MASARYK UNIVERSITY

FACULTY OF SCIENCE

DEPARTMENT OF BOTANY AND ZOOLOGY

A COEXISTENCE HOTSPOT

FROM THE EXTREMELY SPECIES-RICH WHITE CARPATHIAN MEADOWS TOWARDS THE PERI-CARPATHIAN FOREST-STEPPE

HABILITATION THESIS

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Abstract

The meadows of the White Carpathians have long been known as an extremely species-rich plant community and a natural phenomenon of international importance. Although some authors considered them unique, our research has shown that they are not unique in the geographical sense. The core of their species composition is the *Brachypodio pinnati-Molinietum arundinaceae* association, whose distribution has been documented on the margins of the Western and Eastern Carpathians and in some adjacent regions. Admittedly, the association is absent in large areas and rare elsewhere. Its most characteristic species include *Brachypodium pinnatum*, *Carex montana*, *Crepis praemorsa*, *Potentilla alba* and *Pulmonaria mollis* s.lat. Due to its distribution and the considerable representation of forest-steppe species, we refer to it as peri-Carpathian forest-steppe meadows. Our results confirm that it is the most species-rich vegetation on plots sized 10–16 m^2 known worldwide, with up to 115 vascular plant species per 10 m^2 and 119 per 16 m^2. The causes of their extreme species richness are not yet fully understood, but it is clear that they are complex and factors operating at different spatial and temporal scales play a role. Peri-Carpathian forest-steppe meadows are part of habitat mosaics that we refer to as peri-Carpathian forest-steppe. It is a non-equilibrium forest-steppe that is maintained in a non-forest state despite a climate suitable for forest vegetation due to periodic disturbances. At the same time, it is a relict forest-steppe, as light-demanding species have persisted here for millennia, in some places probably throughout the Holocene. They likely originate from the Late Glacial and Early Holocene hemiboreal forests, whose inherited large species pool may contribute to the species richness of the present-day forest-steppe meadows. These features place the peri-Carpathian forest-steppe in a group of specific non-forest ecosystems, scattered all over our planet, whose rich biodiversity is underpinned by the long-term continuity of non-forest habitats enabled by disturbance. Their loose analogy with collapsed Pleistocene ecosystems, whose openness was maintained by grazing of large herbivores and fire, is also suggested.

Abstrakt

Louky Bílých Karpat jsou dlouho známy jako mimořádně druhově bohaté rostlinné společenstvo a přírodní fenomén mezinárodního významu. Byť je někteří autoři považovali za jedinečné, náš výzkum prokázal, že v geografickém smyslu unikátní nejsou. Jádrem jejich druhového složení je asociace *Brachypodio pinnati-Molinietum arundinaceae*, jejíž rozšíření bylo doloženo na okrajích Západních a Východních Karpat a v některých přilehlých oblastech. Nicméně v rozsáhlých oblastech chybí a jinde je vzácná. K jejím nejcharakterističtějším druhům patří *Brachypodium pinnatum*, *Carex montana*, *Crepis praemorsa*, *Potentilla alba* a *Pulmonaria mollis* s.lat. Vzhledem k jejímu rozšíření a významnému zastoupení lesostepních druhů ji označujeme jako perikarpatské lesostepní louky. Naše výsledky potvrzují, že jde o druhově nejbohatší známou vegetaci na ploše 10–16 m^2, s až 115 druhy cévnatých rostlin na 10 m^2 a 119 na 16 m^2. Příčiny jejich extrémního druhového bohatství nejsou dosud zcela objasněny, je však zřejmé, že jsou komplexní a roli zde hrají faktory působící na různých prostorových a časových škálách. Perikarpatské lesostepní louky jsou součástí mozaik biotopů, které označujeme jako perikarpatská lesostep. Jde o nerovnovážnou lesostep, udržovanou v nelesním stavu navzdory klimatu vhodnému pro lesní vegetaci díky režimu

pravidelných disturbancí. Zároveň jde o reliktní lesostep, neboť světlomilné druhy zde přežívají dlouhodobě, na některých místech pravděpodobně po celý holocén. Vývojově jsou zřejmě odvozeny od pozdněglaciální a staroholocenní hemiboreální lesostepi, jejíž zděděný velký druhový fond může přispívat k druhové bohatosti dnešních lesostepních luk. Tyto vlastnosti řadí perikarpatskou lesostep do skupiny specifických nelesních ekosystémů, roztroušeně se vyskytujících po celé naší planetě, jejichž pestrá biodiverzita je podmíněna dlouhodobou kontinuitou bezlesí umožněnou disturbancemi. Nabízí se i jejich analogizace se zaniklými pleistocenními ekosystémy, udržovanými v nelesním stavu pastvou velkých býložravců a požáry.

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Motto: *The promontories of the White Carpathians between Strážnice and Uherský Brod, descending in waves to the Morava river, are home on their slopes facing mainly to the south and southeast to beautiful steppe meadows, unique not only in our country but also in the whole of Central Europe.*

Josef Podpěra (1942)

Preface

The forest-steppe meadows of the White Carpathians are an extraordinary natural phenomenon, well known to Czech and many foreign naturalists, especially botanists. The specific features of the local flora and vegetation were summarised in a comprehensive monograph some time ago (Jongepierová 2008). These include, in the first place, the great species richness of vascular plants, unusual combinations of species of different habitat requirements, numerous retreating and generally rare species or their occurrence in a characteristic landscape mosaic with numerous solitary trees, lines of shrubs and smaller or larger woods. The large extent of the local meadows is also remarkable – in fact it is an entire meadow landscape.

In my PhD thesis on subcontinental oak forests (Roleček 2007) I pointed out the similarity of the species composition of the White Carpathian meadows and subcontinental oak forests and the possible historical roots of this similarity. A hypothetical common ancestor of these vegetation types are the open-canopy forests of the Early Holocene, whose exact species composition is unknown, but whose modern analogue may be the hemiboreal forests extending from the Southern Urals further southeast. In the following research, together with M. Hájek and other colleagues, we focused on testing this historical hypothesis and on other understudied aspects of forest-steppe meadows, such as extreme species richness at the level of individual stands and distribution outside the White Carpathians. The present habilitation thesis summarizes the results of our research so far, supplemented by a review of the relevant literature and a synthesis of the findings. All this is framed by a newly proposed concept of the peri-Carpathian forest-steppe.

Jan Roleček, Náměšť nad Oslavou, June 2023

1. Introduction

Species coexistence in space and time is one of the crucial aspects of biodiversity (Wright 2002, Tokeshi 2009, Levine et al. 2017). The knowledge accumulated over decades of ecological and biogeographical research demonstrates that the patterns of species coexistence and the role of controlling factors are scale-dependent: they are usually affected by multiple processes, which may act non-uniformly across spatial, temporal and organismal scales (Willig et al. 2003, Anderson 2018, Chase et al. 2018). From this perspective, local coexistence of plants at the community level is a special case, where individuals of different species interact directly (Whittaker 1972, Tilman 1982, Silvertown 2004), while other ecological and biogeographical processes such as dispersal, long-term refugial dynamics and speciation still influence community composition. Knowing and understanding these phenomena is important for effective biodiversity conservation (Nicholson et al. 2006, Hart et al. 2017), but it is also an exciting scientific challenge.

Tropical rainforests are notoriously diverse (Wright 2002, Ghazoul & Sheil 2010), however comparisons across scales have shown that on plots ranging in size from fractions to tens of square metres, temperate grasslands are the richest plant communities in the world (Klimeš 1997, Wilson et al. 2012). More than 100 species of vascular plants per 10 m^2 recorded there (Roleček et al. 2021b) are a striking example of coexistence. Several studies published around 2010 drew attention to the fact that extremely high species richness is found mainly in the forest-steppe meadows of central-eastern Europe, particularly in the peri-Carpathian region (Dengler et al. 2009, Hájková et al. 2011, Merunková et al. 2012, Wilson et al 2012). This vegetation type shows also some other peculiarities, including a specific species composition, which has already been pointed out by the old researchers (Procopianu-Procopovici 1892, Rudolph 1911, Soó 1927, 1949, Sillinger 1929, Podpěra 1930, Koczwara 1931).

Previous studies of plant species richness in the peri-Carpathian forest-steppe meadows have focused mainly on fine-scale patterns and processes (e.g. Klimeš 1997, 1999, Klimeš et al. 2013). We have followed a different path: as some of the specific features of the peri-Carpathian forest-steppe meadows, such as the frequent occurrence of otherwise rare species with disjunct distributions, are difficult to explain through fine-scale processes, we focused on the understudied large-scale aspects. In our initial studies we raised a hypothesis about the specific history and continuity of these grasslands on Holocene time scale (Roleček 2007, Hájková et al. 2011). In further research we focused on three main aspects of the peri-Carpathian forest-steppe meadows: i) species composition, its variability and relationship to other steppe vegetation types in Central and Eastern Europe; ii) extreme species richness of stands in landscape and biogeographical context; and iii) origin and dynamics on palaeoecological time scale.

2. Peri-Carpathian forest-steppe meadows: composition, distribution, variability and research history

2.1. Species composition

In this study, we use the term peri-Carpathian forest-steppe meadows for the extremely species-rich semi-dry grasslands, which are most often placed in phytosociological classifications in the broadly conceived *Brachypodio pinnati-Molinietum arundinaceae* association Klika 1939. According to the present-day definition (Willner et al. 2019), the constant species of the association (frequency > 50%) include *Achillea millefolium* aggr., *Brachypodium pinnatum* s.lat. (usually *Brachypodium pinnatum*), *Briza media*, *Carex montana*, *Dactylis glomerata*, *Euphorbia cyparissias*, *Festuca valesiaca* s.lat. (usually *F. stricta* subsp. *sulcata*), *Filipendula vulgaris*, *Galium verum*, *Knautia arvensis*, *Lotus corniculatus* s.lat., *Pimpinella saxifraga* s.lat., *Plantago media*, *Salvia pratensis*, *Trifolium montanum* and *Viola hirta*. The best indicator species against other semi-dry grassland types of the *Brachypodietalia pinnati* class (phi > 0.15) are *Carex montana*, *Inula salicina*, *Lilium martagon*, *Potentilla alba*, *Pulmonaria mollis* s.lat. and *Serratula tinctoria*. The concepts of the association in different studies differ to some extent (Chytrý 2007a, Janišová & Uhliarová 2008, Hegedüšová Vantarová & Škodová 2014, Lengyel et al. 2016, Roleček et al. 2019c, Willner et al. 2019), and to illustrate the best possible agreement of the different concepts, we compiled a list of consensus indicator species of the association (Table 1).

Fig. 1. Ecological spectra of constant species of the *Brachypodio-Molinietum* association and the eight most similar associations of grassland vegetation in the Czech Republic (Chytrý 2007b) sorted into different phytosociological associations (Table 2).

From an ecological point of view, it is a relatively mesophilous vegetation, in which different ecological groups of species intermingle, but semi-dry grassland and forest fringe species predominate (Fig. 1). This is one of the reasons, besides its occurrence in forest-steppe regions (Chapters 2.2 and 5), why we use the term “forest-steppe meadows”, which is uncommon but present in the literature (Illyés & Bölöni 2007, Makunina 2017). With forest communities, they share mainly subxerophilous to mesophilous light-demanding and semi-shade species, which are most abundant in subcontinental oak forests, i.e. open-canopy forests on favourable, deep soils (Roleček 2007). The position of the association within the dry grasslands of the *Festuco-Brometea* class is peripheral: among the 14 most similar non-forest associations in the Czech Republic, a total of eight different alliances are represented, including vegetation of mesophilous meadows, forest fringes, semi-dry grasslands, intermittently wet to wet meadows and submontane acidophilous grasslands (Table 2). The most similar is the *Ranunculo-Arrhenatheretum* association (*Arrhenatherion* alliance, *Molinio-Arrhenatheretea* class), which differs from the *Brachypodio-Molinietum* association mainly by the predominance of mesophilous over semi-dry grassland species and the absence of species of forest fringes and open-canopy forests. Methodological details of these analyses are given in Chapter 7.

2.2. Distribution

The distribution of the *Brachypodio-Molinietum* association covers a large area of central-eastern Europe (Fig. 2), mainly the lower elevations of the Western and Eastern Carpathians, their foothills and adjacent areas such as the North Hungarian Mountains, Romanian Transylvania or the Volyn-Podolian Upland in western Ukraine. We call this distribution “peri-Carpathian”, referring both to the peripheral position of most sites within the Carpathians (often near the boundary between warmer and drier forest-steppe lowlands and more humid, forested higher elevations) and to the occurrence of the association along almost the entire Carpathian arc (peri- [from Greek] = around). However, *Brachypodio-Molinietum* is not distributed continuously, but widely scattered, and within its range it is a rare vegetation type, usually associated with exceptional sites and regions.

The classic area of occurrence is the **White Carpathians**, a medium-high mountain range on the southwestern periphery of the Western Carpathians, extending into the forest-steppe lowlands around the Morava and Váh rivers. The forest-steppe meadows here grow mainly on steep slopes and plateaus on calcareous claystones and sandstones of the Carpathian flysch in a wide range of altitudes (approximately 270–700 m a.s.l.). The association was described from the Czech part of the mountain range (Klika 1939), but its occurrence extends to Slovakia (Sillinger 1929, Hegedüšová Vantarová & Škodová 2014). The forest-steppe meadows in the White Carpathians are famous for their extraordinary species richness, numerous occurrences of rare and declining species (*Orchidaceae*, *Gentianaceae*, biogeographically significant species) and large extent (Jongepierová 2008, Hájková et al. 2011). The most species-rich stands are known from the National nature reserves Porážky (up to 113 species per 16 m^2; Hájek et al. 2020) and Čertoryje (up to 116 species per 25 m^2; Chytrý et al. 2015). On the Slovak side of the mountains, a maximum of 84 species per 10 m^2 has been recorded (M. Janišová & K. Devánová, unpublished). Biogeographically significant species, i.e. those with isolated or marginal occurrences in the region, include mainly *Pedicularis exaltata* (Těšitel et al. 2018), as well as *Danthonia alpina*, *Gentiana acaulis*, *Thalictrum simplex* subsp. *galioides*, *Veratrum nigrum* and *Veronica spuria* (Hájková et al. 2011).

Table 1. Consensus indicator species of the peri-Carpathian forest-steppe meadows. The list was compiled by combining lists of diagnostic species of the *Brachypodio-Molinetum* association from eight different studies (see Chapter 7 for methodological details). The indicator value corresponds to the number of studies in which the species is listed as diagnostic; species included in a single study and taxa identified only at the genus level were not listed. To illustrate the habitat requirements of the species, the vegetation classes for which the species is identified as diagnostic in the EuroVegChecklist (Mucina et al. 2016) are listed. Only type subspecies of the listed species were considered, with the exception of *Cyanus triumfettii* (subsp. *triumfettii*, *axillaris* and *strictus*), *Pulmonaria mollis* s.lat. (subsp. *mollis* and *P. dacica*) and *Symphytum tuberosum* (subsp. *tuberosum* and *angustifolium*). Class abbreviations: Ag – *Alnetea glutinosae*, AP – *Alno-Populetea*, At – *Asplenietea trichomanis*, BB – *Brachypodio-Betuletea*, CF – *Carpino-Fagetea*, Ds – *Drypidetea spinosae*, Ea – *Epilobietea angustifolii*, EP – *Erico-Pinetea*, ES – *Elyno-Seslerietea*, FB – *Festuco-Brometea*, FO – *Festuco-Ononidetea*, KC – *Koelerio-Corynephoretea*, MoA – *Molinio-Arrhenatheretea*, MuA – *Mulgedio-Aconitetea*, Ns – *Nardetea strictae*, Qp – *Quercetea pubescentis*, Qrp – *Quercetea robori-petraeae*, TG – *Trifolio-Geranietea*.

Species	Indicator value	Diagnostic for the class
Carex montana	6	FB, TG
Brachypodium pinnatum	5	FB, TG, MoA
Crepis praemorsa	5	FB, TG
Potentilla alba	5	Qp
Pulmonaria mollis s.lat.	5	Qp, CF
Cirsium pannonicum	4	FB, TG
Clematis recta	4	TG
Hypochaeris maculata	4	FB, Ns
Primula veris	4	FB
Stachys officinalis	4	MuA, Ea, BB
Tanacetum corymbosum	4	TG, Qp
Trifolium montanum	4	FB
Astrantia major	3	MoA
Avenula pubescens	3	FB, MoA
Campanula glomerata	3	FB, MoA
Euphorbia angulata	3	TG, Qrp
Filipendula vulgaris	3	FB, BB
Melampyrum cristatum	3	TG, Qp
Molinia arundinacea	3	FB, MoA, ES, CF, Qpr, EP
Ranunculus polyanthemos	3	FB
Rumex acetosa	3	MoA, MuA, At
Serratula tinctoria	3	MoA, Ns, Qrp
Tragopogon pratensis subsp. *orientalis*	3	MoA
Agrostis vinealis	2	KC
Anemonastrum narcissiflorum	2	ES
Aquilegia vulgaris	2	CF
Arrhenatherum elatius	2	MoA
Campanula persicifolia	2	TG, Qp
Carlina acaulis	2	FB
Crepis biennis	2	MoA
Cruciata glabra	2	FB, TG
Cyanus triumfettii	2	TG, ES, FO
Digitalis grandiflora	2	Ea, BB
Ferulago sylvatica	2	TG
Genista tinctoria	2	MoA
Geranium sanguineum	2	TG
Gladiolus imbricatus	2	MoA
Gymnadenia conopsea	2	MoA
Inula hirta	2	FB, TG, Qp
Inula salicina	2	FB, TG, MoA
Klasea lycopifolia	2	FB, TG
Laserpitium latifolium	2	TG, Qp
Lathyrus latifolius	2	TG
Lathyrus niger	2	Qp, CF
Lathyrus pannonicus subsp. *collinus*	2	TG
Neotinea ustulata	2	FB
Peucedanum oreoselinum	2	TG
Polygala major	2	FB, Ds
Potentilla erecta	2	Ns, Ag
Salvia pratensis	2	FB, MoA
Scorzonera hispanica	2	FB, TG
Stipa tirsa	2	FB
Symphytum tuberosum	2	CF, AP
Thalictrum aquilegiifolium	2	MuA

Species	Indicator value	Diagnostic for the class
Thesium linophyllon	2	FB
Trifolium alpestre	2	TG
Trifolium rubens	2	TG
Veratrum nigrum	2	CF
Vicia tenuifolia	2	TG
Viola hirta	2	FB

Table 2. Vegetation associations of the Czech Republic most similar to the the *Brachypodio-Molinietum* association. The concept of syntaxa corresponds to the compendium Vegetation of the Czech Republic (Chytrý 2007b). The most similar forest association is *Carici fritschii-Quercetum roboris* with a Euclidean distance of 5.541 (after removing woody plants from the analysis). Methodological details in Chapter 7.

Association	Alliance	Class	Euclidean distance
Ranunculo bulbosi-Arrhenatheretum elatioris	*Arrhenatherion elatioris*	*Molinio-Arrhenatheretea*	4.352
Geranio sanguinei-Peucedanetum cervariae	*Geranion sanguinei*	*Festuco-Brometea*	4.596
Trifolio medii-Melampyretum nemorosi	*Trifolion medii*	*Festuco-Brometea*	4.609
Pastinaco sativae-Arrhenatheretum elatioris	*Arrhenatherion elatioris*	*Molinio-Arrhenatheretea*	4.764
Poo-Trisetetum flavescentis	*Arrhenatherion elatioris*	*Molinio-Arrhenatheretea*	4.810
Trifolio medii-Agrimonietum eupatoriae	*Trifolion medii*	*Festuco-Brometea*	5.074
Polygalo majoris-Brachypodietum pinnati	*Cirsio-Brachypodion pinnati*	*Festuco-Brometea*	5.093
Scabioso ochroleucae-Brachypodietum pinnati	*Cirsio-Brachypodion pinnati*	*Festuco-Brometea*	5.118
Geranio sanguinei-Trifolietum alpestris	*Geranion sanguinei*	*Festuco-Brometea*	5.170
Carlino acaulis-Brometum erecti	*Bromion erecti*	*Festuco-Brometea*	5.220
Molinietum caeruleae	*Molinion caeruleae*	*Molinio-Arrhenatheretea*	5.224
Holcetum lanati	*Deschampsion cespitosae*	*Molinio-Arrhenatheretea*	5.258
Potentillo albae-Festucetum rubrae	*Arrhenatherion elatioris*	*Molinio-Arrhenatheretea*	5.296
Campanulo rotundifoliae-Dianthetum deltoidis	*Violion caninae*	*Molinio-Arrhenatheretea*	5.353
Anthoxantho odorati-Agrostietum capillaris	*Cynosurion cristate*	*Molinio-Arrhenatheretea*	5.395

In the warmer and drier regions of southern Moravia, the vegetation of the *Brachypodio-Molinietum* association occurs only sporadically and in a somewhat different species composition. It is most frequent in the area of calcareous Neogene sediments of the **Kyjov Hills**, where these stands were originally described as a separate association *Potentillo albae-Brachypodietum pinnati*, whose characteristics are transitional to the more drought-tolerant association *Polygalo majoris-Brachypodietum pinnati* (Vicherek & Unar 1971, Ambrozek 1989). Chytrý (2007a) synonymized *Potentillo-Brachypodietum* with the *Brachypodio-Molinietum* association, and the results of the synthesis by Willner et al. (2019) support this broader concept. While in the more precipitation-rich White Carpathians *Brachypodio-Molinietum* grows even on southern slopes, when they are not too steep and the soil is deep enough, in the drier Kyjov region it retreats to shady slopes and slope foothills (Fig. 4). On the southern slopes, the most common vegetation is the drought-tolerant *Stipa* steppe of the *Festucion valesiacae* alliance. The biogeographically significant species in the region include e.g. *Artemisia pancicii*, *Daphne cneorum*, *Klasea lycopifolia*, *Potentilla patula* and *Taraxacum serotinum*, which, however, grow partly in drier habitats. In the richest stands of the *Brachypodio-Molinietum* association in this region, up to 71 species per 16 m^2 have been recorded (Vicherek & Unar 1971).

