Using a new database of plant macrofossils of the Czech and Slovak Republics to compare past and present distributions of hypothetically relict fen mosses

Využití nové makrozbytkové databáze k porovnání současného a dávného rozšíření druhů mechorostů, považovaných za glaciální relikty

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Modern databases containing large amounts of botanical data are a promising source of new results based on large data analyses. We used a new database of plant macrofossils of the Czech and Slovak Republics to compare the recent distributions of putative relict species of fen bryophytes with their past distributions since the late glacial. All the species studied occur in late-glacial sediments, but mostly in regions where they are recently recorded (19–21st centuries). There are specific regions rich in putative relict species of fen bryophytes both in late glacial / early Holocene times and recently. In some cases the target species were, however, found outside the recent distribution range where environmental conditions are no longer suitable for their occurrence. We further found that the total number of the glacial and early-Holocene records greatly exceeds the total number of records for the middle Holocene, when succession to woodlands or bogs resulted in a reduction in species of bryophytes that are specific to open rich fens. The observed patterns may imply a relict status of the target species. We especially documented a substantial decline in the abundance of species requiring a high and stable water level (*Drepanocladus trifarius*, *Meesia triquetra* and *Scorpidium scorpioides*), both throughout the Holocene and during the most recent transformations of the landscape. In contrast, those species that tolerate transient decreases in water level persisted into recent times at more localities (*Calliergon giganteum*, *Hamatocaulis vernicosus*, *Paludella squarrosa*). Macrofossil data cannot, however, provide a quantitative analysis of the distribution of a species, because the number of recent data usually greatly exceeds the number of fossil records. The reason is that the area sampled in palaeoecological research is very small as it is time-consuming and expensive; cores or excavations usually are of only a few square centimetres. Despite this shortcoming, macrofossil data are an important, but not the only, source of evidence for the identification of the relict status of a species.

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K e y w o r d s: calcareous fens, central Europe, fossil records, herbarium specimens, Holocene, late glacial

Introduction

In the last few decades, a huge number of different floristic, ecological or palaeoecological data have been collected. An improved possibility to analyse large datasets due to the rapid development of computer technologies has triggered the creation of large databases, which are a very useful and promising tool for answering general questions and testing hypotheses (e.g. Chytrý et al. 2016). Within the field of palaeoecology, pollen databases already exist for both, the Czech Republic and Slovakia (PALYCZ database; Kuneš et al. 2009) and Europe (EPD database, http://www.europeanpollendatabase.net) and are widely used in large-scale synthetical studies (Davis et al. 2003, Feurdean et al. 2014, Fyfe et al. 2015, Giesecke et al. 2017). These databases are also part of the worldwide database Neotoma (https://www.neotomadb.org), which contains not only pollen data but also data from other palaeoecological fields like plant macrofossils, molluscs etc. Analysis of data from such databases could help us answer questions about the relic status of species and habitats or about changes in species distributions with changing climate and the effect of human activity. Unfortunately, in the case of plant macrofossils the availability of data is much worse than in the case of pollen because there are very little data on plant macrofossils for Europe. Neotoma database contains data mostly from North America and virtually no plant macrofossil data for Europe. In 2009, the new late-Quaternary plant macrofossil database for northern Eurasia (from 23° to 180° E and 46° to 76° N) was presented and used for mapping the distribution of some tree taxa (Binney et al. 2009; http://www.geog.ox.ac.uk/research/biodiversity/lel/NEMD.html). This database includes sites in the former Soviet Union and one in Finland, thus it covers only the eastern part of Europe. There are no national plant macrofossil databases for Europe, except for the archaeobotanical data from archaeological sites; Pokorná et al. 2011; http://www.arup.cas.cz/czad; Pokorná et al. 2018). Here we introduce, for the first time, a new database for the Czech Republic and Slovakia (http://www.sci.muni.cz/botany/mirecol/paleo), and utilize data stored in it for the first meta-analysis. This database is the first attempt to gather records of plant macrofossils found in natural sediments like peat, travertines or gyttja into one national database for the area west of 23° E and make the information more widely accessible to botanists.

Plant macrofossils have an advantage over the more widely used plant microfossils, such as pollen and spores, as in the most cases they are identifiable to species level. This holds especially for mosses, for which entire specimens are fossilized unlike vascular plants for which only seeds or fragments of tissues are fossilized. As a result, macrofossil data can be used for comparing the distributions of species in the remote past and in modern times. For bryophytes, however, modern distribution maps are usually not available or less complete than those for vascular plants for which a long tradition of grid cell mapping exists (e.g. Kaplan et al. 2017a, b).

One of the possible applications of macrofossil databases is tracing the species distribution dynamics during glacial/interglacial cycles. Many studies have reconstructed glacial refugia and post-glacial recolonization patterns of individual species at the European scale, including bryophytes (Szövenyi et al. 2006, Kyrkjeeide et al. 2012, 2014, Hedenäs 2017). In central and western Europe, there is a long tradition of identifying which of the regionally rare species are relicts from glacial times, or at least from before the middle-Holocene climate optimum (so called 'glacial relicts' in this concept; see Rybníček 1966, Jankovská 1988, Odgaard 1988, Hájková et al. 2015, Dítě et al. 2018). Macrofossil databases may help with the quantification of the relict status of hypothetically relic fen species, which is the principal aim of the meta-analysis presented in this paper.

Hypothetically relic fen mosses are easily identifiable, often are the main component of peat and as such are frequently detected in fossil material. Some of them are currently rare or declining not only in western and central Europe but also in the boreal zone (e.g. *Hamatocaulis vernicosus*, *Meesia triquetra*; Rehell & Virtanen 2016). One of them, *Hamatocaulis vernicosus*, is even protected by a European directive in the Natura 2000 system (the Council Directive 92/43/EEC). A huge effort is devoted to mapping, monitoring and active conservation of the last remnants of their populations and understanding their dynamics during the Holocene, which could help in devising more effective means of conservation. Knowledge on the recent and historical distributions of these hypothetically relic species of fen bryophytes in the Czech Republic and Slovakia is still incomplete and fragmented. The results of herbarium specimens of some species are published mostly in local journals and manuscripts (Bryonora, Bulletin of SBS, habilitation theses; e.g. Soldán 1987, Váňa 2006, Dítě & Šoltés 2010, Štechová et al. 2012, Šoltés 2014). Moreover, comparison with fossil records, which could indicate their relic status, has never been done before.

One of the aims of this study is to provide detailed information about the new Czech and Slovak database of plant macrofossils from natural sediments, especially those of bryophytes, and evaluate the possibility of using such a database for constructing past and modern distributions. Another, more specific aim is to use this database for mapping the past distributions of particular hypothetically relic species of fen mosses on a millennial scale. Further, we aim to gather all the data on the modern distributions (19–21st century) of the target species of moss, which are currently scattered in local journals and unpublished material. Using the compiled data on modern and past distributions we aim to determine the relict status of particular species of moss.

