional conditions, from lacustrine to terrestrial, which occurred in the Middle Holocene (~4.9 cal. ka BP according to radiocarbon dating).

The palaeo-lakes from the second group exhibited similar lithostratigraphy to the largest palaeo-lakes. However, the thickness of the lacustrine/thelmatic sediment (zone B) was reduced (usually <1 m) and most of the infill was formed by peat (zone C).

Overall, the lithostratigraphy of the studied lakes shows a similar pattern to the sedimentary sequences of most thermokarst lakes. Sediments of recent thermokarst lakes can usually be divided into two general formations (Czudek & Demek 1970; Farquharson *et al*. 2008): (i) basal high-energy colluvial sediment with a massive structure dominated by upland material from bank thaw and collapse events (correlated with zone A), and (ii) an above-lying low-energy central basin environment dominated by lacustrine sediment and peat (zones B and C).

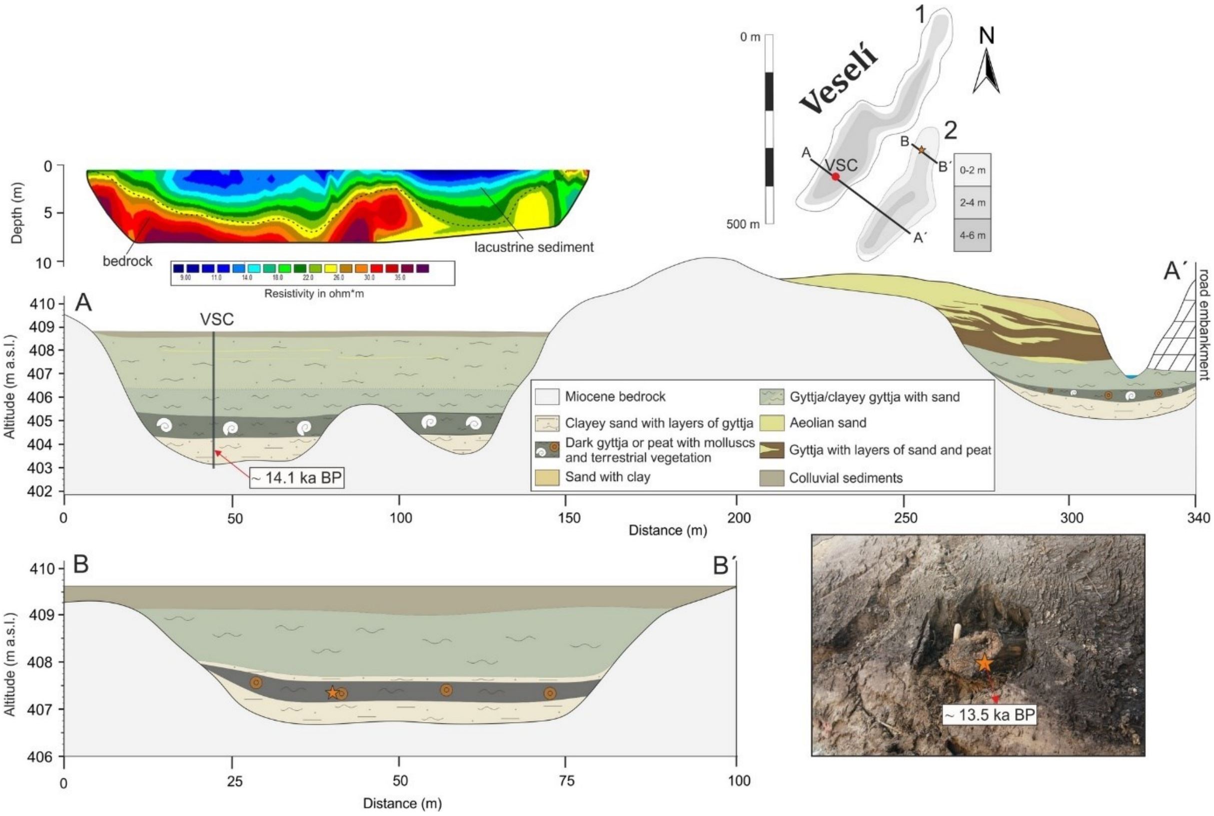

Fig. 4. *Bathymetry and stratigraphic cross-sections of the Veselí_1 and Veselí_2 palaeo-lake basins together with the results of Electrical Resistivity Tomography (adopted from Hošek et al. 2017b), the location of the VSC sampling core and the calibrated radiocarbon ages. The red star refers to the location of the pine branch within the lacustrine sediment exposed in a temporary artificial outcrop (the photograph's bottom right).*

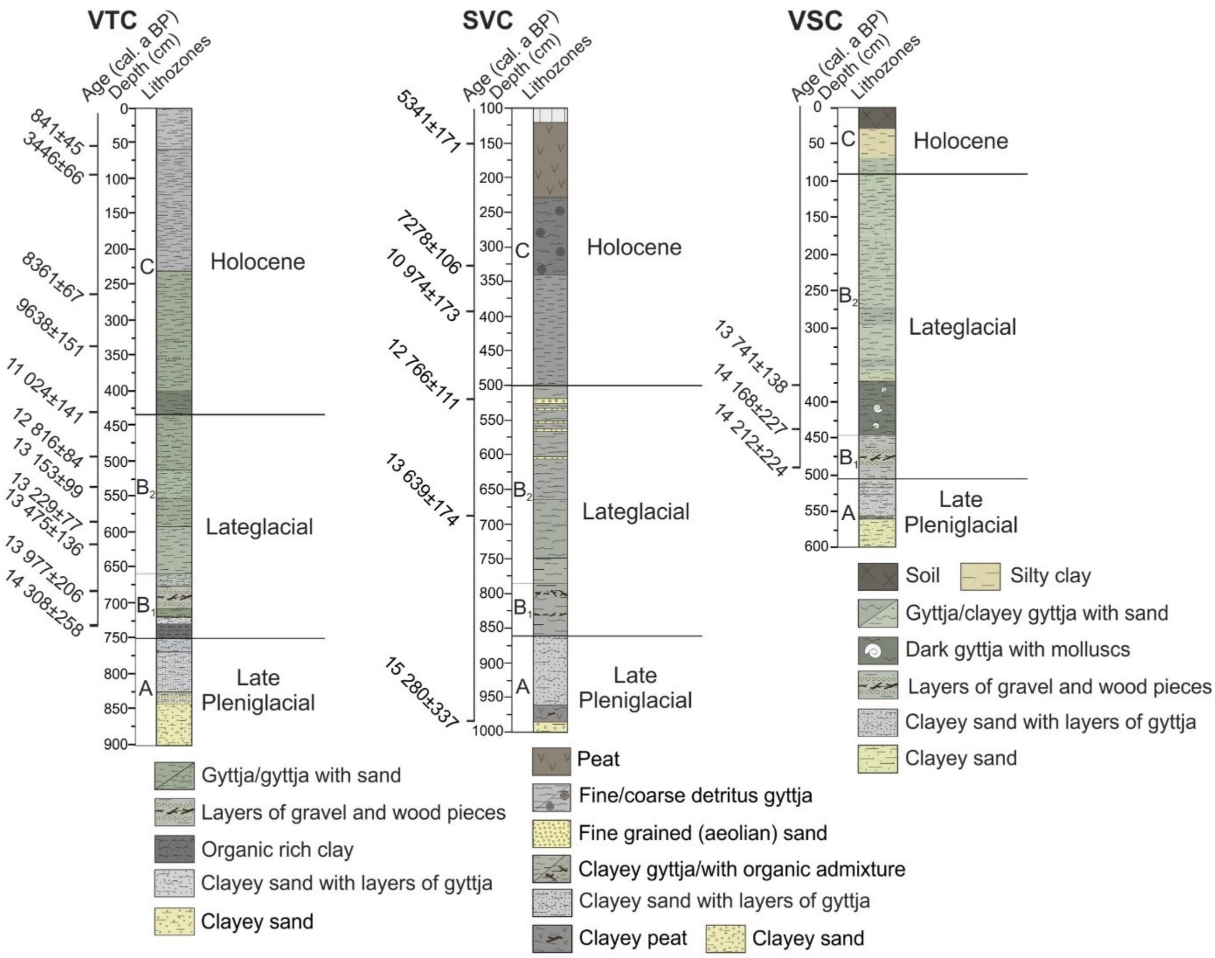

Fig. 5. *Lithology and radiocarbon ages of references cores VTC, SVC and VSC.*

Interpretation and dating of periglacial features

A 153-cm high and 120-cm wide structure exposed in the wall of the Záblatí sand pit (Fig. 6C) was interpreted as pseudomorph of thermal-contraction crack. The host material was unconsolidated sand and gravel of Cretaceous sediment. The pseudomorph infill consisted of sandy silt with larger clasts (up to 2 cm in diameter), which were mostly vertically aligned along the walls of the pseudomorph. The infilling material was loess, which had been (re)deposited in the wedge together with surrounding sand and gravel by both aeolian and colluvial processes. Two OSL samples obtained from the sediment infilling (Fig. 6C) yielded ages of 53.3±2.8 and 58.3±2.5 ka (Table 2), dating the formation of the pseudomorph of thermal-contraction crack to the Early/Middle Pleniglacial (MIS 4/3). The OSL age of the pseudomorph corresponds to the one period of permafrost formation (~60 ka) in northern France described by Bertran *et al*. (2014). Although no direct evidence of the existence of permafrost during the Late Weichselian (MIS 2) was obtained, its presence in the study area was very likely, since, in central Europe, MIS 2 is reported to have been a significantly colder phase of the Weichselian glacial than MIS 4 (Huizer & Vanderberghe 1998).

Hexagonal thermal-contraction-cracking features (10–25 m in diameter), visible in fields in aerial photographs (Fig. 6A), were interpreted as having a polygonal pattern (Liljedahl *et al*. 2016; Kanevskiy *et al*. 2017). Most of the observed polygons had sharp edges, which, in aerial photographs, appeared darker than the surrounding land. However, some polygons had more rounded outlines and were delimited by wide depressions or furrows, which may correspond to former thermal-contraction-cracking features that underwent thermokarstic degradation (Bertran *et al*. 2014; Andrieux *et al*. 2018). Larger terrain depressions often appeared irregularly covered with subcircular or elongated dark places, a few meters to 100 m in length (Fig. 6A). This geomorphologically-determined distinction is clearly visible in historical maps and photographs, since the wet sites, interpreted as thermokarst depressions, were used as meadows, while arable fields were limited to the elevated and thus drier areas (Fig. S2). On the basis of borehole investigations, dark spots up to 3 m in depth corresponded to wet organic-rich fine-grained sediment or peat with minero-clastic diamicton deposits at the base, whereas light spots indicated the coarser well-drained sediment of bedrock. These structures could be remnants of "sediment-filled pots" (Conant *et al*. 1976; French *et al*. 2003), which presumably formed at the intersection of two or more wedges by a combination of thermal erosion and the mixing, slumping, and redeposition of material from both the wedges and the enclosing sediments. The modern permafrost analogue is the "thaw sink" (Hopkins 1949; French 2017).

The mound-like topography observed in the surroundings of some palaeo-lakes can also be interpreted as the remnants of degraded thermal-contraction-cracking features (probably ice-wedges) (badland thermokarst reliefs; Kokelj & Jorgenson 2013; Steedman *et al*., 2016), and the shallow valleys between these reliefs are likely to be meltwater channels (Fortier *et al*. 2007).

In the upper part of the exposed wall at the Záblatí sand pit, distinct large deformation structures occurred in unconsolidated diamicton (grey sandy gravel with silt) above the compact, white sandstone/conglomerate (Fig. 6B). They included ball-and-pillow structures of sand and silt, ~0.6 high and 0.5 m wide, round-topped diapirs of melt-out diamiction up to 1.2 m high and 1 m wide, and other types of cryoturbations in the uppermost part of the outcrop. We interpreted these structures as thermokarst involutions, formed by loading and liquefaction in the permafrost active layer.

Fig. 6. *A. Aerial photograph (source: mapy cz, year 2015) showing distinct structures visible on the agricultural field (49.12°N, 14.7°E) between thermokarst basins (TB) interpreted as permafrost-related features. The structures include hexagonal polygonal nets and asymmetric permanently wet depressions filled by organic-rich fine-grained sediment or peat. B. An outcrop in the former sand pit near Záblatí (49.1°N, 14.67°E) exposing the Cretaceous conglomerate and an upper layer of unconsolidated sandy gravel with silt. The unconformity between these units was interpreted as the base of the palaeo-active layer; accordingly, the sediment deformations visible in the upper part of the outcrop probably occurred during the deepening of the active layer and were interpreted as thermokarst involutions. C. The pseudomorph of thermal-contraction crack, 1.5 m deep and 1.2 wide, filled by sandy silt (redeposited loess) dated by OSL at ~55 ka.*

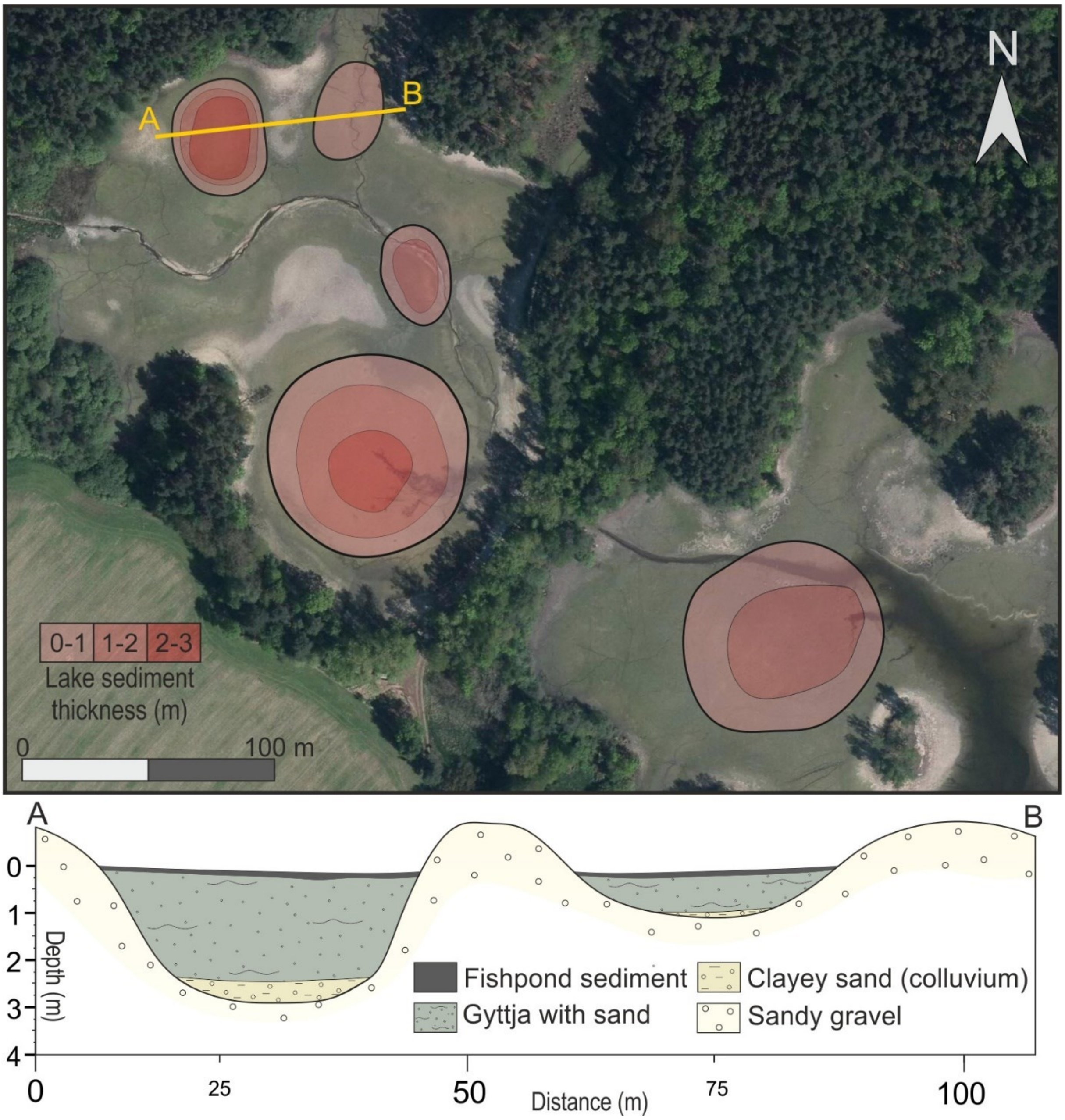

Fig. 7. *Aerial photograph (source: CUZK, year 2013) showing the Blatný fishpond during the low water table stage. Several circular, up to 3 m depth palaeo-lake basins were mapped between distinct crescent-shaped sandy bars. Stratigraphic cross-sections of two palaeo-lake basins at the Blatný site (yellow line) are shown below.*

Discussion

The remnants of thermal-contraction-cracking features, pitted and undulating topography, or structures interpreted as thermokarst involution (Fig. 6A, B) indicate the previous existence of ice-rich permafrost in the study area as well as past thermokarst landforms resulting from its thawing. Irregular, non-ramparted depressions are the most ubiquitous forms resulting from local thermokarst processes. In a broad sense, thermokarst forms originate from climate-induced and site-specific causes (Toniolo *et al*. 2009). With regard to climate change, the main factor is an increase in ground surface temperature that alters the thermal balance. In mid-latitudes of Europe the onset of the Lateglacial was accompanied by a significant increase in temperature as well as precipitation (Walker 1995; Huijzer & Vandenberghe 1998) and subsequently by permafrost degradation within the former periglacial zones (see Vandenberghe *et al*. 2014 and references therein), with the local development of thermokarst features including shallow depressions filled by alluvial and/or colluvial sediments (Bertran *et al*. 2014). We propose that the amelioration (overall warming) of the climate was, similarly as in recent thermokarst regions, the fundamental trigger of intensive thermokarst processes and thermokarst lake development in the study area.

Site-specific conditions influence the patterns and amount of thermokarst settlement or the loss of surficial material. These processes are related mostly to the quantity and type of ground ice (Shur & Osterkamp 2007; Wolfe *et al*. 2014), local hydrology, and terrain configuration (Jorgensen 2013). Therefore, to understand the thermokarst processes in the Třeboň Basin, we need to take into account the geological, hydrogeological, and geomorphological contexts of the study area as well as the palaeoenvironmental conditions along the Late Pleniglacial – Lateglacial transition.

Massive ground ice formation

Due to a lack of information on cryostructures and ground icing in the study area, the type of ground ice can be only estimated on the basis of current hydrological and geological settings. All the studied palaeo-lakes, as well as most of the periglacial features identified from aerial photographs, are located within poorly-drained low-lying areas. These water-saturated zones are derived mostly from bedrock faults with structural controls on groundwater upwelling, in some cases artesian. We assume that during the cold conditions of the Late Pleniglacial, subsurface ice had its highest occurrence along these zones. All basins were formed in Miocene sediments which consist of layers of sandy/silty clays, clayey sands, and sandy gravels with the thickness of particular lithologies varying from several decimetres to several meters. In this sequence, frost-susceptible fine-grained sediments (i.e. layers of silty clay and clayey sand) were particularly prompt in impelling unfrozen water to the freezing front (Wu *et al*. 2012). This action could have induced the formation of discrete bodies of segregation ice (Rampton 1988) and/or intrusive ice, when groundwater was under (artesian) pressure (Mackay 1989; Mackay & Dallimore 1992). Observations from current permafrost areas (e.g. Moorman 1998) imply that such geohydrological conditions could promote the formation of ice lenses up to several meters in thickness, eventually heterogeneous tabular and/or folded massive ice bodies parallel to the ground and subsurface structures. In contrast to the deepest and largest basins formed in the central parts of palaeo-valleys, thermokarst lakes located farther from the down-valley axis tend to be rather shallow, probably because of near-surface ice segregation and shallow ice ground.

Formation of palaeo-thermokarst depressions

Pingo and lithalsa scars. – Keeping in mind the assumed hydrological and climatic conditions of the region, the formation of perennial frost mounds, including both open-system (hydraulic) pingos and mineral palsas (lithalsas), can be expected.

Collapsed forms of these structures have the greatest potential for preservation in the fossil record (French 2017) and have previously been described from numerous sites in the past permafrost zone of north and northwestern Europe, for example in Wales (Watson 1971; Ross 2011), England (Watson & Watson 1972), Scandinavia (Svensson 1971; Seppälä 1972), Denmark (Svensson 1961), Belgium (Pissart 2000), Poland (Dylik 1965), northern France (Van Vliet-Lanoë *et al*. 2016), and the Netherlands (Hoek & Joosten 1995). Both structures usually comprise circular or oval-shaped depressions with flat floor. They are usually surrounded by a rampart, although need not be necessarily present due to either deposition in the scar depression or erosion of the rampart (Flemal 1976). Diameter ranges from several tens (lithalsa) to several hundreds of meters (pingos) (Áhman 1976; Harris 1993; Mackay 1998), depending on the size of the ice core and the amount of material that is relocated to the margins through mass wasting (Wolfe *et al*. 2014).

From this point of view, basins of the second group show some morphological similarities to typical lithalsa or pingo scars, since they are obviously circular with a pan-like shaped bottom (Fig. 7). A possible explanation for the absence of distinct ramparts in the surroundings of the investigated lakes could be human action, which completely disturbed the original geomorphology of the sites during the construction of the fishponds and over six centuries of intensive agriculture practices. This was previously documented in areas of cultivation, for instance from England (Watson 1972) or Paris Basin in France (Pissart 1960), where ramparts were lowered or completely destroyed and overall micro-relief strongly blurred. Another explanation of lacking ramparts may be removing by natural processes such as slumping into the depression or lateral erosion by wave activity, mechanism described from current Arctic areas (e.g. Müller 1964; Wünnemann *et al*. 2008). The impure sand and gravel of the basal sediments (zone A) could partially originate from the original rampart rims destroyed during the later phase of the thermokarst activity in the region (see also discussion below). Relicts of potential ramparts could be preserved at the Blatný site. When the water level of the fishpond is low, distinct crescent-shaped sandy bars are visible (Fig. 7A). These bars separate several circular depressions up to 3 m in depth, which are filled by lacustrine sediments and peat (Fig. 7B).

However, neither the morphometry nor the morphology of the largest investigated basins (the first group) match the typical remnants of pingo/lithalsa scars, since these basins tend to be rather elongated and irregular in shape, with a V-shaped profile (Figs 3, 4). These findings point to the action of another thermokarst formation process as well as a different post-formation history of erosion and deposition. Given that all these basins are associated with shallow valley-form depressions (Fig. 2), it is possible they could have been influenced by processes of fluvio-thermal erosion. The conceptual model of such palaeo-lakes formation is presented in Fig. 8 on the example of the Švarcenberk palaeo-lake.