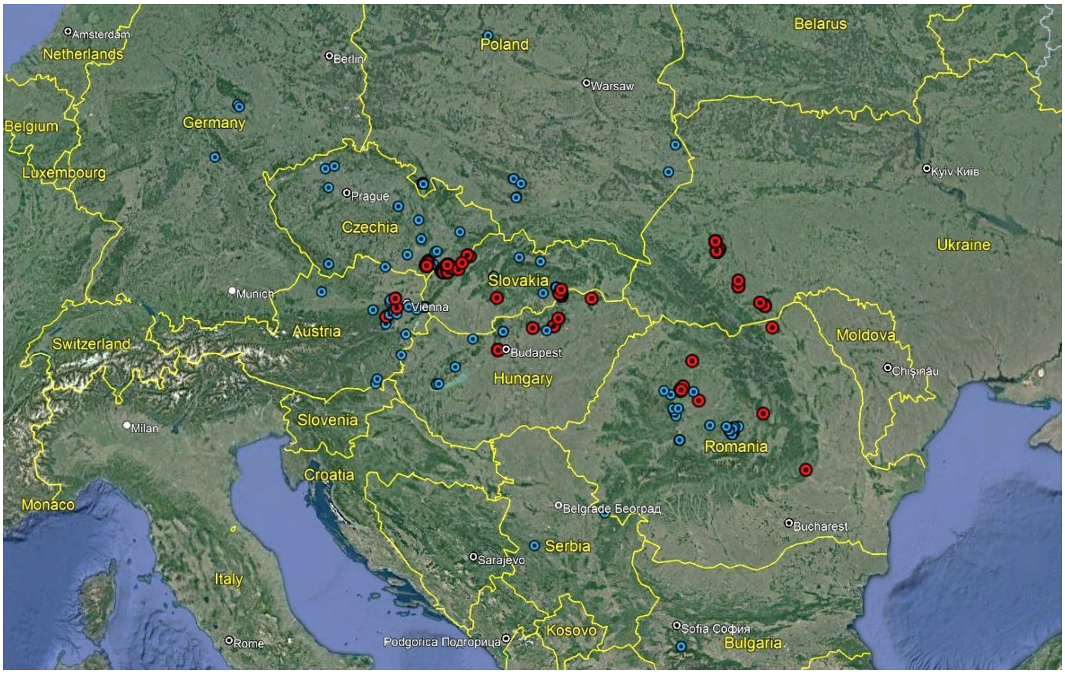

Fig. 2. Distribution of the *Brachypodio-Molinietum* association according to the latest syntaxonomic synthesis of Central and Eastern European semi-dry grasslands (Willner et al. 2019). Several more recent relevés meeting the formal definition of the association are added. Red symbols indicate relevés with a sum of indicator values (Table 1) of at least 50, which better fit the traditional association concept. Relevés marked in blue can be interpreted as less typical or misclassified. Background map taken from GoogleEarth.

Fig. 3. Forest-steppe mosaic in the National nature reserve Čertoryje and the adjacent Vojšické louky meadows in the White Carpathians, Czech Republic. The vegetation matrix consists of forest-steppe meadows of the *Brachypodio-Molinietum* association, influenced to varying degrees by the intensification of farming in the times of socialist agriculture in the second half of the 20th century.

Fig. 4. Transition of a steppe grassland and tall herb-rich vegetation with *Dictamnus albus* on south-oriented slope (right) to forest-steppe meadow (*Brachypodio-Molinietum*) on north-oriented slope (rear left). Nature reserve Louky pod Kumstátem, Kyjov Hills, Czech Republic.

Fig. 5. Karstic plateaus with sinkholes at altitudes above 500 m are typical habitats of forest-steppe meadows of the *Brachypodio-Molinietum* association in the Slovak/Aggtelek Karst. On the northern slopes of the sinkholes, the meadow vegetation grades into the tall herb-rich vegetation of the *Geranion sanguinei* alliance. Meadows in the Mihály láza area on the Hungarian side (top) and in the part of the Silica Plateau called Batova lúka on the Slovak side of the karst (bottom).

In **Slovakia**, apart from the White Carpathians, the best developed vegetation of the peri-Carpathian forest-steppe meadows is found on the **Silica Plateau** in the **Slovak Karst**, from where it extends to the vicinity of Jósvafő in the **Aggtelek Karst** in northern Hungary. Although this area is dominated by limestones and the xerothermic vegetation of the rocky steppe is abundant here, the *Brachypodio-Molinietum* association is also represented in several places, especially on deeper clayey soils on plateaus and in sinkholes at altitudes above 500 m (Fig. 5). Biogeographically significant species in the area include e.g. *Adenophora liliifolia*, *Alyssum gmelinii*, *Pulsatilla patens* and *Tephroseris integrifolia* subsp. *aurantiaca*. In the richest stands of the *Brachypodio-Molinietum* association, up to 79 species per 16 m^2 have been recorded on the Slovak side (P. Dřevojan, P. Hájková & M. Hájek, unpublished) and up to 88 species per 16 m^2 on the Hungarian side (P. Hájková & M. Hájek, unpublished).

Fig. 6. Mount Sitno (1009 m a.s.l.) in the Štiavnické vrchy Mts is the highest site of the *Brachypodio-Molinietum* association in Central Europe. The Tatárska lúka meadow in the foreground is situated on the place of a Late Bronze Age settlement (Zachar 2010).

An isolated site with well-developed vegetation of forest-steppe meadows of the *Brachypodio-Molinietum* association is **Tatárska lúka meadow** in the **Sitno** massif of the **Štiavnické vrchy Mts** (Fig. 6). It is the highest site of this vegetation in Central Europe (approximately 900 m a.s.l., in a somewhat impoverished form also on the top of Sitno around 1000 m a.s.l.). The occurrence of relatively thermophilous species here is made possible both by suitable local conditions (sunny slopes, proximity of relict rocky habitats, long history of non-forest habitats due to the prehistoric settlement of the site; Labuda 1999, Zachar 2010) and by its location near the forest-steppe regions of the Little Danube Plain and the Krupina Plateau. The occurrence of base-demanding species is conditioned by the mineral-rich neovolcanic bedrock (andesites and their tuffs). Biogeographically significant species in the area include e.g. *Adenophora liliifolia*, *Minuartia hirsuta* subsp. *frutescens*, *Valeriana tripteris* and *Tephroseris integrifolia* subsp. *aurantiaca*. In the richest stands of the *Brachypodio-Molinietum* association, up to 74 species per 16 m^2 were recorded (P. Hájková & M. Hájek, unpublished). Similar stands are known from several other regions in Slovakia, for example the Starohorské vrchy Mts (Janišová & Uhliarová 2008) and Slanské vrchy Mts (Ružičková 1987, J. Roleček et al., unpublished), but the available vegetation relevés do not meet the present-day definition of the association (Willner et al. 2019).

In **Hungary**, well-developed vegetation of the *Brachypodio-Molinietum* association is rarely, but regularly, found on the summit meadows of the North Hungarian Mountains. The most species-rich stands are known from the neovolcanic **Mátra Mts**, specifically from the **Tugár-rét meadow** near the settlement of Fallóskút at an altitude of approximately 650 m (Fig. 7). Up to 94 species per 16 m^2 have been found here (Hájek et al. 2020). Among the biogeographically significant species, *Cotoneaster melanocarpus*, *Drymocallis rupestris*, *Rosa arvensis* and *Tephroseris integrifolia* subsp. *aurantiaca* occur in the vicinity.

Fig. 7. Vegetation of species-rich forest-steppe meadows at Tugár-rét in the Mátra Mts. In the background, the Ágasvár hill (788 m a.s.l.) with the remains of a medieval castle and a hillfort from the Late Bronze Age (Tankó 2004).

Species-rich stands of forest-steppe meadows were also recorded in **Zemplén Mts**, again on neovolcanic bedrock. At the **Gyertyán-kúti-rét meadow** (also called Bohó-rét; Fig. 8), located on a plateau north of the village of Regéc at an altitude of approximately 680 m, the vegetation of intermittently wet meadows of the *Molinion* alliance predominates. In the drier places, however, the herb-rich vegetation of the *Brachypodio-Molinietum* association is also represented, where up to 91 species per 16 m^2 were found (P. Dřevojan & J. Roleček, unpublished). Among the biogeographically significant species, *Adenophora liliifolia* and *Dactylorhiza fuchsii* subsp. *sooana* are present, and some other orchid species are also abundant (P. Batoušek in litt.).

Fig. 8. Mosaic of open-canopy forests, intermittently wet meadows and forest-steppe meadows of the *Brachypodio-Molinietum* association on the Gyertyán-kúti-rét meadow on the plateau of the Zemplén Mts.

In the **Bükk Mts**, forest-steppe meadows occur in two distinct landscape contexts: at the foothills in forest-steppe mosaics and on the summit plateau in meadows surrounded by beech forests (Fig. 9). At the foothills, representative stands are preserved on the left bank slopes of the **Tárkányi-patak valley** below the village of Felsőtárkány on neovolcanic bedrock, partly overlain by loess. Here, the *Brachypodio-Molinietum* association grows on shady slopes, while the vegetation of open-canopy forests dominated by *Quercus pubescens* and narrow-leaved dry grasslands (*Festucion valesiacae*, *Stipetum tirsae*; Vojtkó & Farkas 1999) is represented on the sunny slopes. On the summit plateau formed by karstified limestones there occur stands of forest-steppe meadows with a specific species composition at the **Nagy-mező meadow** near the Bánkút settlement. The locality is situated at an altitude of approximately 790 m and is known for its high species richness, with declining groups such as *Orchidaceae* and *Gentianaceae* well represented (Bükki Nemzeti Park Igazgatóság 2015). Biogeographically significant species in the wider area include e.g. *Dracocephalum ruyshiana* (the only Hungarian population together with the neighbouring Kis-mező; Vojtkó & Marschall 1991), *Dactylorhiza fuchsii* subsp. *sooana*, *Lathyrus transsilvanicus*, *Lilium bulbiferum* and *Tephroseris integrifolia* subsp. *aurantiaca*. Herb-rich stands corresponding to the *Brachypodio-Molinietum* association are found mainly on the slopes of larger sinkholes; up to 78 species per 16 m^2 have been recorded here (P. Hájková, P. Dřevojan & M. Hájek, unpublished).

Apart from the above mentioned regions, the peri-Carpathian forest-steppe meadows in Hungary are also known from the **Buda Hills**. At the popular trip site of **Normafa** near Budapest (Fig. 10), where the bedrock consists of Tertiary calcareous sediments, vegetation with a species composition transitional to the *Polygalo majoris-Brachypodietum pinnati* association occurs. Species richness is somewhat lower here, with a maximum of 58 species per 16 m^2 (P. Hájková & M. Hájek, unpublished).

Fig. 9. Contrasting habitats of the *Brachypodio-Molinietum* association in the Bükk Mts: northern slopes in a forest-steppe mosaic on neovolcanic bedrock and loess at the foothills near Felsőtárkány (top) and a limestone plateau divided by sinkholes at Nagy-mező meadow (bottom).

Fig. 10. *Brachypodio-Molinietum* at Normafa site in Buda Hills near Budapest (photo by P. Hájková).

In **Romania**, the **Transylvanian Basin** is a key area for peri-Carpathian forest-steppe meadows. The bedrock of this extensive depression, surrounded by the Eastern, Southern and Romanian Western Carpathians, is mainly composed of easily eroded Neogene calcareous sediments, which give rise to a softly modelled, yet highly structured terrain. This contributes to the formation of diverse habitat mosaics in which the vegetation of the *Brachypodio-Molinietum* association is also present. According to existing knowledge, this association is widely scattered in the region and more common in the peripheral parts of the basin and in relatively wetter habitats.

Fig. 11. The Valea Lui Craiu site is located in the Fânațele Clujului meadow complex near the city of Cluj. Here, the vegetation of the *Brachypodio-Molinietum* association occurs mainly in relatively wet places in a mosaic with other types of dry grasslands. Intensive sheep grazing promotes the spread of ruderal species and the poisonous *Adonis vernalis*, whose numerous tufts are a striking feature of the local vegetation. Together with the stands in the White Carpathians and the Prut-Siret Interfluve in western Ukraine, these are the richest known grassland communities in the world on plots of 10 to 25 m^2.

The **Fânațele Clujului** (Cluj meadows), located on the periphery of the city of Cluj in the northwestern part of the Transylvanian Basin, is an exceptional site in terms of size, preservation and species richness (Fig. 11). The biogeographically significant species in this area include e.g. *Adonis volgensis*, *Cephalaria radiata*, *Colchicum bulbocodium*, *Psephellus trinervius* and *Serratula coronata*. The vegetation of the *Brachypodio-Molinietum* association occurs here, together with related vegetation types (e.g. *Stipetum tirsae*, *Geranion sanguinei*), especially on the gentle northern slopes, particularly in their concave parts. The most species-rich vegetation is known from the northern, higher part of the meadow complex called Valea Lui Craiu (approximately 550 m a.s.l.). Here, up to 118 species per 10.9 m^2 and 115 species per 10 m^2 have been recorded, which are currently world maxima of species richness on these plot sizes (Roleček et al. 2021b).

In the southeastern part of the Transylvanian Basin, forest-steppe meadows are abundant e.g. in the **vicinity of Sighișoara**. The landscape here is more forested, but steppe grasslands are still abundant, especially in areas sculpted by landslides, creating sometimes bizarre scenery (Fig. 12). The vegetation of the forest-steppe meadows in this area has a somewhat different species composition, close to the *Polygalo-Brachypodietum* association, while the more moisture-demanding species typical of the *Brachypodio-Molinietum* association are more common in the tall herb-rich vegetation of the *Geranion sanguinei* alliance (Schneider-Binder 1984, Schneider 1996). However, in a study by Willner et al. (2019), a number of relevés from this area have been assigned to the *Brachypodio-Molinietum* association. As in other warm and dry regions, this association is confined here to the shady slopes of forest-steppe mosaics, which are particularly well developed here due to the ruggedness of the terrain. The biogeographically significant species include e.g. *Adenophora liliifolia*, *Cephalaria radiata*, *Festuca amethystina*, *Lathyrus transsilvanicus* and *Ranunculus breyninus*. In the richest stands, up to 66 species per 16 m^2 have been recorded (Roleček et al. 2019b).

Fig. 12. A system of hills of landslide origin (locally called glimee or Büchel) near the village of Apold near Sighișoara. Forest-steppe meadows and tall herb-rich vegetation closely related to the *Brachypodio-Molinietum* association grows here on the northern slopes and their foothills.

Outside the Transylvanian Basin, the *Brachypodio-Molinietum* association in Romania has been rarely recorded in the intermontane basins of the Eastern Carpathians, specifically in the **Ciuc** (Csík) **Basin** at the foot of the neovolcanic Harghita Mts **near the town of Miercurea Ciuc** (Fig. 13). Due to the considerable altitude (the bottom of the basin is situated approximately 650 m a.s.l.), the peri-Carpathian forest-steppe meadows grow here on the sunny slopes, while acidophilous elements are more abundant on the plateaus. Among the biogeographically significant species, *Actaea europaea* is represented. In the most species-rich stand, 79 species per 16 m^2 were recorded (K. Fajmon & J. Těšitel, unpublished). According to published data, similar vegetation including a limited number of forest-steppe species extends also into the surrounding mountains (Kovács 2015).

According to our latest findings, the well-developed vegetation of the peri-Carpathian forest-steppe meadows, meeting the definition of the *Brachypodio-Molinietum* association (Willner et al. 2019), reaches southeastwards to the **outer foreland of the Arc Carpathians** (the part of the Eastern Carpathians turning westwards and passing into the Southern Carpathians). In the **vicinity of the village of Pâclele**, north of the town of Buzău, an extremely diverse forest-steppe landscape has been preserved on Tertiary calcareous sediments (Fig. 14). While on the southern slopes, dry grasslands with many southern and southeastern elements (e.g. *Centaurea* *orientalis*, *Chrysopogon gryllus*, *Klasea radiata*, *Malabaila graveolens*, *Phlomis herba-venti* subsp. *pungens*) occur, on the northern slopes we find a familiar mosaic comprising the association *Stipetum tirsae* on drier sites, and the tall herb-rich vegetation of the *Geranion sanguinei* alliance on wetter unmown (but burnt and extensively grazed) sites. In the mown stands, which are rare here due to the decline of traditional farming, a typical vegetation of the *Brachypodio-Molinietum* association develops. It differs only in a few species from the stands in the White Carpathians, at the opposite end of the Carpathian arc. For illustration, we present below a full vegetation relevé (Relevé 1). In the most species-rich stand, 82 species per 16 m^2 were recorded (P. Hájková & M. Hájek, unpublished).

Fig. 13. *Brachypodio-Molinietum* at the foot of the Harghita Mts near the town of Miercurea Ciuc.

Fig. 14. Forest-steppe landscape on the border of the Arc Carpathians and the Lower Danube lowland north of the town of Buzău. In the foreground the Pâclele Mari mud volcano complex with its unique halophilous vegetation with *Nitraria schoberi* shrub, in the background a diverse mosaic of forests, scrub and dry grasslands with *Brachypodio-Molinietum* association on the northern slopes.

Relevé 1: Romania, Buzău region, municipality of Pâclele, mown forest-steppe meadow at the base of a shady slope north of the Pâclele Mari mud volcanoes; 45.34694°N, 26.71172°E (WGS-84); 265 m a.s.l.; 22 June 2021; area 16 m^2; slope 25°; slope orientation 360°; herb layer cover 75%; moss layer cover 5%; median herb layer height 45 cm. Recorded by P. Dřevojan & J. Roleček.

E_1: *Carex montana* 2b, *Hypochaeris maculata* 2a, *Brachypodium pinnatum* 2m, *Potentilla alba* 2m, *Prunella* cf. *grandiflora* 2m, *Cirsium pannonicum* 1, *Festuca stricta* subsp. *sulcata* 1, *Geranium sanguineum* 1, *Primula veris* 1, *Stachys officinalis* 1, *Trifolium pannonicum* 1, *Vicia tenuifolia* 1, *Achillea millefolium* aggr. +, *Anthericum ramosum* +, *Avenula pubescens* +, *Briza media* +, *Campanula bononiensis* +, *C. persicifolia* +, *Carex filiformis* +, *C. humilis* +, *C. michelii* +, *Cerastium fontanum* subsp. *vulgare* +, *Convolvulus arvensis* +, *Cruciata glabra* +, *Dactylis glomerata* +, *Dorycnium pentaphyllum* +, *Elytrigia intermedia* +, *Euphorbia cyparissias* +, *E. illirica* +, *Ferulago* cf. *sylvatica* +, *Filipendula vulgaris* +, *Galium verum* +, *Inula hirta* +, *Knautia arvensis* +, *Leontodon hispidus* +, *Leucanthemum adustum* +, *Lotus corniculatus* s.lat. +, *Luzula campestris* +, *Onobrychis arenaria* +, *Phleum phleoides* +, *Pilosella piloselloides* +, *Pilosella* sp. +, *Pimpinella saxifraga* s.lat. +, *Plantago media* +, *Poa angustifolia* +, *Pontechium maculatum* +, *Ranunculus polyanthemos* +, *Rhinanthus* sp. +, *Rosa gallica* +, *Schedonorus pratensis* +, *Solidago virgaurea* +, *Tanacetum corymbosum* +, *Taraxacum* sect. *Taraxacum* +, *Teucrium chamaedrys* +, *Thalictrum aquilegiifolium* +, *Tragopogon pratensis* subsp. *orientalis* +, *Trifolium alpestre* +, *T. montanum* +, *Viola hirta* +, *Campanula glomerata* r, *Cytisus* sp. r, *Daucus carota* r, *Euphorbia nicaeensis* subsp. *glareosa* r, *Falcaria vulgaris* r, *Gladiolus imbricatus* r, *Jacobaea vulgaris* r, *Melampyrum arvense* r, *Myosotis* sp. r, *Polygala comosa* r, *Stachys recta* r, *Thalictrum minus* r, *Valeriana stolonifera* subsp. *angustifolia* r, *Veronica austriaca* subsp. *austriaca* r, *V. chamaedrys* s.lat. r, *Vincetoxicum hirundinaria* r; *Crataegus* sp. +.

Fig. 15. An enclave of tall herb-rich vegetation (*Geranion sanguinei* alliance) and forest-steppe meadows (*Brachypodio-Molinietum* association) in the gently undulating agricultural landscape of the Moldavian Plateau near Calafindești.

Towards the north, the vegetation of the *Brachypodio-Molinietum* association occurs more frequently on the outer periphery of the Eastern Carpathians. Within Romania, its presence has been recorded on the **Moldavian Plateau** around the town of Suceava, in its most typical form in the **Fânațele seculare de la Calafindești reserve** (Fig. 15). The bedrock here is Neogene calcareous sediments of the Carpathian foreland. The protected area is a remnant of herb-rich steppe and meadows in an agriculturally intensive landscape at an altitude of approximately 370 m. The tall herb-rich vegetation of *Geranion sanguinei* is particularly well developer here, both in terms of area and species diversity. Among biogeographically significant species, there is e.g. a large population of *Ligularia glauca* and further *Adenophora liliifolia*, *Pulsatilla patens*, *Salix starkeana* and *Trinia kitaibelii* (Tomescu & Chifu 2009). In the most species-rich stand, 69 species per 16 m^2 were recorded (P. Dřevojan & J. Roleček, unpublished).

Fig. 16. Sampling of the extremely species-rich vegetation of the *Brachypodio-Molinietum* association at the Dzyurkach site near the village of Spaska in the Prut-Siret Interfluve (photo by A. Tokaryuk).