Material and methods

Macrofossil database

For creating the database we used Microsoft Access 2003 software. The structure of the database follows the Arbodat database, which was developed for archaeobotanical data (Kreuz & Schäfer 2002). All data were compiled from published sources or from particular researchers. Macrofossils are macroscopically visible parts of plants, e.g. pieces of wood, seeds and fruits, tissues, oogonia, tree leaves and needles, bryophyte stems and leaves etc. Most of the data is of material collected from organic sediments in fens, mires or lakes. Almost all samples are assigned to a Holocene period according to Mangerud et al. (1974). Hereafter we use the following abbreviations: LG – late glacial, PB – Preboreal, BO – Boreal, AT – Atlantic, SB – Subboreal and SA – Subatlantic. Age of data published before the common use of radiocarbon dating (before 2000 AD only six profiles

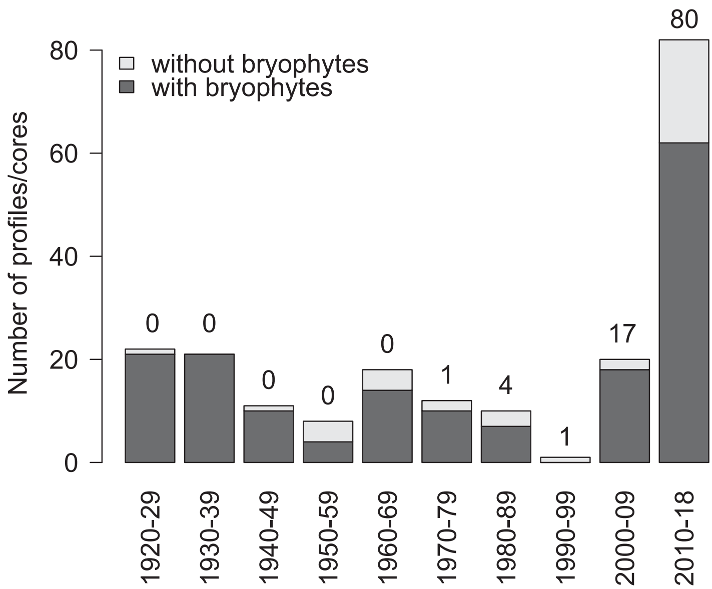

Fig. 1. – Number of profiles and cores in particular periods with (grey colour) and without (white colour) identified bryophytes. The number above the bars indicates the number of radiocarbon-dated profiles.

with C^{14} dating, Fig. 1) was estimated based on results of pollen analyses, mostly by authors. Age of data from profiles analysed and published after 2000 AD is mostly based on radiocarbon dating or dates derived from age-depth models (Fig. 1).

Macrofossil database contains data from 162 complete palaeoecological profiles. Other data come from exploratory drilling (39 sites) in Slovakia, where 2–3 samples were analysed (basal sample + samples after deforestation; for more details see Hájek et al. 2011). Such data are assigned the status of "pilot samples" in the text and maps. Thus, altogether data from 201 sites are included, and mosses were recorded at ~164 sites (for their distribution see Fig. 2). Both, complete profiles and pilot samples without bryophytes include either sediment without bryophytes or sediment with bryophytes that were not identified by the researchers. The lowest number of profiles was analysed after World War II (1950–1959; 8 profiles) and in the 1990s (only one profile). In contrast, higher numbers of profiles were analysed in the period between World Wars, in the 1960s and after the year 2000 (Fig. 1). Within all these profiles and cores, ~3450 samples were analysed and more than 700,000 macrofossils of ~800 plant taxa collected and identified by 29 authors. Information about species and profiles are available on the web page of the Department of Botany and Zoology of Masaryk University (http://www.sci.muni.cz/botany/mirecol/paleo). Published data can be obtained from the database administrator, but unpublished data needs the agreement of particular authors.

A distinctly higher number of profiles and cores collected at high altitudes have been available. Fifty sites occur in the Czech oreofyticum (i.e. high-altitude regions with cold-tolerant flora), 78 sites in the Czech mezofyticum (middle altitudes with a moderately warm-demanding flora) and 48 sites in the Slovak Carpaticum Occidentale region (i.e. middle and high altitudes with a Carpathian flora). In the database there are only data for

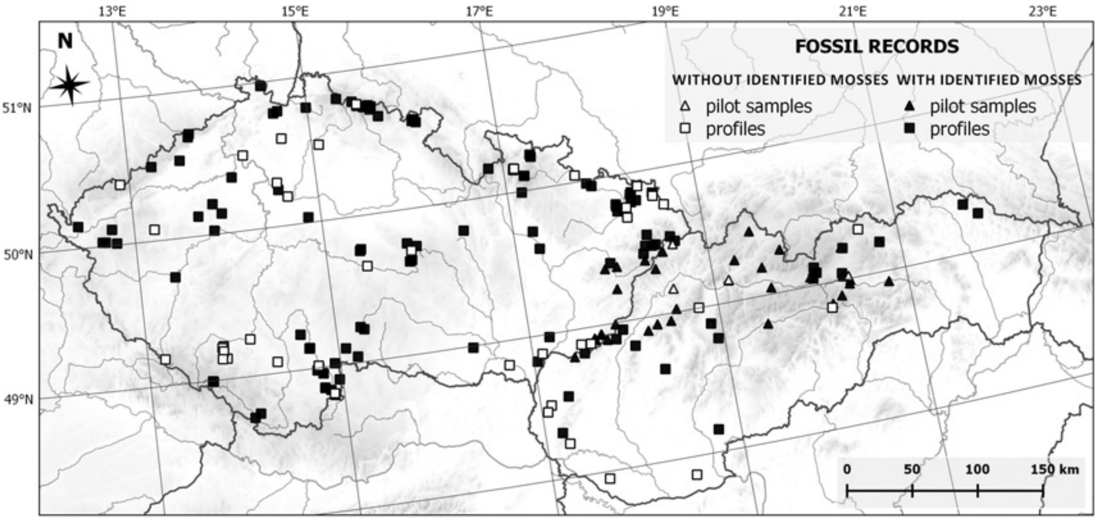

Fig. 2. – Distribution of macrofossil data with and without bryophytes.

25 sites in the lowlands, 14 in Czech thermofyticum (i.e. low-altitude regions with a warm-demanding flora) and 11 in Slovak Pannonicum (i.e. Pannonian lowland regions with a warm-demanding flora). Furthermore, although there is more data for young than for old sediments, the number of localities with old sediments of glacial or early-Holocene age (LG+PB+BO; 102 sites) is also quite high.