Fluvio-thermal erosion

Obviously elongated asymmetrical basins of the first group are located within linear shallow depressions, going from slightly elevated areas of SW slopes toward the axial (Lužnice) river floodplain (Fig. 2). These structures were presumably formed during the Late Pleniglacial, and could be the remnants of short palaeo-tributaries of the Lužnice River braided plain (Chábera & Vojtěch 1975). The drainage of slopes likely occurred preferentially along the zones with ice-rich ground (Fig. 8A). This is a readily identifiable feature of arctic lowland terrain resulting in the common thermokarst landform known as beaded streams (Merck *et al*. 2011; Jorgenson 2013; Arp *et al*. 2015). Beaded streams are generally associated with ice-wedge polygons and locally with massive ground ice and thaw lakes (Washburn 1973). When streams pass over networks of ice-wedges or massive ice, the thermal properties of the flowing water cause complete ground ice degradation, producing elliptical or irregularly shaped pools and thaw pits often connected by long runs (Oswood *et al*. 1989; Arp *et al*. 2015). The highest intensity of thermal erosion and thus the deepest ground ice degradation occurs within low-gradient parts of channels.

The melting of ice and thereby ground subsidence could have been intensified at the beginning of the Lateglacial (Fig. 8B), during periods of climatic amelioration, when surface water discharges were increasing and permafrost was degrading. Increased flow through the valleys was likely connected with lateral and vertical erosion (scour) and the coalescence of separated pools, permafrost scouring usually resulting in the formation of irregular depressions often three to five times deeper than the confluent channels (Rice *et al*. 2008). The strength of bedrock deposits along zones of thawing ground was reduced due to elevated pore pressures, rendering them vulnerable to erosion along channel forms, whereas permafrost zones with low contents of ground ice provided cohesion for bed sediments. This heterogeneous fluvio-thermal erosion could have resulted in the formation of discontinuous gullies. It might also explain the elongated (up to 1 km in length) enclosed morphology of the studied basins. Similar thermokarst processes and landforms were observed, for instance, on Bylot Island in northern Canada (Godin & Fortier 2012) and are suggested to be the driving mechanism for the formation of non-ramparted, up to 15 m deep, elongated depressions ("hollows") described from the former periglacial zone of England (Berry 1979; Banks *et al*. 2014).

Surface subsidence in zones of ice-rich permafrost together with the incision of the Lužnice River at the transition from the cold Pleniglacial to the warmer Lateglacial (Chábera & Vojtěch 1975) led to the disconnection of former streams from the Lužnice floodplain and the sudden change in the hypsometric curve of the stream. The shift of the erosion base toward SW slopes was likely accompanied by backward erosion (Fig. 8B) within developed basins resulting in the formation of steep north-facing slopes revealed at the SV and VT palaeo-lakes (Fig. 3). Water flowing into the depressions was able to amplify the deepening and longitudinal extension of some basins and to cut downward into its bed. The remnants of this process could be internal valleys in the central part running parallel with the longer basin axis (Figs. 4, 5).

The central parts of basins were filled with relocated terrigenous sediments (in some cases, with admixtures of terrigenous plant remains), originating from the watershed of the channel and thaw slumps on adjoining thermokarst slopes. The sedimentation of basal deposits was likely followed by the accumulation of water in initial depressions, as indicated by the presence of aquatic plant macrofossils or Cladocerans (Pokorný 2002). The formation of a perennial water body in the depressions could have significantly intensified thermokarst processes as a result of its asymmetrical heat exchange during warm and cold seasons, resulting in heat accumulation under the water and the development of taliks under the deepening lakes.

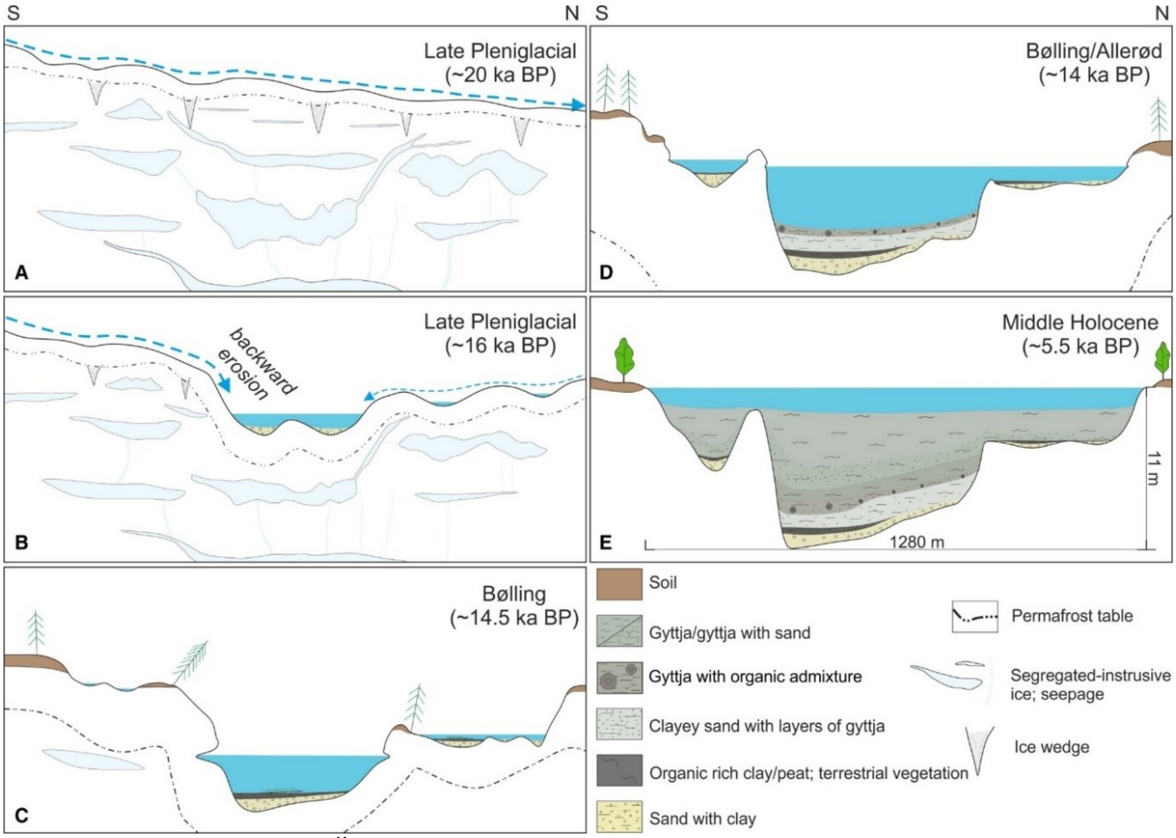

Fig. 8. *Conceptual model of Švarcenberk palaeo-lake formation and evolution; see text for explanation.*

Evolution of lakes in the context of Lateglacial environmental change

The possible mechanism of the formation of palaeo-lake basins, derived mostly from their morphology, was outlined above. The following section provides a chronological framework for their evolution obtained from their sedimentary record.

The initial phase of thermokarst activity in the Třeboň region (Fig. 8B) occurred shortly before ~16 ka, as indicated by palynostratigraphy of the basal sediment of the Švarcenberk palaeo-lake (Pokorný 2002). This can be correlated to the Weichselian Pleniglacial-Lateglacial transition dated in central Europe to around 15 ka (Willis et al. 2000). A sudden increase in air temperatures and precipitation, datable to the onset of the Bølling interstadial (~14.6 cal. ka BP; GI-1e in NGRIP; Björck *et al*. 1998), promoted the rapid deepening of depressions (Fig. 8C). Thermokarst basin subsidence and increasing water depth facilitated the accumulation of lacustrine sediment (fine/coarse detritus gyttja). In many of the studied lacustrine sedimentary records, autochtonous lacustrine sediment alternates with distinct layers of a sand/terrestrial vegetation admixture, which points to a fluctuating lake level and/or the ongoing erosion of lake banks. It also indirectly indicates that the soil surface in the research area was rather unconsolidated and thus vulnerable to erosion.

A decrease in allochtonous components together with the high content of aquatic plants found in the B_1 subzone (Pokorný 2002; Hošek *et al*. 2017b; Žáčková, unpublished data) indicate lacustrine sedimentation with a minimum input of slope material. This distinct change in lacustrine sedimentation corresponds to the onset of the Allerød interstadial and suggests that the main phase of the development of the largest lake basins was established shortly after ~14 cal. ka BP. Consequently, the initial phase of thermokarst subsidence and lake growth must have occurred rapidly during less than one thousand years. This is in concordance with many observations from recent thermokarst regions, where the active phase of thermokarst subsidence is assumed to have been a short-term catastrophic event occurring over a few centuries or even decades (e.g. Ballantyne *et al*. 2018).

Although the deepest parts of the largest thermokarst lakes were formed before the Allerød, thermokarst activity in the study area probably continued also during later phases of the Lateglacial. As indicated by varied palaeoenvironmental records from the study area (Pokorný 2002; Pokorný *et al*. 2010; Hošek *et al*. 2014, 2017b), the Allerød interstadial (~13.8–12.7 cal. ka BP BP; GI-1c) was warmer and significantly wetter compared to the preceding periods. This climatic amelioration likely promoted further permafrost degradation and caused the second (minor) phase of thermokarst activity in the study area. In central Europe, a discontinuous/sporadic permafrost table is assumed to have existed during the Lateglacial (Isarin 1997; Huizer & Vandeberghe 1998). In this environment, reshaping of the existing lake basins occurred and lithalsa scars could form, as indicated by the results of the relative dating of the basal lacustrine sediment of some lake basins of the second group, which suggest Lateglacial (Allerød?) or even Early Holocene age (Hošek *et al*. 2013). Furthermore, the radiocarbon date of ~13.7 cal. ka BP (wood) from the interface between gyttja and basal sands in the lakeshore sediments of the Švarcenberk site (Fig. 3, Table 1) suggests that this part of the lake, semi-separated from the main basin by a distinct ridge (Fig. 3), had developed by the end of the Bølling or at the very beginning of the Allerød (Fig. 8D). Consequently, the final shape of the Švarcenberk palaeo-lake was likely established after this date by the coalescence of two basins during a sudden increase in the water table. An increase in lake level correlating with the Allerød was documented in many boreholes on the basis of changes in sediment lithology and composition (e.g. the dominance of fine detritus gyttja and the algal record; Pokorný 2002; Hošek *et al*. 2016, 2017). At the Veselí_2 palaeo-lake (Fig.4), the rise in lake level at the onset of the Allerød was accompanied by the lateral expansion of the lake surface and subsequently by the flooding of adjacent banks and their intensive erosion. This is indicated by the distinct layer of trunks and large branches of pine found within colluvial sediment and dated to ~13.5 cal. ka BP (Fig. 4). It is reminiscent of observations from recent permafrost regions, where the early development of thermokarst depressions was usually accompanied by the submergence of nearby standing trees (Fig. 8C; Czudek & Demek 1970; Vitt *et al*. 1994). During the lateral expansion of the lake surface and reshaping of the basins destruction of potential ramparts of some basins could occurred.

With the advent of the ***Younger Dryas*** stadial (~12.7 cal. ka BP; GS-1), rapid cooling accompanied by a decrease in precipitation occurred throughout central Europe (Roberts 2014). In the study area, climatic deterioration had a significant impact on both biotic and abiotic processes (Pokorný 2002; Hošek *et al*. 2014), resulting in sparser vegetation cover, and consequently an increase in the input of allogenic material to lake basins (Hošek *et al*. 2017b), as manifested in the high silt content and/or intermittent-to-common silt laminae within lacustrine sediments (Fig. 5). Overall, colluvial and aeolian sedimentation together with physical weathering processes prevailed. The surface was intensively remodelled by cryoturbation, as documented in the area of archaeological excavation at the former shore of the Švarcenberk palaeo-lake (Šída 2013). Wedge structures and cryoturbation phenomena observed throughout the Bohemian Massif (Czudek 2005) suggest the occurrence of at least sporadic permafrost or deep seasonal frost during the Younger Dryas, although permafrost aggradation is rather unexpected at these altitudes during this stadial (Isarin 1997). Some small-size enclosed depressions and hollows abundant throughout the study area could have resulted in intensive landscape remodelling and the final retreat of permafrost (or seasonally frozen ground), which culminated along the Pleistocene-Holocene transition (~11.7 cal. ka BP). These small depressions or thermokarst bogs were filled by colluvial sediment and later, during the Early/Middle Holocene, by peat.

Conclusions

Dozens of large basins and enclosed depressions filled by colluvial deposits, lacustrine sediments, and peat were discovered at the southern limit of the former European permafrost zone. We assume that formation of these basins is the result of a complex of several interdependent thermokarst processes which occurred along the Weichselian Pleniglacial-Lateglacial transition and during the Lateglacial. These processes include the thermal and fluvio-thermal erosion of ice-rich permafrost zones and the consequent formation of discontinuous thermokarst gullies and possibly pingo or lithalsa scars. The development of these rare post-thermokarst landforms was possibly the result of a specific regional geological and hydrogeological setting. The formation and subsequent stabilization of the lakes was climatically driven and had two phases, with the major phase at the onset of Pleniglacial/Lateglacial warming and rise in precipitation (~16–15 cal. ka BP BP) and the minor phase during the Lateglacial climatic oscillations (~14.7–11.7 cal. ka BP). This study contributes the knowledge on the palaeogeography of the former European periglacial zone by showing that Late Pleistocene thermokarst activity could have had a significant impact on the landscape evolution of some regions of central Europe along the southern limit of the continuous permafrost zone. Such findings also point to the involvement of similar processes of physical landscape transformation with respect to the former European periglacial zone and current thermokarst landscapes of the Arctic.

Supporting Information:

Additional Supporting Information may be found in the online version of this article at http://www.boreas.dk.

Fig. S1. Relative probability density functions for samples from Záblatí.

Fig. S2. Approximate extent of the lake sediments (red line) determined by hand boring.

Data S1. Optically stimulated luminescence dating.

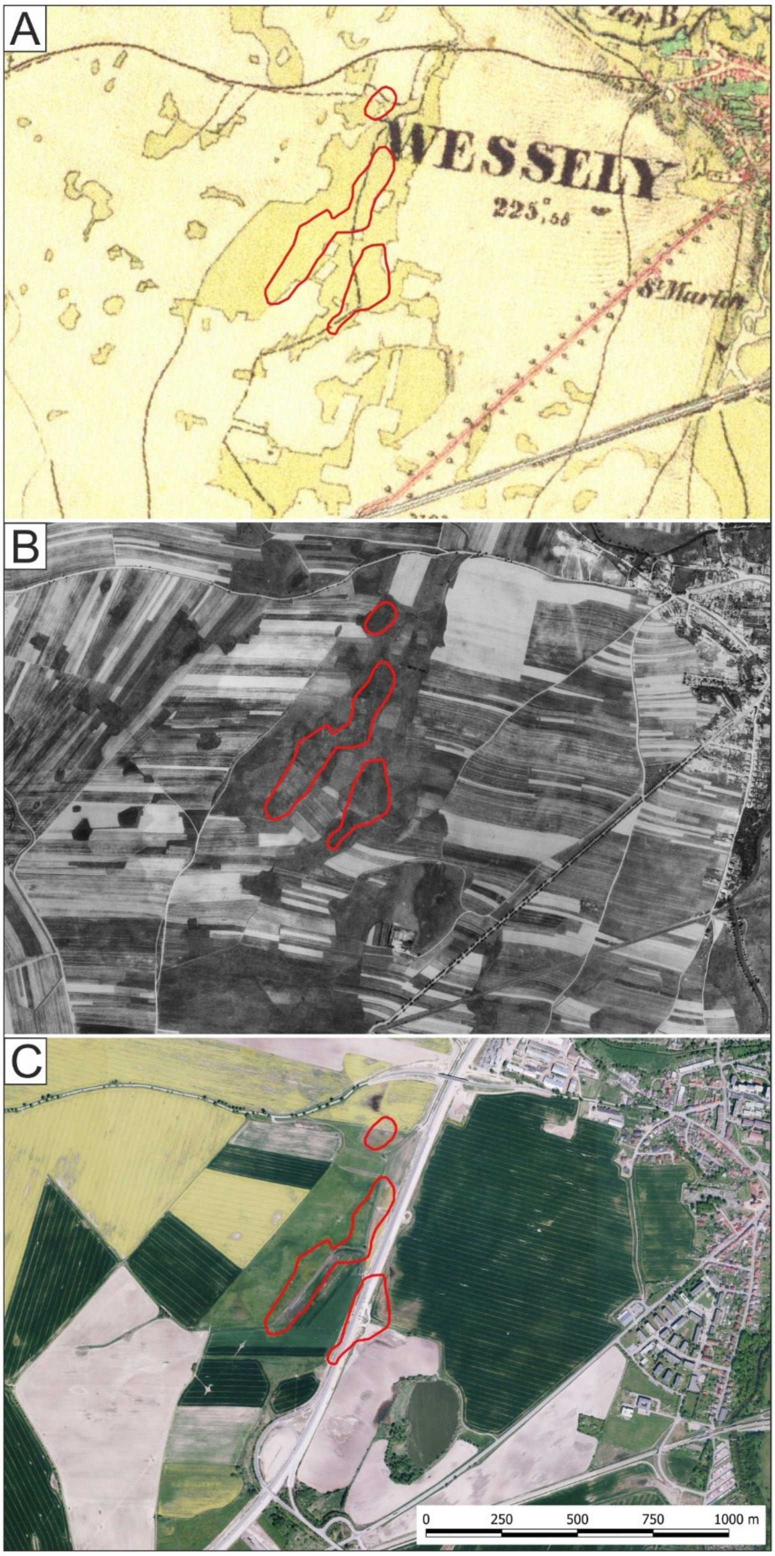

Fig. S2: *Aproximate extend of the lake sediments (red line) proofed by hand boring. The locality near Veselí nad Lužncí town in the northern part of desribed burried tharmokarst landscape. Historical map (A) from 19. century (Second military survey of the Habsburg Empire) shows the fine mosaic of arable fields (in white) and meadows reflecting wetter area in shallow basins (in yellow). Historical aerial photo from 1953 (B) shows remaining morphology of the area, where darker sides are wet meadows in thermokarst depresiions. Nowdays (C), the area and its fine relief is strongly shaped by intensive agriculture practises.*

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case study 3

Late Glacial erosion and pedogenesis dynamics: Evidence from high-resolution lacustrine archives and paleosols in south Bohemia (Czech Republic)

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Abstract

Sediments from three paleolakes and two paleosol horizons in south Bohemia, Czech Republic, provide evidence of climate change and landscape evolution in central-eastern Europe on millennial to centennial timescales over the Late Glacial (~ 16 – 11.5 ky). Based on a combination of geochemical, sedimentological and geophysical proxy indicators, along with the pollen record and soil micromorphology, we propose a relationship between vegetation cover, soil development, and erosional processes. Four major and two minor environmental stages, identified in all investigated paleo-lakes, were broadly correlated with the Late Glacial climatostratigraphy. Short-term (decadal to centennial) climatic deteriorations between the Bølling and Allerød, and within the Allerød, have been correlated with the Older Dryas and the Intra-Allerød Cold Period (IACP) respectively. B horizons of two (gleyic) podzols discovered under aeolian sand dunes in the lake catchments were dated to the Allerød interstadial and were parallelized with Usselo soils – pedostratigraphical marker horizons of west- and northern-central Europe. The upper parts of these soils have signs of colluvial processes. According to the radiocarbon dating, the erosion occurred at 13,155 ± 150 cal. yr BP and can be associated with the IACP event, which is marked by a significant input of allogenic material into the lake basins. We attribute the significant increase in the iron and consequent phosphorus content in the lake sediments during the Allerød to the podzolization that occurred with the humid interstadial conditions.

Key words: Late Pleistocene; landscape evolution; climate; lake geochemistry; soil micromorphology; podzolization

Introduction

As demonstrated by numerous paleoenvironmental studies worldwide, changes in climate regimes associated with the Late Glacial (LG) period (~ 16 – 11.5 ky ago) caused deep ecosystem conversions and evoked distinct interactions within and between the different components of terrestrial environments (Roberts, 2014).

Although most research has demonstrated the effects of the LG climatic oscillations on the biological components of the environment (Firbas, 1949; Watts, 1979; Amman and Lotter, 1989; Amman et al., 1993; Goslar et al., 1993; Hoek 1997), significant insight into the LG climatic and, consequently landscape, dynamics can also be gained by the study of the associated erosion and pedogenesis dynamics. These processes are directly connected with climatic changes: the more favourable climatic conditions would usually favour pedogenesis, greater soil-binding by the denser vegetation, and the limiting of surface erosion, while cooling conditions tend immediately to cause surface instability, limited chemical weathering, increased erosion, and reinforced aeolian activity (Engström and Wright, 1984).

Some studies have shown that lacustrine sediments are able to record physical erosion, weathering, and soil development (Bakke et al., 2010; McKay and Kaufman, 2009; Rosqvist and Schuber, 2003; Simonneau et al., 2014).

In a Pan-European context, the most straightforward evidence on the LG climatic oscillations (including the minor cooling episodes such as the Older Dryas or Intra-Allerød Cold Period) has come from the North-Atlantic (NA) region; further into the European sub-continent, namely into central-eastern Europe (hereafter CEE), the impact of these short-term climatic episodes has as yet been poorly documented. This could be due to: (1) geographical position, since the N and NW Europe is supposedly more heavily influenced by the hydroclimatic changes in the NA; and/or (2) the relative scarcity of suitable CEE sedimentary archives, such that would cover the complete period of the LG in sufficient resolution, compared to N and NW Europe. Consequently, many questions related to particular episodes in paleoenvironmental history remain virtually unclear throughout the territory of the Czech Republic, situated as it is in an important transition zone between the macro-climatic settings of the Atlantic and European continent. Such unanswered questions include those relating to the spatiotemporal variation of the timing of LG climatic changes and their impact on terrestrial ecosystems.

The investigation of Lake Švarcenberk in South Bohemia (Czech Republic) has already proved to be one of the most valuable archives for this period of interest in the entire CEE (Hošek et al., 2014). With a sediment thickness of over 10 m, from which 4-5 m cover just the LG period, this site provides the most complete and detailed record of the last 16 ky in the European interior. Though a wide range of paleoecological information has already been obtained from this site (Pokorný and Jankovská, 2000; Pokorný, 2002; Hošek et al., 2014), some crucial questions remain unclear. These include the interplay between terrestrial and lake ecosystems, and the wide-scale landscape evolution during the Last Termination.