Further to the north, already on the territory of the **Ukraine**, the terrain of the Outer Carpathian Depressions is somewhat more rugged, although it is still underlain by Neogene sediments, mainly calcareous claystones and sandstones. In the area of the **Prut-Siret Interfluve**, the **Dzyurkach** complex of herb-rich meadows has been preserved. It is situated near the village of Spaska, west of the city of Chernivtsi, in the upper part of a ridge at an altitude of approximately 450 m (Fig. 16). It is surrounded on three sides by mesophilous forests (including beech forests), but to the southeast it is connected to the early settled landscape of the Prut Basin, where forest-steppe elements are abundant. The local vegetation thus combines (sub)montane species with relatively thermophilous and drought-tolerant species, similar to the higher elevations of the White Carpathians. While the vegetation on the sandstones has a higher proportion of acidophilous species and its overall composition is closer to the *Koelerio-Phleion* alliance, the *Brachypodio-Molinietum* association occurs on the clays, transitioning into more productive and mesophilous, even truly wetland vegetation on wet sites (including a spring fen of the *Caricion davallianae* alliance). The similarity with the White Carpathians is emphasised by the occurrence of *Pedicularis exaltata*, other biogeographically significant species include e.g. *Adenophora liliifolia*, *Crepis sibirica* and *Potentilla thuringiaca*. The high plant diversity is also reflected at the level of individual stands, with up to 119 species recorded per 16 m^2, which is the current world maximum of species richness on this plot size (Roleček et al. 2019a).

The northwestern continuation of the Moldavian Plateau between the Prut and Dniester rivers in Ukraine is referred to as the **Pokutian-Bessarabian Upland**. This is also an important hotspot of steppe species, partly due to the geological substrate, which consists largely of Neogene gypsum. Here, especially between the towns of Horodenka and Tlumach, a rugged karst terrain is developed at an altitude of approximately 300 m. While relict dry grasslands with continental elements such as *Thalictrum petaloideum* (the only site in Europe), *Draba podolica* and *Helictotrichon desertorum* grow on the rocky slopes of the valleys of the Dniester tributaries, well-developed stands of *Brachypodio-Molinietum* forest-steppe meadows and tall herb-rich vegetation of the *Geranion sanguinei* alliance have been preserved in sinkholes with deeper soil, for example in the **vicinity of the village of Chortovets** (Fig. 17). Among the biogeographically significant species, in addition to those mentioned above, there are *Actaea europaea*, *Anemonastrum narcissiflorum*, *Centaurea ruthenica*, *Ligularia glauca*, *Ranunculus breyninus*, *Sesleria heufleriana*, *Trifolium lupinaster* and *Viola jooi*. In the most species-rich stand, 82 species per 16 m^2 were recorded (J. Roleček & K. Fajmon, unpublished).

Fig. 17. *Brachypodio-Molinietum* association on the slopes of a gypsum sinkhole surrounded by fields at Zalomy site near the village of Chortovets in the Pokutian-Bessarabian Upland.

North of the Dniester river extends the **Volyn-Podolian Upland**, which is already part of the Eastern European Plain and in the past was known for its extensive steppes (Szafer 1935). Smaller, but species-rich, stands of steppe grasslands have been preserved especially in its western part called the **Western Podillia** (referred to as Opillia in more detailed subdivisions). Its relatively humid climate is influenced by the proximity of the Carpathians (Roleček et al. 2019c). Larger concentration of steppe habitats is found, for example, in the **Hnyla Lypa Basin**, where the Halych National Nature Park was declared for their protection. The key site here is **Kasova hora** (Fig. 18), an elongated flat ridge above the left bank of the Hnyla Lypa river near the village of Bovshiv. A diverse mosaic of steppe communities on Neogene gypsum, claystone and Cretaceous sediments, partly overlain by loess, has been preserved here on about 200 ha at an altitude between 250 and 330 m. While on the sunny slopes around the gypsum outcrops the feather grass steppe of the

Festucion valesiacae alliance grows, on the gentle northern slopes and in places also on the plateaus there are stands of the *Brachypodio-Molinietum* forest-steppe meadows, *Geranion sanguinei* tall herb-rich vegetation and other types of mesophilous grasslands, partly influenced by past human activities (grazing, ploughing). Human influence is long-lasting here, as the area includes the polycultural archaeological site Bovshiv I with finds of artefacts from all major archaeological periods between the Neolithic and Early Medieval period (Pankiv et al. 2001, Hájková et al. 2022). Among the many biogeographically significant species are e.g. *Actaea europaea*, *Adenophora liliifolia*, *Anemonastrum narcissiflorum*, *Carlina acanthifolia* subsp. *utzka*, *Cirsium erisithales*, *Crambe tataria*, *Crepis sibirica*, *Crocus heuffelianus*, *Helictochloa hookeri* subsp. *schelliana*, *Helictotrichon desertorum*, *Lathyrus pisiformis*, *Pulsatilla patens*, *Ranunculus breyninus* and *Trifolium lupinaster* (Zamoroka et al. 2018). The mixing of montane and steppe elements is even more striking here than elsewhere. In the richest stands of the *Brachypodio-Molinietum* association, we recorded 93 species per 16 m^2 (Hájek et al. 2020). Similar, although less extensive stands of the peri-Carpathian forest-steppe meadows are also found at several other nearby sites (e.g. Chortova hora, Shchovby, Vynohrad).

Fig. 18. One of the most extensive and representative stands of forest-steppe meadows of the *Brachypodio-Molinietum* association in its entire range growths on the northern slope of the Kasova hora ridge near Bovshiv in the region of Western Podillia.

Vegetation analogous to the peri-Carpathian forest-steppe meadows is also found in the **Alps**. In their northeastern tip, the **Vienna Woods**, it has been described as a separate association *Euphorbio verrucosae-Caricetum montanae* (Karrer 1985). A numerical analysis by Willner et al. (2019) showed that some of its stands are only slightly different from the *Brachypodio-Molinietum* association; this is confirmed by our analysis of the representation of indicator species (Table 1 and Fig. 2). However, a more detailed comparison shows that the two vegetation types are sufficiently distinct, and even stands with intermediate characteristics have an overall species composition closer to the *Euphorbio-Caricetum* association (Fig. 19). Also this association may be extremely species-rich, with up to 83 species per 16 m^2 (P. Dřevojan & J. Roleček, unpublished). Further comparative research is needed to better understand the relationship between semi-dry grasslands in the Alpine region and the peri-Carpathian forest-steppe meadows.

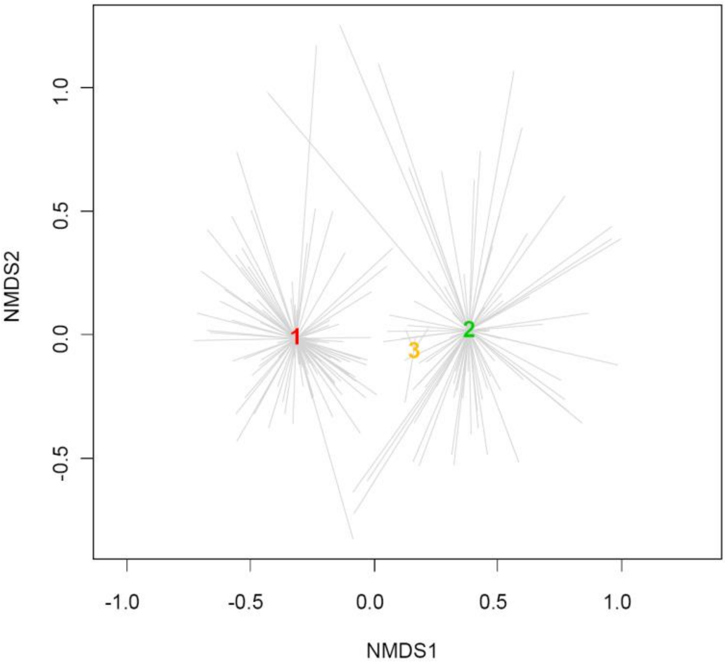

Fig. 19. NMDS plot showing the relationship of the total species composition of the peri-Carpathian *Brachypodio-Molinietum* association (1; only relevés with a sum of indicator values 50 and more are included; see Table 1 and Fig. 2) and the Alpine association *Euphorbio verrucosae-Caricetum montanae* (2). Relevés of group 3 come from the Alps and were originally classified as *Euphorbio-Caricetum*, but meet the definition of *Brachypodio-Molinietum* by Willner et al. (2019). There is a noticeable difference between peri-Carpathian and Alpine stands.

Fig. 20. Vegetation of the *Euphorbio verrucosae-Caricetum montanae* association on the northern margin of the Vienna Woods near Wolfpassing (photo by P. Hájková).

2.3. Variability

In its extensive range, the peri-Carpathian forest-steppe meadows show considerable variability. To illustrate its main features, we classified relevés of the *Brachypodio-Molinietum* association into three subtypes based on the main gradients in species composition (Table 3, Fig. 21, methodological details in Chapter 7). We assumed that three units were sufficient to capture the main features of variability without diluting the description too much.

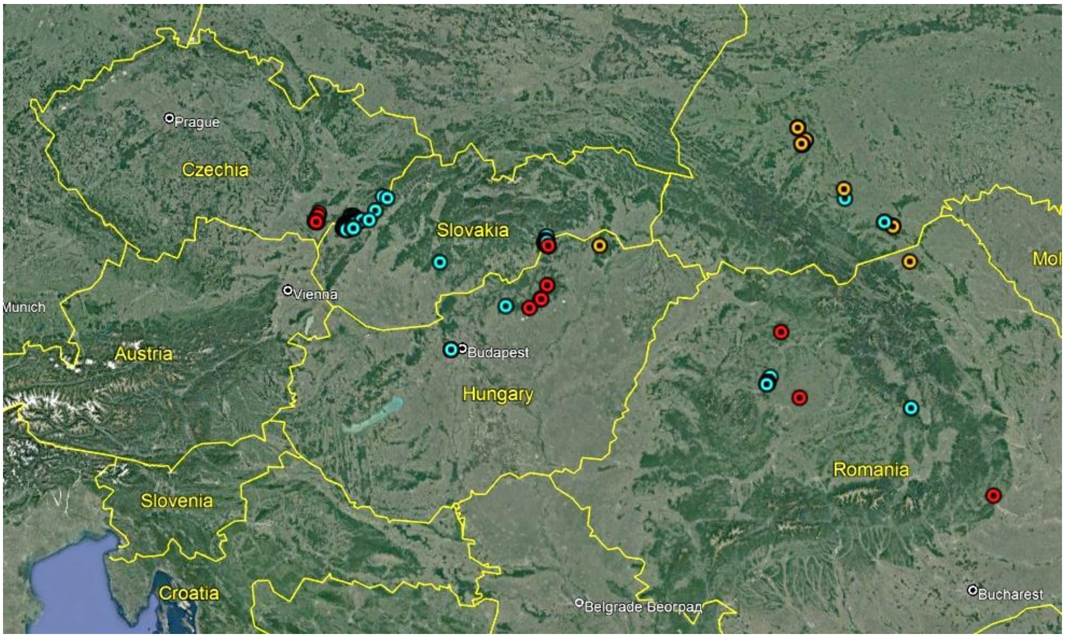

Fig. 21. Distribution of the three main subtypes of the *Brachypodio-Molinietum* association. Only relevés with a sum of indicator values of 50 and more were included in the analysis (see Table 1 and Fig. 2). Relevés from the Alps were not included. Subtype 1 in blue-green, subtype 2 in red and subtype 3 in orange (see Table 3). Background map taken from GoogleEarth.

Subtype 1 is relatively mesophilous and is characterized by a higher abundance of common meadow species (e.g. *Campanula patula*, *Cerastium fontanum* subsp. *vulgare*, *Colchicum autumnale*, *Plantago lanceolata*, *Rhinanthus minor*), mesophilous grassland species of higher elevations (e.g. *Alchemilla* spp., *Traunsteinera globosa*, *Trisetum flavescens*) and some species of forest-steppes, especially those abundant in the White Carpathians (e.g. *Bromopsis erecta*, *Carex flacca*, *Cytisus virescens*, *Lathyrus latifolius*, *Pulmonaria angustifolia*, *Veronica orchidea*). This includes all relevés of the *Brachypodio-Molinietum* association from the Czech part of the White Carpathians (although Klika's description is based on relatively xerophilous stands in the foothills; Klika 1939) and also some rather mesophilous stands from Slovakia, Hungary, Romania and rarely also Ukraine, especially from higher elevations. This is the most species-rich subtype and includes relevés with the maximum number of species in the Czech Republic, Romania and Ukraine. In Romania, this vegetation corresponds to the previously described associations *Festuco sulcatae-Brachypodietum pinnati* Soó 1927 (see nomenclatural note in Electronic Appendix 7 of Willner et al. 2019) and *Pediculari-Caricetum montanae* Soó 1948; both were described from the Fânațele Clujului site.

Subtype 2 includes somewhat more xerophilous vegetation and is distinguished mainly by a lower abundance of mesophilous grassland species and a higher abundance of drought-tolerant species (e.g. *Aster amellus*, *Campanula moravica*, *C. sibirica*, *Pontechium maculatum*, *Pulsatilla vulgaris* subsp. *grandis*) and some southeastern elements (e.g. *Danthonia alpina* and *Helictochloa adsurgens*). It is widespread over most of the range of the association, especially at lower elevations, from the southwestern promontories of the Western Carpathians through the North Hungarian Mountains to Transylvania and the outer foothills of the Eastern Carpathians. It is absent in Ukraine. It includes the previously described associations *Festucetum sulcatae* Soó 1927 (Romania), *Potentillo albae-Brachypodietum pinnati* Vicherek & Unar 1971 (Czech Republic) and *Trifolio medii-Brachypodietum pinnati* Illyés, Bauer & Botta-Dukát 2009 (Hungary).

Subtype 3 is geographically differentiated and includes all but the most mesophilous stands in western Ukraine. It is distinguished by an ecologically diverse group of species that are absent or less common in the western and southern parts of the peri-Carpathian region, or that grow there in different habitats. These include many forest-steppe elements (e.g. *Euphorbia angulata*, *Ferulago sylvatica*, *Peucedanum oreoselinum*, *Polygonatum odoratum*, *Pulmonaria mollis* s.lat, *Pulsatilla patens*, *Veratrum nigrum*), mesophilous species of meadows and open-canopy forests (e.g. *Calamagrostis arundinacea*, *Cruciata glabra*, *Phyteuma orbiculare*, *Solidago virgaurea*, *Trifolium pannonicum*), some predominantly montane species (e.g. *Anemonastrum narcissiflorum*, *Ranunculus breyninus*) and regional endemics (*Cytisus blockianus*). In addition to the western Ukrainian stands, one relevé from northwestern Hungary (Zemplén Mts) was also classified into this subtype. The subtype corresponds to the previously described association *Caricetum montanae* Koczwara 1931.

Given the considerable floristic differences between the subtypes, the question arises whether it is appropriate to group them in a single *Brachypodio-Molinietum* association. The answer, in my opinion, is inevitably subjective and in this particular case ambiguous for various reasons. First of all, I am in favour of a plurality of classifications, which should be tailored to their purpose. I believe that for the purpose of a review of vegetation types at the biogeographical scale, as conceived by Willner et al. (2019) for semi-dry grasslands, a broader concept of basic descriptive units (associations) is useful. In such a case, the different breadth of units within a single classification is not a major problem because it reflects, among other things, differences in the degree of ecological and geographic differentiation of vegetation in different biogeographical regions, as well as persistent differences in the representativeness of vegetation data from different parts of Europe. On the other hand, at local scale and within biogeographical regions, we often need finer-resolution classification and we usually also have more representative data that allow more detailed and balanced classification to be made. Here I am inclined to the view that within the peri-Carpathian area, it is possible and appropriate to distinguish several basic vegetation units of forest-steppe meadows. In that case, the content of the *Brachypodio-Molinietum* association, as conceived by Willner et al. (2019), would correspond rather to a higher hierarchical unit, probably a suballiance. The above subtypes may then become the basis for new, more narrowly conceived associations. However, any alternative classification should be based on the analysis of a new dataset, even more representative of other related vegetation types. In this respect, we are unfortunately still constrained by the limited availability of good quality data from some regions.

Table 3. Indicator species of the three subtypes of peri-Carpathian forest-steppe meadows. Percentage frequencies are shown and their upper indices show species' indicator values (phi coefficient × 100).

Subtype	**1**		**2**		**3**	
Number of relevés	65		30		15	
Campanula patula	62	77	.	-	.	-
Potentilla heptaphylla	68	65	7	-	.	-
Vicia sativa s.lat. (incl. *V. angustifolia*)	34	56	.	-	.	-
Fragaria moschata	32	55	.	-	.	-
Veronica orchidea	31	54	.	-	.	-
Trifolium campestre	29	52	.	-	.	-
Pulmonaria angustifolia	37	48	3	-	.	-
Plantago lanceolata	83	47	20	-	13	-
Danthonia decumbens	23	46	.	-	.	-
Myosotis arvensis	34	45	3	-	.	-
Traunsteinera globosa	22	45	.	-	.	-
Alchemilla spp.	20	43	.	-	.	-
Trisetum flavescens	65	42	3	-	20	-
Rhinanthus minor	51	42	13	-	.	-
Bromopsis erecta	78	42	37	-	.	-
Ononis spinosa	45	42	3	-	7	-
Carex flacca	29	40	3	-	.	-
Lathyrus latifolius	54	38	20	-	.	-
Pilosella bauhini	34	37	7	-	.	-
Cytisus hirsutus (incl. *C. virescens* (Kovács ex Neilr.) A.Kern.)	26	37	3	-	.	-
Linum catharticum	74	35	37	-	7	-
Colchicum autumnale	51	35	7	-	13	-
Carex caryophyllea	62	31	30	-	7	-
Cerastium fontanum subsp. *vulgare*	32	31	10	-	.	-
Campanula rotundifolia (incl. *C. moravica* (Spitzn.) Kovanda)	2	-	27	43	.	-
Campanula sibirica	.		20	43	.	-
Pulsatilla vulgaris (incl. *P. vulgaris* subsp. *grandis*)	14	-	47	32	7	-
Aster amellus	.		27	30	7	-
Euphorbia angulata	3	-	.		67	72
Peucedanum oreoselinum	3	-	.		47	57
Phyteuma orbiculare	.		.		27	50
Ranunculus breyninus	.		.		27	50
Pulsatilla patens	.		3	-	33	44
Calamagrostis arundinacea	8	-	.		40	41
Polygonatum odoratum	6	-	10	-	53	41
Veratrum nigrum	5	-	3	-	40	41
Trifolium pannonicum	8	-	10	-	53	39
Inula ensifolia	8	-	7	-	47	38
Ferulago sylvatica	2	-	10	-	40	36
Cruciata glabra	49	-	27	-	93	34
Pulmonaria mollis s.lat. (incl. *P. dacica*)	22	-	37	-	80	32
Solidago virgaurea	3	-	30	-	60	32

2.4. Contact vegetation

As already shown in Section 2.2, peri-Carpathian forest-steppe meadows may occur in different vegetation and landscape contexts. Despite the regional peculiarities described above, two basic ones can be distinguished: in more humid regions it occupies average habitats and may form the matrix of the vegetation mosaic, while in drier regions it retreats to somewhat wetter habitats on northern slopes and in shallow depressions (Figs 22–24).

Typical contact vegetation in both contexts is the **thermophilous fringe and tall herb-rich vegetation of *Geranion sanguinei* alliance**, which occupies somewhat wetter (but not waterlogged) and nutrient-richer habitats in depressions and forest margins (Roleček et al. 2019c, 2022, Klinkovská 2022). It may also represent successional stage of forest-steppe meadows on abandoned and irregularly managed sites. Due to similar species composition and often small-scale occurrence, this vegetation is frequently overlooked (Klinkovská 2022). In addition to the characteristic physiognomy given by the abundance of herbs, often tall ones (e.g. *Clematis recta*, *Laserpitium latifolium*, *Veratrum nigrum*), the vegetation of the *Geranion sanguinei* alliance is characterised by the occurrence of a number of plant species that are absent or less frequent in forest-steppe meadows. These are relatively moisture-demanding or cold-tolerant species (e.g. *Aconitum moldavicum*, *A. variegatum*, *Cirsium erisithales*, *Gladiolus imbricatus*, *Picris hieracioides* subsp. *umbellata*, fleaworts from the *Senecio doria* group (Calvo & Aedo 2015), *Veratrum lobelianum*, *Thalictrum aquilegiifolium*, *Trollius europaeus*), as well as rare light-demanding species with disjunct distributions (e.g. *Actaea europaea*, *Adenophora liliifolia*, *Crepis sibirica*, *Ligularia glauca*, *Pedicularis exaltata*; Roleček et al. 2018, 2022). We suggest that, as in the case of the peri-Carpathian forest-steppe meadows, these are, at least at some sites, relicts of ancient vegetation that used to be widespread in mesic habitats before the expansion of shady forests, as discussed in Chapter 4. Corresponding vegetation in Romania has been described as the *Trollio-Clematidetum recti* association (Täuber & Weber 1976, Roleček et al. 2019b), into which also analogous vegetation in western Ukraine may be classified (Roleček et al. 2022). Our recent research shows that similar vegetation occurs also in the White Carpathians and some other regions in the range of the peri-Carpathian forest-steppe meadows (Roleček et al. 2018, Klinkovská 2022, J. Roleček et al., unpublished) and a comparison of all available vegetation data is needed to better understand their interrelationships. Although some stands of the *Geranion sanguinei* alliance may be extremely species-rich, the number of species here is usually significantly lower than in the *Brachypodio-Molinietum* association (it averages about 45 species per 16 m^2 in western Ukrainian stands; Roleček et al. 2019c). The factor limiting coexistence here is probably high productivity, promoting the development of robust, competitively strong species that occupy space, reduce light availability and limit the persistence of competitively inferior species.

On somewhat drier sites, *Brachypodio-Molinietum* transitions into the **more drought-tolerant semi-dry grassland types of the *Cirsio-Brachypodion pinnati* alliance**. Depending on habitat conditions and the landscape pool of steppe species, these are most often the steppe meadows of the *Stipetum tirsae* association and the semi-dry grasslands of the *Polygalo majoris-Brachypodietum pinnati* association (Table 4). The species composition of the two vegetation types is somewhat similar. Compared to the *Brachypodio-Molinietum* association, they are depleted of mesophilous species and enriched with some xerophytes (e.g. *Carex humilis*, *Eryngium campestre*, *Inula ensifolia*, *Koeleria macrantha*, *Potentilla incana*). *Stipetum tirsae* is more common in large forest-steppe complexes on deep chernozem-like soils and is distinguished by a greater abundance of e.g. *Falcaria vulgaris*, *Galatella linosyris*, *Inula hirta*, *Scabiosa canescens* and *Veronica spicata* in addition to the frequent dominance of *Stipa tirsa* (Willner et al. 2019). In contrast, the *Polygalo majoris-Brachypodietum pinnati* is a calciphilous community more common on shallower soils in rugged terrain. In addition to the usual dominance of *Brachypodium pinnatum*, it is characterized by higher abundances of e.g. *Aster amellus*, *Bupleurum falcatum*, *Centaurea stoebe*, *Dorycnium pentaphyllum*, *Lembotropis nigricans* and *Sanguisorba minor* (Willner et al. 2019). Although both communities are species-rich, they reach lower maxima of species richness than the *Brachypodio-Molinietum* association. A factor limiting coexistence here is probably soil drought, reducing productivity and preventing the occurrence of large numbers of more moisture-demanding species.