Moss data

For this case study seven species of hypothetically relic fen mosses were selected: *Calliergon giganteum*, *Drepanocladus trifarius*, *Hamatocaulis vernicosus*, *Helodium blandowii*, *Meesia triquetra*, *Paludella squarrosa* and *Scorpidium scorpioides*. We compiled all the data on modern occurrences of these species, which are published mainly in local journals or in manuscripts. In Slovakia, data on the recent and historical distributions of all the species studied except *Hamatocaulis vernicosus* are summarized in the habilitation thesis of Šoltés (2014) and in a high number of studies published in local journals (for the complete list of references see Electronic Appendix 8). For the Czech Republic, distribution of *H. vernicosus* is summarized in Štechová et al. (2012), distribution of *H. blandowii* and *S. scorpioides* in Štechová et al. (2010b) and that of *M. triquetra* and *P. squarrosa* in Soldán (1987), Váňa (2006) and Štechová et al. (2010a). Other data came from the bachelor theses of Bradáčová (2011; *H. blandowii*) and Bartošová (2014; *C. giganteum*) and a number of studies published in local journals (see Electronic Appendix 8).

Recent distributions (after 2000) are based on our own data and that of some of our colleagues (Electronic Appendices 1–7), which were collected during the intensive research on mires and fens done in the last two decades. In addition, we completed a revision of herbarium specimens of species previously published and of herbarium specimens of species that have not been previously revised (*D. trifarius* and *C. giganteum* in

Table 1. – Frequencies of particular species of relict bryophytes in the Czech Republic and Slovakia. F/R – ratio between all fossil and all (sub)recent occurrences, LG – late glacial, PB – Preboreal, BO – Boreal, AT – Atlantic, SB – Subboreal, SA – Subatlantic. The first number refers to the Czech Republic, the second to Slovakia.

Species	(Sub)recent data				Fossil data				F/R
	Recent	Before 2000	Literature	Total	LG+PB+BO	AT+SB	SA	Total	
Calliergon giganteum	53+68	31+23	0+18	84+109	10+2	1+5	6+2	17+9	0.135
Drepanocladus trifarius	1+1	7+2	5+5	13+8	5+1	0	3+0	8+1	0.429
Hamatocaulis vernicosus	71+38	71+7	15+0	157+45	2+1	1+0	1+0	4+1	0.025
Helodium blandowii	7+13	23+3	5+4	35+20	2+0	1+0	1+0	4+0	0.073
Meesia triquetra	5+10	22+9	26+4	53+23	6+0	4+2	5+0	15+2	0.224
Paludella squarrosa	19+10	44+6	22+2	85+18	7+0	1+0	0+1	8+1	0.087
Scorpidium scorpioides	8+2	26+4	14+6	46+12	6+3	2+1	1+0	9+4	0.224

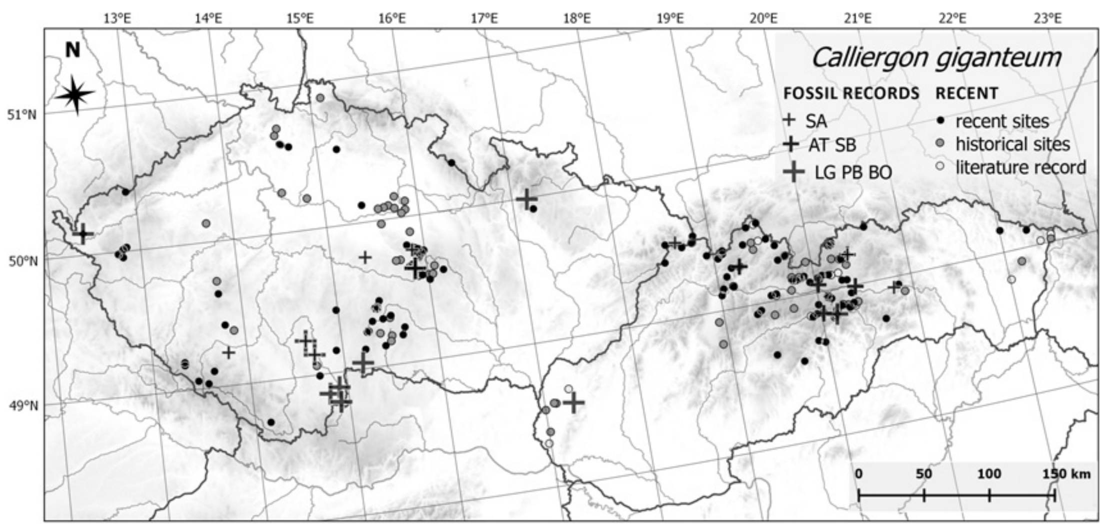

Fig. 3. – Distribution of *Calliergon giganteum* in the Czech and Slovak Republics based on fossil, herbarium and published data. See Methods for the abbreviations of periods.

the Czech Republic). Specimens from the most important Czech and Slovak herbaria and some of those in adjacent countries were checked (for list of checked herbaria and their abbreviations see Electronic Appendix 6). Published data without herbarium specimens were also considered, but such data are presented and mapped separately (see Table 1 and Figs 3–9), as they are not as reliable as the data documented by herbarium specimens. Fossil data were obtained from the newly established macrofossil database.

The recent occurrences of species (after the year 2000) are based on coordinates measured by a GPS device directly in the field or coordinates obtained from Google Earth by

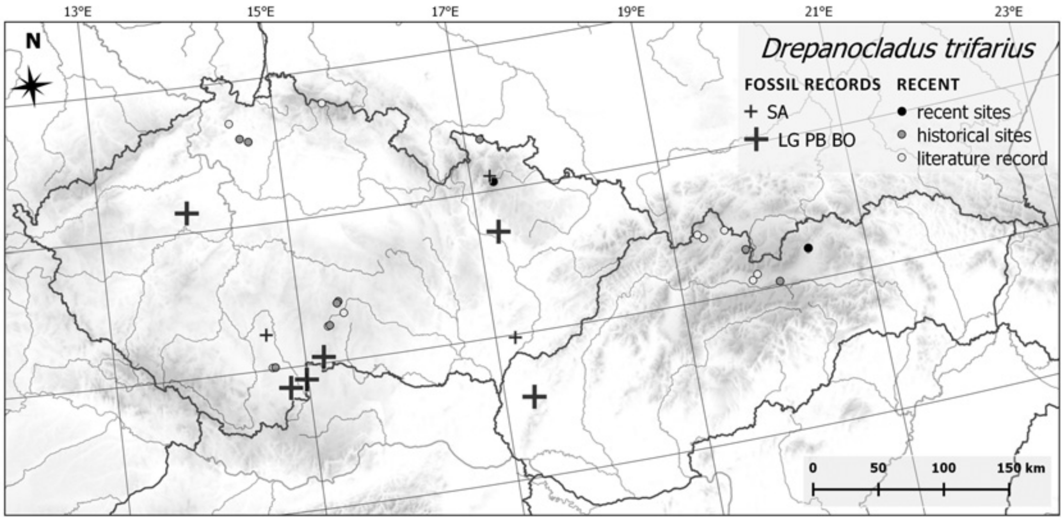

Fig. 4. – Distribution of *Drepanocladus trifarius* in the Czech and Slovak Republics based on fossil, herbarium and published data. See Methods for the abbreviations of periods.