To fill in some of those gaps, we hereafter report on some high-resolution lacustrine records discovered recently in in two other individually-closed paleolakes and the LG interstadial paleosol horizons that represent the former catchment surfaces.

Our aim has been to obtain evidence for the environmental changes surrounding the LG in high temporal resolution, with particular focus on how the rapid climatic shifts had affected pedogenesis, erosion, and weathering. To address these questions, we have applied geochemical, sedimentological, rock-magnetic and micromorphological methods to both the lacustrine sequences and paleosol horizons. Because of the crucial role of vegetation cover in erosion-weathering processes, we compared the geochemical data with the pollen record, currently available from Lake Švarcenberk (Pokorný, 2002, Hošek et al., 2014).

Last, but not least, this study has highlighted some challenges for paleoenvironmental reconstruction from the geochemistry and rock-magnetism of non-laminated lacustrine sequences.

Regional setting

The study area is situated in South Bohemia, the Czech Republic, in the north-eastern margin of the Třeboň Mega-basin (Fig. 1). This Mega basin is filled mostly by Cretaceous clastic sediments consisting of sandstones, conglomerates and mudstones. Cretaceous sediments are partially covered by Middle and Late Miocene fluvio-lacustrine clayey sands filling the NNE-SSW graben.

During the Last Glacial Maximum (c. 24-22 ky BP) the study area was located ~110 km north of the Alpine piedmont glaciers and ~420 km from the southern edge of the North European continental Ice Sheet. Quaternary periglacial sediments include Pleistocene colluvial loamy sands, fluvial sandy gravels and the Holocene floodplain of the Lužnice River. Along this axial river, numerous aeolian sand dunes formed during the Younger Dryas (Pokorný and Růžičková, 2000). The sand dunes were formed, according to their morphology, by north-westerly winds. The source material originated both from fluvial sand and unconsolidated Cretaceous sandy bedrock. Because of its altitudinal position (420 m asl) and flat landscape, the loess cover has not been preserved in the Třeboň Mega-basin. Nevertheless, remnants of loess-like sediments can be found in the NW neighbourhood of this vast area.

Due to the nature of the geological substratum of this Mega basin, local soils are deficient in calcium carbonate. Currently, most soils are leached and show a tendency towards podzolization. The soils are thus mostly acidic (pH down to 3.3).

The study area is located in the temperate transitional climatic zone between west oceanic and east continental climatic settings. The present climate is controlled by prevailing westerly air masses, already significantly reduced in moisture by their passage across central Europe. Present mean annual precipitation is 627 mm and mean annual temperature is 7.8 °C (at the town of Třeboň; 30-year observation sequence).

Nineteen depressions filled by lacustrine sediments were recently discovered in the study area (Fig. 1, for details see Hošek et al., 2013; Hošek et al., 2016), most of them covered by artificial fishponds of Medieval and Modern foundation. These basins vary in size (several tens up to several hundreds of metres in diameter), and in the depth of their post-glacial infilling (2-12 m);

nevertheless, they share several common features such as their location on Miocene sedimentary bedrock, elongated shape, and the presence of tectonic faults that often run along their major axis. Although research on the origin of the lake basins is still in progress, we assume that these basins are the result of the complex of thermokarst processes (formation and collapse of alases/pingos and surface degradation of the permafrost) that occurred during the periglacial conditions of the late LGM. Another explanation which should be taken into account is that their origin is connected with short-distance neotectonic horizontal movements (pull-apart basins). The local geological settings of these study lakes and the bathymetry of the lake basins are shown in Figures 1 and 2.

The stratigraphy of the infilling of all the basins under investigation is very similar, and the time-successive changes in sediment character are highly contrasting, reflecting well the changes in environmental conditions during the millennia of sedimentation.

Material and methods

This paper is based on data obtained from the three most-intensively investigated lakes: Velký Tisý– 'VT' (49°02´58.01´´N; 14°43´39.60´´E), Švarcenberk – 'SV' (49°08´42.01´´N; 14°42´45.22´´E) and Lake Veselí – 'VS' (49° 10´14.67´´N; 14°40´36.06´´E). All of them were closed in terms of their hydrology and with relatively small catchments (4-6 km^2).

Reference cores VTC and VSC were taken in the summer seasons of 2014 and 2015 with a pneumatic hammer-operated piston corer (tube 50 mm in diameter). The SVC core from the central part of the SV lake was taken already in 2000 (Pokorný, 2002). After a visual description of the cores, these were subsampled continuously with intervals of 2.5 cm (core VTC) and 1 cm (VSC). In the case of Lake Švarcenberk, we used archived samples from the central core (SV), sampled with 4 cm intervals.

Although the study area has been severely influenced by agricultural management over the last centuries, we were able to discover Late Glacial paleosols within two (from the total of three) investigated catchments (Fig. 1), and the erosional surfaces associated with them, preserved under thick aeolian sand dune deposits. These sections were dug manually and the soils subsampled continuously for micromorphological, geochemical and rock-magnetic investigations.

Chronology and depth-age modelling

The chronology of the VTC core is based on seven radiocarbon ages determined on terrestrial plant macroremains (2 samples) and 5 bulk sediment samples (due to the general scarcity of macroremains). From the VSC core, two samples of terrestrial plants and one bulk sediment sample were used for dating. In the case of the SVC core, we used the already published radiocarbon measurements (Pokorný 2002; Hošek et al., 2014).

From the soil buried under the Vlkovský přesyp sand dune (VLK), two charcoal samples were taken for radiocarbon dating, and one radiocarbon date (also obtained from a charcoal sample) used from a previous investigation of the site (Pokorný, 2002) (Table 1). Samples were prepared for ^{14}C accelerated mass spectrometry (AMS) and dated at the Poznan radiocarbon laboratory in Poland (abrr. Poz-), at the Center for Applied Isotope Studies, University of Georgia in USA (abrr.

UGAMS-), and at the Radiocarbon Dating Laboratory, Department of Quaternary Geology, Lund/Sweden (abrr. LuA-; see Table 1).

The depth-age relationship of the cores was performed using a depth-age model constructed in the software CLAM 2.2 (Blaauw, 2010). The model is based on the linear interpolation of dates calibrated according to the northern hemisphere terrestrial curve IntCal13.14C (Reimer et al., 2013).

Geochemical, LOI, δ^{15}N, and grain-size analyses

We included data on the elemental concentration of titanium (Ti), rubidium (Rb), strontium (Sr), iron (Fe), calcium (Ca) and phosphorus (P) in our study in order to detect changes in the lithogenic influx and chemical weathering intensity in the catchments. X-ray fluorescence (XRF) measurements were performed on split cores at a resolution of 1-2.5 cm using a NITON XL3t 950 GOLDD + (Thermo Scientific) spectrometer with 50 kV Ag tube and large-area SD detector (used for the cores VTC and SVC) and Delta Professional spectrometer with 50 kV Rh tube (used for the core VSC).

For better assessment of the erosion-weathering processes in the study area, samples from the VTC core were used to carry out additional analyses.

The stable isotopic composition of nitrogen was measured from samples at a depth of 770-400 cm in 2.5-8 cm intervals at the Laboratory of Geochemistry of the Faculty of Science of Charles University in Prague. Samples were decarbonized with 0.5 mol/L HCl, wrapped in tin capsules and combusted or high-temperature pyrolysed. δ^{15}N was determined using a Thermo Flash 2000 elemental analyzer connected to a Thermo Delta V Advantage isotope-ratio mass spectrometer in a Continuous Flow IV system and oxygen. δ^{15}N is expressed relative to atmospheric nitrogen and normalized to a calibration curve based on international standards.

LOI (%) was calculated as the difference in weight between the sediment dried at 110 °C and ash produced at 550 °C within a high temperature muffle furnace (Heiri et al., 2001).

Ash residual material from the VTC core was used for granulometric analyses using a laser size analyzer CILAS 1190 LD that provides a measurement range from 0.04 to 2500 µm. Following Syvitski (1991) and Sperazza et al. (2004), the samples were treated with 0.5 mol/L HCl, dispersed with 5.5g KOH 24 hours prior to analysis, and 60 seconds of ultrasonication was used during analysis.

Rock-magnetic measurements

Rock-magnetic investigations were applied on the VTC core. The core was subsampled continuously at 2.5 cm intervals using plastic cubes with an inner volume of 6.7 cm^3. Values of saturated isothermal remanent magnetization (SIRM) were imparted with a MMPM 10 pulse magnetizer using a field of 2 T. The sample was then imparted in a back field at 200 mT (IRM_200mT). Remanence measurements were made using a JR6-A spinner magnetometer with a noise level of 0.1×10^{-8} A/m^2. The S-ratio was calculated conventionally as IRM_200 mT/SIRM.

For the correlation of magnetic and geochemical parameters, as well as the chemical element concentration and pollen record, the Pearson´s correlation coefficient r was used.

Micromorphology

Four oriented soil samples were taken in small Kubiena boxes (dimensions 3 × 5 cm) from the buried soil in the "Vlkoský přesyp" sand dune (VLK) and one from the paleosol in the proximity of Lake Velký Tisý (VT8) (Fig. 1). Upon slow drying followed by impregnation with resin, thin sections were produced from samples in the laboratory of the Czech Geological Survey (equivalent to Bullock et al., 1985; Stoops, 2003). The thin sections were studied under polarizing microscopes at a magnification of 16–800× and interpreted according to Stoops et al. (2010).

Table 1. Results on radiocarbon dating from the cores VTC, SVC, VSC and paleosol VLK:

Lab. code	Profile, depth (cm)	Type of material	^{14}C age BP	Calibrated age range cal. yr BP	Reference
LuA-4590	SVC, 390–393	Woody stem fragment	9640 ± 115	10,801–11,147 (68%)	Pokorný, 2002
LuA-4591	SVC, 520–523	Bulk gyttja sample	10,780 ± 115	12,654–12,877 (68%)	Pokorný, 2002
LuA-4738	SVC, 680–683	Bulk gyttja sample	11,750 ± 120	13,464–13,813 (68%)	Pokorný, 2002
LuA-4737	SVC, 985–995	Salix twigs	12,800 ± 120	14,943–15,617(68%)	Hošek et al., 2014
Poz-72027	VTC, 422–423	Bulk gyttja sample	9670 ± 60	11,061–11,214 (50.7%) 10,786–10,981 (39.2%) 10,986–11,033 (5.1%)	This study
Poz-72212	VTC, 487–488	Bulk gyttja sample	10.840 ± 60	12,672–12,823 (95%)	This study
Poz-72071	VTC, 536–537	Bulk gyttja sample	11.250 ± 60	13,019–13,249 (95%)	This study
UGAMS-25537	VTC, 590	Bulk gyttja sample	11.400 ± 30	13,152–13,306 (95%)	This study
Poz-72028	VTC, 617–618	Bulk gyttja sample	11.730 ± 70	13,448–13,717 (95%)	This study
Poz-71860	VTC, 678–679	Betula (fruit, seeds)	12.000 ± 60	13,729–14,037 (95%)	This study
Poz-71861	VTC, 730–735	Woody fragment	12.240 ± 60	13,960–14,449 (95%)	This study
UGAMS-25536	VSC, 282.5	Bulk gyttja sample	11.890 ± 35	13,580–13,776 (95%)	This study
UGAMS-23611	VSC, 355–360	??? Carex	11.830 ± 70	13,534–13,772 (89.8%) 13,483–13,527 (5.2%)	This study
UGAMS-23612	VSC, 420–422	Salix/Populus (wood fragment)	12.140 ± 30	13,905–14,152 (94.7%) 13,880–13,884 (0.3%)	This study
Poz-80136	VLK_surface, 185	Charcoal fragments	10.560 ± 70	12,380–12,705 (92.5%)12,239–12,274 (1.8%) 12,308–2325 (0.6%)	This study
LuA-4645	VLK_subsurface, 190	Charcoal fragments	11,260 ± 120	12,829–13,343 (95%)	Pokorný and Růžičková, 2000
Poz-80137	VLK_bottom, 198	Charcoal fragments	11,530 ± 60	13,263–13,475 (95%)	This study

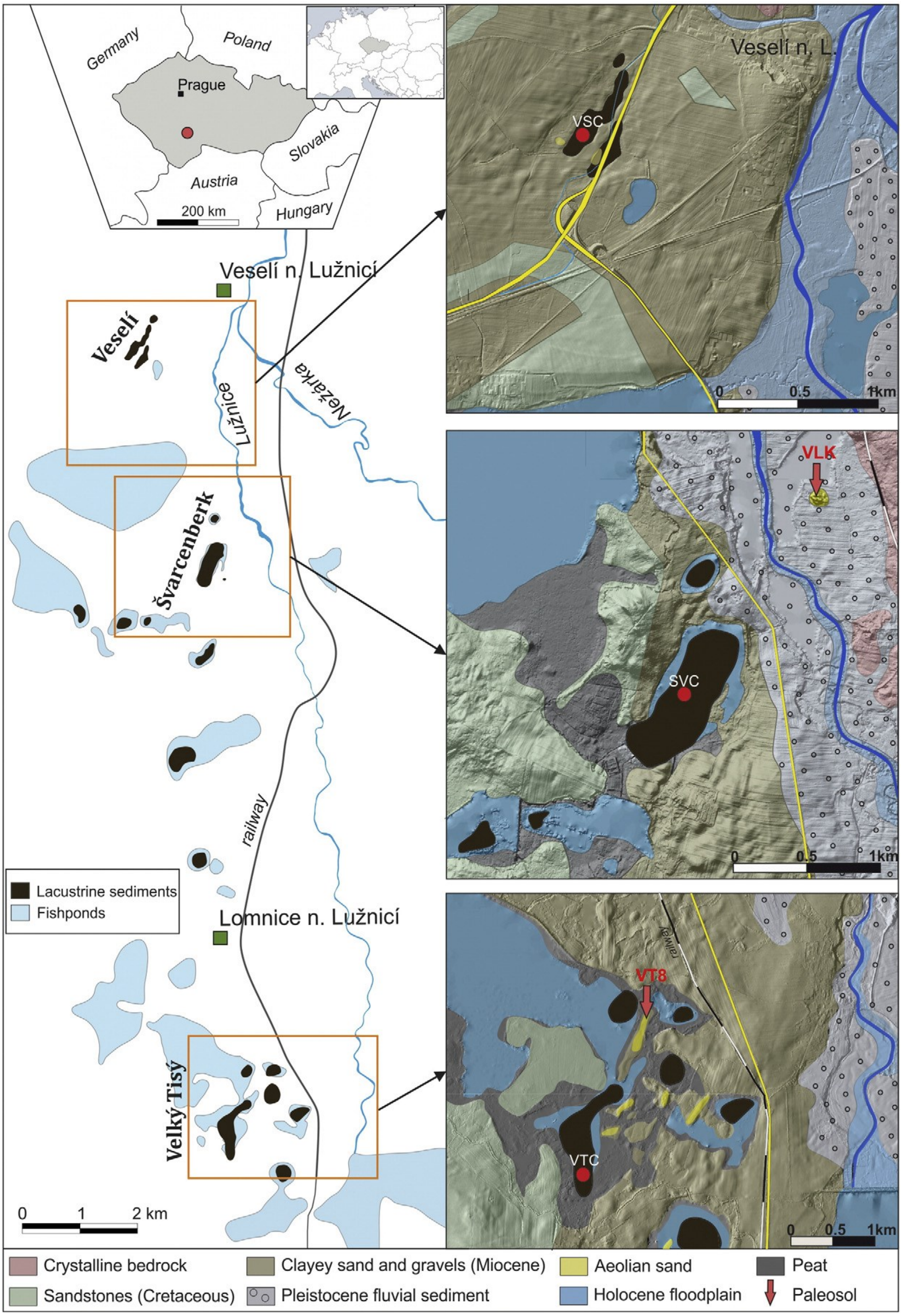

Fig. 1. *Location of the study area and simplified geological map with positions of coring sites. Red arrows mark the sites with paleosol horizons buried by sand dunes.*

Results

Lithostratigraphy and chronology of lake sediments

General lithological descriptions of the studied cores are shown in Figures 2 – 4. We were able to divide the studied sedimentary records into three main zones (A-B-C), corresponding to major environmental changes in the study area. Within these zones, particular lithological units (LUs) for each studied core were differentiated. The basal parts of the studied sections (zone A) consist of minerogenic sediments (clayed sand/gravel) with a very low content of organic matter. In the overlying 3 to 4-m-thick zone B, a slightly grey/greenish grey, fine-detritus gyttja prevails. In the lower part of this zone, an increased input of allochthonous mineral (fine-grained sand and silt) is found, whereas in the upper part the zone is characterized by quiet lacustrine sedimentation. The uppermost part of the studied cores (zone C) consists of organic-rich, fine- and coarse-detritus gyttja, sometimes rich in microscopic charcoal. In the case of the VSC core, only a thin layer from this upper zone is preserved, due to the destruction caused by agriculture management.

Based on 7 radiocarbon dates from the VTC, 3 dates from the VSC, and 3 dates from the SVC core (Table 1), zone B represents the Late Glacial period and the sediment from the studied cores provide a complete high-resolution record of this period. The underlying zone A was accumulated probably during the Pleniglacial (LGM), and zone C corresponds with the Holocene. In this paper, mainly the zone B (LG) are investigated.

Elemental variations in the sediment cores VTC, SVC, and VSC

The stratigraphic variations of selected elements in the individual cores from the three studied lakes are shown in Figures 3 and 4. The gross trends in these proxies show considerable regularity between the three cores. Common features of the geochemical record of the Late Glacial part of all the studied cores (zone B) allowed us to subdivide this zone into particular subzones B1, B2, and B3.

In lacustrine environments, titanium has been found to be a good measure of the intensity of detrital input, similarly as in, for example, Whitlock et al. (2008). The highest concentrations of Ti were found in zones A (VTC, VSC) and B3 (SVC) (Figs. 3 and 4), denoting the significant input of mineral-clastic material to the lakes. In general, distinct phases of increased influx of detrital material are visible on the LG part of the records (zone B). The highest Ti concentrations have been found within subzones B3, whereas subzones B2 and the lower part of subzone B1 show rather lower concentrations. In zone C, Ti concentration significantly decreases.

The iron record of the lacustrine sediments (Figs. 3 and 4) is characterized by high values within subzone B2, relatively low (SVC) or descending (VTC and SVC) values within subzone B3, and rather low to moderate values with subzone B1 and zone A, except for the lithological units VTC_7 and 8 and VSC_5, where increased concentrations of Fe were found. A weak correlation between Fe and Ti in VTC and SVC (r=~0.10, 0.22) and even a weak negative correlation in VSC (r= -0.14) suggest that the enrichment of the lake sediments in Fe cannot be attributed to enhanced detrital input.

Although lacustrine sediments in the research area are found to be acidic and carbonate-poor, some horizons showed an enrichment in calcium. Depth variations of the Ca records have generally shown opposite trends to that of Fe (Figs. 3 and 4). In the VTC core (Fig. 3), the high concentrations of Ca correspond with the upper part of zone A (LU VTC_9) and subzone B1, whereas subzones B2 and B3 show a significantly lower concentration as well as a descending trend in Ca concentration. A similar record has also been found in the SVC core (Fig. 4); in this profile the highest Ca concentration relates to the LU SVC_10 (zone A) and SVC_7 (subzone B1).

In the core VSC (Fig. 4) a higher content of Ca has been found within LU VSC_5 (subzone B1) and subzone B2. In contrast, Zone A and subzone B3 seem to be almost calcium- (carbonate-) free.

Phosphorus reaches maximum concentrations within subzone B2, whereas zone A shows low values, both similarly in all cores. In the VTC and SVC cores (Figs. 3 and 4) there is some increase in the lower part of subzone B3 and, in the case of VTC, also in the middle part of subzone B1 (LU VTC_7). Phosphorus concentrations show a good positive linear relationship with Fe in the LG part (Zone B), in core VTC (r= 0.61) and SVC (r= 0.71). In the VSC core this relationship has only a weak correlation (r= 0.44).