The *Brachypodio-Molinietum* association is also closely related to the **semi-dry grasslands of the *Orchido militaris-Seslerietum heufleranae* association** (Dengler et al. 2012, Willner et al. 2019). In contrast to the previous two communities, this vegetation is usually found on steep shady slopes. It is characterized by the dominance of *Sesleria heuflerana* and *Carex humilis* and a species composition largely intermediate between the *Polygalo majoris-Brachypodietum* and *Brachypodio-Molinietum* associations. In contrast to the peri-Carpathian forest-steppe meadows, thermophilous and drought-tolerant species and some species of shallow soils (e.g. *Inula ensifolia*, *Lembotropis nigricans*, *Linum flavum*, *Teucrium chamaedrys*, *T. montanum*, *Thesium linophyllon* or *Veronica spicata*) are more frequently represented here. However, some indicator species of the peri-Carpathian forest-steppe meadows are also present (Table 4) and, given the habitat conditions (steep slopes), some of them could probably have survived here even during periods when the vegetation on deeper soils was subject to successional changes. Mesophilous meadow species and forest-steppe species of deep soils (e.g. *Anthoxanthum odoratum*, *Carex montana*, *Galium verum*, *Plantago lanceolata*, *Potentilla alba*, *Pulmonaria mollis* s.lat., *Rumex acetosa* and *Veratrum nigrum*) are less represented than in the *Brachypodio-Molinietum* association. In western Ukraine, semi-dry *Sesleria* grasslands are mostly found in more rugged terrains on Cretaceous sediments, less frequently on Neogene gypsum. They were described by Koczwara (1931) under the name *Seslerietum heufleranae*. In Romania, on the other hand, they may occur together with the *Brachypodio-Molinietum* association on Neogene claystones (Fig. 24). The species richness of these stands is comparable to the *Polygalo majoris-Brachypodietum pinnati* association, i.e. it is lower than in the *Brachypodio-Molinietum* association (Dengler et al. 2012). Coexistence here is probably not so much limited by drought, but the limited availability of nutrients and other resources on shallower soils, and different stand structure due to terrain, management or different dominant species may play a role.

In longer-term waterlogged depressions in contact with peri-Carpathian forest-steppe meadows, **wet meadow vegetation** often occurs, especially stands of *Molinion caeruleae* alliance on nutrient-poor sites and *Calthion palustris* alliance on nutrient-rich sites. Particularly the intermittently wet meadows of the *Molinion* alliance share a number of species with the

Brachypodio-Molinietum association (Table 4); besides the dominant *Molinia arundinacea* also the so-called species of intermittently wet habitats, which include e.g. *Galium boreale* subsp. *boreale*, *Potentilla alba*, *Serratula tinctoria* and *Stachys officinalis*. These species also co-occur in other vegetation types (e.g. the subcontinental oak forests; Roleček 2007) and form a distinct sociological group *Serratula tinctoria* (Chytrý 2007b). The drier types of *Molinia* meadows on mineral-rich soils may be close to the peri-Carpathian forest-steppe meadows in their species composition and in some cases can even be understood as their local analogues. Such stands, sometimes classified as *Molinietum caeruleae caricetosum tomentosae* subassociation (Koch 1926, Řezníčková 2007), are known from the White Carpathians, the Elbe Basin, the eastern part of the Drahanská vrchovina Upland and the area at the confluence of the Morava and Dyje rivers (Hájek 1998, Vicherek 2000, Řepka & Roleček 2002, Roleček & Novák 2008), outside the Czech Republic also from Romania and a number of sites in the Balkans (M. Hájek & P. Hájková, unpublished). It is a species-rich vegetation type (usually 35–50 species per 16 m^2, in some cases considerably more; Hájek 1998, Řezníčková 2007), yet its species richness is lower than in the peri-Carpathian forest-steppe meadows. Coexistence may be limited here by waterlogging or lower nutrient availability, however habitat differences between the two vegetation types are not yet sufficiently studied.

On permanently waterlogged sites, the **vegetation of tall sedges and reeds** of the *Phragmito-Magnocaricetea* class, sometimes with fragments of willow carrs of the *Salicion cinereae* alliance, may also be present in the peri-Carpathian forest-steppe meadow complexes. A typical component of the vegetation mosaics on the Carpathian flysch are tufa-forming springs with sedge-moss vegetation of calcareous fens of the *Caricion davallianae* alliance (Hájek 1998, Hettenbergerová et al. 2013).

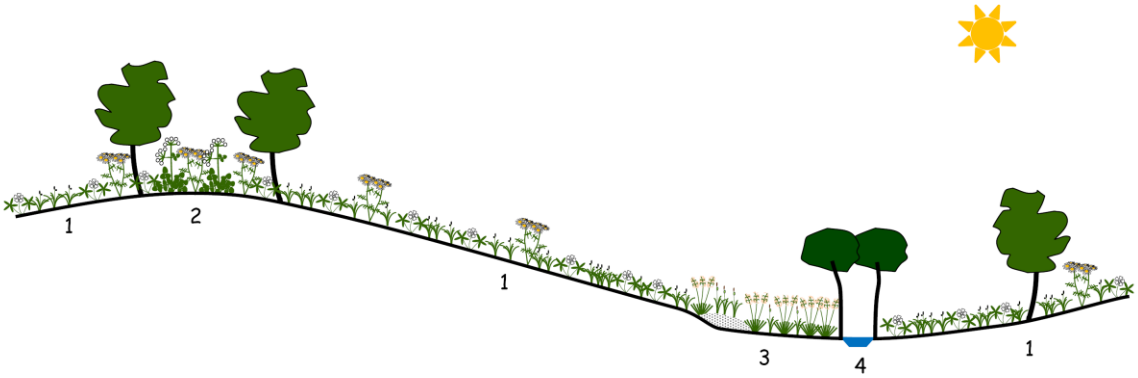

Fig. 22. *Brachypodio-Molinietum* association may form the matrix of the vegetation mosaic in relatively humid regions such as the White Carpathians. On forest margins and in wetter depressions, it transitions into the tall herb-rich vegetation of the *Geranion sanguinei* alliance. The species composition of more intensively managed (fertilised, ploughed) stands changes towards mesophilous meadows of the *Arrhenatherion elatioris* alliance. 1 – *Brachypodio-Molinietum*, 2 – *Geranion sanguinei*, 3 – *Molinion caeruleae*, *Caricion davallianae*, *Calthion palustris*, 4 – *Alnion incanae*.

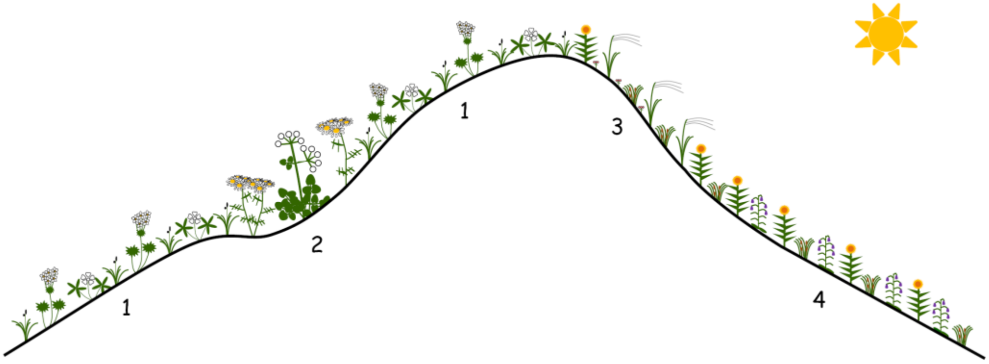

Fig. 23. In somewhat drier regions such as Western Podillia in Ukraine, the vegetation of the *Brachypodio-Molinietum* association retreats to shady slopes. Here it occupies convex or flat areas, while in wetter and more nutrient-rich depressions it transitions to the tall herb-rich vegetation of the *Geranion sanguinei* alliance. The drier types of steppe grassland grow on the sunny slopes. 1 – *Brachypodio-Molinietum*, 2 – *Geranion sanguinei*, 3 – *Festucion valesiacae*, 4 – *Polygalo majoris-Brachypodietum pinnati*.

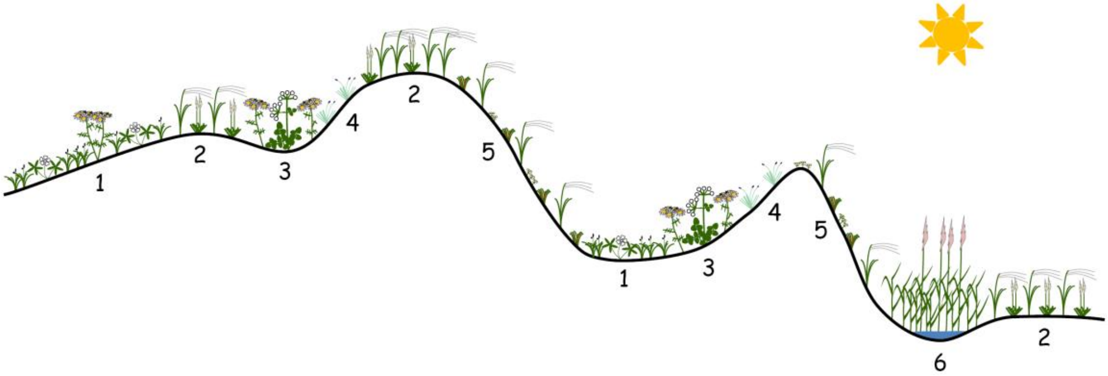

Fig. 24. *Brachypodio-Molinietum* is associated with relatively wetter habitats on shady slopes and in shallow depressions also in the diverse forest-steppe mosaics of Transylvania, which are formed by landslides. On plateaus with chernozem-like soils, slightly more drought-tolerant vegetation of the *Stipetum tirsae* association predominates. 1 – *Brachypodio-Molinietum*, 2 – *Stipetum tirsae*, 3 – *Geranion sanguinei*, 4 – *Orchido militaris-Seslerietum heufleranae*, 5 – *Stipion lessingianae*, 6 – *Molinion caeruleae*, *Phragmito-Magnocaricetea*. Adapted from A. Bădărău, http://www.floraofromania.transsilvanica.net.

2.5. Analogous vegetation

In addition to the above described *Euphorbio-Caricetum* association from the northeastern periphery of the Alps, there occur analogues of the peri-Carpathian forest-steppe meadows also in other parts of Europe. Some are floristically very close to the *Brachypodio-Molinietum* association and contain a large number of its indicator species (Table 4), others are related mainly by the ecological spectra and habitat requirements of the species involved. In most cases, these analogues also share a common traditional management practice, which is usually mowing and hay production.

On the **southeastern periphery of the Alps**, analogous vegetation occurs in Slovenia and in the adjacent part of Austria (Styria), where Alpine, Balkan and Pannonian biogeographical influences intermingle. In Slovenia, it is largely classified in the *Bromo-Danthonietum* association (Šugar 1973, Willner et al. 2019), while in Styria it has been described as the *Cirsio pannonici-Brometum* association (Steinbuch 1995). The latter association was classified by Willner et al. (2019) in the broadly conceived *Festuco rupicolae-Brometum* association described from southern Germany (Zielonkowski 1973). These vegetation types are distinguished from the peri-Carpathian forest-steppe meadows by a greater abundance of (pre-)Alpine and sub-Mediterranean species (e.g. *Buphthalmum salicifolium*, *Euphorbia verrucosa*, *Genista sagittalis*, *Hippocrepis comosa*, *Knautia drymeia*, *Noccaea praecox*, *Orobanche gracilis*, *Rhinanthus glacialis*, *Thymus longicaulis*), but at the same time they share a large number of indicator species (Table 4) and are jointly classified within the *Cirsio-Brachypodion* alliance (Willner et al. 2019). The stands may be extremely species-rich (Steinbuch 1995, Sengl & Magnes 2008, J. Roleček et al., unpublished), but the maxima recorded so far are lower than in peri-Carpathian stands (about 80 species per 16 m^2).

Further southeast, analogous vegetation occurs on the **plateaus of the Balkan mountain ranges**. Probably the first to notice these communities was Šmarda (1966) on the Lovech Plateau in Bulgaria. Later, for example, the *Galio lovcensis-Artemisietum chamaemelifoliae* association was described from the wider Stara Planina Mts (Pedashenko et al. 2010, Willner et al. 2019). It shares a number of indicator species with the peri-Carpathian meadows (Tab. 4), but differs in the occurrence of many, largely sub-Mediterranean-(sub)continental species (e.g. *Bromopsis riparia*, *Cerastium banaticum*, *Festuca dalmatica*, *Galium rhodopeum* (syn. *G. lovcense*), *Genista sagittalis*, *Hypericum linarioides*, *Pimpinella tragium*, *Seseli peucedanoides*, *Thymus longicaulis*). This vegetation is also notable for the isolated occurrence of *Artemisia chamaemelifolia*, a rare light-demanding species with a disjunct distribution (Pedashenko et al. 2010). The vegetation of this association, classified in the *Cirsio-Brachypodion* association, reaches an altitude of almost 1500 m.

Towards western Europe, the grasslands of the *Cirsio-Brachypodion* alliance are being replaced by the suboceanic semi-dry grasslands of the *Mesobromion erecti* alliance. However, this change is not uniform in space, and especially in areas with a continentally inclined climate, or for other reasons enriched with (sub)continental elements, vegetation in some respects surprisingly close to peri-Carpathian forest-steppe meadows may occur (Meusel 1940, Krausch 1961, Mahn 1965, Willner et al. 2019). These areas also include the **broader surroundings of the Swabian Alb** in southwestern Germany, where, for example, species-rich semi-dry grasslands of the *Gentiano vernae-Brometum* association are found (Kuhn 1937, Willner et al. 2019). Although these include suboceanic and (pre-)Alpine elements (e.g. *Buphthalmum salicifolium*, *Cirsium acaulon*, *C. tuberosum*, *Euphorbia verrucosa*, *Festuca ovina*, *Gentiana verna*, *Gentianella germanica*, *Hippocrepis comosa*, *Potentilla verna*), they share a number of indicator species (Table 4) and ecological features with peri-Carpathian forest-steppe meadows. These include, in particular, common dominants (e.g. *Brachypodium pinnatum*, *Carex montana*), the common occurrence of mesophilous and drought-tolerant species, a significant representation of herbs, including submontane and fringe species, and numerous competitively inferior, retreating species (e.g.

Orchidaceae, *Gentianaceae*). Swabian Alb and the adjacent Baar are also known for concentrated occurrences of rare light-demanding species (e.g. *Anemonastrum narcissiflorum*, *Bistorta vivipara*, *Festuca amethystina*, *Gentiana lutea*, *Pleurospermum austriacum*, *Salix starkeana*; Witschel 1980, Wilmanns 2003), but these often grow in other vegetation types.

Fig. 25. Forest-steppe meadow of the *Vicio craccae-Centaureetum pseudophrygiae* association on the northern slope of the Petrin log hollow in the unmown part of the Streletskaya Steppe near Kursk in the Central Russian Upland.

As the peri-Carpathian forest-steppe meadows show clear continental links (Roleček et al. 2014, Willner et al. 2019), it is tempting to look for their analogues in the forest-steppe zone of Eastern Europe. From this point of view, the **Central Russian Upland** is a crucial region, where numerous fragments of forest-steppe vegetation are still preserved (Alyekhin 1951, Poluyanov & Averinova 2012). It is also situated on the borderline between forest and steppe zones with climatic conditions favourable for the occurrence of both drought-tolerant and mesophilous species. Within the Russian forest-steppe, this area is distinguished by the mixing of different biogeographical influences and isolated occurrences of rare light-demanding species (e.g. *Betula humilis*, *Bupleurum ranunculoides*, *Daphne cneorum*, *D. sophia*; Kozo-Polyanskiy 1931, Petrov & Terechina 2013, Roleček 2018). Vegetation most similar to the peri-Carpathian forest-steppe meadows grows here on gentle northern slopes on deep chernozem-like soils. It is classified in the *Vicio craccae-Centaureetum pseudophrygiae* association, which has been assigned by the authors to the *Geranion sanguinei* alliance (Dorofeyeva & Poluyanov 2013), but its species composition and physiognomy corresponds to the *Cirsio-Brachypodion* alliance in the Central European understanding (Willner et al. 2019). It shares a number of indicator species with the *Brachypodio-Molinietum* association (Table 4), some of which attain significantly higher constancy here (notably *Klasea lycopifolia*, *Stipa tirsa* and *Veratrum nigrum*). On the other hand, it is distinguished by the absence of many species, particularly mesophilous ones, and by a greater abundance of (sub)continental elements (e.g. *Bromopsis riparia*, *Campanula stevenii*, *Cytisus ruthenicus*, *Delphinium cuneatum*, *Dracocephalum ruyschiana*, *Euphorbia semivillosa*, *Iris aphylla*, *Phlomis tuberosa*, *Stipa pennata*, *Veronica spuria*), some of which have somewhat different habitat requirement here than in Central Europe. A photograph and a record of the species composition is shown to illustrate the species composition of this vegetation at the classic site of the Central Russian steppes, the Streletskaya Steppe near Kursk (Fig. 25, Relevé 2). On the adjacent plateaus with deep soils, the somewhat more drought-tolerant vegetation of the *Stipo tirsae-Bromopsietum ripariae* association predominates (Averinova 2010). The richest mown stands are characterized by extreme species richness, with up to 86 species per 1 m^2 and 141 per 100 m^2 (Zolotukhina & Zolotukhin 2012); the former is the world maximum for a given plot size.

Relevé 2: Russia, Kursk region, Streletskaya Steppe, abandoned forest-steppe meadow at the base of the shady slope of the Petrin log hollow; 51.58014°N, 36.10658°E (WGS-84); 225 m a.s.l.; 31 July 2018; area 16 m^2; slope 13°; slope orientation 350°; herb layer cover 80%; moss layer cover 1%; median herb layer height 30 cm. Recorded by J. Roleček, J. Těšitel & A. V. Poluyanov.

E$_1$: *Carex montana* 2b, *Arrhenatherum elatius* 2m, *Stachys officinalis* 2m, *Achillea millefolium* aggr. 1, *Brachypodium pinnatum* 1, *Calamagrostis epigeios* 1, *Fragaria viridis* 1, *Potentilla alba* 1, *Primula veris* 1, *Agrostis capillaris* +, *Anthoxanthum odoratum* +, *Arabis* sp. +, *Asperula tinctoria* +, *Avenula pubescens* +, *Bistorta officinalis* +, *Bromopsis inermis* +, *B. riparia* +, *Campanula persicifolia* +, *Carex pallescens* +, *Centaurea jacea* +, *Centaurea phrygia* subsp. cf. *stenolepis* +, *Clematis recta* +, *Dactylis glomerata* +, *Draba sibirica* +, *Dracocephalum ruyschiana* +, *Equisetum* cf. *pratense* +, *Euphorbia semivillosa* +, *Festuca rubra* +, *Filipendula vulgaris* +, *Galium album* +, *G. boreale* +, *G. verum* +, *Geranium sanguineum* +, *Hypericum maculatum* +, *Inula hirta* +, *Klasea lycopifolia* +, *Knautia arvensis* +, *Leontodon hispidus* +, *Lotus corniculatus* +, *Luzula multiflora* +, *Lysimachia nummularia* +, *Origanum vulgare* +, *Peucedanum oreoselinum* +, *Phleum pratense* +, *Plantago lanceolata* r, *Poa angustifolia* +, *Potentilla thuringiaca* +, *Pulmonaria angustifolia* +, *Ranunculus polyanthemos* +, *Rumex acetosa* s.lat. +, *Sanguisorba officinalis* +, *Serratula tinctoria* +, *Silene viscaria* +, *Solidago virgaurea* +, *Stellaria graminea* +, *Tanacetum vulgare* +, *Thalictrum lucidum* +, *Trifolium alpestre* +, *T. campestre* +, *T. montanum* +, *Veronica chamaedrys* s.lat. +, *Viola canina* subsp. *ruppii* +, *Viola hirta* +, *Agrimonia eupatoria* r, *Anthriscus sylvestris* r, *Carex caryophyllea* r, *Cerastium fontanum* subsp. *vulgare* r, *Geum rivale* r, *Hypericum hirsutum* r, *Jacobaea erucifolia* r, *Lathyrus pannonicus* subsp. *collinus* r, *Leucanthemum vulgare* aggr. r, *Linaria vulgaris* r, *Melampyrum cristatum* r, *Prunella vulgaris* r, *Stachys recta* r, *Stipa tirsa* r, *Tanacetum corymbosum* r, *Taraxacum* sect. *Taraxacum* r, *Thalictrum simplex* subsp. *simplex* r, *Vicia tenuifolia* r; *Prunus spinosa* r, *Pyrus pyraster* r.