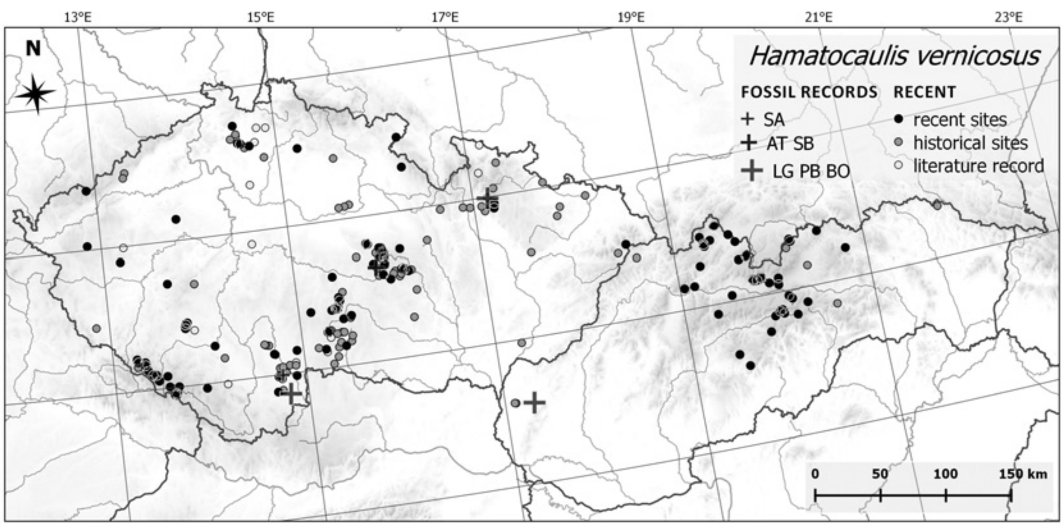

Fig. 5. – Distribution of *Hamatocaulis vernicosus* in the Czech and Slovak Republics based on fossil, herbarium and published data. See Methods for the abbreviations of periods.

the author who sampled the species in the field or who knows the position of the locality. For the purposes of creating maps, the coordinates of old records not well localized were those of the nearest villages. The same rules were also applied to records of fossils. All localities in Electronic Appendices 1–7 were included in a particular phytogeographic unit according to Futák (1984) for Slovakia and Skalický (1988) for the Czech Republic.

The nomenclature of mosses follows Kučera et al. (2012).

The distributions of particular species were plotted on maps using QGIS 2.18.14 (version 2, June 1991) software. Figure 2 was created in the R v. 3.2.3 (R Core Team 2015).

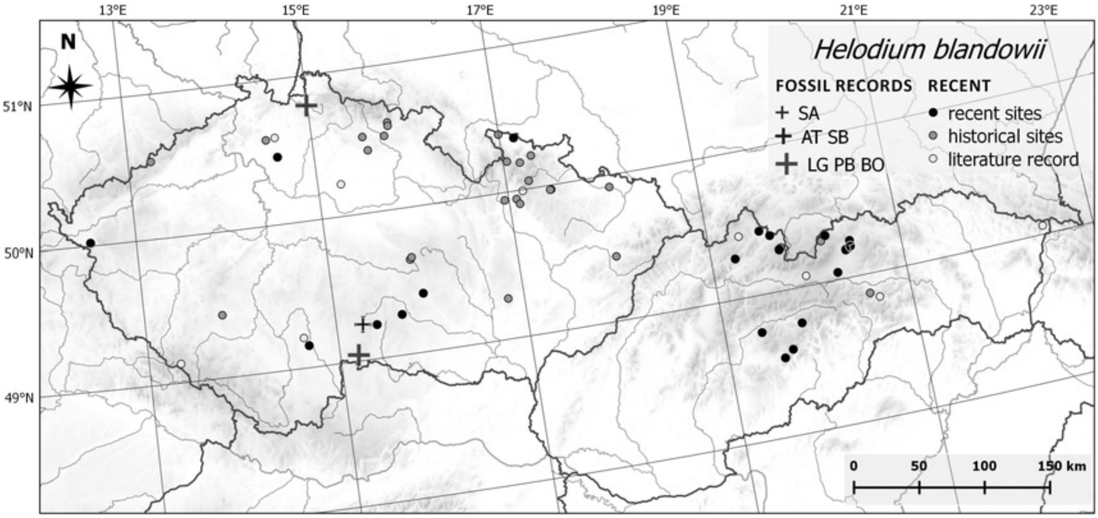

Fig. 6. – Distribution of *Helodium blandowii* in the Czech and Slovak Republics based on fossil, herbarium and published data. See Methods for the abbreviations of periods.

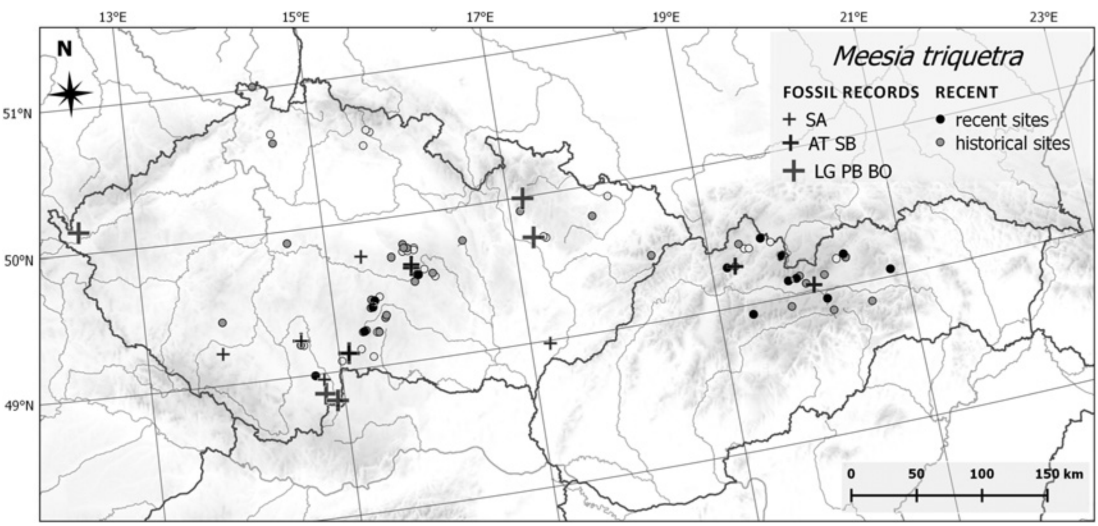

Fig. 7. – Distribution of *Meesia triquetra* in the Czech and Slovak Republics based on fossil, herbarium and published data. See Methods for the abbreviations of periods.