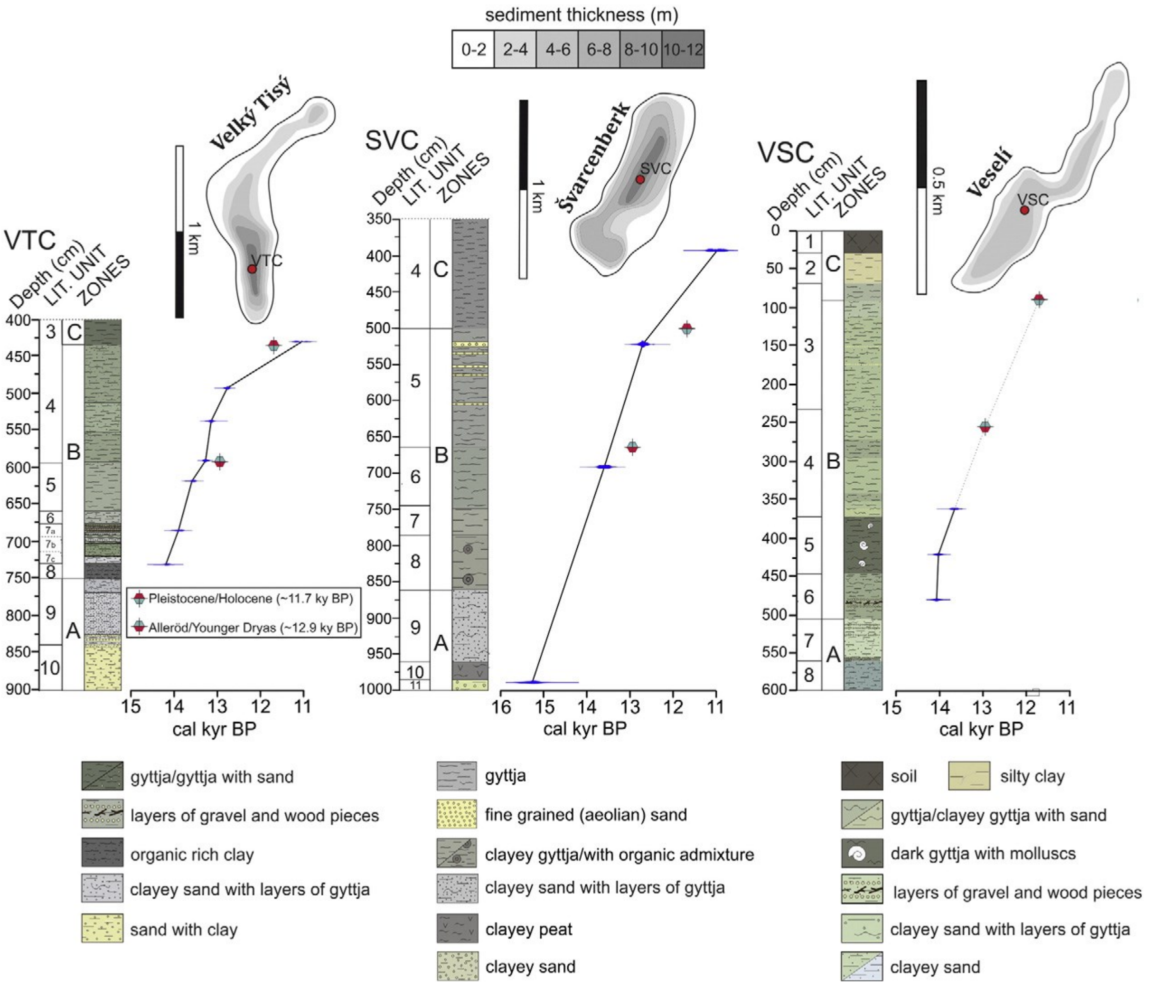

Fig. 2. *Lithology and age-depth relation for VTC, SVC and VSC cores together with the bathymetry of studied lakes. Boundaries between Alleröd-Younger Dryas (~12.9 ky BP) and Pleistocene-Holocene (~11.7 ky BP; both defined following Lowe et al., 2008) were added based on chemostratigraphy and, in the case of the SVC core, also based on palynostratigraphy (adopted from Hošek et al., 2014).*

Results from the VTC core

C/N and LOI

The organic matter (OM) in sediments is able to record the relative contributions of the particulate detritus of plants coming from a catchment (allochthonous) or from the aquatic environment (autochthonous). The origin of aquatic organic matter is conventionally distinguished from allochthonous (terrigenous) material by the C/N ratios. Lacustrine algae have low C/N ratios, commonly between 4 and 10, whereas upland vascular plants have C/N ratios of 20 or more (Meyers and Lallier-Vergès, 1999). In subzone B1, the C/N ratio ranges from 28 to 11 (Fig. 3), indicating the significant contribution of terrestrial OM in the lacustrine sediment. The maximum values correspond with LU VTC_8 (clayey peat) and the upper part of LU VTC_7 (silty gyttja with an admixture of plant macro-remains). Within subzones B2 and B3, the C/N ratios are rather stable, being around 11, denoting that the organic component of gyttja is mainly composed of the remains from autochthonic aquatic production. This interpretation is supported by microscopic examinations that revealed remnants of microscopic organisms, mainly algae.

Based on this finding, the values of LOI (Fig. 3) in the B2 and B3 subzones can be taken mostly as a proxy for primary lake productivity, which was definitely driven mainly by climate conditions (Heiri, 2001). The LOI values show an opposite trend to the Ti concentrations discussed above. The content of OM within zone A is very low, ranging from 0 to 3 %. The highest content of OM (up to 60%) coincides with the layer of clayey peat in the bottom of subzone B1 (LU VTC_8). Subzone B2 also shows a higher content of OM (~ 25%), whereas within subzone B3 the content of OM again progressively decreases (~16 %). The uppermost part of subzone B3 is characterized by a sudden increase of OM content, which reaches its maximum at the LG/Holocene boundary.

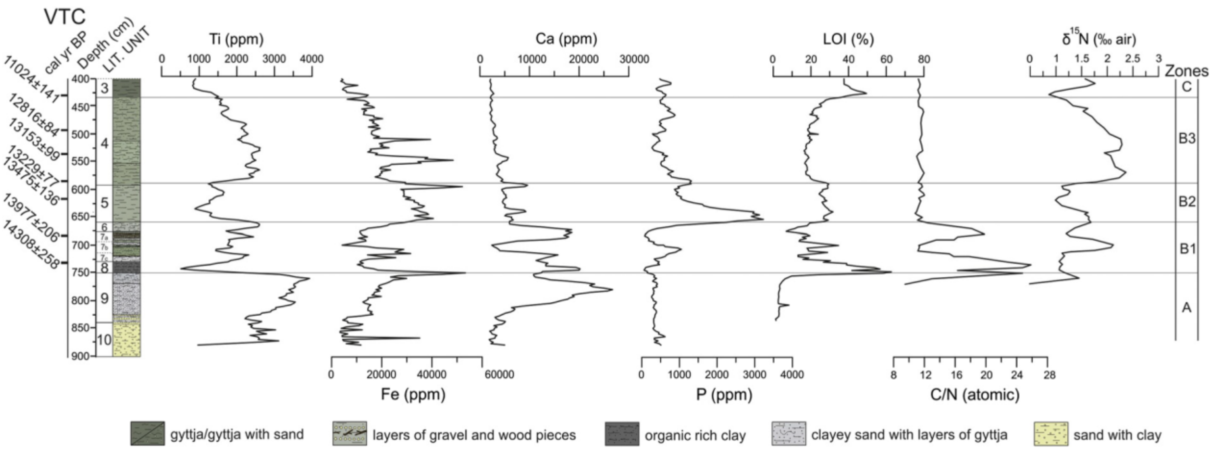

Fig. 3. *Graphs of selected elements concentration, Loss on Ignition (LOI), C/N and $\delta^{15}N$ in the core VTC plotted by depth.*

$\delta^{15}N$ and paleoclimatic interpretations

Although nitrogen isotope composition ($\delta^{15}N$) in lake sediments can be influenced by several mechanisms (see Xu et al., 2014 and references therein), a considerable factor influencing $\delta^{15}N$ can be, similar to C/N, the amount of terrigenous organic matter entering the lake. Lowering $\delta^{15}N$ values can thus be associated with a higher amount of terrigenous organic matter and *vice versa*. Consequently the denser vegetation cover and soil development during a warm-humid period leads to low $\delta^{15}N$ values in lake sediments, while elevated $\delta^{15}N$ values can indicate sparser vegetation, weak pedogenesis, and thus a cool (and dry) climate (Watanabe et al., 2004; Zhang et al., 2014).

The values of $\delta^{15}N$ (Fig. 3) vary between 0.47 and 2.73 % with an average value of 1.54. The depth profile shows rather low values in subzone B1, except for its middle part (LU VTC_7), where a significant increase of $\delta^{15}N$ was found (Fig. 3). Another peak in $\delta^{15}N$ occurs at the B1/B2 boundary. Subzone B2 is characterized by a range of lower values ~1.1 ‰; slight increases of $\delta^{15}N$ have been detected in the upper part of this subzone (617.5-600 cm). In subzone B3 there is a sudden increase of $\delta^{15}N$; peak values are high (~2.3 ‰) within the lower part of the subzone (500 cm) and then continuously decrease up to the LG/Holocene threshold, when they rise again.

During the whole of LG the $\delta^{15}N$ values show very similar depth variations as the Ti record (r= 0.54) (Fig. 3). In subzone B1, the increases of $\delta^{15}N$ lag behind the peaks of Ti, resulting in a low/moderate correlation coefficient (r= 0.20), whereas in subzones B2 and B3 a strong correlation (r= 0.85) between these proxies has been found.

Grain-size variations

Depth-variations of clay-, silt-, and sand-grain sizes of the mineral clasts, together with the mean grain size (MGS), are shown in Figure 5. Basal sediments in LU VTC_10 (880-750 cm) consist mainly of coarse silt to fine/medium coarse sand. In the over-lying grey sandy silt (LU VTC_9) the fraction 16-42 µm prevails. Average grain size in subzone B1 is 34 µm. This subzone is characterized by the higher dynamics of the coarse-grained input. The most prominent input of the coarse-grained clasts is coincident with LU VTC_6 (650-700 cm, MGS up to 72 µm, maximum grain size up to 500 µm). Within subzone B2 (LU VTC_3) a medium-coarse silt (23 µm) prevails. In the upper part of the unit gyttja is enriched by clay (up to 8 %). Average grain-size of subzone B3 (LU VTC_4) is 27 µm; the striking feature of the upper part of this subzone is the high content of the clay fraction (up to 12%). By contrast, the middle part (depths 475-550 cm) is characterized by a distinct input of a coarse-grained fraction (MGS up to 45 µm, maximum grain size up to 200 µm).

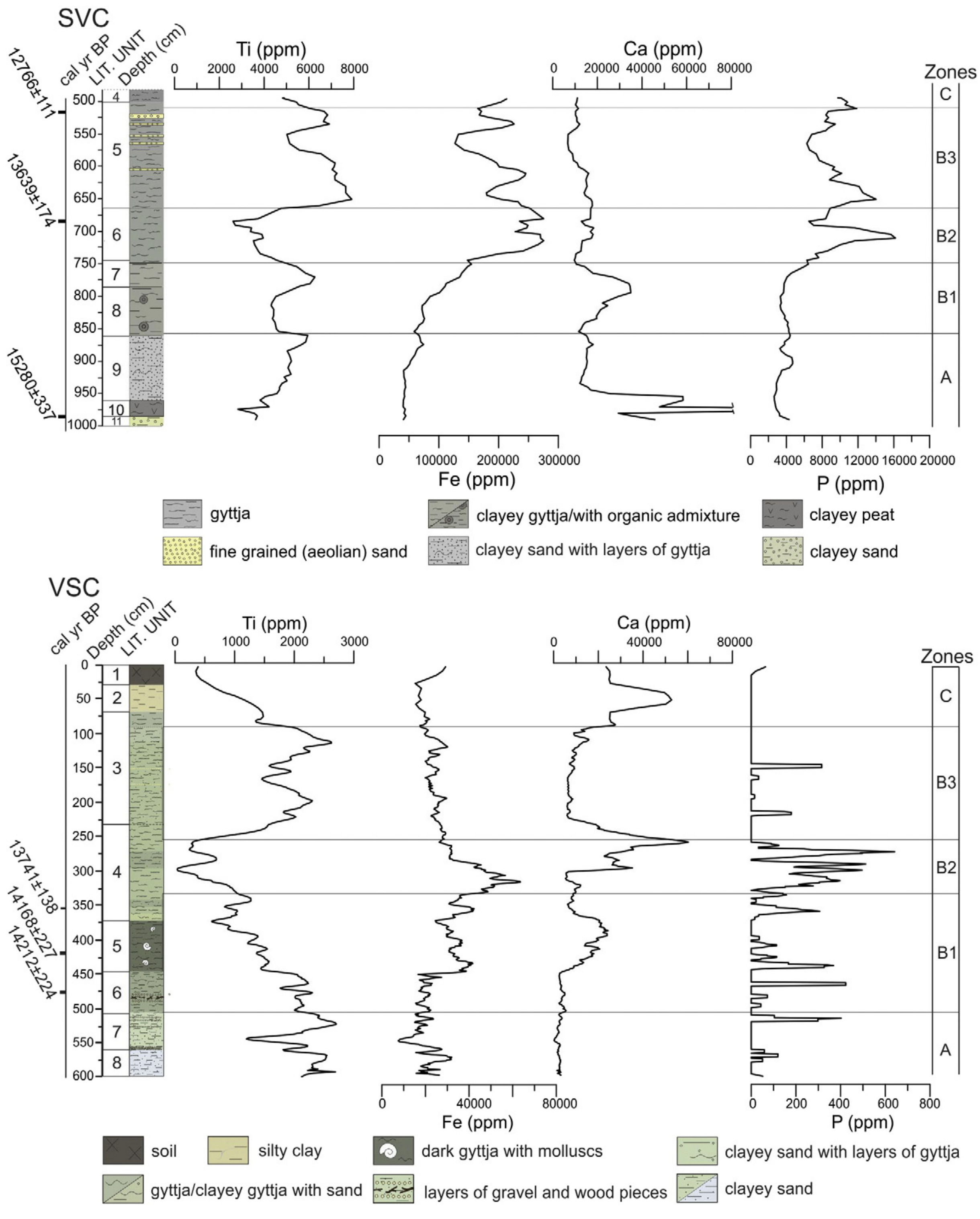

Fig. 4. *Graphs of selected elements concentration in the cores SVC and VSC plotted by depth.*

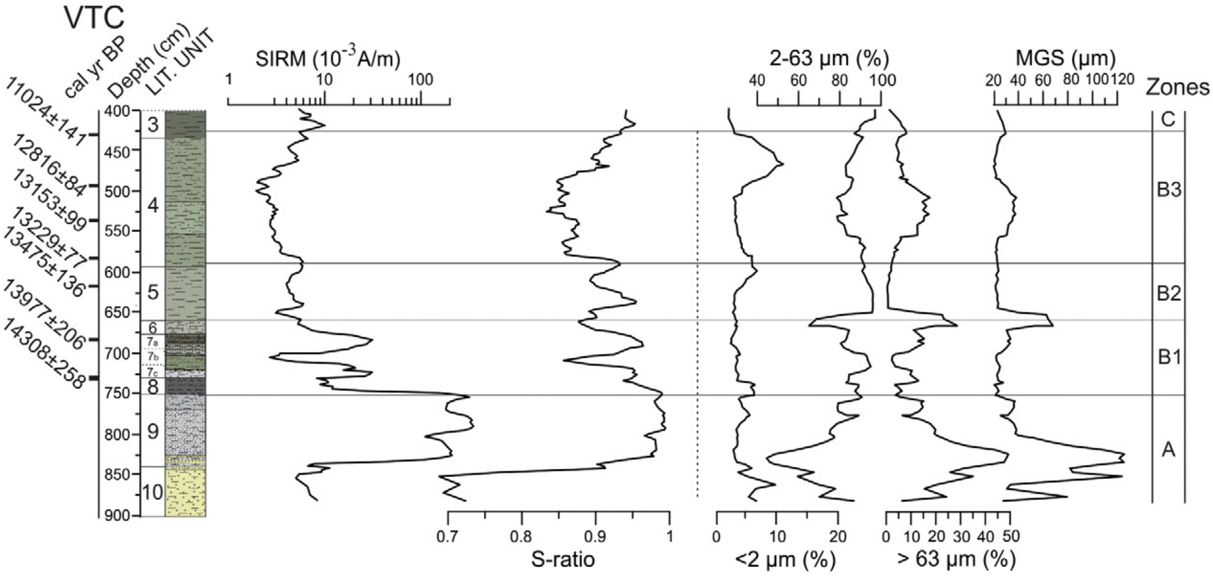

Fig. 5. *SIRM, S-ratio and grain-size variations in the core VTC.*

SIRM and S-ratio

Rock-magnetic parameters, in concert with the geochemical and sedimentological characteristics, provide a valuable contribution to environmental reconstructions, since the magnetic properties can mirror both the environmental conditions on land and the intra-lake processes (Just et al., 2016).

Depth-variations of the SIRM and S-ratio are shown in Figure 5. SIRM is a parameter providing information mostly on the concentration of fine-grained magnetite preferably formed by pedogenesis (Heller and Evans, 1995). The values of SIRM (in 10^{-3} A/m) vary between 0.5 and 610. In zone A and subzone B1, the rock magnetic record correlates with the lithology. On the bottom of zone A (LU VTC_10) are very low values of SIRM, apparently due to the presence of diamagnetic quartz sand. Maximum values correspond with LU VTC_9, where clayey silt dominates. A sharp decrease of magnetic values in zone B1 (LU VTC_8) is caused by a significantly high content of diamagnetic organic matter (up to 80%), which reduces the magnetic signal. Peaks of SIRM within subzone B1 correlate with layers of increased influxes of silt and fine-grained sand mixed with plant macro-remains (LU VCTC_7). Within subzones B2 and B3 (homogenous fine-detritus gyttja) rather low SIRM (2–12) was found. Increased values of SIRM (lower and upper part of B2, upper part of B3) have no lithological correlates.

The S-ratio is a concentration-independent proxy for the relative abundance of ferrimagnetic to antiferromagnetic minerals (Maher, 1986; Wang et al., 2012). Elevated values reflect the dominance of magnetite (or maghemite), while lower values represent increasing contributions from antiferromagnetic minerals, i.e. hematite or goethite. The S-Ratio is in general high and varies less in zone A (0.9 to 1), whereas in zone B the S-ratio is scattered between 0.75 and 1 (Fig. 5). The positive correlation of SIRM with the S-ratio (r= 0.61) suggests magnetically-soft ferrimagnetic minerals (magnetite or maghemite) as the main carriers of magnetic remanence. Consequently, the lower S-ratio values observed in some horizons (lower part of LU VTC_7, VTC_6, middle part of VTC5, VTC_4) signalize an increased presence of magnetically-harder antiferromagnetic minerals (hematite or goethite), which have overall weak magnetic signals (Robinson, 1986).

Elevated SIRM, and consequently a high S-ratio, within zone A indicates a magnetite/maghemite population that is probably of detrital origin because it occurs in mineral-clastic-rich sediments deposited with a minimum of organic matter (LOI 0.1-3 %).

SIRM shows a weak/moderate positive correlation with Ti content within zone A (r=0.44), a very weak correlation within subzone B1 (r= 0.11), and a strong negative correlation within subzones B2 and B3 (r= -0.66, Fig. 6). The correlation between the S-ratio and Ti shows a similar behaviour as the SIRM. It is slightly positive in zone A (r= 0.32), very weak in B1 and strongly negative in B2 and B3 (r= -0.88). Both magnetic parameters show positive correlation with Ca (r=0.43 for SIRM and 0.57 for S-ratio) for zones A and B1, whereas in subzones B2 and B3 this relationship does not occur. Within subzones B2 and B3, where the fine-detritus gyttja dominates, the S-ratio as well as SIRM are obviously positively correlated with LOI (r= 0.81 and 0.72, Fig. 6), denoting that the magnetic enhancement of the lacustrine sediment occurred during periods with increased lake productivity, which we can assign to a warmer climate. Within subzone B1, SIRM and the S-ratio show linear correlation with C/N (r= 0.58 and 0.61, respectively) suggesting that the magnetic signal is positively influenced by an influx of terrestrial organic material.

The S-ratio and $\delta^{15}N$ have a significant strong correlation (r= -0.75) during the whole LG (Fig. 6). The SIRM and $\delta^{15}N$ anti-correlate moderately within subzone B1 (r= -0.42) and strongly (r= -0.64) within subzones B2 and B3.

The paleosols - field observations, micromorphological description, dating

We have discovered two paleosols under aeolian sand: VT8 paleosol, situated in the proximity of the former shore of Lake Velký Tisý, and VLK paleosol, located in the NE proximity of Lake Švarcenberk (Fig.1). The profiles of these paleosols and superimposed sand dunes are sketched in Figure 7. The basal part of the VLK profile consists of non-stratified, medium and coarse sand with fine gravel. A charcoal sample from the top of this basal layer provided a radiocarbon age of 13,427 ± 116 cal yr BP. The over-lying, 21-cm-thick, brownish-yellow (10YR6/8) soil horizon is characterized by its massive texture and low organic content (0.6-1.2 %). The over-lying, 170-cm-thick, aeolian accumulation consists of well-sorted, fine to medium sand with a layer of coarse sand and gravel.

At the base of the profile from the VT8 site, clayey sand (Miocene sediment) has been found. This basal sediment is overlain by a 15-cm-thick layer of brownish-yellow (10YR6/6) clay mixed with fine- to medium-grained sand. Macroscopic charcoals and features of oxidation-reduction features (Fe and Mn nodules) are present. This layer is buried under a 90-cm-thick horizon of aeolian sand. A 15-cm-thick, podzol, horizon sequence (O-E-Bhs) developed on the top of this sequence and some placic horizons were recognized within the aeolian sand.

Four samples from the VLK paleosol and one sample from the VT8 paleosol were obtained from the above-discussed sequences; their significant micromorphological features are summarized in Table 2 and shown in Figure 8.

According to the field and micromorphological observations on the VLK paleosol (see Table 2), the lower part (21-9 cm, sample VLK_2, Fig. 8a) consists of an intact, gley-spodic horizon of podzol, whereas the upper part (8-0 cm; VLK_1, 3, 4) is probably a redeposited B horizon mixed with sand and poorly-decomposed organic matter. Apart from the fragments of B horizon, possible fragments of humic A horizon (Fig. 8b) and albic E horizon (Fig. 8d) were found. This pedo-colluvial horizon was post-sedimentarily illuviated and gleyed. It contains abundant charcoal fragments that was dated to 13,155 ± 150 cal yr BP. The pedo-colluvial horizon is overlain by a 2 to 4-cm-thick layer reddish yellow clay (7.5YR6/6) with sand and abundant size-sorted, charcoal and mineralized, wood fragments (average size 0.3 cm in diameter). The sample obtained from these organic fragments yielded a radiocarbon age of 12,492 ± 169 cal yr BP.

Micromorphological analyses of the VT8 site (Figs 8e-f, Table 2) have proved the nature of the material: soil sediment. This layer is similar to that found in the upper part of the VLK site; nevertheless, fragments of former soil horizons are rather rare. Post-sedimentary illuviation also took place, but its intensity was significantly lower compared to that from the VLK site.

Discussion

Titanium and magnetic proxies as indicators of erosion and pedogenesis processes

In order to remove the effects of the detrital chemistry, titanium (Ti) was taken to represent an element that is relatively immobile during weathering and stays predominantly in the allogenic phase (Young and Nesbitt, 1998). The minerals containing Ti are not dissolved in an exogenic environment (Demory et al., 2005) and are biologically not very active (Eusterhues et al., 2005), so their concentration in lacustrine sediment is mostly related to the erosion rate in the lake catchment. Since Ti is most enhanced in fine-grained, clastic-rich sediments (it is especially strongly bounded on the clay fraction) its higher values could also have originated from wind-blown/eroded loess or the intensive erosion of catchment mineral soils (Yancheva et al., 2007; Dietrich and Sirocko, 2011).

In the study area, the Miocene clayey sand can be considered an appreciable contributor to Ti in the lake sediment. This is demonstrated in the relationship between Ti and concentration of reworked Tertiary palynomorphs in the SVC core, which shows an obvious similarity throughout zone A and subzones B2 and B3 (Fig. 9). A negative correlation (a decrease in the concentration of Tertiary palynomorphs with increasing content of Ti in LU SVC_7, subzone B1) could have been caused by the erosion of a former loess cover from the lake catchment. This interpretation is supported by a substantially-elevated concentration of Ca in these sedimentary strata (Fig. 4). Eroded (water-, or wind-transported) loess could also be the source of Ti in zone A and partially also in subzone B1. In these horizons the calcium content is ten times higher than in the present bedrock. The higher content of Ca further correlates with an increased presence of medium/coarse silt, i.e. grain-size fraction 16-42 µm typical for loess (Smalley, 1995).