The relationship with peri-Carpathian forest-steppe meadows can also be traced in the forest-steppes of the **Central and Southern Urals**. This region hosts relatively mesophilous steppe vegetation, extending beyond the 55th degree of latitude (Zolotareva et al. 2019). Its diversity has been documented in considerable detail (Jamalov et al. 2012), but Willner et al. (2019) summarized it under a single broad association *Poo angustifoliae-Stipetum pennatae*, described from the Southern Urals (Jamalov et al. 2013; Fig. 26). Despite the dominance of feather grasses (*Stipa pennata*, *S. tirsa*), it is classified within the *Cirsio-Brachypodion* association due to the large proportion of subxerophilous and mesophilous species (Willner et al. 2019, Zolotareva et al. 2019). It shares a number of indicator species with the peri-Carpathian stands (Table 4), however, it differs by the absence of many meadow, suboceanic and sub-Mediterranean species, and conversely by the higher abundance of species that are absent (e.g. *Artemisia armeniaca*, *A. sericea*, *Campanula stevenii*, *Dianthus versicolor*, *Helictochloa hookeri* subsp. *schelliana*, *Potentilla humifusa*, *Salvia dumetorum*), less common (e.g. *Cytisus ruthenicus*, *Dracocephalum ruyschiana*, *Lathyrus pisiformis*, *Phlomis tuberosa*, *Potentilla thuringiaca*, *Seseli libanotis*, *Thalictrum simplex* subsp. *simplex*, *Trifolium lupinaster*, *Veronica spuria*) or have different habitat preferences (e.g. *Aconogonon alpinum*, *Linaria vulgaris*, *Potentilla argentea*) in Central Europe. In the local context, it is the most species-rich steppe community, although its species richness does not approach that of peri-Carpathian forest-steppe meadows (about 65 species per 100 m^2 on average; Zolotareva et al. 2019). Herb-rich types on somewhat wetter sites resemble Central European vegetation the most; they are usually classified by Russian authors as separate associations transitional between dry grasslands of the *Festuco-Brometea* class and tall herb-rich vegetation of the *Carici macrourae-Crepidetalia sibiricae* order within the *Molinio-Arrhenatheretea* class (e.g. *Drabo sibiricae-Primuletum macrocalycis* and *Carici caryophylleae-Fragarietum viridis* associations; Jamalov & Kucherova 2009, Jamalov et al. 2012, Zolotareva et al. 2019).

Fig. 26. A stand of *Poo angustifoliae-Stipetum pennatae* association in a forest-steppe mosaic on chernozem-like soil near the village of Annovka, Zilair Plateau, Southern Urals.

This overview shows that the peri-Carpathian forest-steppe meadows are by no means a singularity – a geographically restricted and developmentally isolated phenomenon. Analogous vegetation is known from many places in Central and Eastern Europe and, in addition to shared species, there are similarities in habitats, landscape contexts and management practices. At the same time, it is far from being a commonplace vegetation; on the contrary, these analogues are often interpreted as distinctive, even unique, and are given special attention by botanists in several regions. For example, the extremely species-rich forest-steppe meadows around Kursk are referred to by Russian authors as the "Kursk botanical anomaly" (Alyekhin 1934, Filatova 2012). The archaic nature of this vegetation, its characteristic species, sites or entire regions of occurrence are also often highlighted (e.g. Kozo-Polyanskiy 1931, Wilmanns 2003, Sengl & Magnes 2008, Pedashenko et al. 2010). Thus, we can conclude that the interplay of ecological and historical factors that shaped the peri-Carpathian forest-steppe meadows happened to occur more frequently in the European temperate zone and contributed to the emergence of these coexistence hotspots.

Table 4. Frequencies of indicator species of the *Brachypodio-Molinietum* association (see Table 1) in selected contact (C; similarly distributed but ecologically distinct) and analogous (A; ecologically similar but distributed elsewhere) associations of dry grasslands of Central and Eastern Europe. Similarity was calculated using the Sørensen index by comparing the frequencies of indicator species in a given association and the *Brachypodio-Molinietum* association (maximum 1, minimum 0). Frequency data were taken from the paper of Willner et al. (2019). 1 – *Euphorbio verrucosae-Caricetum montanae*, 2 – *Bromo-Danthonietum*, 3 – *Polygalo majoris-Brachypodietum*, 4 – *Gentiano vernae-Brometum*, 5 – *Vicio craccae-Centaureetum pseudophrygiae*, 6 – *Galio lovcensis-Artemisietum*, 7 – *Orchido militaris-Seslerietum heufleranae*, 8 – *Festuco rupicolae-Brometum*, 9 – *Stipetum tirsae*, 10 – *Poo angustifoliae-Stipetum pennatae.*

Association	***Brachypodio-Molinietum***	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Contact/Analogous association		A	A	C	A	A	A	C	A	C	A
Similarity		0 .76	0.66	0.64	0.61	0.60	0.56	0.55	0.54	0.54	0.48
Brachypodium pinnatum s.lat.	82	51	85	75	77	6	47	43	62	52	14
Trifolium montanum	69	68	77	26	48	44	27	13	27	48	75
Carex montana	64	72	37	8	46	31	.	13	6	2	3
Salvia pratensis	64	66	81	58	52	50	.	23	50	48	.
Filipendula vulgaris	63	32	42	29	10	100	73	27	18	75	78
Viola hirta	55	40	22	32	29	69	7	13	30	17	14
Arrhenatherum elatius	45	60	47	29	13	13	.	7	42	11	.
Ranunculus polyanthemos	44	47	19	22	27	44	.	33	15	11	65
Primula veris	38	34	.	13	54	56	7	33	13	3	34
Stachys officinalis	38	38	42	13	21	81	53	23	12	11	19
Thesium linophyllon	38	25	16	33	12	.	27	43	6	19	.
Campanula glomerata	33	26	9	25	33	6	33	13	8	11	11
Trifolium alpestre	33	13	.	10	2	38	87	17	7	23	1
Avenula pubescens	31	53	24	13	25	25	13	.	21	8	.
Vicia cracca s.lat.	30	47	33	10	28	75	20	10	23	17	47
Carlina acaulis	29	53	39	17	34	.	20	17	26	.	.
Cirsium pannonicum	29	38	55	12	.	.	.	27	6	2	.
Inula salicina	29	17	2	5	5	13	33	7	2	9	4
Tanacetum corymbosum	29	15	8	16	3	38	13	7	3	8	26
Potentilla alba	28	8	3	2	2	44	13	.	1	2	.
Genista tinctoria	27	2	8	15	5	13	7	10	6	17	24
Cruciata glabra	26	19	44	8	.	.	47	20	7	3	.
Rumex acetosa	26	30	13	2	4	6	33	.	12	5	13
Geranium sanguineum	25	6	15	12	4	75	40	13	2	17	8
Tragopogon pratensis	25	58	29	14	26	31	33	3	18	3	9
Hypochaeris maculata	19	11	18	12	8	13	33	.	2	16	38
Polygala major	19	6	.	25	.	.	33	23	2	16	.
Serratula tinctoria	19	.	.	3	.	38	.	7	1	5	.
Campanula persicifolia	18	17	3	3	4	25	7	10	4	3	13

Association	***Brachypodio-Molinietum***	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Contact/Analogous association		A	A	C	A	A	A	C	A	C	A
Similarity		0 .76	0.66	0.64	0.61	0.60	0.56	0.55	0.54	0.54	0.48
Pulmonaria mollis	18	.	.	2	.	.	.	.	1	2	2
Inula hirta	13	2	4	9	1	69	33	.	1	34	45
Lathyrus pannonicus	13	8	.	3	.	25	.	.	1	6	.
Clematis recta	12	4	4	2	.	13	.	.	1	.	.
Crepis praemorsa	11	4	1	1	5	.	.	17	1	.	2
Molinia caerulea s.lat.	11	26	1	1	4	.	.	.	1	2	.
Peucedanum oreoselinum	11	21	55	10	3	6	.	17	9	5	.
Gymnadenia conopsea	10	13	35	3	38	.	.	.	4	.	.
Laserpitium latifolium	9	6	3	2	2	.	.	23	1	.	.
Potentilla erecta	9	23	32	1	19	6	.	.	4	.	1
Cyanus triumfettii	8	.	.	7	.	.	7	3	1	11	.
Ferulago sylvatica	8	.	.	1	.	.	20	3	1	3	.
Scorzonera hispanica	8	.	.	7	.	.	13	7	1	11	5
Euphorbia angulata	6	.	.	3	.	.	.	7	.	.	.
Lathyrus latifolius	6	8	.	5	.	.	.	.	1	8	.
Trifolium rubens	6	2	5	1	.	.	.	.	1	3	.
Veratrum nigrum	6	2	.	1	.	19	20	.	1	5	.
Aquilegia vulgaris	5	4	.	.	.	.	.	.	1	.	.
Digitalis grandiflora	5	.	.	1	.	.	.	.	1	.	3
Klasea lycopifolia	5	.	.	1	.	44	.	.	.	3	.
Agrostis vinealis	4	2	.	1	.	.	.	.	.	6	2
Crepis biennis	3	21	3	3	3	.	.	.	4	.	.
Lathyrus niger	3	.	.	1	.	.	.	.	1	.	.
Melampyrum cristatum	3	2	.	1	1	19	.	.	1	2	20
Neotinea ustulata	3	11	12	4	7	.	20	.	2	.	.
Thalictrum aquilegiifolium	3	.	.	1	.	.	.	13	1	.	.
Symphytum tuberosum	2	.	.	.	.	.	.	.	.	2	.
Anemonastrum narcissiflorum	1	.	.	1	.	.	.	.	.	.	.
Astrantia major	1	6	2	1	7	.	13	7	.	.	.
Gladiolus imbricatus	1	.	.	.	.	.	.	.	.	.	.
Stipa tirsa	1	.	.	1	.	25	.	.	1	100	3

2.6. Research history

In order to better understand the phenomenon of peri-Carpathian forest-steppe meadows and its current perception, it may be useful to review older botanical literature. Our aim is not to provide an exhaustive overview, but to illustrate the views of selected prominent authors on those characteristics of peri-Carpathian forest-steppe meadows that are the subject of our research: species composition, distribution, extreme species richness and historical origin.

2.6.1. White Carpathians

The first author who devoted an entire study to the vegetation of the White Carpathians was the Slovak botanist **Pavel Sillinger** (1905–1938). His work (Sillinger 1929) is detailed, modern for its time in more ways than one, and later authors often returned to it. Many of Sillinger's conclusions can still be agreed with today, and his observations are a valuable testimony to the appearance of White Carpathian nature almost a century ago. He wrote about the local forest-steppe meadows: *Meadows with a rich accompaniment of xerothermic plants, transitioning into meadow steppes (*Stipa stenophylla *as a formation plant), are characteristic of this area.*[1] He also emphasised their species richness: *The floristic diversity*, *species richness, is remarkable* [speaking about meadows with *Carex montana*]. *I have counted for example 60–70 species in a single association stand in the Vrbovce region and even 70–90 species in the Radějov and Velká regions.*[2] He distinguished between meadow and steppe stands using the following criteria: *...the different types of meadows of soft-leaved sedge* [Carex montana] *are ecologically marked by a mixture of meadow and steppe elements, the former of which predominate and condition the overall physiognomy of the stand. However, the same interesting mixture can also be found in communities in which steppe plants have achieved a high dominance and thus become determinants of the physiognomy, which is then more or less, sometimes distinctly, steppe-like. These communities can be classified as meadow steppes (steppe meadows). In the southern part of the White Carpathians, the leading species of these meadow steppes is the horsetail feather grass:* Stipa stenophylla *Čerň.*[3]

Sillinger also commented on the historical origin of these communities: *In the Pannonian period* [meaning the Boreal, i.e. the younger phase of the Early Holocene], *steppes spread here, probably covering a large area and suppressing the montane flora. In the following period, the Atlantic, with the climate cooling and the precipitation increase, the steppe communities were pushed back by the forest, especially the beech descending to low elevations at this time, along with some submontane and montane species. However, steppe flora did not disappear in the area; it survived in the low-elevation hilly area in the southwest, where climatic conditions were also favourable, probably in the more xerophilous open woodlands, perhaps mainly oak-dominated (in the so-called "forest-steppe"). Thermophilous and montane species have mixed. Finally, man, through his culture, has once again enabled a new expansion of thermophilous flora by clearing forests over large areas, thus also changing the climatic conditions in favour of greater aridity. In the places of the "forest-steppe", meadow-steppes were formed, overgrown with the horsetail feather grass* [*Stipa tirsa*]*, the steppe species spread to the deforested slopes and hillsides and advance towards the northeast; secondarily, but in a natural way, those semi-steppe and semi-xerophilous meadow communities arise which are famous for their floristic richness.*[4] It is

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[1] Orig.: *Ze společenstev jsou pro toto území charakteristické louky s bohatým doprovodem rostlin xerothermních, přecházející do luhových stepí (*Stipa stenophylla *jako rostlina formační).*

[2] Orig.: *Význačná je floristická pestrost, bohatství druhové* [luk s *Carex montana*]. *Napočítal jsem v jediném asociačním porostu na př. na Vrbovčansku 60–70, na Radějovsku a Velečsku dokonce 70–90 druhů.*

[3] Orig.: *...jsou různé typy luk ostřice horní ekologicky vyznačeny mísením prvků lučních a stepních, z nichž první převládají a podmiňují celkovou fyziognomii porostu. Tutéž zajímavou směs nalezneme však i ve společenstvech, v nichž stepní rostliny dosáhly vysoké dominance a staly se tak směrodatnými pro fysiognomii, která je pak víceméně, někdy význačně stepní. Společenstva ta můžeme zařadit mezi luhové stepi (stepní louky). V jižní části Bílých Karpat vůdčím druhem těchto luhových stepí je kavyl tenkolistý:* Stipa stenophylla *Čerň.*

[4] Orig.: *V době pannonské rozšířily se tu stepi, jež zabíraly asi velkou rozlohu a zapuzovaly horskou květenu. V následující době, atlantické, za ochlazování klimatu a přibývání srážek byla společenstva stepí zatlačována lesem, zejména buk sestupuje v této době do nízkých poloh a s ním některé druhy submontanní a montanní. Stepní květena však v území nevymizela; zachovala se v nízké pahorkatinné oblasti na jihozápadě, kde jí byly příznivé také poměry klimatické, pravděpodobně v xerofilnějších světlých hájích, asi převážně dubových (v t. zv. „lesostepi"). Přichází k mísení druhů teplomilných a horských. Konečně člověk svou kulturou umožnil opětně novou expansi teplomilné květeně, když vykácel lesy na velkých plochách a změnil tím také klimatické poměry ve prospěch větší*

remarkable in what detail the author has attempted to reconstruct the Holocene development of the vegetation of the area without having relevant palaeoecological data. This approach to palaeoecological reconstruction will be discussed later (Chapter 4.1). However, we should not miss an important fact: Sillinger assumed the survival of light-demanding species, which today largely make up the White Carpathian forest-steppe meadows, in climatically determined (i.e. warm and dry) open-canopy deciduous forests at the foothills of the White Carpathians. In his opinion, the most xerophilous variant of the local steppe meadows, dominated by *Stipa tirsa* (*Stipetum tirsae* association in the current concept; Chytrý et al. 2007, Willner et al. 2019), developed on the sites of former open-canopy forests after human deforestation by humans, while the "semi-steppe" meadows with *Carex montana* (*Brachypodio-Molinietum* association in the current concept) developed in wetter habitats and at higher elevations of the White Carpathians.

The only significant aspect of the forest-steppe meadows, on which Sillinger did not take a clear position, is the relationship to similar vegetation elsewhere in Central Europe. It seems (although he did not explicitly comment on the matter) that he considered the meadows to be a local manifestation of the mixing of Pannonian and Carpathian influences. However, as noted above, he did not hesitate to refer to the drier types as meadow steppes or steppe meadows, clearly referring to their continental analogues. This is despite their presumed anthropogenic origin and differences in species composition from the "true xerophilous steppes", which he reported from the periphery of the White Carpathians near Skalice or Trenčianske Bohuslavice: [Steppe meadows] *are far less xerophilous, hosting a whole selection of more hygrophilous meadow plants, the European and Eurasian element having a numerical predominance.*[5]

Josef Podpěra (1878–1954), one of the most important Czech botanists of the first half of the 20th century, was an influential promoter of the analogy between Central European and continental steppes and forest-steppes. He paid great attention to the White Carpathians, repeatedly wrote about the local flora and vegetation, and in 1928 he brought the participants of the Fifth International Phytogeographical Excursion here (Rübel 1930). As part of the outcomes of this excursion, he published his first comprehensive work on the vegetation of the White Carpathians, in which he focused on the species composition, origin and biogeographical relationships of the local forest-steppe meadows and the overall distribution of their dominant species *Stipa tirsa* (Podpěra 1930). He raised the following questions: *Are the meadow steppes of the White Carpathians indigenous? Are the meadow steppes in this area climatically or edaphically determined? Is a comparison with the steppe associations of southern and central Russia possible?*[6] The answer to the first question was: *I consider the meadow steppe vegetation in this area to be indigenous. The current distribution of forest and meadow steppe goes back centuries.* [...] *Originally, the area was probably more forested. On the steep slopes, in places with rocky soil*

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suchosti. Na místech „lesostepi" vznikají luhové stepi, zarůstající kavylem tenkolistým, stepní druhy šíří se na odlesněné svahy a úbočí vrchů a postupují k severovýchodu; druhotně, ale cestou přirozenou vznikají ona polostepní a poloxerofilní lučinná společenstva, která jsou proslulá svým floristickým bohatstvím.

[5] Orig.: [Stepní louky] *jsou daleko méně xerofilní, hostí celý výběr hygrofilnějších rostlin lučních, element evropský a eurasijský má číselnou převahu.*

[6] Orig.: *Sind die Wiesensteppen der Weissen Karpathen ursprünglich? Sind die Wiesensteppen des Gebietes klimatisch oder edaphisch bedingt? Ist ein Vergleich mit den Steppenassoziationen Süd- und Mittel-Russlands möglich?*

that is unfavourable for forest, vegetation similar to the meadow steppe has probably always been preserved. Steppes on plateaus (plakor steppes) were probably not indigenous to the area. After research into the chernozems (rendzinas) [we now understand rendzinas differently], *pedologists will be able to give us important insights into the former distribution of meadow steppes.* [...] *The natural, little human-influenced development of forests, forest-steppes and steppes is probably subject to much deeper natural influences (e.g. fires) than rational human culture can produce.*[7] Podpěra demonstrated a remarkably dynamic understanding of steppe and forest-steppe for his time: disturbances, whether caused by human activity or natural factors (fire), are part of them, and may even be necessary for them. He expressed this in a pregnant way in one of his last works, in which he returned to the White Carpathians (Podpěra 1951): *Due to human influence (pastoralism and hay farming), a beautiful forest-steppe developed on the southern edge of the White Carpathians between Uherský Brod and Strážnice.*[8] It is therefore paradoxical from today's point of view that he answered the second question about the factors determining the occurrence of these steppes in 1930 as follows: *I consider the extensive meadow steppes of the White Carpathians, where* Stipa stenophylla *plays such an important role, to be primarily edaphic (substrate, slope) and secondarily climatic or microclimatic (shaded slopes of the rugged area).*[9] In contrast, the area with the best developed steppe meadows (the foothills between Radějov and Hluk) has a mild terrain and climate, to which Podpěra himself commented: *The precipitation conditions seem to be too high for a steppe region.*[10] Apparently he did not count on the possibility that disturbances could play a significant role in the long-term (Holocene) survival of species here.

The third question, concerning the relationship between the White Carpathian and Russian steppes, was answered by Podpěra in the spirit of his belief, influenced by his rich experience with the continental steppes during World War I (Chytrý et al. 2017). Referring to Alyokhin's classification of steppes, he wrote: *Our steppe meadows can thus be described as herb-rich feather grass steppes with* Stipa stenophylla (Stipetum stenophyllae) *predominating in the more exposed places and as herb-rich steppe meadows on flatter slopes.*[11] He was not quite clear about the existence of possible analogues in Central Europe, but from some of his statements it seems that he considered the White Carpathian forest-steppe meadows to be unique in Central Europe. However, with regard to their most drought-tolerant type (*Stipetum tirsae* association in today's concept), he mentioned multiple sites in Bohemia and Moravia (Podpěra 1930).

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[7] Orig.: *Ich halte die Wiesensteppenbestände im Gebiete für ursprünglich. Die heutige Verteilung des Waldes und der Wiesensteppe geht weit in die Jahrhunderte zurück.* […] *Ursprünglich war das Gebiet wohl mehr bewaldet. An steilen Hängen, an Stellen mit für den Wald ungünstigem, felsigem Boden hat sich wohl immer eine wiesensteppenartige Vegetation erhalten. Flache (plakore) Steppen waren im Gebiete ursprünglich wohl nicht zu Hause. Die Pedologen werden uns später nach der Erforschung der Schwarzböden (Rendzinen) des Gebietes wichtige Ausschlüsse über die ehemalige Verbreitung der Wiesensteppen verschaffen können.* […] *Die natürliche, vom Menschen wenig beeinflusste Entwicklung des Waldes, der Waldsteppe und der Steppe unterliegt wohl weit mehr tiefgreifenden natürlichen Einflüssen (z. B. Bränden), als sie die rationelle Kultur des Menschen hervorrufen kann.*

[8] Orig.: *Vlivem lidským (pastevnictví a senařství) rozvinula se na jižním okraji Bílých Karpat mezi Uherským Brodem a Strážnicí nádherná lesostep.*

[9] Orig.: *Die grossen Wiesensteppen der Weissen Karpathen, auf denen die* Stipa stenophylla *eine so bedeutende Rolle spielt, halte ich in erster Linie für edaphisch (Unterlage, Hang), in zweiter Linie für klimatisch, besser gesagt mikroklimatisch (Schattenhänge eines reich gegliederten Gebietets) bedingt.*

[10] Orig.: *Die Niederschlagsverhältnisse kommen mir für ein Steppengebiet zu hoch vor.*

[11] Orig.: *Wir können also unsere Steppenwiesen an mehr exponierten Stellen als bunte Federgrassteppen mit vorherrschender* Stipa stenophylla (Stipetum stenophyllae*), an flachen Hängen als bunte Steppenwiesen bezeichnen.*

Jaromír Klika (1888–1957), one of the founders of the Czech school of phytosociology, was also quick to address the question of the White Carpathian forest-steppe meadows. Already in the first of a series of studies on the xerothermic vegetation of Central Europe, mainly devoted to the Pavlov Hills (Klika 1931), he distinguished and (invalidly) described the community *Molinietum arundinaceae* cum *Stipa stenophylla*, which more or less corresponds to Podpěra's (also invalid) association *Stipetum stenophyllae*. A few years later (Klika 1939), he described the *Brachypodieto-Molinietum* association, which is now used under the full name *Brachypodio pinnati-Molinietum arundinaceae* for forest-steppe meadows in the White Carpathians and elsewhere in the peri-Carpathian area (Chytrý 2007a, Willner et al. 2019).