Results

Bryophytes in macrofossil database

Generally, the number of localities (profiles and pilot samples) with identified bryophytes greatly exceeds the number of localities without identified bryophytes (164 versus 39), but this result is strongly determined by the oldest data. Out of 43 profiles published before World War II (1920–1939), only one was without identified bryophytes. The palynologists at that time (Karl Rudolf, Franz Firbas, Hugo Salaschek or Marie Puchmajerová)

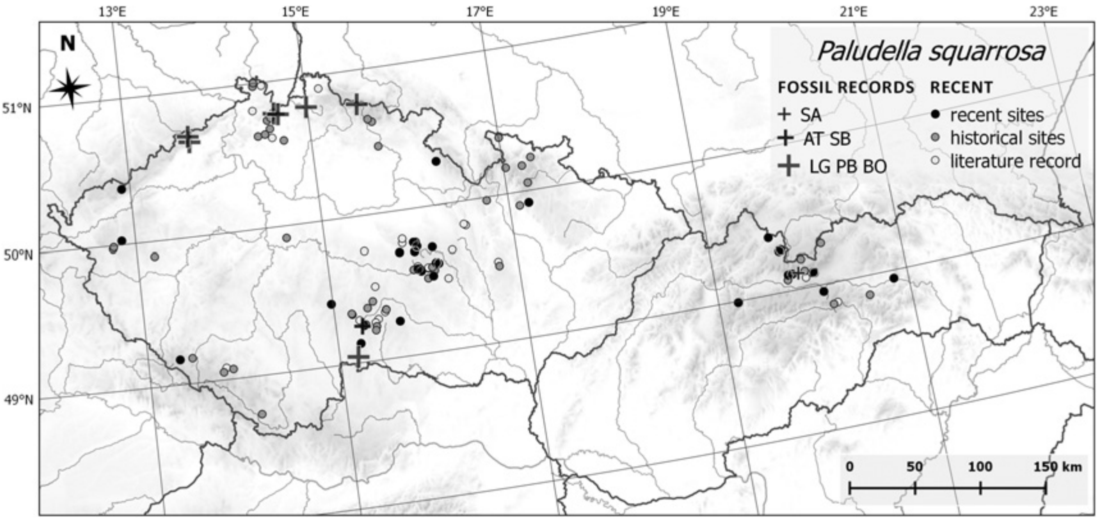

Fig. 8. – Distribution of *Paludella squarrosa* in the Czech and Slovak Republics based on fossil, herbarium and published data. See Methods for the abbreviations of periods.

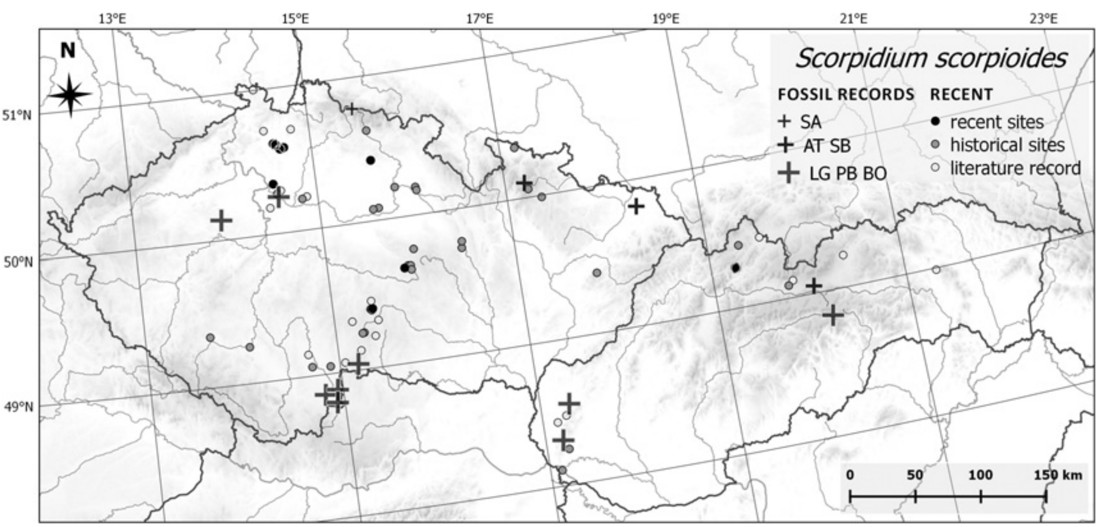

Fig. 9. – Distribution of *Scorpidium scorpioides* in the Czech and Slovak Republics based on fossil, herbarium and published data. See Methods for the abbreviations of periods.

identified macrofossils in profiles, including bryophytes, themselves or with bryologists, before starting the pollen analysis in order to understand the stratigraphy of the profile. Later, the proportion of profiles without identified bryophytes slightly increases, except in the sixties. A number of fossil data on bryophytes strongly increased after the year 2000, which coincides with the overall progress in palaeoecological research (Fig. 1).

All seven species of moss studied were found in late-glacial or early-Holocene sediments, which is one of the important indices of their glacial-relict status (Table 1). Moreover, the number of late-glacial and early-Holocene records is higher than the number of middle-Holocene records, which indicates the existence of a bottleneck for glacial-relict species of fen mosses in the middle Holocene.

Frequencies of modern and fossil specimens of target mosses

We found that *D. trifarius* is currently the rarest species in both countries (considering the records after 2000), with only one locality in the Czech Republic and one in Slovakia, but it was the rarest species also historically, with nine localities documented by herbarium evidence and further 10 localities reported in publications (see Table 1 for frequency of all species). In contrast, *C. giganteum* and *H. vernicosus* are currently the most frequent, the first being more frequent in Slovakia (68 sites versus 53) and the second in the Czech Republic (71 sites versus 38). *Paludella squarrosa* is the third currently and historically most frequent species (altogether 103 localities), being more common in the Czech Republic (or at least more frequently collected in the case of historical localities) than in Slovakia. Another three species (*M. triquetra, H. blandowii* and *S. scorpioides*) are generally rarer than the former and there are distinct differences between the two countries. In the Czech Republic, there were a greater number of localities for these species in the past (before 2000) and then the number of localities substantially declined. In contrast, in Slovakia these species were distinctly less frequently sampled and recorded before 2000 and the number of localities has not declined, or has only declined a little, since then. *Scorpidium scorpioides* is more common in the Czech Republic than in Slovakia, where it is extremely rare with only two subpopulations in the Kubínska hoľa Mts.