Since humic soil horizons are usually enriched by fine-grained (single-domain and superparamagnetic) magnetite and maghemite (Jordanova et al., 2013), the elevated magnetic values in the monotonous, organo-mineral, lacustrine sediment can be connected with a more intensive pedogenesis in the lake catchment (Maher and Taylor, 1988). The good correlation between S-ratio and SIRM with LOI and $\delta^{15}N$ (Fig. 6) in the sediment strata where the fine-detritus gyttja dominates (subzones B2 and B3) suggests that the magnetite/maghemite enhancement of the lacustrine sediments can be attributed to warmer (more humid) periods and thus a humic soil-horizon development in the lake catchment.

On the other hand, a higher content of ferrimagnets in zone A and also in LU VTC_7a and 7c (subzone B1) can be attributed to the presence of eroded (wind-blown) loess, which is, in general, enriched in coarse-grained (lithogenic) magnetite (Maher and Thompson, 1991). This assumption is supported by the very similar depth variation of SIRM and Ca in these horizons (Figs. 3 and 5).

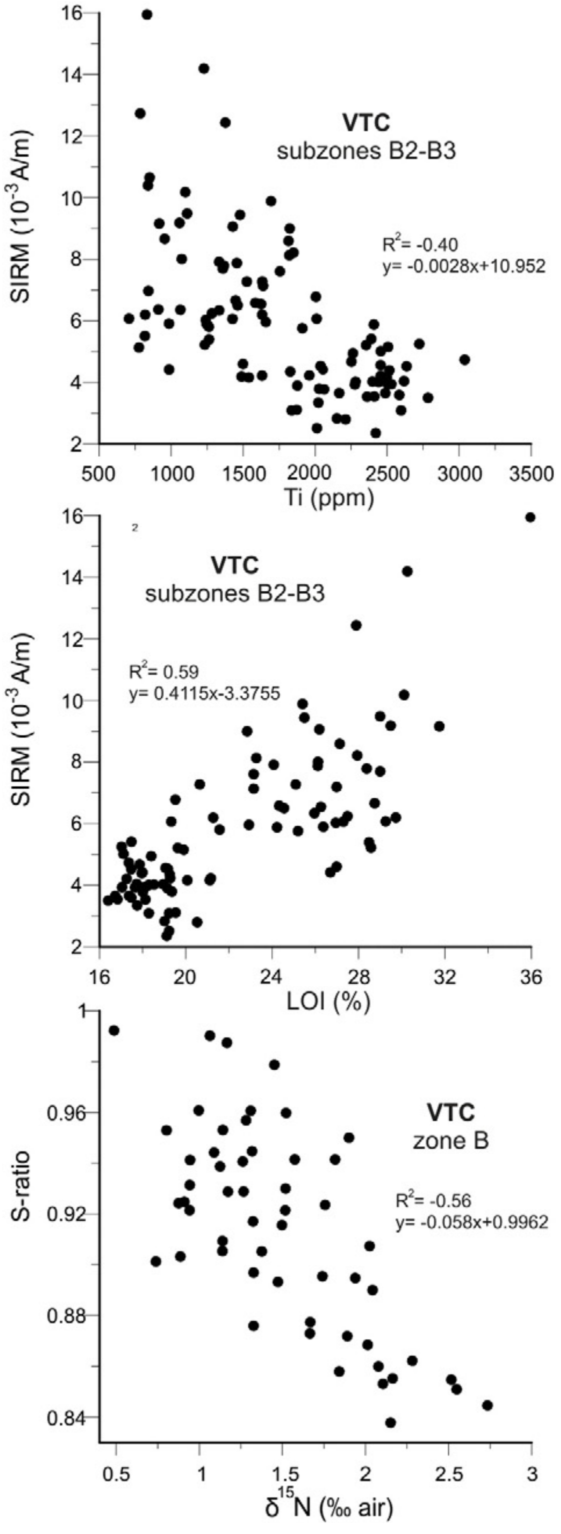

Fig. 6. *Scatterplots of (a) SIRM versus Ti, (b) SIRM versus LOI and (c) and S-ratio versus $\delta^{15}N$ in the core VTC.*

Paleoenvironmental implications and local climatostratigraphy

The close similarity of the Ti depth-variations in all studied lacustrine sedimentary sequences suggests that the dynamics of the allogenic input into the three studied lake basins was driven by the same mechanisms, most probably triggered by the climatic changes. We assume that the relationship between cold climate and higher amounts of Ti in the lake sediment was caused by the following process: when the climate deteriorated, vegetation was destabilized by ecological stress. Events, such as blowdowns and fires, became more frequent under such circumstances. The resulting disturbed surface was more prone to erosion, including aeolian transport and such processes would result in higher Ti contents in the lake basins as compared with more stable warm periods. In the study area this assumption is supported by: 1) the positive relationship between Ti and pollen percentages of *Artemisia* (Fig. 10), which is commonly used as an indicator of cold and dry climate and thus sparse vegetation cover (Hongyan et al., 2013); and 2) the strong positive correlation between Ti and $\delta^{15}N$ (Fig. 6). The former finding also confirms the observations from some other sites: that measurements of $\delta^{15}N$ in lacustrine sediments can be considered as a powerful proxy for climate reconstructions.

The idea that Ti is a suitable tracer of the climatic record in our study area is further supported by the close similarity between the $\delta^{18}O$ Greenland record (NGRIP Members, 2004) and the depth-variations of Ti content in all the studied lakes (Fig. 11). These findings allow us to subdivide the records into particular units, corresponding to already-known LG biostratigraphy (*sensu* Mangerud et al., 1974) and comparable with the event stratigraphy proposed by Lowe et al. (2008). Based on this syllogism, subzone B1 very probably corresponds with Bølling, subzone B2 with Allerød, subzone B3 matches to Younger Dryas and B/C threshold correlates with the Younger Dryas/Holocene transition.

Apart from this kind of wiggle-matching, our correlation is supported by radiocarbon dating, and in the case of the SVC core by the regional pollen stratigraphy as well (Pokorný, 2002; Hošek et al., 2014).

In addition to the prominent stages, some minor climatic events were identified in the study area.

Bølling-Allerød warm period and two minor cooling events within

In comparison with the preceding Pleniglacial, sudden climatic amelioration occurred during the onset of the Bølling interstadial (see e.g. steep increase of the LOI in the VTC core, Fig. 3). Nevertheless, Ti records in the VTC and VSC cores show that the soil surface in the research area was still rather unconsolidated, inclinable to erosion. The higher level of catchment erosion during the pre-Allerød period has also been referred to, for example, in the case of Łukie Lake in eastern Poland (Zawiska et al., 2015). In all study lakes, the most prominent erosion event has been found in the uppermost part of the B1 subzone, in the time interval that separates the Bølling and Allerød interstadials. This cooling episode could be associated with the Older Dryas (GI-1d reported by Björck et al, 1998). This short-lived climatic deterioration is generally recognized in the pollen record in northern and western Europe (e.g. Walker, 1995; Brauer et al., 2000) and has also been found in the oxygen isotopic record of several lakes in southern central Europe, where it is dated to 14,044 - 13,908 yr BP (von Grafenstein et al., 1999; van Raden et al., 2013). Radiocarbon data 13,977 ± 206 cal. yr BP and 13,741 ± 138 cal. yr BP obtained from the discussed horizons of the VTC and VSC cores support this correlation. Identifying the Older Dryas outside of the NA region has been regarded as problematic, particularly due to the low temporal resolution of most sites already studied and/or the weak response of local vegetation to this climatic event (Lotter et al., 1992). Within the territory of the Czech Republic it has not been clearly detected in pollen records up to now.

The prominent peak of the sand fraction associated with the Older Dryas period in the VTC core (depth 648-677 cm, Fig. 5) could have been caused by a high intensity of erosion and/or by a higher level of aeolian activity. A significant aeolian influx in organic deposits during the Older Dryas has been reported from many sites in the Netherlands (e.g. Bohncke et al., 1993). The increasingly severe conditions during this period are indicated by the expansion of pine, suggesting a fall in mean winter temperatures, and an increase in the continentality of the climate (Pokorný, 2002).

Another signal of the erosion event (climatic deterioration) has been found within the Allerød interstadial (the upper part of subzone B2). This event can be associated with cooling and surface erosion of mineral soils, as suggested by the higher values of Ti and $\delta^{15}N$, and the lower S-ratio (Figs. 3–5). The stratigraphic position, together with the radiocarbon data in the VTC and SVC cores (Fig. 2 and Table 1), suggests that this climatic shift was coeval with the *Intra-Allerød Cold Period* (Amphi-Atlantic Oscillation of Levesque et al, 1993; GI-1b *sensu* Björck et al, 1998). This centennial-scale cooling event has been reported, for example, from Switzerland (the Gerzensee oscillation; Lotter et al, 1992), Canada (the Killarney Oscillation; Lesveque et al, 1993), Wales (Walker and Harkness 1991), and England (Gransmoor; Walker et al, 1993). At Lake Gerzensee, this event is dated to 13,274 – 12,989 varve yr BP (Raden et al., 2013). From lakes in Denmark, the onset of the oscillation is dated between 11,400 and 11,300 ^{14}C BP (Andersen et al., 2000). In the Greenland oxygen isotopic record this event spans the period approximately 13 311– 13 099 calendar yr BP (Rasmussen et al., 20006).

Evidence of IACP in all the studied lakes denotes the strong response of the regional environment to this event, which has been recorded only exceptionally and as a weak disruption outside the North Atlantic region (Björck et al., 1996; Velichko et al., 2002; Battarbee et al., 2004).

Younger Dryas

In subzone B3, a sudden increase of allogenic input (higher Ti content, Figs. 3 and 4), and a simultaneous decrease of aquatic and terrestrial organic production (lower LOI and higher $\delta^{15}N$ values in the VTC core; Fig. 3) occurred. These findings point to a rapid cooling, an acceleration of erosion intensity and thus a sparser vegetation cover than that during the preceding Allerød. We attribute this subzone to the Younger Dryas, although the radiocarbon data obtained from the same horizons seem to be obviously older (Table 1, Fig. 11). The discrepancy between radiocarbon measurement results and the rich contextual information provided by chemo- and palyno-stratigraphy (Pokorný, 2002; Hošek et al., 2014, see also Fig. 2) can best be explained by the significant radiocarbon plateaus that are repeatedly reported for the YD period (Ammann and Lotter 1989; Björck et al. 1996; Wick, 2000).

The maxima of the aeolian dynamics are supposed to occur during the middle period of the YD, as visible on the grain-size record of the VTC core (zone B3, Fig. 5). This period is connected with a significant input of a coarse mineral fraction. In the SVC core, several layers of well-sorted sand are preserved in a position corresponding with the middle and upper part of the YD (see Fig. 4).

These aeolian sand layers had already been correlated with the formation of the VLK sand dune, and with the opening up of forest cover (Pokorný and Růžičková, 2000). Higher aeolian activity during this period within the YD is in accordance with observations from numerous other sites of northern-central Europe (Hoek, 1997).

From this point of view, the later part of the YD seems to be climatically more favourable. In all cores, Ti content declines. In the VTC core, the same period is associated with a distinct dominance of clay in the sediment (Fig. 5), which can be attributed to an increase of the lake level and/or enhanced pedogenesis in the catchment. The idea of accelerated soil formation in the catchment under more humid conditions (and its connection with the formation of fine-grained pedogenic magnetite/maghemite) is also supported by the magnetic and $\delta^{15}N$ records, which gradually increase (decrease) within the upper part of the YD toward the Holocene. The climatic amelioration associated with increased humidity has been previously observed throughout northern-central Europe (e.g., Kulesza et al., 2014; Karpińska-Kołaczek et al., 2016), eastern-central Europe (Hájková et al., 2016), and eastern Europe (Druzhinina et al., 2015; Stančikaite et al., 2015; Zawiska et al., 2015). On the other hand, grain-size analyses of the littoral core from the Švarcenberk Lake (Hošek et al., 2014) suggest a lake-level rise in the later phase of the YD and thus rather drier conditions along the Pleistocene/Holocene transition.

Evidence from paleosols

An exceptional opportunity to study the above-discussed processes is provided by the fossil soils discovered in the proximity of the Švarcenberk and Velký Tisý paleolakes (Fig. 1). On the surface of the Pleistocene sandy-gravel terrace of the Lužnice River, a spodic horizon of podzol was identified (VLK, Fig. 7). This soil is buried by up to 4 m of sand, which has been previously interpreted as aeolian by origin (Pokorný and Růžičková, 2000). Based on the radiocarbon data obtained from the base and top of this soil (Fig. 7, Table 1), the soil had developed during the second part of the Allerød. It can be parallelized with the stratigraphically-identical Usselo and Finow soils reported from west- and northern-central Europe, where they are usually considered to be stratigraphical-marker horizons for Late Glacial, aeolian landscapes (Hijszeler 1957; Schlaak, 1997; Kowalkowski et al., 1999; Kasse, 2002; Kaiser et al. 2006; Kaiser et al. 2009; Jankowski, 2012). These paleosols consist of various soil types; nevertheless, the Finow soils are mostly characterized by silicate weathering, clay translocation and redoximorphism, whereas for the Usselo soils organic matter accumulation and podzolization are rather more characteristic (Kaiser et al., 2009). On the basis of the micromorphological investigations (Table 2), the latter type is pedologically more similar to that found within the VLK sand dune. Because of the influence of water table oscillations within the fluvial terrace, podzolization took place - consequently with the oxidation of iron and manganese after water saturation and desaturation. The buried soil horizon thus corresponds rather with the Gleyic Podzol. This type of Usselo soil has been previously described, for instance, in a closely-resembling, geomorphological and hydrological context from Poland, as the result of soil-forming processes and diagenesis along a buried slope (Jankowski, 2012). The Usselo horizon is usually 5–20 cm thick and is characterized by slight humus accumulation, the presence of charcoal and well-developed humic (Ahb), albic (Eb), and spodic (Bhs) horizons (Kaiser et al., 2009 and references therein). Nevertheless, in our studied profile the humic and albic horizons have not been detected. This we attribute to the erosion of the former Ah and Eb horizons shortly before the soil was buried under the aeolian sand. The same observations have also been made in some loess/paleosols sequences in central Europe where the Ah horizons of the Eemian Luvisol were eroded immediately after the climate deterioration at the end of the Last Interglacial (Hošek et al., 2015). Micromorphological investigations (Table 2) have shown that the upper part of the soil profile has signs of colluvial processes and surface runoff, such as horizontal lamination and the changing of 1 to 2-mm-thick layers of coarse- and fine-grained particles over a dense, structural seal. The higher content of the poorly-decomposed organic matter visible in the micromorphological sample VLK_1 (Fig. 8b) can be interpreted as the preserved fragment of a disturbed Ah horizon, which was mixed with the sand and underlying gley-spodic horizon during colluviation. Owing to the fact that the matrix in the lowermost part of sample VLK_3 is obviously depleted (Fig. 8c), only a relic of the albic horizon (E) could be preserved in this layer. All these findings indicate that some climatically-driven erosion event occurred within the Allerød. Based on the radiocarbon date 13,005 – 13,305 cal yr BP obtained from the pedo-colluvial horizon, this event fits the above-described IACP cool event (GI-1b) dated from western Europe to 13,274 – 12,989 varve yr BP (Raden et al., 2013). This clearly demonstrates a direct relationship between landscape processes, such as surface runoff / soil erosion, and the allogenic input to the lake basins, as indicated by the geochemical/magnetic records in all the lakes studied by us.

Another pedo-colluvial horizon buried by aeolian sand found in the proximity of Lake Velký Tisý (VT8, Figs. 1 and 7) seems to be the result of the same erosion event. Unfortunately, no radiocarbon date was obtained from this horizon. Nevertheless, a Late Paleolithic artifact (Federmesser culture; personal communication by P. Šída) discovered in the over-lying aeolian sand denotes that the sand accumulated during the YD (from the age of the Federmesser culture in central Europe; see Joachim, 2008). Thus we suggest that the soil was formed (and eroded) in the preceding warmer period. This horizon is, similarly to the VLK site, very rich in charcoal, pointing to the observation from northern-central Europe that towards the end of Allerød the occurrence of forest fires had increased (van der Hammen, 1951).

The pedo-colluvial horizon and the uppermost part of the intact B horizon from the VLK paleosol are marked by a relatively strong clay illuviation connected with the gley process demonstrated by micromorphological analysis (sample VLK_4, Fig. 8d). The same, but less intensive, post-sedimentary illuviation was also recognized in the pedo-colluvial horizon from VT8 (Fig. 8e). It denotes that another pedological process took place on these sites after the erosion event. This soil weathering process could be related to a relatively short humid phase of the late Allerød (GI-1a in the NGRIP record) which occurred after the IACP cold event. Favourable climatic conditions during this period are indicated by all the abiotic proxies from the three studied lakes (Figs. 3-4) and it is also reflected in the biotic indicators from Lake Švarcenberk (Pokorný, 2002; Hošek et al. 2014). Nevertheless, due to the relatively short distance between the buried soils and recent surface, it should also be taken into account that the illuviation of the particular soil horizons could have taken place during the Holocene.

The formation of soils during the Allerød period required stable climatic conditions with little aeolian activity and a relatively-dense vegetation cover. The catchments of the lakes were covered by pine-dominated forest, which then became more closed, as reflected by a decrease in open-community indicators in the pollen spectra (Pokorný, 2002; Hošek et al., 2014). Woodland cover helped to prevent surface washes and slope processes. Considering this, it is not surprising that generally little erosion occurred in the lake catchments during the Allerød.

A combination of the acidic nature of the bedrock, the relatively dense cover by coniferous trees, and increased precipitation would have ensured that podzolization occurred in the study region (see Fig. 8a). The increase in precipitation, in particular, would have been the crucial factor for this process (Section 5.4.). A supposed increase of precipitation in the study area at the beginning of the Allerød is in accordance with the higher lake level of the VT lake (see the fall in the mean grain size of the lacustrine sediment in this particular horizon, Fig. 5) and with the pollen record from Švarcenberk Lake (Hošek et al., 2014).

By contrast, the formation of aeolian sand dunes indicates severe climatic conditions. In the upland record from the VLK buried soil, the sudden climatic change at the Allerød/YD threshold is represented by the thin layer of sandy clay and abundant charcoal dated to 12,322 – 12,661 cal yr BP (Fig. 7), i.e. the beginning of the YD. This layer with abundant charcoal has been referred to from numerous Usselo soils as well (Kaiser et al, 2009 and references within). Charcoal presence on the top of the soil probably resulted from the climatic deterioration which led to a wide-scale dieback of coniferous forests and subsequent extensive fire events. This climatic event is also probably reflected in the regional pollen record (Pokorný, 2002; Hošek et al., 2014), where a peak in microscopic charcoal particles precedes a phase of significant opening up of the vegetation during the Allerød/YD transition. A good size-sorting of the charcoal and rotten-wood particles (0.5 cm in diameter, see Fig. 7) denotes that the fragments of dead coniferous vegetation were wind transported together with the sand.

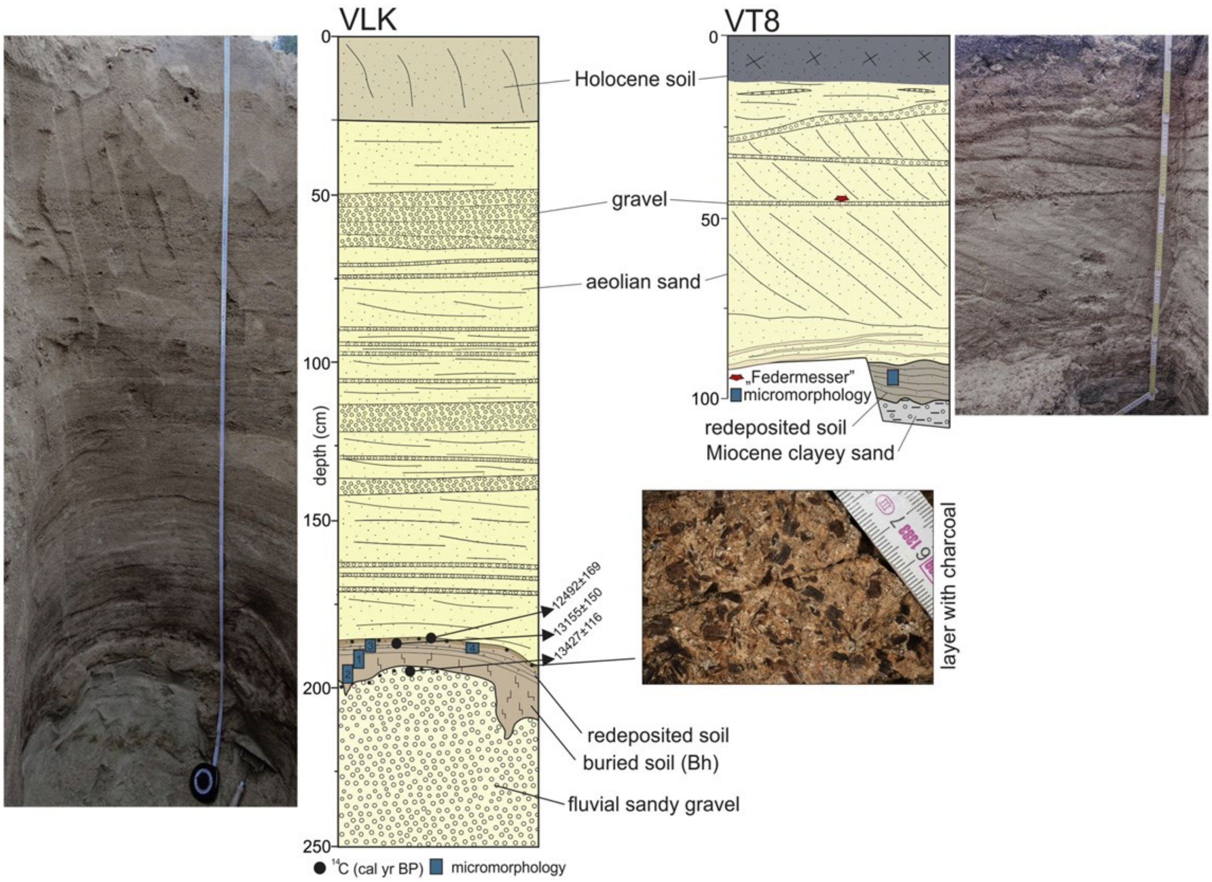

Fig. 7. *Profile sketches of paleosol sections Vlkovský přesyp (VLK) and Velký Tisý (VT8). Photo shows a detail of the layer with abundant charcoal and wood fragments.*