Klika (1931) also commented on the origin of the White Carpathian meadows: *An important, so far too little appreciated influence on the expansion and formation of the steppes has the man. One of the most brilliant examples of this are the steppe stands of* Stipa stenophylla *near Blatnička and Suchov* [i.e. the White Carpathian foothills] *in southern Moravia. The indigenous open oak forest probably harboured* Molinia arundinacea *as the predominant indigenous understorey. After deforestation,* Stipa stenophylla *prevailed on the south and southeast facing slopes, which is no longer accompanied by* Molinia *only on the driest sites.* [...] *...our steppes are conditioned edaphically and microclimatically.*[12] To a large extent, therefore, he shared the views of his predecessors, but unlike them (especially Podpěra) he emphasised the climatic differences between the Central European and continental steppes: *...in a true steppe, which occurs as a climax, the very low temperatures in some winter months are decisive.*[13] He then came to the opposite conclusion regarding the biogeographical links of the Central European steppes, which he subsequently referred to only in quotation marks and concluded: *It would not be correct, however, to consider these communities as extensions or continuations of the Russian steppes.*[14] Thus, Klika thought of the White Carpathian forest-steppe meadows in a dynamic way (as did Sillinger and Podpěra), but placed great emphasis on their hypothetical climax state in his interpretation. Over time he sharpened his assessment and found biogeographical links elsewhere (Klika 1939): Brachypodieto-Molinietum *Klika. A parallel community to* Molinietum litoralis *Scherrer* [described from the Swiss Plateau; Scherrer 1925] *on Tertiary claystones and sandstones of the White Carpathians up to an altitude of 690 m, with mountain species increasing from 500 m. The soil is calcareous rendzina* [not in the present-day understanding]. *The black impermeable fine soil is sometimes influenced by man (fertilization). According to the dominant species a number of facies partly conditioned by human influence can be distinguished. The association was formed*

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[12] Orig.: *Einen bedeutenden, bisher zu wenig gewürdigten Einfluss auf die Ausdehnung und Entstehung der Steppen hat der Mensch. Eines der glänzendsten Beispiele hierfür sind die Steppenbestände von* Stipa stenophylla *bei Blatnička und Suchov in Südmähren. Der ursprüngliche lichte Eichenwald beherbergte wahrscheinlich als vorherrschenden ursprünglichen Unterwuchs* Molinia arundinacea. *Nach der Abholzung überwiegt auf den nach Süden und Südosten gekehrten Hängen* Stipa stenophylla, *welche nur an den trockensten Stellen nicht mehr von* Molinia *begleitet wird.* […]*...unsere Steppen edaphish und mikroklimatisch bedingt sind.* […]

[13] Orig.: *...in der wirklichen Steppe, die als Klimax vorkommt, auch die sehr niedrigen Temperaturen während einiger Wintermonate entscheidend sind.* […] *Es wäre aber nicht richtig, diese Gesellschaften für Ausläufer oder für die Forsetzung der russischen Steppen zu halten.*

[14] Orig.: *Es wäre aber nicht richtig, diese Gesellschaften für Ausläufer oder für die Forsetzung der russischen Steppen zu halten.*

secondarily by degradation of xerothermic oak forests.[15] The emphasis on the secondary nature and human influence on the White Carpathian meadows is obvious. The observation about the occurrence of similar vegetation on the periphery of the Alps is useful, although the mentioned Scherrer's community also contains a number of regionally specific (pre-Alpine) species and within the Czech vegetation resembles most closely some communities on the eroded marl slopes in Bohemia (Studnička 1980, Toman 1981). It also grows in different climatic conditions (annual rainfall over 1000 mm), and it is noteworthy that this time it does not prevent Klika from drawing parallels.

Nevole (1947), in his overview of the meadow vegetation of the White Carpathians, and Holzknecht (1952), in his study on the local forest-steppe vegetation, mostly repeated the ideas of the previous authors, so we will stop only at the excellent expert on the flora of the White Carpathians, **Stanislav Staněk** (1903–1982). He wrote about the local meadows in his regional floristic synthesis (Staněk 1954): *In the hilly area on the outskirts of the Carpathians, there is a zone of forest-steppe characterised by hills with downy oak accompanied by numerous shrubs with white violet and low fumewort* [i.e. *Viola alba* and *Corydalis pumila*] *in the spring undergrowth. Extensive steppe meadows have developed in this zone, especially in the southern part of the White Carpathians.* [...] *Forest-steppe meadows of similar composition, with even richer flora, are known from Transylvania.*[16] To our knowledge, he was the first Czech author to point out the close analogies of the White Carpathian forest-steppe meadows in Romania.

Podpěra's successor in the research of Moravian flora and vegetation, **Jan Šmarda** (1904–1968), did not pay special attention to the White Carpathian forest-steppe meadows, but he knew the area well and expressed his view on the origin of the local meadows in a paper devoted to the discovery of analogous vegetation on the Lovech Plateau in Bulgaria (Šmarda 1966): *In both cases, the indigenous deciduous forest was cleared and solitary oaks were left as standards. As a result of the sudden opening, i.e. changes in light, heat and humidity regimes, the species composition of the indigenous herbaceous understorey of the forest has changed. Many moisture- and shade-loving species have disappeared, while others have adapted to the influx of light and heat and are thriving in the new conditions. These areas have been and continue to be gradually enriched with additional species: steppe, grassland and weedy. This has resulted in a rich mosaic of phytosociologically poorly defined stands that would be very difficult to characterise using conventional phytosociological methods. I refer to these cenologically heterogeneous stands, very rich in species, which gradually spread to the areas of cleared forest, as meadow steppes.*[17] It is

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[15] Orig.: Brachypodieto-Molinietum *Klika. Eine parallele Gesellschaft zum* Molinietum litoralis *Scherrer auf tertiären Tonnmergeln und Sandsteinen der Weiss-Karpathen bis zur Höhe von 690 m, von 500 m ab nehmen montane Arten zu. Der Boden ist eine kalkreiche Rendzina. Die schwarze undurchlässige Feinerde wird manchmal vom Menschen beeinflusst (Düngung). Nach den überwiegenden Arten ist eine Reihe von durch menschliche Einflüsse teilweise bedingten Fazien zu unterschieden. Die Assoziation ist durch Degradierung sekundär aus den xerothermen Eichenwäldern entstanden.*

[16] Orig.: *V pahorkatině na okraji Karpat šíří se pásmo lesostepi význačné chlumy s dubem šipákem doprovázeným četnými křovisky s violkou bílou a dymnivkou nízkou v jarním podrostu. V tomto pásmu rozvinuly se zvláště v jižní části Bílých Karpat rozsáhlé stepní louky.* […] *Lesostepní luka podobného složení, s květenou ještě bohatší, jsou známa až ze Sedmihradska.*

[17] Orig.: *V obou případech došlo k vykácení původního listnatého lesa a byly ponechány solitérní duby jako výstavky. V důsledku náhlého prosvětlení, resp. změny ve světelném, tepelném i vlhkostním režimu, došlo k změnám v druhové skladbě původního bylinného podrostu lesa. Mnohé vlhko- a stínomilné druhy vymizely, jiné se přílivu světla a tepla přizpůsobily a v nových podmínkách dobře prosperují. Tyto plochy byly a jsou i nadále postupně obohacovány o další druhy: stepní, luční i plevelné. Tak vznikla bohatá mozaika fytocenologicky nevyhraněných porostů, které by jen velmi obtížně bylo lze charakterizovat běžnými metodami fytocenologickými. Tyto*

evident that Šmarda's view of the origin of these meadows was close to Sillinger's and Podpěra's. As noted in Section 2.5, recent research (Willner et al. 2019) confirmed the considerable similarity of forest-steppe meadows in the wider Stara Planina Mts in Bulgaria (Pedashenko et al. 2010) to White Carpathian forest-steppe meadows.

One of the greatest experts of steppe flora among Czech botanists was **Jan O. Martinovský** (1903–1980). In addition to the taxonomy of feather grasses (Martinovský 1980), he became interested in the biogeographical relationships of Czech steppes and forest-steppes (Martinovský 1967, 1971, Martinovský & Kolbek 1984). He advocated the equivalence of continental and Central European steppes (he avoided the terms analogue and homologue because of their alleged ambiguity) and, like Podpěra, tried to place our steppes in the classification framework used by Russian authors. He viewed the White Carpathian forest-steppe meadows similarly to the steppes in the vicinity of the Russian towns of Orel or Penza, i.e. as a northern, mesophilous type of steppes of the forest-steppe zone (Martinovský 1967): *I guess the analysis sufficiently justifies the opinion that even the so-called meadow steppes in the White Carpathians cannot be considered a separate* [i.e. unique] *community, but that they are essentially the same plant formation as the Bohemian forest-meadow steppes* [where he classifies in the first place the steppe meadows of the České středohoří Mts, the so-called Babiny meadows]. *I choose the name White Carpathian facies of forest-meadow steppes for them.*[18] The unusual term "forest-meadow steppe", emphasising the mesophilous character of these communities, has been used in Russian literature. Regarding the origin of the White Carpathian meadows, Martinovský inclined to the above-mentioned view of Sillinger (1929), which he considered to be intermediate between the "extreme" views of Podpěra (1930) and Klika (1931).

At the turn of the 1960s and 1970s, an intense discussion about steppes and forest-steppes and their origin in Central Europe took place among Czech botanists and palaeoecologists (Jeník 1969, Jeník & Ložek 1970, Moravec 1970, Ložek 1971). On this occasion, the influential phytosociologist **Jaroslav Moravec** (1929–2006) wrote about the ecology and origin of the White Carpathian forest-steppe meadows (Moravec 1970): *The "steppe" or "forest-steppe" phytocenoses of the White Carpathians are found in a more humid climate than the xerothermic phytocenoses of the Lounské středohoří Hills* [...]. *They occupy pararendzinas, pseudorendzinas (pelozems) or eutrophic brown soils on more or less calcareous neogene* [in fact Cretaceous to Palaeogene] *sandstones and marlstones. These phytocenoses are much more clearly replacement communities after the forest, as evidenced by their numerous contacts with forest phytocenoses and their dependence on regular mowing once a year. They are therefore thermophilous meadows conditioned by a warmer climate, not by greater aridity. Their secondary nature is confirmed by the intensive management of some of these meadows in recent years, which has transformed them into mesophilous oat grass meadows of the* Arrhenatherion *alliance, even though many of the indigenous species are still present.* [...] *It has already been mentioned that the White Carpathian*

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cenologicky heterogenní porosty, druhově velmi bohaté, nastupující postupně na plochy po vykáceném lese, označuji jako luhové (luční) stepi.

[18] Orig.: *Soudím, že provedený rozbor dostatečně zdůvodňuje názor, že ani tzv. luhové stepi v Bílých Karpatech nelze považovat za samostatné společenstvo, nýbrž že běží v podstatě o týž rostlinný útvar, jako jsou české lesoluční stepi. Volím pro ně název bělokarpatská facie lesolučních stepí.*

meadows with scattered trees cannot be regarded as a forest-steppe as a climax.[19] Moravec thus followed Klika's argumentation when he emphasised mesophilous, secondary, non-climax character of the White Carpathian meadows. However, in the general debate on steppes, he acknowledged two essential circumstances: i) *The existence of steppes as primary xerothermic phytocenoses on deep soil – chernozem – would only be possible in the form of a relict community preserved by human activity since Neolithic agricultural settlement*;[20] and ii) *It is likely that the northern part of the subzone of the meadow steppes in the USSR also includes similar secondary vegetation.*[21] However, he did not draw from these considerations any significant consequences for his assessment of Czech forest-steppe meadows.

The author of the most detailed vegetation study of the White Carpathian forest-steppe meadows to date is **Vlastimil Tlusták**. In his diploma thesis (Tlusták 1972) he published a large number of phytosociological relevés of the White Carpathian forest-steppe meadows and in a subsequent scientific paper (Tlusták 1975) he placed them in the broader framework of the meadow vegetation of the White Carpathians. Both studies, especially the paper, are characterized by the compact form of contemporary syntaxonomic works. It is certainly worth mentioning that the author has placed the vast majority of forest-steppe meadows within the broadly conceived *Brachypodio-Molinietum* association. Even the driest stands with *Stipa tirsa* he classified, like Klika, in the subassociation *B.-M. stipetosum stenophyllae*. However, he also distinguished other types of dry grasslands, which is in line with the present-day idea of the variability of this vegetation in the region, where the stands of the *Brachypodio-Molinietum* association form the most widespread, but not exclusive, dry grassland type (Chytrý et al. 2007). He classified this association in the *Cirsio-Brachypodion pinnati* alliance, thus emphasizing its continental biogeographical links. The issue of species richness was not particularly addressed by him, despite the fact that he took a large number of rather good quality relevés. He only mentioned the fact that *Brachypodio-Molinietum* is a "very species-rich community", and then referred to the driest subassociation, *B.-M. stipetosum stenophyllae*, as a "species-unusually rich community" (today we know that the driest stands are, on the contrary, species poorer; Fajmonová et al. 2020). He took a position similar to that of Klika on the history of the grasslands, i.e. he considered them to be secondary vegetation after deforestation, with the more mesophilous stands in his opinion derived from oak-hornbeam and beech forests (he mentions the alliances *Carpinion betuli* (Meyer 1937) Oberdorfer 1953 and *Eu-Fagion* Oberdorfer 1957 emend. Tx. 1960) and the drier from thermophilous oak forests (he mentions the alliance *Quercion pubescenti-petraeae* Br.-Bl. 1931). As a necessary condition for the existence of the community, he identified low-intensity human

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[19] Orig.: *„Stepní" resp. „lesostepní" fytocenosy Bílých Karpat se vyskytují v humidnějším klimatu než xerothermní fytocenosy Lounského středohoří* […]. *Osídlují pararendziny, pseudorendziny (slínovatky) příp. eutrofní hnědozemě na více či méně vápnitých neogenních pískovcích a slínovcích. U těchto fytocenos je mnohem zřetelnější, že jde o náhradní společenstva po lese, což dokládají četné kontakty s lesními fytocenosami i jejich závislost na pravidelném kosení jednou do roka. Jsou to tedy thermofilní louky podmíněné teplejším klimatem, nikoliv větší ariditou. Jejich druhotnost potvrzuje i intensivní obhospodařování některých těchto luk v posledních létech, které je mění v mesofilní ovsíkové louky svazu* Arrhenatherion, *i když se v nich řada druhů z původního složení dosud udržuje.* […] *Že za lesostep jakožto klimax nelze pokládat bělokarpatské louky s roztroušenými stromy, bylo již zmíněno.*

[20] Orig.: *Existence stepí jako primárních xerothermních fytocenos na hluboké půdě – černozemi – by byla možná jen v podobě reliktního společenstva konservovaného lidskou činností od neolitického zemědělského osídlení.*

[21] Orig.: *Je pravděpodobné, že severní část podzony lučních stepí v SSSR zahrnuje též podobné druhotné porosty.*

management (single mowing, no fertilization). He then devoted a separate chapter of his thesis to the question whether the White Carpathian meadows can be considered as steppes or forest-steppes. He rejected the use of these terms by Sillinger (1929) and Podpěra (1930, 1931), arguing that he understands steppe as a climax vegetation type confined to true chernozems and kastanozems, whose species composition is dominated by plants of continental origin, which in his opinion the vegetation under study does not meet. Forest-steppe is, in his bold statement, "in fact a completely different type of vegetation from that envisaged by the authors cited above". He referred to Walter's (1968) definition, according to which a forest-steppe is "a macromosaic in which sharply delimited forest complexes alternate with a steppe completely devoid of woody plants". He fully subscribed to the views of Moravec (1970) and Vicherek (1971), but admitted that "opinion on this question is far from uniform" and briefly referred to the works of Jeník, Klika, Ložek, Martinovský and Meusel, some of which are quoted here.

To summarise the above, I think that the old authors paint a very realistic picture of the White Carpathian forest-steppe meadows. I would like to highlight P. Sillinger's timeless study, which goes into valuable detail in the description and at the same time discusses the findings in a broad context. The then twenty-four-year-old author did an extraordinary job. The ensuing debate did not have one prevailing direction and, despite the differing opinions, was not a clash of sharply defined positions. The views of some authors changed over time, sometimes even contradicting themselves to some extent. Nevertheless, several trends are evident. With regard to the relationship of the White Carpathian forest-steppe meadows to grassland communities in other regions, Sillinger, Podpěra, Staněk, Šmarda and Martinovský referred to analogues in continental forest-steppe regions to varying degrees, while Klika, Moravec and Tlusták were dismissive of this analogue to varying degrees. Analogues in the pre-Alps (Klika), the Balkans (Šmarda) and Transylvania (Staněk) were also mentioned. One of the arguments for analogizing with continental communities is the assumed origin of these meadows in the long-term persistence of their species from the time of the wider extent of the steppes (e.g. Sillinger and Podpěra). However, it is significant that both authors assumed survival of light-demanding species in open-canopy forests, determined climatically or edaphically, rather than in non-forest communities (mainly due to the relatively humid climate in the area, unfavourable for the maintenance of steppes; they have not considered the possible influence of disturbances much). In this respect, they were largely in agreement with their apparent opponent, Klika. Rather, then, it is a conceptual disagreement over what either author calls primary and natural versus secondary and anthropogenic. As far as species richness is concerned, most authors emphasise the extraordinary diversity of the White Carpathian forest-steppe meadows. It was expressed in numbers of vascular plant species only by Sillinger (1929), who listed 70–90 species "in a single association stand" in the vicinity of Radějov and Velká nad Veličkou.

More recent views, where relevant to our discussion, are incorporated in the following chapters.

2.6.2. Other regions

In other parts of the range, the peri-Carpathian forest-steppe meadows have also attracted the attention of old botanists for their specific species composition and extraordinary richness. **Aurel Procopianu-Procopovici** (1862–1918), the author of the first vegetation map of Romania, wrote about the meadows in the vicinity of the town of Suceava (Procopianu-Procopovici 1892): *As far as the second type of meadows is concerned, which are made dispensable by the increasingly common, more profitable cultivation of clover, these are at present almost everywhere confined to remote, mostly narrow strips in the middle of fields, on the steepest parts of the hills, where at present they are exploited to the fullest by mowing. The above-mentioned circumstances mean that the extremely lush flora of these less dry meadows, which I would like to call indigenous meadows for the sake of brevity, can only be considered to be superficially known.*[22] It is clear from the author's list of species that the vegetation is close to the *Brachypodio-Molinietum* association and the tall herb-rich vegetation of the *Geranion sanguinei* alliance, which can still be found, for example, in the nearby Fânațele seculare de la Calafindești reserve (see Chapter 2.2). It is worth noting that the author emphasises the presumed archaic nature of these meadows by referring to them as indigenous, natural (*ursprünglich*).

The Czech-German botanist and palaeoecologist **Karl Rudolph** (1881–1937) pointed out similar vegetation just a few dozen kilometres to the north, in the vicinity of the town of Chernivtsi in the territory of present-day Ukraine (then part of the Austro-Hungarian Empire). In the first monographic study of the vegetation of this region, he wrote about the local vegetation mosaics including forest-steppe meadows (Rudolph 1911): *If the steep, unforested slopes of the clay hills are not used as pastures or cultivated, a plant community of a special character develops on them.... The flora of these hills cannot really be described as uniform, but consists of a colourful mosaic of different sub-formations, which are sometimes purely developed on small stretches, sometimes completely interpenetrate each other, but which together form the picture of a meadow formation in the popular and economic sense. This juxtaposition and intermingling of the different sub-formations is caused by the diversity in the soil properties of the hills (varying slope, exposure, moisture) already described in the introduction. This also explains the strikingly large number of species in the flora of the hills. The actual character of this flora, however, is given by the occurrence of a community of thermophilous species on the steeper, sunnier places that form the grassland* [*Trift* in German] *formation in the narrower sense. These "grassland sites" then gradually change into "meadow sites" of different facies (dry mountain meadows, wet valley meadows, meadow mires, etc.), which differ from the grassland sites by the absence of these thermophilous plants and the new appearance of typical meadow plants. In the hollows and on the slopes, pools continue to form with their own flora, and in addition to all this, all these sub-formations are interspersed with typical forest plants, which can probably be considered relicts of*

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[22] Orig.: *Was die zweite Art Wiesen anbelangt, welche durch den immer allgemeiner werdenden, vorteilhafteren Kleeanbau entbehrlich gemacht werden, so ist diese gegenwärtig nahezu überall auf entlegene, meist schmale Streifen mitten in Feldern, an den allersteilsten Stellen der Hügel beschränkt, wo sie derzeit durch die Mahd wohl ihre höchste Verwerthung erfahren. So brachten es diese oben erwähnten Umstände mit sich, dass die überaus üppige Flora dieser mehr weniger trockenen Wiesen, die ich der Kürze halber als ursprüngliche Wiesen bezeichnen möchte, bisher höchstens nur als flüchtigst bekannt angesehen werden kann.*

the former forest stand on the hills.[23] The fact that the vegetation of the *Brachypodio-Molinietum* association is part of the described mosaic is also evident from Rudolph's photograph and the list of species in the accompanying text to the site Okruh near Chernivtsi in the monograph *Die Pflanzendecke Österreich-Ungarns* (Hayek 1914). This vegetation still occurs here today (Roleček et al. 2014) and is protected in the Malovanka botanical reserve.