Generally, there is a much lower number of fossil (late glacial, Holocene) than modern (19–21st centuries) records, which correlates with greater demands of palaeoecological studies. Nevertheless, frequencies of fossil records differ for different species. *C. giganteum* and *M. triquetra* are the most frequently recorded species in palaeoecological profiles (26 and 17 occurrences, respectively), whereas *H. blandowii* is recorded only in four and *H. vernicosus* in five profiles. The latter two species are extremely rare in fossil samples from Slovakia, with no record of *H. blandowii* and only one record of *H. vernicosus*. The most pronounced differences between these two countries are for *D. trifarius, M. triquetra* and *P. squarrosa*, which were more frequently recorded in the Czech Republic than in Slovakia. This is partly correlated with the lower number of profiles analysed in Slovakia.

Distribution of relic mosses and comparison with fossil records

There are several regions in both countries where almost all species have frequently occurred in the past and also recently. In the Czech Republic, occurrences of the target species are concentrated in the Czech-Moravian highlands including the Žďárské vrchy and Jihlavské vrchy hills (all species with the exception of *D. trifarius* in the Žďárské vrchy), the Třeboňská pánev basin (all species with the exception of *P. squarrosa*), Ralsko-bezdězská table (all species) and Jeseníky Mts (all species, but *M. triquetra* and *C. giganteum* with only a single locality). A low number of occurrences are recorded in middle and eastern parts of the Labe river basin (*C. giganteum*, *H. vernicosus* and *S. scorpioides*), Moravskoslezské Beskydy Mts (*C. giganteum, H. vernicosus*, *M. triquetra*), Šumava Mts, Český les and Slavkovský les Mts (*C. giganteum, H. vernicosus, H. blandowii*, *P. squarrosa*) and Krkonoše Mts and their foothills (Podkrkonoší region;

D. trifarius, H. blandowii, M. triquetra, P. squarrosa and *S. scorpioides*). In the other regions studied these species are extremely rare. In Slovakia, target moss species are most frequently recorded in the Tatra Mts and adjacent basins (phytogeographical units Západné Beskydy, Podtatranské kotliny and Západné Tatry). Regions harbouring three or four target species are situated in the central and northern part of Slovakia (Stredné Pohornádie, Nízké Tatry, Fatra, Slovenský raj, Slovenské rudohorie, Spišské vrchy and Východné Beskydy phytogeographical units). In contrast, Slovak lowlands are rather poor in the target species except for the Záhorská nížina lowland where three target species are recorded, one of which is not documented by herbarium specimens (*S. scorpioides*).

Fossil records come mostly from the same regions as the recent and historical records. In the late glacial and early Holocene, some of the mosses studied occurred also in regions where currently they do not occur, like the Džbán (*D. trifarius*, *S. scorpioides)*, the Zábřežsko-uničovský úval lowland (*D. trifarius, M. triquetra*), the Horní Poohří (Upper Ohře) valley (*C. giganteum*, *M. triquetra*), the Lužické hory Mts and Podještědí region (*P. squarrosa*), the Lužická kotlina basin (*H. blandowii*), the Muránska planina Mts (*S. scorpioides*), the Záhorská nížina lowland (*D. trifarius*) and the Malé Karpaty Mts (*S. scorpioides*). These localities are at low or middle altitudes. Nevertheless, there are also younger fossil records from the Subatlantic period, which are in regions without historical or recent records of the target species, like the Jihomoravské úvaly phytogeographical unit (*D. trifarius*, *M. triquetra*) and the Hornosázavská pahorkatina hills (*C. giganteum*, *M. triquetra*).

Discussion

How can the fossil record help us in assessing the relic status of a species?

The definition of relict species is usually based on a comparison of their modern and past distributions, but the knowledge on the past distribution is never definite and is estimated using biogeographical and ecological indices (Dítě et al. 2018), genetic structure of the species (Reisch et al. 2003, Sabovljević et al. 2006, Habel & Assmann 2010) or macrofossil records. A species is categorized as relict if its modern distribution is a remnant of a wider distribution in the past (Habel & Assmann 2010, Grandcolas et al. 2014). The target species of mosses belongs to so-called glacial relicts, i.e. relicts from the cold past, which were more frequent in the last glacial period (Herzog 1926, Holmquist 1962, Pearson 1965, Rybníček 1966) and during the present interglacial (Holocene) restricted greatly in their distribution. The relic statuses of the target species of fen mosses were suggested mostly based on indirect biogeographical evidence such as a modern distribution restricted to isolated areas with specific climatic or soil conditions (Dítě et al. 2018), whereas relevant genetic data are rather scarce. Hedenäs & Eldenäs (2007) report quite complicated phylogeographical structure within *Hamatocaulis vernicosus*, even with signs of cryptic speciation, but consider it to be unrelated to European glacial history. Glacial history, however, matters for North-American populations of *Meesia triquetra*, whose genetic diversity decreases significantly with increasing latitude and within-site diversity varies among regions (Montagnes et al. 1993). For *S. scorpioides* worldwide, Hedenäs (2009) reports a pattern analogous to most arctic-temperate and some arctic-alpine species, which indicates it spread from southern into northern latitudes after the last glaciation.

Another indirect index of relict status is a species' affinity for sites with a long history. A previous study in the Western Carpathians tested this assumption (Hájek et al. 2011) but only included strongly calcareous fens where target species are rare and hence could not be tested statistically. The few radiocarbon-dated fens where target species of mosses currently occur (or occurred in the last decades), indeed, appear to have originated thousands years ago in most cases, either in the late glacial (Brezové fen – Hájková et al. 2015; Bobrov fen – Rybníček & Rybníčková 2002) or early Holocene (Belanské lúky – Hájková et al. 2012a; fen close to the Puchmajerovej lake – Čierniková 2017), but some are only a few hundred years old (e.g. the Kaľava site with *Paludella squarrosa* – Horsák et al. 2015b).

Direct evidence that a species was more common in the past than today is rather scarce and could be provided only by palaeoecological data. This study based on an extensive macrofossil database reveals that the number of fossil records of putative relic species is always lower than the number of modern records. This result does not refute the relict status of these species, because the spatial coverage of macrofossil research is very low as few areas have been sampled for palaeoecological data. Individual samples usually are only for a few square centimetres in the case of cores. The number of samples per region is very low, because palaeoecological research is time-consuming and expensive and often limited by the poor availability of sediments. Macrofossil data inherently cannot provide a quantitative analysis of a species' distribution, because past distribution will always be underestimated relative to the modern distribution, which is based on extensive research by generations of botanists who have explored most of the fen habitats in central Europe.