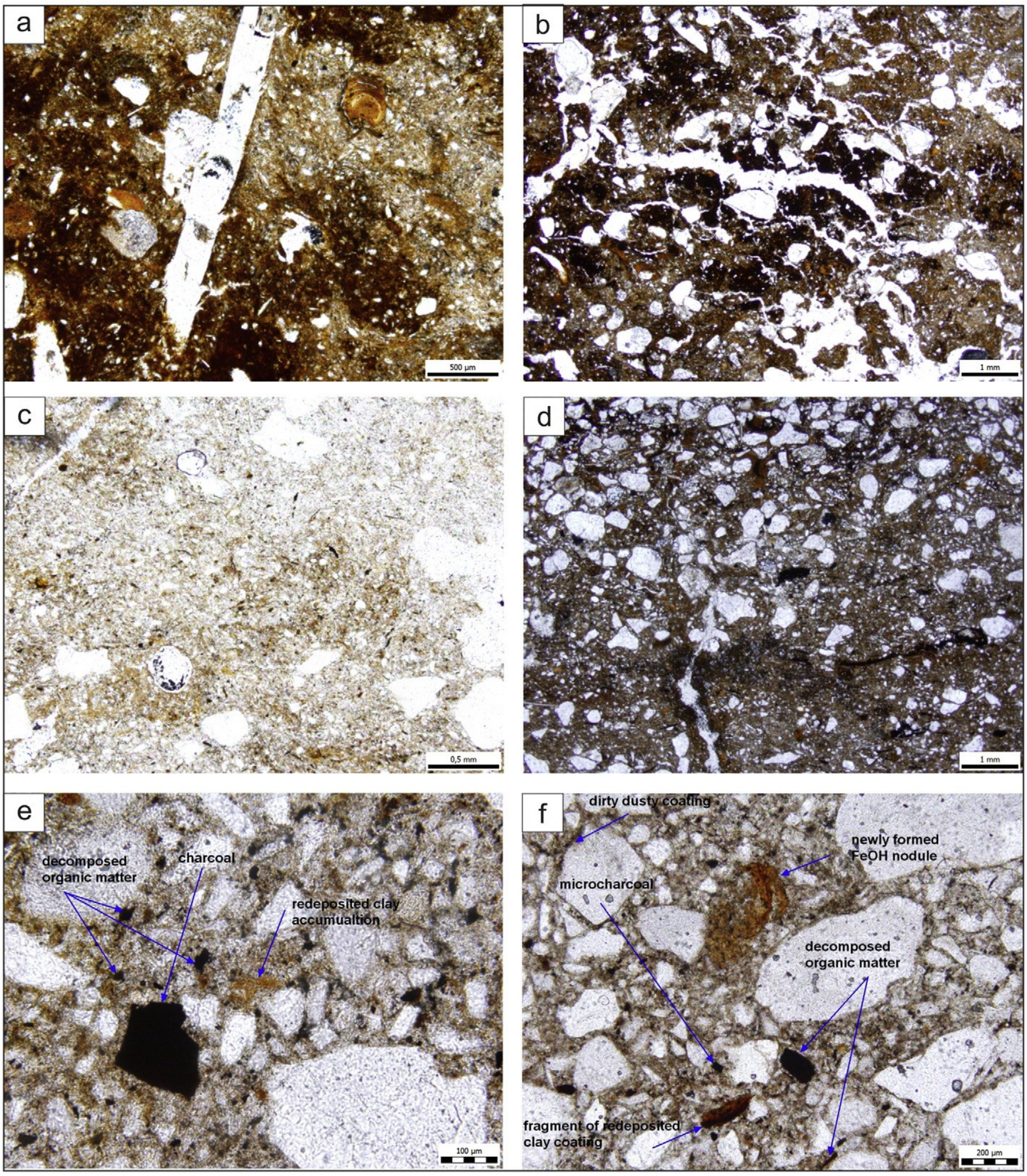

Fig. 8. *Micromorphological features of the paleosols from the VLK (a–d) and VT8 (e, f); a – sample VLK_2, Fe oxide depleted groundmass (right part), Fe/Mn oxide quasi-coatings and impregnative nodules (central lower part and left corner) (PPL); b – sample VLK_1, horizon of black particles composed of partly and fully decomposed organic matter and coated by clay minerals. Visible crack pores (PPL); c – sample VLK_3, depleted silty matrix with vughs; d – sample VLK_4, the transition between silty loam and sands. Pieces of buried organic matter and microcharcoal are preserved there; e – sample VT8, microcharcoal, as well as relict of clay accumulation and dark pieces of buried organic matter (PPL); f – sample VT8, fragment of redeposited clay coating, black, decomposed organic matter, dirty dusty coating, microcharcoal and newly forming FeOH nodule (PPL).*

Table 2. Micromorphological description of the paleosols from the VLK and VT8 sites:

VLK_2 (Fig. 8a)	Complex microstructure, horizontal pores, cracks, channels, vughs, complex packing voids C/F(500 μm) = 15:85; C/F(500 μm) = 30:70; sandy loam Coarse fraction: subrounded and rounded quartz and plagioclase, mica Matrix brown to dark brown stipple speckled to porostriated Organic components: fragment of partly decomposed organic matter – rare but present; brown decomposed elongated fragments of organic matter (50–100 μm – cca 5%); dark decomposed angular pieces of organic matter (50–100 μm – cca 20%) Pedofeatures: Fe oxide depleted groundmass, Fe/Mn oxidequasicoatings and impregnative nodules, clay infilling and coating	Gley-spodic horizon of podzol
VLK_1 (Fig. 8b)	Cracky microstructure; cracks pores, channels, vughs, complex packing voids C/F(500 μm) = 10:90; C/F(500 μm) = 30:70; sandy loam Coarse fraction: subrounded and rounded quartz and plagioclase, mica Matrix: orange brown, dark brown to black, stipple speckled, grano and porostriated Organic components: black partly decomposed and decomposed organic matter – preserved as fragments, but composing horizon, brown decomposed elongated fragments of organic matter (50–100 μm – cca 20%); dark decomposed angular pieces of organic matter (50–100 μm – cca 30%) Pedofeatures: Fe oxide depleted groundmass, Fe/Mn oxidequasicoatings and impregnative nodules, Fe/Mn capping, clay infilling and intensive multilayered coating	Redeposited B horizon with fragments of A horizon; features of postsedimentary illuviation
VLK_3 upper part	Vughy microstructure; cracks pores, vughs, chambers C/F(500 μm) = 5:95; C/F(500 μm) = 30:70; sandy loam Coarse fraction: subrounded and rounded quartz and plagioclase, mica Matrix: brown to light brown, stipple speckled, striated Organic components: dark decomposed angular pieces of organic matter (50–100 μm – cca 5%) Pedofeatures: clay and Fe/Mn oxide depleted matrix, occasional mottles of Fe impregnative nodules	Redeposited soil with features of postsedimentary illuviation and gleying
VLK_3 middle part	Vughy microstructure; cracks pores, vughs C/F(500 μm) = 5:95; C/F(500 μm) = 30:70; sandy loam Coarse fraction: subrounded and rounded quartz and plagioclase, mica Matrix: orange brown, dark brown to black, stipple speckled, grano and porostriated Organic components: brown decomposed elongated fragments of organic matter (50–100 μm – cca 20%); dark decomposed angular pieces of organic matter (50–100 μm – cca 30%), charcoal – rare Pedofeatures: Fe/Mn oxidequasicoatings and impregnative nodules, Fe/Mn capping, clay infilling and intensive multilayered coating	Redeposited soil with features of postsedimentary? gleying
VLK_3 lower part (Fig. 8d)	Single packing void microstructure; single packing voids C/F(500 μm) = 15:85; C/F(500 μm) = 30:70; sandy loam Coarse fraction: subrounded and rounded quartz and plagioclase, mica Matrix: orange, clayely, granostriated Organic components: charcoal, microcharcoal, black particle in clay coating Pedofeatures: clay coating	Relict of E horizon?
VLK_4 (Fig. 8d)	Complex microstructure; horizontal pores, cracks, channels, vughs, chambers, complex packing voids C/F(500 μm) = 20:80–50:50; C/F(500 μm) = 30:70; sandy loam to sands Coarse fraction: subrounded and rounded quartz and plagioclase, mica Matrix: stipple speckled to porostriated, brown to dark brown Organic components: fragment of partly decomposed organic matter – rare but present; brown decomposed elongated fragments of organic matter (50–100 μm – cca 10–50%); dark decomposed angular pieces of organic matter (50–100 μm – cca 20–50%) Pedofeatures: Fe oxide depleted groundmass, Fe/Mn oxidequasicoatings and impregnative nodules, clay infilling and coating	Redeposited soil influenced by illuviation of clay minerals and Gleying process
VT8 (Fig. 8e–f)	Massive microstructure; missing pores, only few channels filled with recent partly decomposed roots or rarely compose packing voids C/F(500 μm) = 20:88; C/F(50 μm) = 70:30; unsorted sandy loam Coarse fraction: subangular to subrounded quartz and plagioclase, mica Matrix: brown to light brown, crystalic Organic components: partly decomposed organic matter as roots in recent channels, brown decomposed elongated fragments of organic matter (50–100 μm – cca 1%); dark decomposed angular pieces of organic matter (50–100 μm – cca 20%), microcharcoal (50–100 μm – cca 20%) Pedofeatures: Fe oxide depleted groundmass, Fe/Mn oxide impregnated matrix, rare redeposited Fe/Mn nodules and clay coating, dirty dusty coating on grain surfaces	Redeposited soil with fragments of organic matter and charcoal; slightly postedoposition illuviation

Evidence of early soil leaching and acidification

A striking feature of the geochemical records of all the studied lacustrine records of that particular period is the significant increase in iron, as well as phosphorus concentrations, which correspond with the beginning of the Allerød interstadial (subzone B2, Figs. 3-4). Because of the low correlation between these elements and Ti (r= 0.1-0.3) and the Fe/Ti ratio exceeding the mean upper-crustal value (approximately 10) by an order of magnitude, the enrichment of the lake sediments by iron and phosphorus probably did not occur *via* physical (colluvial or aeolian) processes. We attribute this phenomenon to the climate amelioration, particularly the increase in precipitation. It resulted in the onset of reducing conditions in soils (during podzolization), leaching of iron, and subsequent P loss related to the leaching of Fe as its main inorganic sorbent. The beginning of the Allerød was characterized by the establishment of relatively-dense coniferous forests (Pokorný, 2002; Hošek et al., 2014). Both the more humid climate and coniferous forests are factors that highly promote podzolization (Lundström et al., 2000). The relationship between Fe-mobilization (podzolization) and coniferous forest development is clearly illustrated through the correlation of Fe content and *Pinus* pollen concentration in the SVC core (Fig. 9).

The relatively high *Helianthemum* percentages (up to 3%) in the basal sediments of Lake Švarcenberk (Pokorný, 2002) indicate initially-carbonate-rich substrates in the area, most probably loess (see discussion above). All this is in obvious contrast with the acidic substratum that prevails there today. At the present time, most soils are leached, highly-acidic, and almost completely lacking calcium carbonate.

This finding indicates that in our research area, with its sandy and relatively acidic bedrock, mineral-rich soils were replaced by increasingly well-leached ones during the Allerød.

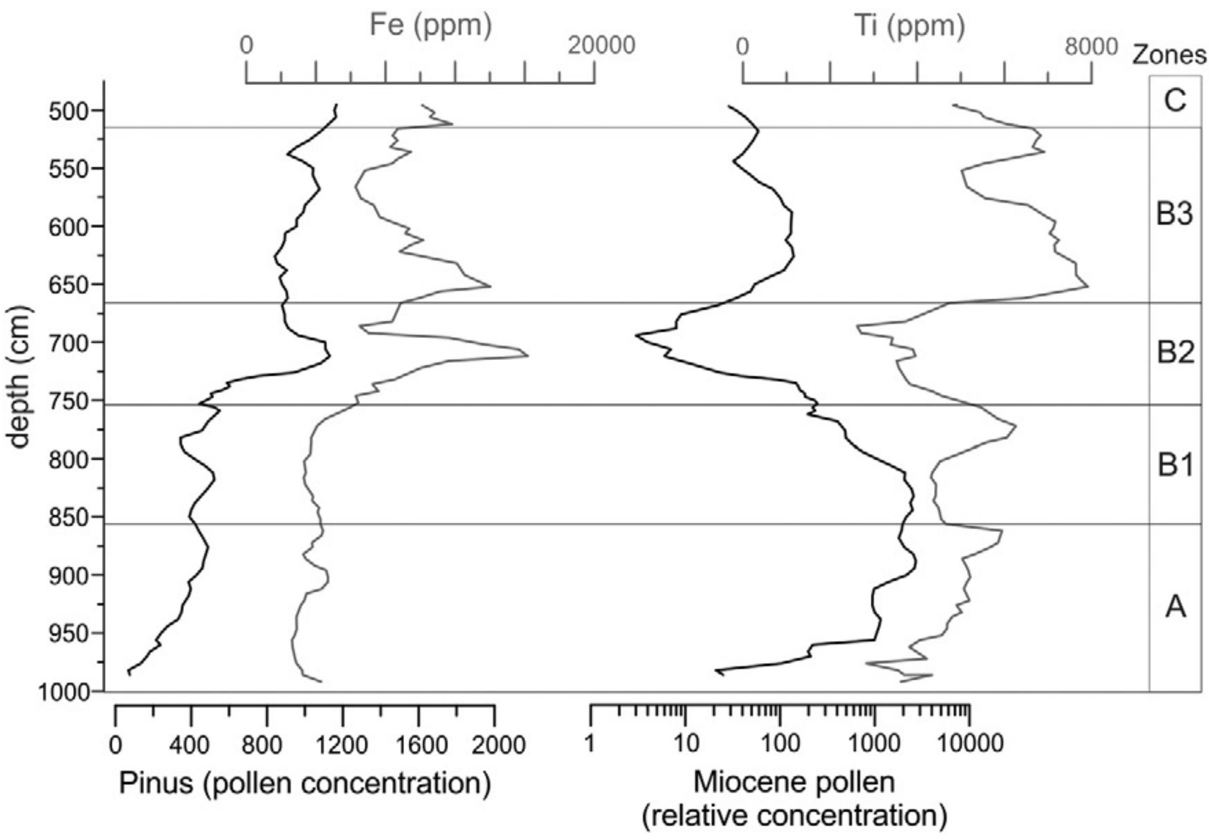

Fig. 9. *SVC core: Depth variation of the Fe, Pinus pollen concentration, Ti and concentration of the Miocene reworked palynomorphs.*

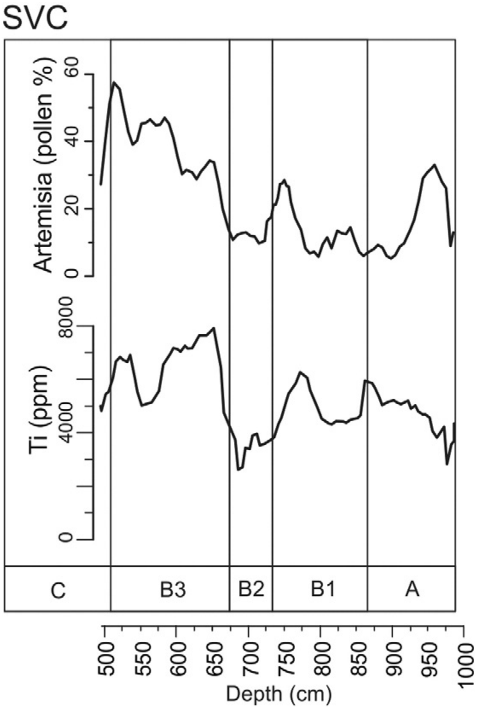

Fig. 10. *SVC core: Comparison of the Ti-recordwith Artemisia pollen record (% of terrestrial pollen total sum).*

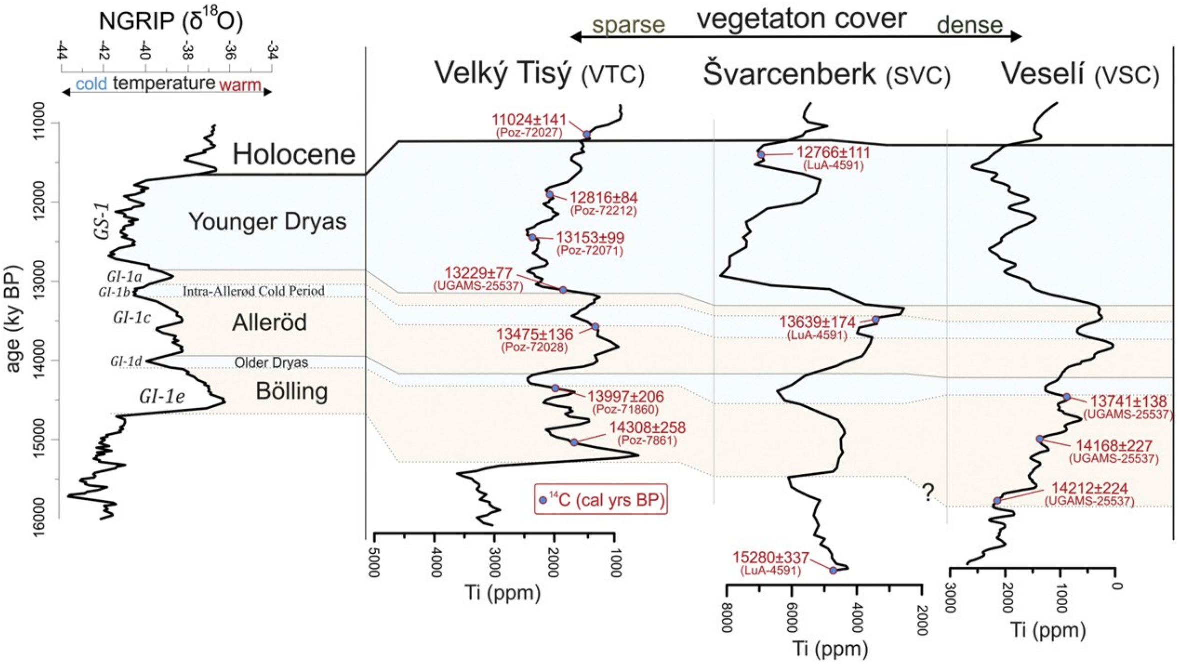

Fig. 11. *Correlation of Ti-records from Velký Tisý, Švarcenberk and Veselí with δ^{18}O record from NGRIP (NGRIP Members, 2004).*

Conclusions

Although the eastern part of central Europe is rather poor in Pleistocene lacustrine sequences, in recent years a large number of lake basins with relatively fast sediment deposition have been discovered in south Bohemia (Czech Republic). In this study we present the first results on newly-studied Late Glacial paleolakes and paleosols. Using a multi-proxy approach that combined sedimentological, geochemical, and geophysical methods with the pollen record and soil micromorphology, we have reconstructed the evolution of the erosion and pedogenic processes during the Last Termination (~ 16 to 11 ky BP). The conclusions of this study can be summarized as follows:

(i) Ti content in lacustrine sediment is a good tracer for erosion in the lake catchments. The highest erosion intensity occurred during cold periods with sparse vegetation cover, as suggested by the direct correlation between Ti and the pollen percentages of the *Artemisia* pollen record.

(ii) Four major and two minor environmental stages, identified geochemically in all the investigated paleo-lakes, were broadly correlated with Late Glacial climatostratigraphy. Based on wiggle-matching of the Ti record with the $\delta^{18}O$ Greenland record, local palynostratigraphy and ^{14}C-AMS dating, the main stages correspond with the Late Pleniglacial (geochemical zone A), Bølling (subzone B1), Allerød (subzone B2) and Younger Dryas (subzone B3). Short-term (centennial) climatic deteriorations situated between the Bølling and Allerød, and within the Allerød, have been correlated with the Older Dryas and the Intra-Allerød Cold Period, respectively. It suggests that the landscape of the study area responded sensitively to the climatic changes in the North Atlantic region and measurement of Ti in lacustrine sediments can be used as a reasonable climatostratigraphical tool for the subdivision of the Late Glacial part of studied records.

(iii) Magnetic properties (SIRM, S-ratio) are shown to be useful indicators of pedogenesis in the catchment, since the magnetic enhancement of the gyttja is probably connected with the development of humic soil horizons in the lake catchment. During the Late Pleniglacial, and partially also during the Bølling, the magnetic signal was influenced by the presence of eroded/wind-blown loess in the lake sediment.

(iv) Measurement of $\delta^{15}N$ in lacustrine sediments seems to be a promising method for the reconstruction of the humidity in the study area. Low $\delta^{15}N$ values relate with a warm-humid period, while elevated $\delta^{15}N$ values indicate a cool (and dry) climate.

(v) The B horizons of two (gleyic) Podzols discovered under aeolian sand dunes in the lake catchments were dated to the Allerød interstadial absolutely, by the ^{14}C-AMS dating (VLK section), and relatively, based on the stratigraphic position (VT8 section). These paleosols were parallelized with Usselo soils, up to now only known from northern-central Europe. According to the micromorphology investigations, the uppermost soil horizons had been eroded. In the case of the VLK paleosol, this erosion event was dated to 13,155 ± 150 cal. yr and associated with the IACP cold event. This clearly demonstrates a direct relationship between landscape processes, such as surface runoff / soil erosion, and allogenic input into the lake basins - as indicated by the geochemical/magnetic records in all studied lakes.

(vi) The geochemical, sedimentological, rock-magnetic, as well as pollen, records suggest that during the Late Pleniglacial and Bølling the study area was covered by a carbonate-rich substrate (loess), which is in sharp contrast with the acidic substratum that prevails in the study area at the present time. The significant increase in the iron and phosphorus content found in the lake sediments during the Allerød indicates that mineral-rich soils in the study area were replaced by increasingly-leached ones during the podzolization that took place under the humid, interstadial conditions.