In the interwar period, part of western Ukraine belonged to Poland, and therefore the local vegetation of the peri-Carpathian forest-steppe meadows was described phytosociologically for the first time by Polish researchers M. Koczwara (Koczwara 1927, 1931) and A. Kozłowska (Kozłowska 1930, 1931). **Marjan Koczwara** (1893–1970), in his modern study *Zespoły stepowe Podola Pokuckiego*, described the habitat and species richness of the *Caricetum montanae* association as follows (Koczwara 1931): *It occurs on gentle slopes and in terrain depressions, on gypsum and limestone, often on the margin of or near oak forests, most often on northern or northwestern slopes. It stands out among all communities for its greatest* [species] *richness.*[24] About the species composition and origin of this vegetation he wrote: *The characteristic plants of this community also include species listed as characteristic of forest meadows, especially those characterized by a high degree of constancy (*Clematis recta, Laserpitium latifolium, Veratrum nigrum, *etc.). The significant number of forest plants in the soft-leaved sedge* [*Carex montana*] *community indicates – in addition to similar ecological conditions – a certain developmental link between these communities. This is based on the fact that the soft-leaved sedge community, as to some extent a succession after the open-canopy oak forests, inherits these forest species.*[25]

We can see that Koczwara interpreted the occurrence of forest and fringe species in a similar way to Rudolph, i.e. as a remnant of the original forest stands. However, this does not mean that he considered this vegetation to be young in terms of its development: *The latter* [montane species] *represent species with relatively strongly fragmented ranges and some systematic features that indicate greater age.* [...] *This would suggest a somewhat relict character of these communities. This is also evidenced by the fact that the above communities are linked to exposures*

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[23] Orig.: *Soweit die steil geböschten, unbewaldeten Abhänge der Lehmhügel nicht als Weiden benutzt oder angebaut werden, entwickelt sich auf ihnen eine Pflanzengesellschaft von besonderer Eigenart... Die Flora dieser Hügel kann eigentlich nicht als eine einheitliche bezeichnet werden, sondern sie besteht aus einem bunten Mosaik verschiedenartiger Subformationen, welche bald auf kleinen Strecken rein entwickelt sind, bald sich gegenseitig völlig durchdringen, die aber zusammengenommen das Bild einer Wiesenformation im volkstümlichen und volkswirtschaftlichen Sinne geben. Dieses Neben- und Durcheinanderauftreten der verschiedenen Subformationen ist durch die schon einleitend geschilderte Mannigfaltigkeit in der Bodenbeschaffenheit der Hügel (wechselnde Böschung, Exposition, Feuchtigkeit) bedingt. Sie erklärt auch mit die auffallend große Artenfülle der Hügelflora. Das eigentliche Gepräge verleiht dieser Flora aber doch das Auftreten einer Gesellschaft von thermophilen Sippen an den steileren, sonnigeren Stellen, welche die Triftformation im engeren Sinne bilden. Diese „Triftstellen" gehen dann ganz allmählich bei geringfügiger Änderung der Bodenverhältnisse in „Wiesen" stellen verschiedener Fazies über (trockener Bergwiesen, feuchter Talwiesen, der Wiesenmoore etc.), die sich durch das Fehlen dieser thermophilen Pflanzen und das Neuhinzutreten typischer Wiesenpflanzen von den Triftstellen unterscheiden. In den Mulden und auf den Absätzen kommt es dann weiter zur Tümpelbildung mit der ihr eigenen Flora und zu alledem gesellt sich noch, daß alle diese Subformationen von typischen Waldpflanzen durchsetzt sind, die wohl als Relikte des einstigen Waldbestandes auf den Hügeln bezeichnet werden können.*

[24] Orig.: *Występuje po łagodnych zboczach i zagłębieniach terenu, na gipsach i wapieniach, nierzadko na skraju lub wpobliżu dąbrów, najchętniej na północnych lub półn.-zach. stokach. Z pośród wszystkich zespołów wyróżnia sie największym bogactwem.*

[25] Orig.: *Do charakterystycznych roślin tego zespołu można zaliczyć również w dalszej mierze gatunki wymienione jako charakterystyczne dla halaw i lak śródleśnych, zwłaszcza te wśród nich, które wyróżniaja się dużym stopniem stałości (Clematis recta, Laserpitium latifolium, Veratrum nigrum i i.). Znaczna ilość śródleśnych roślin w zespole turzycy górskiej wskazuje – obok podobieństwa warunków ekologicznych – na pewien związek genetyczny, jaki istnieje między temy zespółami. Związek ten polega na tem, że zespoł turzycy górskiej jako w pewnej mierze sukcesja po świetlistych dąbrowach przejmuje w spadku po nich owę gatunki leśne.*

which, differing from the general climatic conditions of present-day Podolia, are also relict in character.[26] He reconciles this apparent paradox as follows: *Overall, these facts suggest that, although the soft-leaved sedge community today has been fully developing after the abandonment of the oak forests, and in this sense is a young community, it was already formed to some extent in previous geological epochs, the Diluvial* [Pleistocene] *and probably also the Tertiary, and in this sense is a relict community.*[27]

On the matter of the origin of the *Caricetum montanae* association in recent deforestation, another prominent Polish botanist, **Władysław Szafer** (1886-1970), disputed with Koczwara. In his extensive study *Las i step na zachodniem Podolu* he wrote (Szafer 1935): *Taking the position of A. Rehmann, one could – I believe – with a high degree of probability assume that the non-forest character of the eastern (steppe) part of the Pokutian Podolia is ancient and natural, and looking for its causes, one could find them in the soil conditions of this sub-district of the Pokutian Podolia.*[28] And further: *If we wanted to reconcile the fact of a widespread distribution of forest plants in this part of Podolia today, which are part of the steppe community* Caricetum montanae, *understanding them as relicts of oak forests, we would have to assume that these forests grew here before the main period of karst erosion in a different, drier climate, at a time when the layer of soil covering the gypsum rock was thicker than today. If we consider this assumption as probable, then the time of existence of oak forests in the steppic Pokutia should be transferred to the post-glacial period 3* [i.e. probably the first phase of the Middle Holocene, when mixed oak forests predominated] […], *and their natural disappearance should be causally and temporally connected with the humid period 4* [i.e. probably the younger phase of the Middle Holocene and the subsequent phase of the Late Holocene, when beech, fir and hornbeam were spreading].[29]

In Transylvania, the eminent Hungarian botanist **Rezső Soó** (1903–1980) began his extensive phytosociological research in the interwar period, focusing his first monographic study on the vegetation around the regional metropolis of Cluj. He paid great attention to the Cluj meadows (Fânațele Clujului), which he regarded as an extraordinary phenomenon (Soó 1927): *...the extensive Szénafű (Fânatele = hay meadows) – lying to the northeast of the town, from the Kajántó valley to the Szamos valley – is one of the most prominent landscapes of the Mezőség* [i.e.

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[26] Orig.: *Te ostatnie reprezentują częściowo gatunki o dość silnie poszarpanych zasięgach i pewnych cechach systematycznych, wskazujących na poważniejszy wiek. Wskazywałoby to na zabytkowy, w pewnej mierze, charakter tych zespołów. O tem samem świadczy fakt przywiązania powyższych zespołów do ekspozycyj, które odbiegając od dzisiejszych ogólnych warunków klimatycznych Podola, noszą również charakter zabytkowy.*

[27] Orig.: *V sumie wskazują powyższe fakty na to, że jakkolwiek zespól turzycy górskiej rozwija się w pełni dzisiaj po opuszczeniu dąbrów i w tem znaczeniu jest zespołem młodym, to jednak formował się już w pewnej mierze ubiegłych epokach geologicznych, dyluwjalnej i prawdopodobnie i trzeciorzędowej i w tym sensie jest zespołem zabytkowym.*

[28] Orig.: *Stojąc na stanowisku A. Rehmanna, możnaby bowiem – jak sądzę – z dużem prawdopodobieństwem przyjąć, że bezleśność wschodniej (stepowej) części Podola pokuckiego jest odwieczna i naturalna, szukając zaś jej przyczyn, można je znaleźć w warunkach glebowych tego podokręgu Podola pokuckiego.*

[29] Orig.: *Gdybyśmy chcieli z tem pogodzić fakt szerokiego rozpowszechnienia dziś w tej części Podola roślin leśnych, wchodzących w skład zespołu stepowego* Caricetum montanae, *pojmując je jako relikty lesów dębowych, trzebaby przypuścić, że lasy te rosły tutaj przed głównym okresem erozji krasowej w innym, suchszym klimacie, w czasie, gdy warstwa gleby, pokrywająca skałę gipsową, była grubsza, aniżely jest dzisiaj. Jeżeli przypuszczenie takie uznamy za prawdopodobne, to czas istnienia na Pokuciu stepowem lesów dębowych wypadnie przenieść do okresu postglacialnego 3* [...], *zaś ich naturalny zanik związać przyczynowo i czasowo z wilgotnym okresem 4.*

Transylvanian Plain], *although it was once undoubtedly covered by forests.*[30] He then described the vegetation close to the *Brachypodio-Molinietum* association as *Festuceto* (*sulcatae*)-*Brachypodietum* (*pinnati*). In a later study, he classified this vegetation into the *Danthonio-Stipion stenophyllae* alliance, which he characterized as follows (Soó 1949): *Forest-steppe grasslands, rich in herbs, mostly used as mesophilous hay meadows. These are the most beautiful "hay grasslands". They are of secondary origin on the sites of former oak forests and contain shrub and forest species as survivors.*[31] He did not adhere to the name he had previously proposed and distinguished three different associations within the alliance: *Pediculari-Caricetum montanae* (the closest in species composition to the *Brachypodio-Molinietum* association and also the richest in species, 70 or more species per 10 m^2), *Agrostideto-Danthonietum* (more mesophilous, poorer in species, transitional to the meadow vegetation of the *Arrhenatherion* alliance) and *Stipetum stenophyllae* (the driest, transitional to dry steppe of the *Stipion lessingianae* alliance). Soó was aware of the extraordinary number of rare light-demanding species that in the past could not survive in the forest environment here and explained it as follows (Soó 1927): *...Since the Bronze Age, the forest had been cleared, burnt down, grazed and thus prevented from regenerating; in its place, pastures, dry or oligotrophic meadows developed, these artificial cultivated steppes joined the areas where the forest – due to geomorphological and edaphic conditions – was not able to settle, on the sliding marl or on the saline soils, so that a steppe formation developed there – which conveyed the flora of the former climatic steppes for the present – and could form a centre for their further expansion.*[32] Finally, he admitted the possibility that at least some of the steppe species have persisted in the places settled by humans in an otherwise forested environment, i.e. that there is a direct continuity between the Early Holocene and anthropogenic open landscape.

The famous German botanist and biogeographer **Hermann Meusel** (1909–1997) was also familiar with the Cluj meadows, and he classified the vegetation growing on the foothills of the northern slopes as the most mesophilous type of steppe, which he called "dense-grass meadow steppe" (*dichtrasige Wiesensteppe*), a term roughly corresponding to our (forest-)steppe meadows. He emphasised their affinity with the vegetation of more westerly areas (Meusel 1940): *We meet many species here that are also widespread in Germany and even occur in regions where* Stipa *meadow-steppe communities are completely absent (in the Danube region, for example, in the Swabian Alb).*[33] He included *Brachypodium pinnatum*, *Carex montana* or *Helictochloa pratensis* among the dominant species of this vegetation type and *Anemone sylvestris*, *Astragalus danicus*, *Crepis praemorsa*, *Filipendula vulgaris*, *Fragaria viridis*, *Galium boreale*, *Hypochaeris maculata*,

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[30] Orig.: *…zeigt das weitausgedehnte – von der Stadt nordöstlich, vom Kajántótal bis zum Szamostal liegende – Szénafű (Fânatele = Heuwiesen) eines der praegnantesten Landschaftsbilder der Mezőség obwohl es einst zweiffellos waldbedeckt gewesen war.*

[31] Orig.: *Prairies steppiques boisées, riches en fleurs, servant de prairies de fauche mésophiles pour la plupart. Ce sont les plus belles „herbes de foin". Elles sont d'origine secondaire sur les emplacements d'anciennes chênaies et contiennet des espèces arbustives et forestières comme survivants.*

[32] Orig.: *...der Wald wurde seit der Bronzezeit gerodet, niedergebrannt, geweidet und so an der Regeneration gehindert, an seiner Stelle entstanden Weiden, Trocken- oder Hartwiesen, diese künstlichen Kultursteppen schlossen sich den Flächen an, wo der Wald - infolge geomorphologischer und edaphisher Verhältnisse - nicht fähig war, sich auch den rutschenden Mergel, oder auf den Salzböden niederzulassen, sodass sich daselbst eine Steppenformation entwickelte - die die Flora der früheren klimatischen Steppen für die Gegenwart vermittelte - und ein Zentrum für deren weitere Ausdehnung bilden konnte.*

[33] Orig.: *Wir treffen hier sehr viele Arten, die auch in Deutschland weit verbreitet sind und da selbst noch in Bezirken auftreten, wo* Stipa-*Wiesensteppevereine gänzlich fehlen (im Bereich Donauraums z. B. in der Schwäbischen Alb).*

Peucedanum officinale, *Potentilla alba*, *Pulsatilla patens*, *P. vulgaris*, *Seseli libanotis*, *Tephroseris integrifolia*, *Trifolium montanum* and *Viola rupestris* among the "leader" species. He wrote about the origin of this vegetation: *In more extensive stands, the dense-grass meadow steppe usually only occupies areas that have been kept artificially free of forest. Its elements can also be found for the most part in sparse copses at forest edges and in forest meadows. The boundary between grassland and heath forest* [*Heidewald*; meaning an open-canopy forest with a rich understorey of non-forest species] *can therefore not be drawn sharply.*[34] Like Sillinger before him, he pointed out the specific biogeographical relationships of forest-steppe meadows, which are different from those of feather grass steppes: *The dense-grass meadow steppes are composed primarily of species whose developmental centre is situated in the temperate zone and here again often on the border of the boreal zone. The leading elements of this vegetation type show the richest development in the area of the southern Siberian mountains.*[35] We can see that Meusel looked far to the east in his search for analogues of Central European forest-steppe meadows.

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[34] Orig.: *Die dichtrasige Wiesensteppe besiedelt in ausgedehnteren Beständen meist nur künstlich waldfrei gehaltene Gebiete. Ihre Elemente sind größtenteils auch in lichten Gehölzen an Waldrändern und auf Waldwiesen zu finden. Die Grenze zwischen Grasflur und Heidewald ist deshalb nicht scharf zu ziehen.*

[35] Orig.: *Die dichtrasigen Wiesensteppen werden vorzüglich aus Arten zusammengesetzt, deren Entwicklungszentrum in der temperierten und hier wieder vielfach an der Grenze der borealen Zone liegt. Reichste Entfaltung zeigen die Leitelemente der Arten dieses Vegetationstyps im Bereich der südsibirischen Gebirge.*

3. Extreme species richness

3.1. State and dynamics

The results of our field investigations and other studies published in the last decade confirm that the forest-steppe meadows of the *Brachypodio-Molinietum* association and some stands of the *Geranion sanguinei* alliance with similar species composition are the most species-rich vegetation on areas of 10–16 m^2 known worldwide (Wilson et al. 2012, Roleček et al. 2014, 2019a, 2021b, Chytrý et al. 2015, Biurrun et al. 2021). This is a spatial scale corresponding to the size of the usual vegetation relevé in meadow and steppe habitats (Chytrý & Otýpková 2003), for which a large amount of data is available from around the world (Biurrun et al. 2021). Comparison of maximum species numbers in different parts of the peri-Carpathian region (Table 5) shows that while extremely high values (over 80 species per 16 m^2) were recorded in this vegetation at a number of sites, three regions are exceptional, with maxima well exceeding 100 species per 16 m^2. These are the Prut-Siret Interfluve in western Ukraine (Dzyurkach site), the northwestern part of the Transylvanian Basin around Cluj (Fânațele Clujului site) and the southwestern part of the White Carpathians (multiple sites; Hájek et al. 2020).

Table 5. Maximum species numbers recorded in the peri-Carpathian forest-steppe meadows and related tall herb-rich vegetation sorted by regions.

Maximum species richness	Plot size [m^2]	Region	Site	Country
119	16	Prut-Siret Interfluve	Dzyurkach	UA
118	10.9	NW Transylvanian Basin	Fânațele Clujului	RO
113	16	White Carpathian Mts	Porážky	CZ
94	16	Mátra Mts	Tugár-rét	HU
93	16	Western Podillia	Kasova hora	UA
91	16	Zemplén Mts	Gyertyán-kúti-rét	HU
88	16	Aggtelek Karst	Between Jósvafő and Silica	HU
84	10	Slovak White Carpathian Mts	Bošáca (Janišová & Devánová, ined.)	SK
82	16	Pokutian-Bessarabian Upland	Chortovets-Zalomy	UA
82	16	Buzău Subcarpathians	Pâclele Mari	RO
79	16	Slovak Karst	Batova lúka	SK
79	16	Ciuc Basin	Ciba	RO
78	16	Bükk Mts	Nagy-mező	HU
74	16	Štiavnické vrchy Mts	Sitno-Tatárska lúka	SK
71	16	Kyjov Hills	Špidláky (Vicherek & Unar 1971)	CZ
69	16	Moldavian Plateau	Fânațele seculare de la Calafindești	RO
66	16	SE Transylvanian Basin	Movilele de la Păucea	RO
58	16	Buda Hills	Normafa	HU

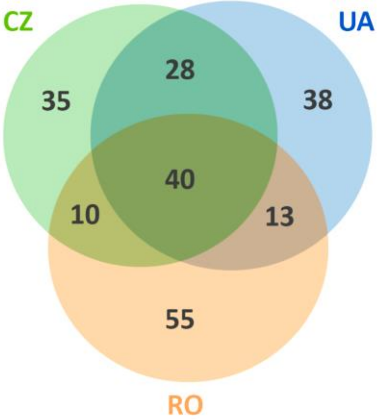

Fig. 27. Venn diagram showing the numbers of species shared among the richest relevés from the White Carpathians (CZ), the Prut-Siret Interfluve (UA) and Transylvania (RO).

The observation that the extreme species numbers are not confined to a single site, but are repeated over a wide geographical area in and around the Carpathians, may be important for understanding the phenomenon studied and assessing the hypotheses put forward to explain it (see Chapter 3.2). At the same time, we know that the extreme richness is largely restricted to a single vegetation type, the broadly understood *Brachypodio-Molinietum* association. The degree of similarity of the vegetation plots with the highest numbers of species in the three richest regions is illustrated by the Venn diagram (Fig. 27). The 40 shared species/taxa include *Achillea millefolium* aggr., *Anthericum ramosum*, *Anthoxanthum odoratum*, *Arabis hirsuta* s.lat, *Arrhenatherum elatius*, *Avenula pubescens*, *Brachypodium pinnatum*, *Briza media*, *Campanula glomerata*, *C. persicifolia*, *Carex filiformis*, *C. montana*, *Cruciata glabra*, *Dactylis glomerata*, *Dianthus carthusianorum* s.lat. (incl. *D. pontederae*), *Festuca rubra*, *Filipendula vulgaris*, *Leucanthemum vulgare* aggr., *Linum catharticum*, *Lotus corniculatus*, *Luzula campestris*, *Plantago lanceolata*, *P. media*, *Poa pratensis* s.lat., *Polygonatum odoratum*, *Primula veris*, *Pulmonaria mollis* s.lat., *Ranunculus polyanthemos*, *Rumex acetosa*, *Salvia pratensis*, *Schedonorus pratensis*, *Securigera varia*, *Serratula tinctoria*, *Stachys officinalis*, *Tanacetum corymbosum*, *Taraxacum* sect. *Taraxacum*, *Trifolium montanum*, *Valeriana stolonifera*, *Veronica chamaedrys* s.lat. and *Viola hirta*. When assessing the similarity of these stands, it should be taken into consideration that the average geographical distance between them is almost 450 km.

We also know that all three regions with the highest recorded species richness values harbour multiple stands with similar species numbers. Although we recorded over 100 species per 16 m^2 in only two relevés about 10 m apart at the Ukrainian site Dzyurkach, it was in three relevés up to 2.3 km apart at the Romanian site Fânațele Clujului, and in multiple relevés up to 16 km apart (Čertoryje, Jazevčí, Porážky and Dolnoněmčanské louky sites) in the White Carpathians (Hájek et al. 2020, Roleček et al. 2021b).

Thanks to the established permanent plots (Hájek et al. 2020), we also have first insights into the dynamics of extreme species richness (Table 6). It is clear that on the scale of a few years, extreme species richness is a constant feature of the studied stands. At all three sites surveyed, it was even found to be increasing – a somewhat surprising finding that may have different causes. First of all, it may be to some extent a sampling artefact due to the fact that the author teams were not identical in the years compared (although at least one author was present in both years) and the sampling effort may not have been identical either (although we worked according to a uniform methodology; Hájek et al. 2020). However, it appeared that at least at the Fânațele Clujului site, changes in species composition are due to intensification of sheep grazing (Roleček et al. 2021b). These changes include the increase in ruderal species, probably due to disturbance of vegetation and diaspore import by grazing animals; these interventions may promote colonization also by other species. Conversely, populations of formerly established species are mostly still surviving, although they may not be in balance with increasing grazing pressure and may disappear from stands if it continues. This observation is consistent with published data on traditional management at the site (mowing) and on the species composition of the local stands prior to our investigations (Soó 1949, Dengler et al. 2012). We also cannot exclude that the colonization of the new species is supported by the sampling itself, which involves a moderate disturbance of the stand by the researchers (Roleček et al. 2019a); indeed, our methodology does not include special measures to eliminate it.

Table 6: Changes in species richness on permanent plots in the peri-Carpathian forest-steppe meadows.

Site	**Porážky (CZ)**	**Dzyurkach (UA)**	**Fânațele Clujului (RO)**
Plot size [m²]	16	16	10.9
Year sampling	2014	2015	2018
Year resampling	2018	2018	2021
Species richness sampling	109	111	106
Species richness resampling	113	119	118

It should be mentioned that comparable values of fine-scale diversity were recorded in the 1950s–1960s on the Streletskaya Steppe near Kursk in the Central Russian Upland (Zolotukhina & Zolotukhin 2012): up to 86 species per 1 m^2 (Golubev 1962) and 141 species per 100 m^2 (Redulesku-Ivan 1965). These values are somewhat higher than the maxima found at corresponding plot sizes in peri-Carpathian forest-steppe meadows (82 and 133, respectively; Chytrý et al. 2015). On the other hand, the species numbers reported from plots of 10–16 m^2 from the Kursk region are lower than the maxima recorded in peri-Carpathian stands (probably in part due to less intensive sampling at these plot sizes by the Russian authors). If we compare the maximum numbers of species recorded in the two areas on differently sized plots and assume a power-law dependence of species richness on plot size (Lomolino 2000, Dengler et al. 2020), we find closely comparable values (Fig. 28). At the same time, it is worth noting that the maximum species numbers in the peri-Carpathian and Central Russian regions were recorded in analogous vegetation (see Section 2.5), which not only shares many species, but has also been similarly managed for a long time (the Streletskaya Steppe has been used mainly as a meadow for hay production since the 17th century at the latest; Semenova-Tyan-Shanskaya 1966). More recent research confirms the extreme species richness of Central Russian forest-steppe meadows, but such high values as in the past have not been recorded there (Zolotuchina & Zolotuchin 2012). A full-fledged comparison will be possible when data collected by a unified methodology are available for both regions.