Even if we cannot compare absolute commonness in glacial and modern times using the macrofossil database, we can (i) verify the occurrence of a target species in the glacial or early postglacial period, which is a basic prerequisite for assigning species as a glacial or early postglacial relict (this kind of evidence has a long tradition in malacology; Ložek 2001, Horsák et al. 2015a); (ii) reveal past occurrences in the regions where the species does not currently occur, such as the glacial occurrence of mountain and boreal species in the central-European lowlands (e.g. *Catoscopium nigritum* and *Drepanocladus trifarius* in the Borská lowland or *Sarmentypnum sarmentosum* in the Labe river lowland; Hájková et al. 2012b), (iii) trace the disappearance of putative glacial relict species in individual profiles throughout the middle or late Holocene (Hájková et al. 2015). This study based on the meta-analysis of the macrofossil database indeed verified the occurrence in the late glacial of all the species of fen mosses studied. For some of them, similar results are also reported in other European countries, including the glacial occurrence of *S. scorpioides* in northern Hungary and in Switzerland (Krisai 1985, Magyari et al. 1999), late-glacial occurrence of *Calliergon giganteum* in north-eastern Poland (Karpińska-Kołaczek et al. 2013) and early-Holocene occurrence of *D. trifarius* and *S. scorpioides* in Denmark and northern Germany (Odgaard 1988, Michaelis 2002). We further found fossil evidence that almost all the target species once occurred in regions in which they were not recorded by botanists in the 19–21st centuries, thus they had a wider geographical range in the remote past than today, as is also documented for *Meesia triquetra* on a European scale by Odgaard (1988). This result implies that climatically and environmentally suitable habitats for the occurrence of the target species were more widespread in the late glacial and early Holocene. This pattern is especially evident for *D. trifarius* (Fig. 4). Moreover, we recorded a higher number of fossils in the late glacial and early Holocene than in the middle Holocene. The latter period is generally known as a climatic optimum within the Holocene for the development of woodlands (Pokorný et al. 2015, Hájek et al. 2016, Jamrichová et al. 2017), including woodlands growing on fen soils (Hájková et al. 2015). In addition, the successional transition from fens to bogs, i.e. ombrotrophic ecosystems lacking the target moss species, occurred frequently in the middle Holocene in central Europe (e.g. in the Třeboň basin; Jankovská 1988), perhaps as a consequence of a fluctuating groundwater level and generally humid summers (Hughes & Barber 2003, Vicherová et al. 2017). In both cases (woodland encroachment, fen-to-bog transition) suitable conditions for the target open-fen species of mosses were strongly restricted. In the first case there is insufficient light for mosses under a tree canopy, while in the second case they were not supplied by mineral-rich groundwater and were therefore outcompeted by sphagnum (Vicherová et al. 2017). The middle Holocene hence seems to be a strong bottleneck for the occurrence of open-fen mosses. Hydrological fluctuations were probably more important than warm climate, because in calcium-rich spring fens air temperature is poorly correlated with groundwater temperature because of a thermal buffer (Horsák et al. 2018).

After the human colonization and extensive deforestation of the landscape in medieval and modern, yet pre-industrial times (Jamrichová et al. 2017), open-fen mosses, including putative relic species, spread again (Hájková et al. 2012a, 2015). This pattern is further indicated by a rather high number of historical records, especially from the first half of the 20th century. The effect of human activity in the second half of the 20th century triggered a second bottleneck, which is comparable to the distinct bottleneck during the middle Holocene. The number of localities of putative relic species was greatly reduced (cf. Electronic Appendix 1–7) as a consequence of extensive drainage (Růžička 1989, Stanová 2000), abandonment (Štechová et al. 2014) and eutrophication, which favoured the spread of more generalist species of mosses (Hájek et al. 2015).

Recent distribution of relict species: what are the crucial drivers?

If we look at the recent distributions of the target species they differ between species and regions. Some of these differences are determined by the different intensity of botanical research, including an increasing focus on *H. vernicosus* because of the Habitat Directive of the EU and more botanists sampling mosses in the Czech Republic than in Slovakia. However, some of the differences might be caused by different habitat affinities or migration histories of individual species. For example, *H. blandowii* sites are concentrated in the northern part of the study area, for which there are very few fossil records. These populations could have been initiated by migration from the North European Plain where this species was more common (Górski et al. 2015, Hugonnot & Celle 2015), but for which there is no genetic evidence.

The general pattern which is obvious from the data is that hypothetically relict fen species occur predominantly in regions where they were in the past, even since the late glacial. The environmental condition in these regions are suitable for the occurrence of mires: high annual and summer precipitation, suitable topographical and hydrological conditions determining low surface run-off and a high number of springs. These conditions might prevent encroachment by woodland or complete transition to ombrotrophic bogs and hence might have facilitated the survival of the target species during the middle-Holocene bottleneck.

Some species have retreated more in the last decades than others. Species sensitive to any disturbance in water regime like *D. trifarius, M. triquetra* and *S. scorpioides,* which require a very stable water level close the surface of the mire or even small pools and inundated depressions (Hedenäs 1989, Štechová et al. 2010a, b, Peterka et al. 2018), are among the rich-fen species of mosses that have retreated most and are endangered (Hodgetts 2015). The effect of a lowering of the water table on the vitality and growth of *S. scorpioides* is confirmed by Kooijman & Whilde (1993). Thus, the water regime together with the Holocene continuity of fen habitats, are the most important determinants of the recent distribution and survival of these species. Generally, the glacial relict species of mosses are associated with the initial successional phases of fens that are characterized by high water level and low productivity, which were common in the glacial landscape. In order to sustain such species in the currently warming and eutrophicated landscape, where late-successional phases prevail, it is necessary to reintroduce disturbances into fen ecosystems (Emsens et al. 2015, Hájek et al. 2015, van Diggelen et al. 2015). Other species like *C. giganteum, H. vernicosus* and *P. squarrosa*, which tolerate slight decreases in water level, which naturally occur on small hummocks, or regenerate well after desiccation (cf. Manukjanová et al. 2014), declined less and some of them are still frequent in calcium-rich fens (e.g. *C. giganteum* and *H. vernicosus*). *Hamatocaulis vernicosus* can further benefit from the recent increase in phosphorus concentration (Hájek et al. 2014, Vicherová et al. 2015, Mettrop et al. 2018) if competition with fast-growing species of moss and vascular plants is reduced by mowing (Štechová & Kučera 2007).