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Dynamics in the Anthropocene

Šumava, from the research on forest vegetation changes

case study 4

Landscape-scale vegetation homogenization in Central European sub-montane forests over the past 50 years

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Abstract

Questions: How did plant species richness and spatial heterogeneity of the vegetation change across sub-montane forests over the past 50 years? Did the vegetation changes reflect eutrophication, acidification and management changes, which the area underwent during the second half of the 20th century?
Location: Ordinary managed forests sampled across 2500 km^2 of a typical Central European sub-montane landscape in the southern part of the Czech Republic.
Methods: We resampled 156 quasi-permanent plots sampled in the 1950s-1970s and covering the whole range of forest vegetation in the region. We compared understorey plant species richness and community composition between the surveys and tested for temporal changes in the spatial heterogeneity (beta diversity) of vegetation.
Results: Species richness and dissimilarity in species composition among plots decreased significantly between the surveys. The vegetation of the plots also changed significantly, but the changes varied considerably, and there is no clear directional trend across all plots. The vegetation homogenization was driven by local extinctions of specialist species, especially competitively weak species adapted to nutrient-poor conditions. Few generalist species expanded between the surveys.
Conclusions: We found evidence of taxonomic homogenization of forest understoreys across a large sub-montane region. This vegetation homogenization was probably driven by complex landscape changes which took place in the last century. Varied traditional management was replaced by largely uniform management, and the once spatially diverse landscape mosaic has become simpler. The resulting transition to species-poor and less variable vegetation was probably further accelerated by environmental eutrophication. Our results thus complement previous forest herb layer resurveys, which focused mostly on lowland forests and small nature reserves, and suggest that landscape-scale taxonomic homogenization is occurring across Central European forests.
Keywords: beta diversity; biotic homogenization; eutrophication; forest understorey; landscape change; semi-permanent plots; species richness; temperate forests; vegetation resurvey

Nomenclature: Kubát et al. (2002)

Introduction

Human impact alters biodiversity at local as well as regional spatial scales (McKinney & Lockwood 1999; Baiser et al. 2012; McGill et al. 2015). Numerous studies have explored changes in species richness at particular localities (Vellend et al. 2013; Bernhardt-Römermann et al. 2015). Much less is known, however, about temporal trends in spatial beta diversity at meta-community and regional scales (McGill et al. 2015). It has been suggested that compositional heterogeneity among sites is rapidly decreasing by the process called biotic homogenization (McKinney & Lockwood 1999). Biotic homogenization can have different forms, of which the most often studied is taxonomic homogenization (Olden & Rooney 2006). Taxonomic homogenization is the temporal decrease of beta diversity or, in other words, increasing similarity of species composition among sites. This process can occur independently of other changes in local or regional diversity (Baiser et al. 2012; Dornelas et al. 2014). Taxonomic homogenization has so far been studied mostly on animal assemblages (Baiser et al. 2012) and substantially less in known about the temporal trend in the spatial beta diversity of plant assemblages, especially in temperate forests.

Several processes have been identified as possible drivers of temporal changes in vegetation composition and diversity in temperate forests. Environmental eutrophication and acidification alter soil conditions (Diekmann & Dupre 1997; Verheyen et al. 2012), and shifts of plant species' optima to higher elevations have been linked to climate change (Lenoir et al. 2008, 2010). Other important drivers of vegetation changes are changes in forest management such as the abandonment of coppicing in lowland forests (Van Calster et al. 2007; Baeten et al. 2009; Szabó 2010; Kopecký et al. 2013) or cessation of litter raking (Douda et al. 2016). Vegetation changes have also been linked to plant invasions and expansions (McCune & Vellend 2013) and to altered game pressure (Hédl et al. 2010; Boulanger et al. 2015; Vild et al. 2016). These processes act at different spatial scales, they often interact, and their contribution to vegetation change depends on the landscape context and local conditions (Bernhardt-Römermann et al. 2015; Naaf & Kolk 2016). Although all these drivers can potentially lead to vegetation homogenization, the actual drivers of vegetation homogenization at the landscape scale remain unexplored.

Most resurvey studies conducted in Europe so far have focused on lowland deciduous forests (Verheyen et al. 2012; Bernhardt-Römermann et al. 2015). Substantially less is known about montane and sub-montane forests (Hédl 2004; Hülber et al. 2008; Lenoir et al. 2010). Existing resurveys usually cover only spatially restricted and relatively homogenous forest stands such as small nature reserves (Šamonil & Vrška 2008; Baeten et al. 2009; Hédl et al. 2010; Heinrichs & Schmidt 2016). The taxonomic homogenization of forest vegetation at the landscape scale is therefore hardly documented. Homogenization processes are poorly understood, especially in ordinary managed high forests, which cover a considerable part of the Central European landscape.

To fill this gap, we explored changes in the diversity and composition of understorey vegetation in sub-montane forests across a Central European landscape. We resurveyed plots across a wide range of forest vegetation, ranging from artificially planted spruce and pine stands to semi-natural fir-beech and mountain spruce forests. This allows us to explore decadal changes of vegetation and its diversity at the landscape scale. Specifically, we asked:

1) Is there any general pattern of vegetation change across various forests in the region under study?

2) Does forest vegetation heterogeneity decrease by the process of biotic homogenization?

3) Which species and ecological processes contributed the most to the observed vegetation changes?

Methods

Study area

To cover diverse forest stands, we chose a region in the southern part of the Czech Republic - the Bohemian Forest (Šumava Mountains) and its foothills (Fig. 1). This 2500-km^2 large region represents a typical Central European landscape with an undulating topography. Elevations in the study region range from 450 to 1300 m a.s.l. Forests cover about 50 % of the area, and the rest is a mosaic of agricultural land, villages and several towns.

The prevailing bedrock types are intensely metamorphosed rocks and granitoids with local admixtures of other rocks, often covered by colluvial and alluvial deposits, and locally by peatbogs. Soils are mostly acidic Cambisols and Podzols, locally also Gleysol and Histosols. The climate in most of the region is characterized by mean annual temperatures of around 5-6°C and mean annual precipitation of around 700 mm. There is an elevational temperature gradient of climatic conditions with the mean annual temperature and precipitation decreasing to around 3°C and 1200 mm, respectively, at 1200 m. a.s.l. (Tolasz et al. 2007).

Depending on the natural conditions, forests should cover almost the entire region (Neuhäuslová 2001). Most of the area was naturally dominated by *Fagus sylvatica* and *Abies alba* whereas *Picea abies* prevailed at higher elevations and probably occurred also in valleys and on waterlogged soils. *Pinus sylvestris* occurred in ecologically extreme sites such as rock screes and mires (Pišta 1982, Abraham et al. 2016). These natural forests were mostly logged during the last centuries and gradually turned into spruce and pine forests for timber production. Old-growth fir-beech forests remain in several isolated nature reserves (Šamonil & Vrška 2008).

This region has been shaped by human presence for millennia, but settlements were relatively sparse (Beneš 1996; Kozáková et al. 2015). Settlements and surrounding meadows, pastures and arable fields reached their greatest spatial extent in the 19th and the first half of the 20th century. In this period, the intensity of traditional forest management probably culminated, at least at accessible sites. The population in the region strongly declined after World War II when German inhabitants were forced out. Dramatic landscape changes continued later when the region experienced the nationalization of private property, collectivization and state planned agriculture and forestry during the communist regime in the 1950s–1980s. In the last two decades, arable agriculture in the region decreased, but forest management remains mechanized and spatially uniform.

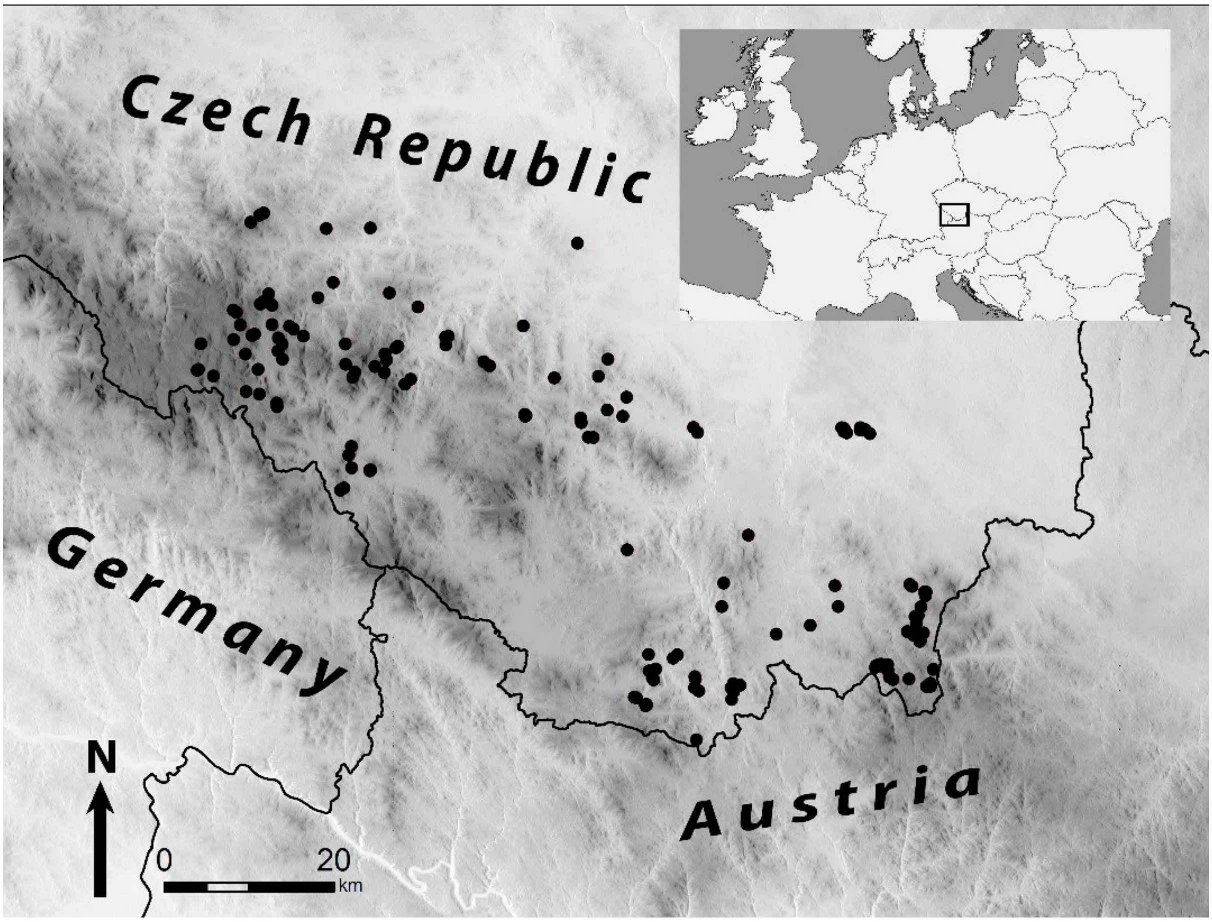

Fig. 1 *Location of the study area within Central Europe and the distribution of 156 resurveyed plots covering varied forest vegetation across a large region (2500 km²) and broad elevational gradient (450–1250 m a.s.l.).*

Vegetation sampling

To explore temporal changes in the vegetation of sub-montane forests, we resurveyed historical vegetation plots (Kapfer et al. 2016). These historical vegetation plots from the study region are available from a detailed study of regional forest vegetation (Pišta 1982) and from the Database of Czech Forest Classification System (Zouhar 2012). The aim of the original sampling was to document forest vegetation heterogeneity and to provide a basis for forest type classification (Pišta 1982). The location of each plot was indicated in detailed forestry maps, usually with a spatial resolution of 1:10,000.

For the resurvey, we selected 156 plots (Fig. 1) sampled between 1955 and 1980 and with at least about 40 years old canopy trees at the time of both surveys. The age was assessed from detailed forest management plans. To relocate these plots, we used geographic coordinates of the plots stored in the Database of Czech Forest Classification System. These coordinates were derived from historical maps, and a previous study in another region found that they are surprisingly accurate (Kopecký & Macek 2015).

In the field, we navigated to the location of each plot using a GPS receiver. We checked the relocation using information about the original plot slope, orientation and tree layer composition. We did not resurvey plots in cases when we found a strong discrepancy between the GPS-indicated location and original plot attributes. We estimated the possible relocation error to be a few tens of metres to up to 100 m in extreme cases. We consider this accuracy sufficient, given the low spatial heterogeneity of the forest stands under study and the relatively large plots size.

We resurveyed the plots in 2009-2011 in the same part of the vegetation season and used the same plot size of 500 m^2 as in the original survey. Within each plot, we recorded all vascular plant species and estimated their percentage cover.

Data analysis

We analysed the species composition of understorey vascular plant only, because the tree species composition was used to verify the plot relocation. To ensure comparability of the compositional data between the surveys, we converted the species percentage cover data recorded in the new survey to 11 ordinal classes of Zlatnik's scale (Zlatník 1953) used in the original survey. Zlatnik's scale is in general similar to the Braun-Blanquet scale (it has 11 ordinal classes; the first two express species abundance - cover below 1%, and the rest express species cover up to 5, 15, 25, 37, 50, 62, 75, 87 and 100%). For the purpose of analyses, we transformed these ordinal classes back to species percentage cover using intermediate values. Additionally, we grouped several closely related species into broader taxa if related species were not distinguished during the first survey (e.g. *Dryopteris carthusiana/dilatata)* or were difficult to reliably identify in the field (e.g. *Viola reichenbachiana/riviniana)*.

Species richness. To analyse temporal changes in species richness, we tested whether the number of understorey vascular plant species differ between the surveys using a 2-sample permutation test as implemented in the *oneway_test* function from the *coin* R package (Hothorn et al. 2008). This test is a non-parametric alternative to the classical t-test and calculates the probability of observing a difference in species richness based on 999 permutations restricted between paired samples.

Vegetation heterogeneity. To explore temporal changes in vegetation heterogeneity (beta diversity), we compared plot dispersion around multivariate centroids between the old and the new survey (Anderson et al. 2006). To account for different aspects of vegetation heterogeneity, we used three different dissimilarity indices. This approach can indicate whether a change in heterogeneity is driven mainly by (a) turnover in species occurrences (presence/absence), (b) by changes in species richness (not real turnover but the situation that the species composition in a plot is a nested subset of the species composition in another plot), or (c) a change in species proportions. Specifically, we used the Simpson index (describing the species turnover without the influence of richness differences), Sørensen index (which incorporates turnover in species occurrences and differences in richness) and Bray–Curtis index calculated from square-rooted species cover data standardized by sample totals (capturing changes in species proportions). To calculate the statistical significance of the difference between the old and the new survey, we used the test of multivariate homogeneity of group dispersions (Anderson 2006). We performed the test with 999 permutations restricted within temporally paired samples.

To identify which species contributed the most to the homogenization/differentiation, we calculated the difference in mean plot distance to the multivariate centroid of the samples from the old survey and the same dataset where we replace the occurrence of the focal species by its occurrence in the new survey. This novel approach answer the question: How would compositional heterogeneity change if the occurrence of the focal species did not change but all other species changed exactly as was observed. The difference between the multivariate dispersion of plots from the old survey and the multivariate dispersion of plots from new survey, but with unchanged occurrence of focal species, shows the effect of individual species changes. As a result, for each species in the dataset, we get the measure of individual species' contributions to the temporal change in compositional heterogeneity.

Species composition. To explore changes in species composition between the surveys, we used the same indexes as for compositional heterogeneity. To test the statistical significance of the compositional change between the old and the new survey, we used permutational MANOVA (Anderson 2001). For the test we used 999 permutations restricted within temporally paired samples.

To visually compare vegetation patterns between the old and the new survey, we performed non-metric multidimensional scaling (nMDS) ordination on the Bray-Curtis dissimilarity matrix. The two-dimensional configuration with the lowest stress after 100 random starts was centred and rotated by principal component analysis to maximize variance along the first ordination axis. To visualize vegetation shifts between surveys, we used 95 % dispersion ellipses based on (1) the SD of plot coordinates from the particular survey - showing overall changes in compositional heterogeneity and (2) the SE of mean plot coordinates from the particular survey – showing the overall shift in species composition (Newton et al. 2012; Oksanen et al. 2015).

To identify species that have significantly decreased or increased in frequency between the surveys (i.e. loser and winner species), we tested whether the proportion of plots occupied by each species changed over time. For the test, we used 999 permutations and adjusted the resulting P-values using Šidák's correction for multiple testing (De Cáceres & Legendre 2009).

To facilitate the interpretation of the observed vegetation changes, we also compared mean Ellenberg indicator values between surveys (Ellenberg et al. 1992). We calculated mean Ellenberg indicator values for each plot (disregarding taxa lacking indicator values) and compared the old and the new survey using the Wilcoxon signed-rank test.

For the analyses, we used R 3.0.2 (R Core Team 2015) with the packages vegan (Oksanen et al. 2015), betapart (Baselga et al. 2013), coin (Hothorn et al. 2008) and indicspecies (De Cáceres & Legendre 2009).

Results

Changes in species richness

Plant species richness decreased in most of the plots (Fig. 2), and this impoverishment was statistically significant ($Z = -2.62$, $p = 0.008$). Mean plot species richness decreased from 15 species in the old survey to 12 species in the new survey. Despite this relatively low alfa diversity, the study plots harboured varying vegetation; in total 269 vascular plant species were recorded: 222 species in the old survey, 201 in the new survey.

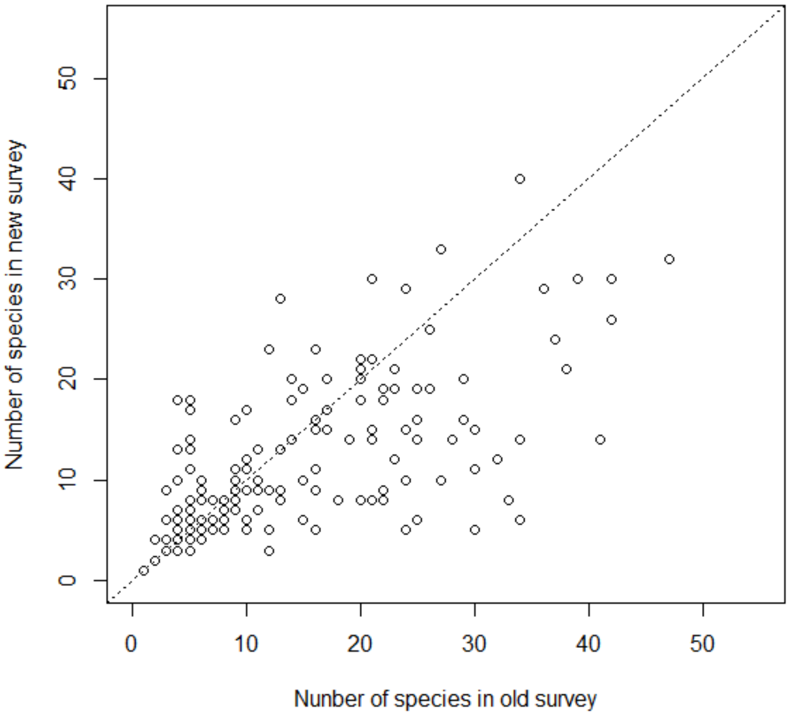

Fig. 2. *Species richness of vascular plants within the study plots decreased between the old survey (1955-1980) and the new survey (2009-2011) of Central European sub-montane forests. Each point represents species richness within an individual plot, and the dashed line represents the null hypothesis of no change in species richness between the surveys.*

Changes in vegetation heterogeneity

Vegetation heterogeneity decreased between the surveys (Fig. 3). The difference in multivariate dispersion among plots was statistically significant for Bray-Curtis dissimilarity (change in species proportions) and Sørensen dissimilarity (species identity including the effect of species richness differences) (Table 1). Multivariate dispersion based on the Simpson dissimilarity (turnover in species identities) also decreased, but the decrease was not statistically significant. Together, these results show that vegetation homogenization was driven by selective species extinction rather than temporal species turnover.

The species contributing the most to vegetation homogenization by changes in their occurrence in the plots were *Dryopteris carthusiana/dilatata, Oxalis acetosella, Vaccinium myrtillus, Rubus idaeus and Calamagrostis villosa*. The species contributing the most to homogenization by changes in their cover were *Vaccinium myrtillus, Dryopteris carthusiana/dilatata, Calamagrostis villosa, Vaccinium vitis-idaea* and *Calluna vulgaris.* This analysis of species' contributions to homogenization does not tell us whether the species increased or decreased.

Table 1. Changes in overall compositional heterogeneity and in local species composition in 156 forest vegetation plots surveyed in 1955–1980 and resurveyed in 2009-2011. The changes were assessed using three dissimilarity indices – Simpson (species turnover without the influence of richness differences), Sørensen (species turnover and differences in richness) and Bray-Curtis (changes in species proportions):

	Compositional heterogeneity			Species composition		
Dissimilarity	Δ dispersion	pseudo F	p-value	R^2 (%)	pseudo F	p-value
Simpson	-0.02	1.31	0.255	1.3	3.97	0.001
Sørensen	-0.04	9.68	0.002	1.3	4.03	0.001
Bray-Curtis	-0.02	10	0.003	0.8	2.52	0.001

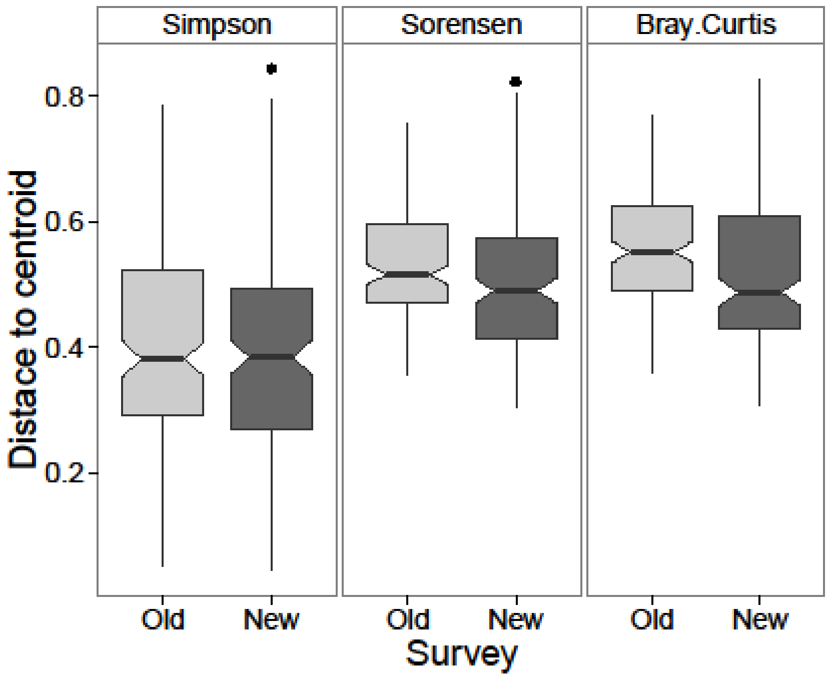

Fig. 3. *Decreasing vegetation heterogeneity between old (1955-1980) and new (2009-2011) surveys of understorey vegetation in Central European sub-montane forests was mainly caused by non-random species extinctions. Boxplots show plot distances to their multivariate centroid in each survey assessed using three dissimilarity indices. The Simpson index measures species turnover without the influence of richness differences, the Sørensen index measures species turnover and differences in richness¸ and the Bray-Curtis index measures changes in species proportions. Thick lines represent medians, boxes encompass 25–75% of values, whiskers extend to the most extreme value within 1.5 times the interquartile range, and dots are values outside the whiskers. Notches indicate approximate 95 % confidence intervals for the medians.*

Changes in species composition

Temporal changes in species composition were substantially smaller than vegetation variability across the space captured by the plots (Fig. 4). Nevertheless, the changes in species composition were statistically significant (Table 1). While the frequency of 21 species decreased significantly, it increased significantly between the surveys in the cases of only three species (Table 2). Winner species were generalists common in disturbed forests - *Rubus fruticosus* agg., the invasive alien *Digitalis purpurea* and *Dryopteris carthusiana/dilatata.* Losers, by contrast, were mostly habitat specialists occurring at nutrient-poor sites, e.g. *Veronica officinalis, Festuca ovina, Danthonia decumbens* and *Hieracium pilosella.*

The mean Ellenberg value for nutrient content increased on average by 0.16 (p = 0.013), and the mean Ellenberg value for soil reaction decreased by 0.14 (p = 0.014). Changes in other mean Ellenberg values were only small and statistically not significant.