The importance of the current frequency of putative relict species of fen bryophytes for assessing their relict status is, however, not straightforward if it is not possible to determine the extent of their distribution in the glacial period. Moreover, a substantial decrease in their distributions was caused subrecently by human activities rather than by climate change. In fact, putatively relict fen mosses can be categorized as both, climate relicts from a cold past and cultural relicts from times characterized by a different management of the landscape (Hengeveld et al. 2015, Roleček et al. 2015).

Focusing on the ratio of all modern to fossil records, *D. trifarius* is the strongest relict followed by *S. scorpioides* and *M. triquetra.* These three species are the most sensitive to a deterioration in the water regime. Moreover, these species were historically more common in the Czech Republic than Slovakia, which could indicate their tendency to occur where the climate is oceanic-like rather than continental. Such a tendency is also well documented by the distribution of *S. scorpioides* in Belarus, where this species occurs only in the western part of the country close to the Baltic, where it is common (Pakalne & Kalniņa 2000, Maslowsky 2017). This pattern, however, calls into question their frequent occurrence in glacial times, which were characterized by a distinctly continental climate (Horsák et al. 2015a). Although they can grow in distinctly continental landscapes such as those at high altitudes in the Altai Mts (Ignatov 1994), they were probably restricted in their distributions during the full glacial times and spread there as long ago as in late glacial times (Rybníček 1966, Dítě et al. 2018).

Comparing the most common species *C. giganteum* and *H. vernicosus,* the latter is less frequently recorded in fossil sediments, but this could be partly due to difficulties with identification. This species is more often identified in late-glacial and early-Holocene deposits in Poland, a neighbouring country of the Czech Republic and Slovakia (e.g. Dobrowolski et al. 2012, Gałka et al. 2013). The relict character of these two species is not as obvious as that of other species, because they are currently rather common and there is little evidence of past occurrence in regions where they currently do not occur. General decline of *H. vernicosus* throughout the Holocene could be due to its affinity for nitrogen-limited sites (Pawlikowski et al. 2013, Hájek et al. 2014), which were more common in early postglacial times (Vitousek et al. 2010), but on the other hand this species thrives in phosphorus-enriched yet disturbed or strongly waterlogged cultural habitats such as fen grasslands and fishpond margins.

Future prospects of the macrofossil database

Even if macrofossil databases do not include unequivocal evidence for the relict status of species in terms of a direct comparison of absolute or relative frequencies in the landscape over time, they contain indirect evidence that is independent of recent biographical and ecological indices. By bringing new kinds of arguments into the debate databases can be useful in many studies dealing with the modern and past distributions of relict fen species of both vascular plants and bryophytes (Dítě et al. 2013, 2018). As the species of bryophytes co-occurring in one small sample (~50–100 ml of sediment) had to grow together at a small scale, fossil data could be useful for predicting the occurrence of those types of vegetation that are defined by a particular combination of bryophyte species, as is demonstrated for the *Stygio-Caricion limosae* alliance (Peterka et al. 2018). Macrofossil data can also be used in searching for changes in the co-existence patterns, because peat profiles provide a "permanent plot" of in situ deposited mire bryophytes over thousands of years (Rydin & Barber 2001). Further, macrofossil databases can be used for tracking the changes in continental or global distributions of species, as illustrated by the records of *Blysmus rufus* in Slovakia (Hájková et al. 2015) or *Warnstorfia tundrae* in Germany (Hölzer & Hölzer 1994). *Blysmus rufus* is currently confined to seaside salt marshes or continental areas in central Asia and absent in central Europe. *Warnstorfia tundrae* (Arnell) Loeske currently only occurs at one site in central Europe (French Alps, http://herbarium.nrm.se) and in Europe is restricted to central and northern Scandinavia (Behre et al. 2005). All these challenges, however, are limited by little data from regions where mires are currently rare or absent. In the future, it would be useful to search for appropriate sediments in these regions and utilize the macrofossil data obtained to provide robust answers to biogeographical questions.

See www.preslia.cz for Electronic Appendices 1–9.

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Souhrn

Moderní databáze botanických dat jsou slibným nástrojem k získání nových výsledků, založených na analýze velkých objemů dat. V této práci představujeme novou paleoekologickou databázi makrozbytkových nálezů rostlin z území České republiky a Slovenska. Zároveň využíváme data z této databáze ke srovnání současného a dávného rozšíření těch druhů mechorostů, které jsou považovány za glaciální relikty flóry střední Evropy. Shromáždili jsme aktuální data o jejich rozšíření od začátku botanického výzkumu ve studovaných zemích až po současnost a rozlišili historické a současné údaje. Za současné jsme považovali údaje zaznamenané po roce 2000. Paleobotanická data pokrývají období od pozdního glaciálu do pozdního holocénu. Všechny druhy považované za glaciální relikty se opravdu vyskytovaly v pozdně glaciálních sedimentech, ale většinou ve stejných oblastech, odkud byly zaznamenány botanickým výzkumem od 19. století. Některé oblasti se tedy vyznačují častějším výskytem těchto druhů v minulosti i v současnosti. V některých případech se ale studované druhy vyskytovaly během pozdního glaciálu nebo raného holocénu i v oblastech, kde už se dnes nevyskytují z důvodu nevhodných podmínek prostředí. Rovněž jsme zjistili, že celkový počet pozdně glaciálních a raně holocenních výskytů studovaných druhů výrazně převyšuje počet jejich výskytů ve středním holocénu, kdy často probíhala sukcese k mokřadním lesům nebo vrchovištím. Tyto výsledky naznačují, že se opravdu může jednat o relikty z období pozdního glaciálu a raného holocénu. Zejména jsme zaznamenali ústup druhů, které vyžadují stabilně vysokou hladinu vody (*Drepanocladus trifarius*, *Meesia triquetra* a *Scorpidium scorpioides*). Tyto druhy ustoupily jak během holocénu, tak během současných antropogenních změn v krajině. Druhy, které jsou tolerantnější k poklesům hladiny vody, přežily dosud na větším množství lokalit (*Calliergon giganteum*, *Hamatocaulis vernicosus*, *Paludella squarrosa*). Makrozbytková data ale nemohou úbytek druhů přesně vyčíslit, protože počet současných lokalit vždy převyšuje počet fosilních dokladů. Důvodem je malé prostorové pokrytí makrozbytkového výzkumu, který je časově náročný a drahý. Jednotlivé analyzované vzorky navíc pokrývají jen několik čtverečních centimetrů tehdejší rašeliništní vegetace. I přes toto omezení jsou makrozbytková data důležitou, ale ne jedinou, indicií k rozpoznání reliktnosti našich druhů.

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