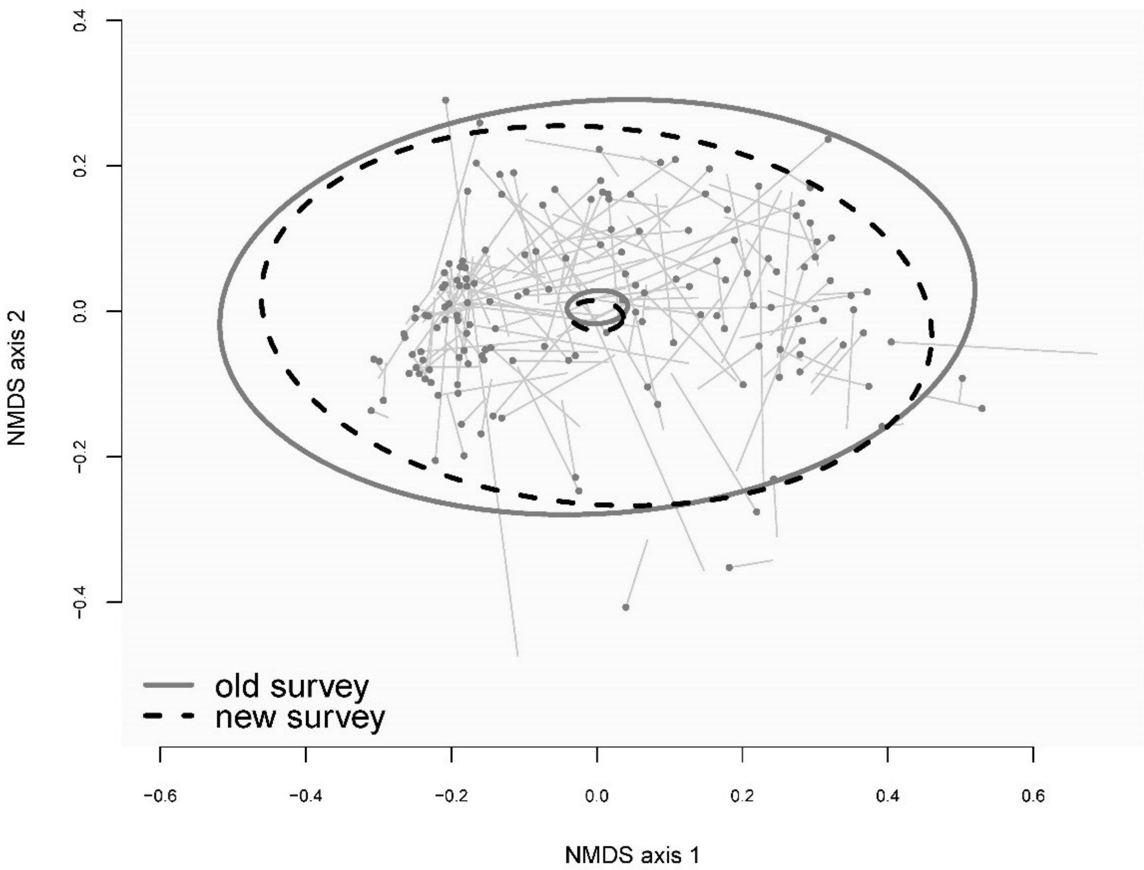

Fig. 4. *Nonmetric multidimensional scaling of the temporal change in understorey species composition. The species composition in the old survey was more heterogeneous than in the new survey, indicating taxonomic homogenization of the forest understorey. The larger ellipses show changes in compositional heterogeneity and represent 95 % dispersion ellipses based on the SD of plot coordinates from each survey. The smaller ellipses show the overall shift in species composition and represent 95 % dispersion ellipses based on the SE of mean plot coordinates from each survey. Filled symbols represent samples from the old survey, the lines connect both samples from the same plot, and the ends of the lines represent samples from the resurvey.*

Table 2. Changes in plant species occurrences in Central European sub-montane forests. The table shows species whose frequency of occurrence changed significantly between the surveys (loser and winner species) and 10 most frequent species with no significant temporal change. The significance of the change was tested by a permutation test, and resulting the p-values were adjusted using Šidák's correction for multiple testing:

Species	Species frequency (N plots)		p-value
	Old survey	New survey	
Loser species			
Veronica chamaedrys	13	2	0.005
Ajuga reptans	19	5	0.006
Viola reichenbachiana/riviniana	35	16	0.006
Veronica officinalis	29	12	0.008
Paris quadrifolia	18	5	0.009
Fragaria vesca	21	7	0.01
Festuca ovina	12	2	0.012
Adoxa moschatellina	7	0	0.016
Hieracium murorum	65	44	0.017
Carex sylvatica	9	1	0.02
Potentilla erecta	11	2	0.022
Petasites albus	19	7	0.024
Mycelis muralis	47	29	0.025
Epilobium montanum	12	3	0.029
Luzula campestris	6	0	0.029
Danthonia decumbens	6	0	0.029
Hieracium pilosella	6	0	0.029
Luzula multiflora	6	0	0.031
Anthoxanthum odoratum	6	0	0.032
Actaea spicata	21	9	0.034
Galeobdolon luteum agg.	35	20	0.041
Most frequent species with no significant changes			
Vaccinium myrtillus	113	118	0.519
Avenella flexuosa	116	109	0.41
Oxalis acetosella	83	94	0.234
Rubus idaeus	44	61	0.058
Calamagrostis villosa	48	60	0.18
Senecio ovatus	51	59	0.37
Athyrium filix femina	58	53	0.53
Luzula luzuloides	48	47	0.755
Carex pilulifera	60	46	0.125
Winner species			
Dryopteris carthusiana/dilatata	73	109	0.001
Rubus fruticosus agg.	13	31	0.006
Digitalis purpurea	2	10	0.035

Discussion

We resurveyed forest vegetation plots across a large sub-montane region and found significant vegetation homogenization despite highly variable compositional changes within individual plots. This provides evidence that large-scale vegetation homogenization is occurring across Central European forests. The temporal change of spatial beta diversity at such landscape - or meta-community - scales is still understudied even though it potentially represents a universal trend and occurs also in other regions (McGill et al. 2015). Whereas vegetation homogenization caused by succession following the cessation of traditional management has been documented in lowland forest reserves (Kopecký et al. 2013; Heinrichs & Schmidt 2016), evidence from managed forests at middle elevation is missing. Our results fill this gap and suggest that species impoverishment and landscape scale homogenization is occurring even in sub-mountain forests. In the following discussion we explore several processes leading to the impoverishment and homogenization of sub-mountain forests in Central Europe.

Species richness decline

Vegetation resurveys have detected decreases as well as increases in local species richness (Vellend et al. 2013; Bernhardt-Römermann et al. 2015). In our study region, species richness has declined significantly. The declining species richness of European lowland forests is considered to be a result of the cessation of traditional forest management (Hédl et al. 2010; Kopecký et al. 2013), and environmental eutrophication and acidification (Baeten et al. 2009). The species richness of our study region declined significantly, but the magnitude of these changes is relatively small compared to lowland forests (Bernhardt-Römermann et al. 2015). This difference can be explained by the relatively species-poor vegetation in our sub-montane region compared to species-rich lowland forests.

The vegetation can respond slowly to environmental changes and sometimes there is a lag between an environmental change and the induced vegetation change (Bertrand et al. 2011; Savage & Vellend 2014). The current state of the vegetation is therefore partly a reflection of the current conditions and partly a reflection of previous conditions (McCune & Vellend 2013). In our study region, the centuries-long human presence sharply declined after World War II. We therefore suggest that the relatively species-rich vegetation captured by the old survey possibly, at least in part, reflected some transitional stage. Species typical of open forests and grassland habitats were still present as a legacy of traditional management and ruderal species, supported by modern management, were already present, albeit only in a few individuals. We therefore think that the observed decline in species richness can be partly explained also by this relatively species-rich transitional stage of the landscape captured in the original survey.

The winner and loser species

Only a few species benefit from the observed vegetation change. The increasing frequency of *Rubus fruticosus* agg. and *Rubus idaeus* reflects the ongoing ruderalization of forest understoreys and can be linked to nitrogen deposition (Walter et al. 2016). A similar increase in the frequency of *Rubus* species has been observed also in other European regions (Verheyen et al. 2012). The single significantly expanding non-native species was *Digitalis purpurea*, but its occurrence is still restricted to the south-eastern part of the region under study. This confirms that European sub-montane forests are only marginally affected by plant invasions, unlike European lowland forests (Chytrý et al. 2005).

Other expanding species are the ferns *Dryopteris dilatata* and *Dryopteris carthusiana*, recorded as one taxon in the original survey. These ferns are expanding also in other European regions, probably due to increasing canopy closure (Verheyen et al. 2012; Bernhardt-Römermann et al. 2015). An alternative explanation is increasing game pressure, as many studies report increasing cover of ferns in response to increasing ungulate densities in North America (Frerker et al. 2014; Nuttle et al. 2014).

Many species have declined significantly between the surveys. They are mostly competitively weak species typical of nutrient-poor sites on acid soils, such as *Veronica officinalis, Festuca ovina, Potentilla erecta, Hieracium murorum, Danthonia decumbens, Hieracium pilosella, Anthoxanthum odoratum, Luzula campestris* agg. Their historical presence was probably facilitated by a more open canopy, widespread litter raking and pastoral management (see Fig. 5a). Significantly declining species are also specialist of humus-rich forests, namely *Paris quadrifolia*, *Mycelis muralis, Galeobdolon luteum* agg. and *Actaea spicata*. These species are on the decline also in other regions (Hédl 2004; Verheyen et al. 2012). In contrast to the first group of species, the decline of these species is probably caused by the opposite process – opening of the forest canopy by logging in certain previously almost unmanaged places (Fig. 5b). These results may appear contradictory at first sight, but they make good sense in our study landscape whereas the first group of species is declining in one subset of the plots, the second group is declining in another. This points to the huge variability among past forest stands across the landscape and is in accordance with the observed overall vegetation homogenization.

Vegetation homogenization at the landscape scale

We found significantly higher vegetation similarity among the plots in the new survey. In other words, the proportion of species shared among plots at different sites increased during the second half of the 20th century. This homogenization was driven by species extinctions rather than overall vegetation turnover or expansion of generalists. As a result, the current species composition of most plots represents a subset of the former community. Besides the numerous loser species (see Table 2), several rare species sensitive to environmental eutrophication (e.g. *Antennaria dioica* and forest orchids) disappeared from the landscape almost completely. To disentangle the different processes leading to vegetation homogenization, we compared several dissimilarity indices, which is a rarely taken approach (Naaf & Wulf 2010; Heinrichs & Schmidt 2016). Our results highlight the great potential of this approach and we encourage its wider use in studies of vegetation homogenization.

Some common and dominant species also contributed to the observed homogenization. For example, *Calamagrostis villosa* has expanded between the surveys, possibly as consequence of its spreading with the planting of spruce. Its increase has already been reported using smaller datasets from the same region (Wild et al. 2004; Šamonil & Vrška 2008). Historically, *Calluna vulgaris* and *Vaccinium vitis-idaea* dominated the forest understorey at extremely acid and nutrient-poor sites. Between the surveys, the cover of these species decreased, and this substantially contributed to the observed vegetation homogenization. However, the contribution of *Calluna vulgaris* and *Vaccinium vitis-idaea* to vegetation homogenization was apparent only from the Bray-Curtis index and is obscured when considering only presence/absence data because few individuals still persist in the plots though the abundance of these two species apparently declined between the surveys. This highlights the necessity of using different metrics when exploring vegetation homogenization.

The ability to detect biotic homogenization does not only depend on the temporal and spatial scale, but also on the overall variability of vegetation types under consideration (McCune & Vellend 2013). Despite that, the vegetation homogenization of Central European forests has been reported by studies focused on only one or a few forest vegetation types at small spatial scales (Hülber et al. 2008; Šamonil & Vrška 2008; Durak & Holeksa 2015; Heinrichs & Schmidt 2016). Few studies have explored changes in vegetation variability at a spatial scale comparable with that considered in our study: forest patches in the South of England homogenized since the 1930s (Keith et al. 2009) and a broad-leaved forest in northern Germany homogenized during the 1990s (Naaf & Wulf 2010). Studies conducted in North American forests have reported forest vegetation homogenization, for example, on Vancouver Island (McCune & Vellend 2013) or in a pine forest in Wisconsin (Li & Waller 2015). Homogenization processes occurring at the landscape scale therefore appear similar across distant regions with different species pools. Biotic homogenization might thus be the sole integrated and universal pattern occurring over large spatial scales, as suggested by Dornelas et al. (2014). We therefore think that the observed decline of vegetation heterogeneity (beta diversity) at the landscape scale reflects the slow, human-driven complex biosphere impoverishment of all regions better than changes in alpha diversity, which vary from site to site (Vellend et al. 2013).

Landscape changes leading to vegetation homogenization

Management changes and environmental eutrophication are the most probable drivers of decreasing plant diversity in our study region, but disentangling the relative roles of these processes is extremely hard. Both culminated in the second half of the 20 century, and observational studies cannot differentiate between artificial nutrient inputs and increasing nutrient levels caused by a decline of nutrient output from the ecosystem.

Historical management was probably the main factor maintaining a spatially variable and locally species-rich mosaic of plant communities in the Central European landscape. The abandonment of this traditional management and the transition to the current coarse-grained and mechanized forestry was probably the main driver of the observed changes (Fig. 5). Former forest pasturage (officially forbidden in the 18th century but locally practised until the 20th century) was probably one of the determinants of species-rich open habitats (e.g. Samojlik et al. 2016). Historical litter raking caused substantial nutrient output from forests (Bürgi & Gimmi 2007, Hofmeister et al. 2008) which also influenced plant communities (Dzwonko et al. 2002; Vild et al. 2015; Douda et al. 2016). Since the cessation of widespread litter raking around the middle of the 20th century, nutrient levels are expected to have increased in the forests under study.

Eutrophication as a driver of vegetation change in temperate forests has been widely tested and discussed (Gilliam 2006; Verheyen et al. 2012). Atmospheric emissions and deposition of NO_3^- and NH_4^+ have been quite high in the study region, peaking in the 1980s (about 160 mmol m^{-2} yr^{-1} of dissolved inorganic nitrogen, Kopácek et al. 2001; Kopáček et al. 2012). Environmental eutrophication probably altered the vegetation in at least some previously nutrient-poor plots. Another artificial source of nutrients, which probably also played a role in our region, is agricultural fertilization. It probably affected at least plots that are close to forest edges and in alluvial forests (Lameire et al. 2000). Generally, there is an interaction of eutrophication and local conditions, as has been reported from lowland forests in Germany, where eutrophication was most pronounced at previously acidic and nutrient-poor sites (Naaf & Kolk 2016).

Soil acidification is another common driver of vegetation changes (Thimonier et al. 1994; Diekmann & Dupre 1997; Baeten et al. 2009; Dirnböck et al. 2014). The amount of acidic deposition, which culminated in 1980–1985 (Kopáček et al. 2012), were quite high in our study region (~140 mmol m^{-2} yr^{-1} atmospheric inputs of sulphur), but plant community shifts toward more acidophilic vegetation are less clear than the consequences of eutrophication discussed above. The mean Ellenberg indicator value for soil reaction decreased slightly, but at the same time we found that species adapted to acidic soils were among the most declining. We suggest two possible explanations: (1) Plant communities were already dominated by acidophilus plant species at the time of the old survey, so further acidification could not have caused local extinctions of basiphillous species, which were absent already in the original survey (because of generally acidic soils on prevailing granite bedrock); or (2) Acidification is often associated with eutrophication through atmospheric deposition of SOx and NOx, so even strong soil acidification can be masked because plant species more strongly respond to the eutrophication (Thimonier et al. 1994; Diekmann & Dupre 1997).

We did not find any climate change-driven vegetation changes described in other regions (Lenoir et al. 2010; Bertrand et al. 2011; Savage & Vellend 2014). Ellenberg indicator values for temperature did not show any significant changes. A possible climate change effect on the forest understorey could be moderated by its interaction with local environmental factors like changes in the canopy cover (De Frenne et al. 2013) and masked by other processes such as management changes and eutrophication.

Implications for biodiversity conservation

Our results suggest that the biodiversity of the forest understorey is decreasing throughout the landscape. The old-growth forests, targeted by previous studies and protected in nature reserves, do not cover all components of decreasing plant biodiversity. For more complete conservation of the plant biodiversity of Central European sub-mountain forests, it would be necessary to (i) also protect forest stands that have been managed for centuries and not only old-growth forests; (ii) restore a diverse mosaic of traditionally managed patches; and (iii) protect species-poor forest patches less influenced by eutrophication and still harbouring regionally declining competitively weak species.

Vegetation changes observed at the landscape scale can signal possible biodiversity losses at different trophic levels. For example, taxonomic homogenization of bird communities has been reported from the Czech Republic (Reif et al. 2013). This homogenization can be - at least partly - a consequence of ongoing vegetation homogenization. While this link is hypothetical, future research should explore this possibility because it has profound consequences for biodiversity conservation in the face of global change.

Although we have found that landscape-scale vegetation homogenization is occurring across sub-mountain forests in Central Europe, more landscape-scale studies from other regions are desirable for a robust synthesis at the continental scale. We nevertheless conclude that formerly spatially diverse and species-rich forest plant communities are vanishing under the present coarse-grained forest management and ongoing environmental eutrophication. To maintain forest species richness and heterogeneity at the landscape scale, spatially more differentiated management is needed.

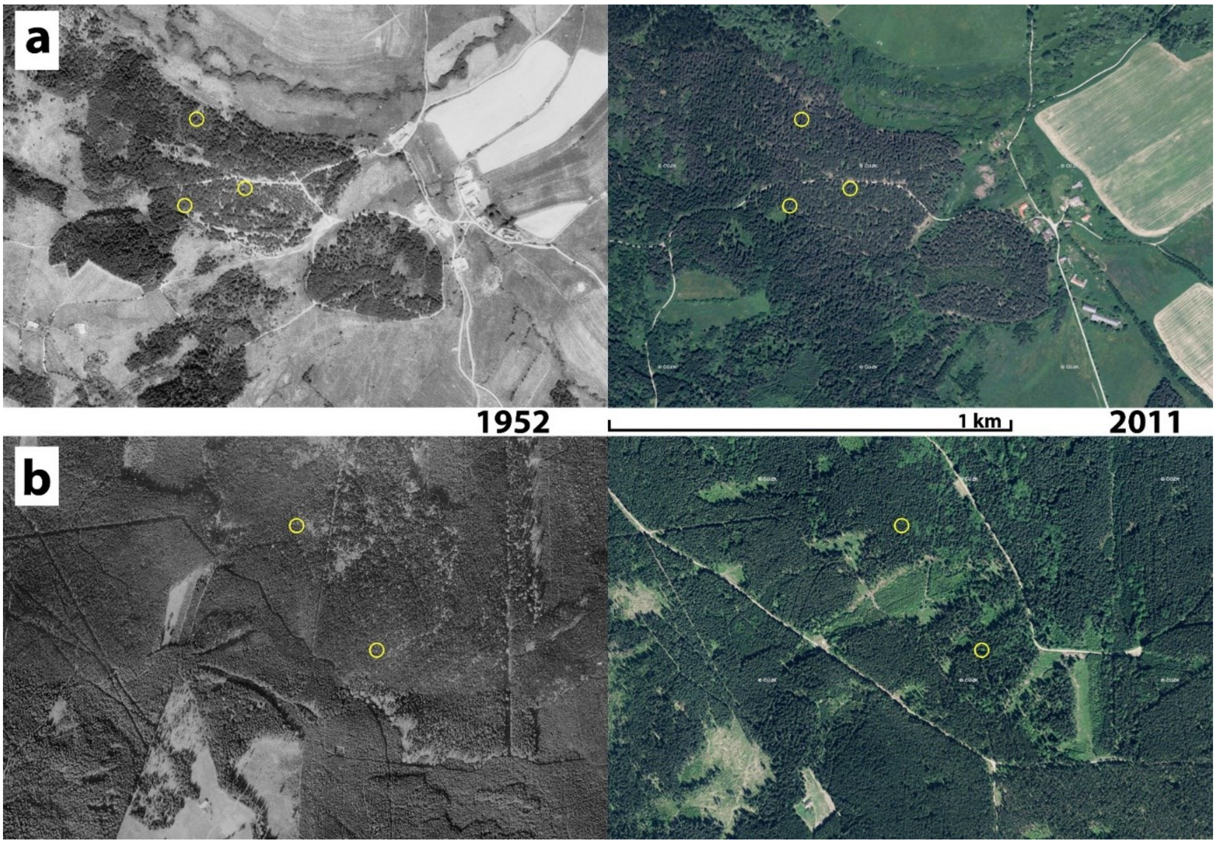

Fig. 5. *Two examples of landscape changes in the study region in the Czech Republic; aerial photographs from 1952 (left) and 2011 (right) of the same area. (a) The once diverse mosaic of open forests neighbouring with a settlement, meadows and pastures has become a dense forest, and the surrounding grasslands have been overgrown by woody species or have been transformed into arable fields. (b) Previously compact forests are now patchy after intensive logging in the last decades. Both these changes have resulted in landscape-scale taxonomic homogenization of understorey plant communities. Circles indicate resurveyed quasi-permanent vegetation plots. The aerial photographs were provided by the* Office *of Military* Geography and Hydrometeorology *(VGHMÚř) of the Ministry of Defence of the Czech Republic and by the Czech Office for Surveying, Mapping and Cadastre.*

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