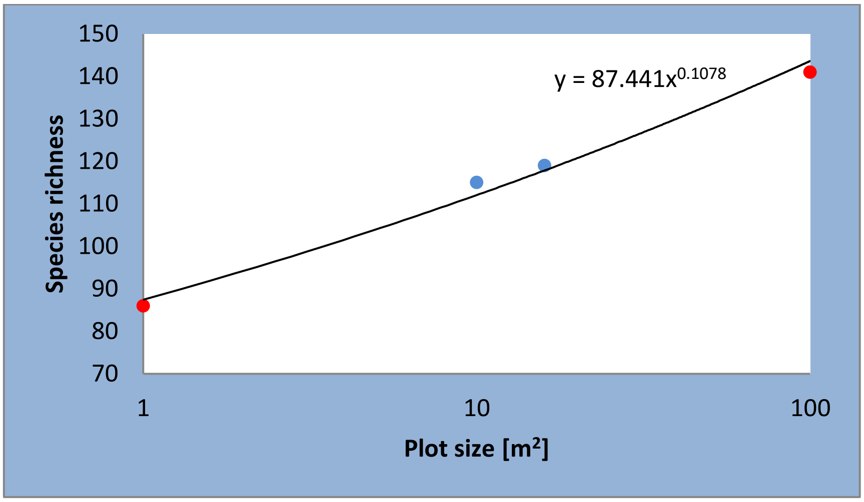

Fig. 28. Comparison of the maximum numbers of species found in forest-steppe meadows in the peri-Carpathian region on plots of 10 and 16 m^2 (blue) and in the Central Russian Upland on plots of 1 and 100 m^2 (red); note the logarithmic scale of the X-axis. Assuming a power-law dependence of species richness on plot size (black line), the values appear to be closely comparable.

3.2. Overview of opinions on the causes of extreme species richness

If we are to comment comprehensively on the possible causes of the extraordinary fine-scale diversity of peri-Carpathian forest-steppe meadows, it is appropriate to summarise the hypotheses put forward so far. At the most general level, dozens of mechanisms have been proposed that enable species coexistence and thus increase local species richness (Wilson 1990, Palmer 1994, Chesson 2000, Tokeshi 2009). As far as peri-Carpathian forest-steppe meadows are concerned, a number of factors that may promote species richness of stands in the White Carpathians have been proposed by Kubíková & Kučera (1999). In particular, they mention (i) the geographical location at the border of important floristic regions and the broad altitudinal gradient causing the intermingling of thermophilous and submontane species, (ii) the high fertility of clay soils, preventing a nutrient gradient from oligotrophic to eutrophic habitats, (iii) a climate on the border between warm and moderately warm regions with large inter-annual variations in precipitation, (iv) the presence of solitary trees, promoting the occurrence of forest species in the meadows and preventing soil disturbance, (v) the presence of species-rich open-canopy oak forests, which enriched the forest-steppe stands with species after deforestation, (vi) non-extreme, average soil properties, allowing a large number of species to realize their physiological amplitude, (vii) extensive management involving regular mowing with only occasional grazing, (viii) rich generative reproduction due to the inter-annual variability in the timing of mowing depending on weather patterns.

Later, Klimeš (2008) highlighted (i) moderate disturbance, (ii) the disruption of multiple conditions necessary to maintain the equilibrium state of species populations, e.g. through mowing and summer droughts that suppress dominants and thus allow their coexistence with other species, and (iii) the presence of scattered trees, especially oaks, which compete with herbs for limiting resources, limit vegetation development by slowly decomposing litter, and promote the occurrence of forest species.

We subsequently proposed that the extreme species richness of the *Brachypodio-Molinietum* association can be at least partially attributed to the long history and continuity of these grasslands maintained by human activities (grazing, mowing and burning; Hájková et al. 2011). Later, we have developed this line of reasoning (Roleček et al. 2014) and proposed a conceptual model of the species richness of peri-Carpathian forest-steppe meadows combining primarily (i) a large common species pool inherited from species-rich Early Holocene light-demanding and basiphilous communities, resulting from long-term disturbances associated with prehistoric human activities, (ii) the structured microrelief of the richest sites, underpinning a fine-grained mosaic of wet, mesic and dry habitats; and (iii) mechanisms balancing the fitness of coexisting species, such as intermittent moisture and regular mowing without fertilization.

Meanwhile, Dengler et al. (2012) proposed for the extremely species-rich grasslands in Transylvania (i) reduced competition due to low nutrient supply and periodic biomass removal by mowing, (ii) favourable intermediate environmental conditions allowing the survival of dry grassland, meadow, fen, forest fringe and woodland species, and (iii) the accumulation of a large species pool due to the long continuous history as a grassland and the generally richer flora on base-rich soils.

At the same time, Merunková et al. (2012) highlighted the unique combination of i) regional factors (long history of grasslands, large size of individual grassland areas and their existence in a landscape mosaic with forests, shrubs and small wetlands), ii) local abiotic factors (soil pH, soil nutrient content, moisture regime and the resulting productivity of the grasslands, which are suitable for many species from the regional species pool) and iii) management practices (low fertiliser inputs and mowing once a year in late spring or summer).

Michalcová et al. (2014) argued, based on their analytical results, that the high local species richness in the White Carpathians is not a consequence of a larger grassland species pool than in the compared regions, but of the local coexistence of many grassland species, leading to communities with high alpha but low beta diversity. They attributed this pattern in part to (i) the large extent of local grasslands, limiting random extinctions, (ii) the high similarity of soils across the landscape (i.e. the absence of a strong environmental filter, allowing many species to occur in many places), and (iii) the high diversity of vegetation cover, promoting mixing of species with different habitat requirements.

Chytrý et al. (2015), comparing species richness on different scales in the Czech Republic and Slovakia, found that while the maximum values on plots smaller than 0.5 m^2 come from different regions and probably depend mainly on local grassland management, on plots larger than 0.5 m^2 they come from only two regions, one of which is the White Carpathians. They interpreted this result as support for the importance of regionally specific landscape processes. However, referring to the results of Michalcová et al. (2014), they questioned the importance of species pool size and suggested that processes associated with past and present seed dispersal at the landscape scale may be more important.

Hájek et al. (2017), in their local study from the central part of the White Carpathians, where the meadows are somewhat less species-rich (but still fall within our definition of extreme species richness), highlighted the role of a large pool of species adapted to phosphorus-deficient soils. They pointed out that neighbouring grasslands on phosphorus-enriched soils show much lower plant diversity at fine spatial scale.

In a recent study including all major steppe types in the Ukrainian Western Podillia (Roleček et al. 2019c), we showed that species richness is unimodally related to (estimated) productivity in this region. The richness peaks in the *Brachypodio-Molinietum* association (around 350 g dry weight/m^2) on mesic sites, in places with a high evenness of species abundances and a relatively even representation of species with different moisture requirements (species of semi-dry sites predominate). We identified the topography-driven gradient of moisture and nutrient availability as the main factor influencing species composition.

Most recently, Fajmonová et al. (2020) questioned the significance of seasonal moisture fluctuations based on field measurements of moisture in the White Carpathians and highlighted the high average soil moisture. Their results also show that distance from prehistoric human settlement does not have a significant effect on species richness, although the species composition of grasslands shows a significant relationship with settlement history.

3.3. Synthesis on the horizon?

As can be seen from the overview above, there is no clear consensus on the causes of the extreme species richness of the peri-Carpathian forest-steppe meadows. However, we can find important common points in the different studies, especially if we try to unify their different terminology and disregard some interpretive inconsistencies. Almost all the authors mentioned above agree that extreme species richness is not driven by one key factor, but is a complex phenomenon involving mechanisms operating at different spatial and temporal scales. With some simplification, we can distinguish three main levels: the stand level (represented by a relatively homogeneous relevé, in our case typically 16 m^2 in area), the site level (corresponding to a mosaic of stands of different vegetation types, typically covering from ones to tens of hectares), and the landscape level (corresponding to a repeated pattern of vegetation and terrain mosaics, typically covering tens to hundreds of km^2). As the development of vegetation in individual regions is to some extent influenced by the wider surroundings, the biogeographical level (corresponding to biogeographical regions covering thousands to millions of km^2) is also relevant. This scheme therefore includes both internal and external mechanisms of species richness maintenance that must interact to achieve maximum species richness, in other words, maximum species coexistence at the stand level (Fig. 29).

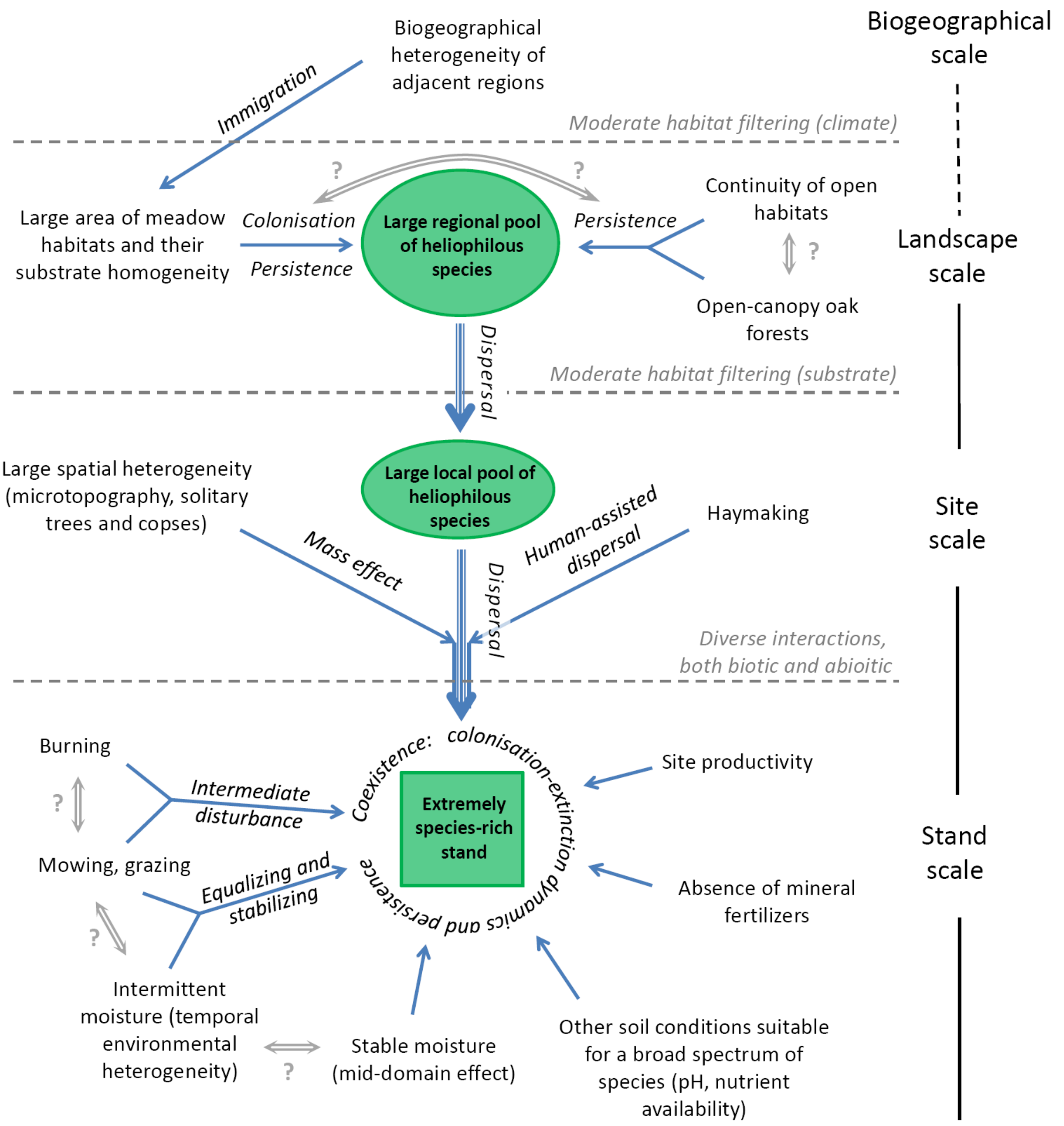

Fig. 29. Hierarchical model of extreme species richness of the peri-Carpathian forest-steppe meadows. Factors repeatedly reported in the literature are included. Grey arrows with a question mark indicate factors whose relationship is the subject of intense debate.

3.3.1. Landscape level

A fundamental landscape-scale factor that is a prerequisite for the coexistence of a large number of species at the stand level is their availability in the **landscape species pool** (Taylor et al. 1990, Zobel 1992). The number of species in extremely species-rich stands is many times smaller than the usual size of the landscape species pool in Central Europe: in the Austrian Alps, up to 980

(Moser et al. 2005) and in the Czech Republic up to 1347 (Wild et al. 2019) taxa per quadrant of less than 35 km^2 are found. It may therefore seem surprising that extreme values of species richness are confined to certain areas, to a certain vegetation type, and thus to a certain group of species. Which group of species is it? An analysis of the consensus indicator species of the *Brachypodio-Molinietum* association (Table 1) and the species shared among the most species-rich relevés (Section 3.1) shows that it is for the most part a mixture of widespread meadow species (e.g. *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Avenula pubescens*, *Briza media*, *Dactylis glomerata*, *Festuca rubra*, *Lotus corniculatus*, *Luzula campestris*, *Plantago lanceolata*, *Poa pratensis* s.lat., *Rumex acetosa*, *Schedonorus pratensis*, *Taraxacum* sect. *Taraxacum*) and species of open-canopy forests, fringe habitats and semi-dry grasslands (e.g. *Anthericum ramosum*, *Campanula glomerata*, *Carex montana*, *Cirsium pannonicum*, *Clematis recta*, *Crepis praemorsa*, *Filipendula vulgaris*, *Polygonatum odoratum*, *Pulmonaria mollis* s.lat., *Tanacetum corymbosum*, *Valeriana stolonifera*). The distribution of the latter group in Central Europe is largely restricted to warmer and drier regions with long-term continuity of open habitats or open-canopy forests (i.e. forest-steppe regions). As can be seen from Fig. 1, species with such habitat requirements make up more than half of the constant species of the *Brachypodio-Molinietum* association, thus their availability in the landscape species pool is essential for the high species richness of these stands. In this way, the **Holocene continuity of non-forest habitats** may increase local species richness.

An alternative or complementary factor contributing to the enrichment of the landscape species pool may be the position of the area on the border of important floristic regions and on a significant altitudinal gradient, i.e. the **biogeographical heterogeneity of the surrounding areas**. The latter is reported for the White Carpathians (Kubíková & Kučera 1999) as well as for the Prut-Siret Interfluve and northwestern Transylvania (Roleček et al. 2014). It may promote immigration and subsequent coexistence of species with different geographical and ecological characteristics. This circumstance raises the question of the relative importance of the long-term survival of light-demanding species in the regions with extremely species-rich grasslands versus their later immigration from surrounding areas, which will be addressed in Chapter 4.

Another repeatedly mentioned factor that may have influenced the formation of the landscape species pool is the **occurrence of open-canopy oak forests**, whose species-rich herb layer with forest-steppe species may have contributed to the formation of forest-steppe meadows after deforestation (Sillinger 1929, Koczwara 1931, Soó 1949, Kubíková & Kučera 1999). This mechanism may certainly have operated, but current knowledge suggests that these open-canopy forests were similarly dependent on disturbances as forest-steppe meadows, at least those in more humid regions (Roleček 2007). Therefore, this hypothesis does not contribute much to resolving the question of the origin of the rich pool of light-demanding species here – perhaps only by pointing out that many of the aforementioned forest-steppe species tolerate semi-shade and could therefore have survived in the past even in more advanced successional stages of scrub and open-canopy forests. In terms of long-term vegetation dynamics, this group of species is more persistent than strictly light-demanding species.

Several authors highlight the **extraordinary extent of grasslands**, in other words, the great abundance of grassland habitats in the landscape, and their relative **substrate homogeneity**

(Kubíková & Kučera 1999, Merunková et al. 2012). Consistent with the predictions of the theory of **island biogeography** (MacArthur & Wilson 1967), these may increase the number of species in the landscape pool by promoting the survival of populations that have a lower probability of extinction due to their larger size, and also increase the likelihood of immigration of new grassland species from surrounding areas. It is true that not only the White Carpathians but also northwestern Transylvania around the Fânațele Clujului site are landscapes with an extraordinary extent of grassland and steppe vegetation. On the other hand, the record-holding Ukrainian site Dzyurkach in the Prut-Siret Interfluve was still a polana, i.e. a small meadow enclave surrounded by forests, in the 18th century. However, steppe meadows were widespread in the wider area (Rudolph 1911, https://maps.arcanum.com).

How to understand the results of studies that question the importance of the species pool size for the local species richness of peri-Carpathian forest-steppe meadows? Michalcová et al. (2014), based on an analysis of data from flora grid mapping, report that the White Carpathians have a comparable pool of meadow and dry grassland species to regions where species richness at the stand level is much lower. From this observation they conclude that local species richness is more likely to be the result of the fine-scale co-occurrence of many grassland species. One can certainly agree with this conclusion to some extent, but at the same time it should be stressed that the grassland species pool is large in all the regions compared in the above study. This is quite trivial in the case of the Pálava Protected Landscape Area and the Podyjí/Thayatal National Park, i.e. topographically diverse territories, notoriously rich (by Central European standards) in flora and habitats (Danihelka & Grulich 1995, 1996, Němec 2021). In contrast, in the White Carpathians, where average habitats with deep soils predominate, the richness of the non-forest flora is surprising and requires a special explanation (Grulich 1992, Kubíková & Kučera 1999). Finally, Chytrý et al. (2015), who also refer to the work of Michalcová et al. (2014), acknowledge the existence of a large pool of grassland species in the White Carpathians, but stress the necessity of its interaction with other factors, especially those favouring dispersal, such as large population sizes, landscape structure without migration barriers and the long-term existence of suitable habitats. In this respect, however, most studies agree.

3.3.2. Site level

At the site level, the **spatial environmental heterogeneity** appears to be a major factor supporting the extreme species richness of the peri-Carpathian forest-steppe meadows. The *Brachypodio-Molinietum* association is linked to areas whose mesorelief is usually not very rugged (plateaus, flat ridges), so that extreme habitats such as rock outcrops or scree are practically absent and the above-mentioned substrate homogeneity is manifested. However, the **microrelief** creates a fine-grained mosaic of habitats with varying moisture and productivity (landslide slopes with wet depressions and drier elevations, karst sinkholes, the vicinity of springs). Thus, both vegetation more drought-tolerant (e.g. *Stipetum tirsae*, *Polygalo majoris-Brachypodietum*, *Festucion valesiacae*) and more moisture-demanding (e.g. *Molinion*, *Calthion*, *Caricion davallianae*) than *Brachypodio-Molinietum* is typically represented in the local vegetation mosaics (again, this is true for all three record-holding sites). Due to the absence of sharp transitions on deep soils formed over fine-grained sediments and their eluvia, the different communities often grade seamlessly into each other. Thus, **mass effect** (Shmida & Ellner 1984) is likely to play an important role in the coexistence of species with different habitat requirements, assuming that colonization from nearby stands (partially) compensates for extinctions caused by differences in the fitness of species with different habitat requirements. The spread of diaspores can be promoted by **haymaking**, which is the traditional use of many species-rich stands (Jongepierová 2008, Dengler et al. 2012, Roleček et al. 2014). **Solitary trees and groups or lines of shrubs and trees** are often also part of vegetation mosaics on extremely species-rich sites, supporting the occurrence of fringe and forest species (e.g. *Asarum europaeum*, *Symphytum tuberosum*, *Viola mirabilis*) and seedlings of woody plants. Sometimes forest species are also present in purely non-forest sites, where they can probably survive in the long term, for example in wetter depressions with tall herb-rich vegetation of *Geranion sanguinei* alliance. Due to their scattered occurrence, the forest species themselves do not contribute much to the local species richness of the meadows. However, fringe species do, and these may theoretically, due to less intensive disturbance in the vicinity of trees and shrubs, form strong source populations, replenishing any declining populations in the meadow itself. However, the influence of trees on the species composition of the surrounding meadows may be multi-faceted (Klimeš 2008) and requires further study.

3.3.3. Stand level

At the stand level, many factors modify the coexistence of an extreme number of species. A basic prerequisite for the growth of large numbers of individuals in a small area is **sufficient habitat productivity** (productivity-diversity relationship; Tilman 1982, Chase & Leibold 2002). Species richness in grassland ecosystems typically has a unimodal relationship to productivity (hump-backed model; Grime 1973, Brun et al. 2019), with species numbers often peaking at biomass around 300–400 g/m^2. This is consistent with data from peri-Carpathian forest-steppe meadows (Merunková et al. 2012, Roleček et al. 2019c). Productivity here seems to be mainly determined by sufficient moisture (Roleček et al. 2019c, Rozbrojová et al. 2020) and balanced availability of essential nutrients (Merunková et al. 2012), but some studies highlight the limitation of productivity by relatively low phosphorus availability (Hájek et al. 2017). Species-rich stands are usually **not fertilized with mineral fertilizers**, so they do not exhibit various, not yet fully understood mechanisms reducing species richness when the availability of nutrients, especially nitrogen and phosphorus, is increased. Among the many mechanisms proposed in the literature are, for example, (i) productivity increase, leading to an increase in biomass and hence increased competition (Grime 1973, Keddy et al. 1997, DeMalach et al. 2017), (ii) a shift from colimitation by multiple elements, promoting coexistence (nitrogen and phosphorus colimitation seems to be particularly important; Palpurina et al. 2019), to limitation by a single element, promoting interspecific competition (Tilman 1982, Palmer 1994, Braakhekke & Hooftman 1999, Merunková et al. 2012), iii) a phenological shift leading to an earlier onset of competition for light (Goldberg & Miller 1990), iv) toxicity of elevated concentrations of phosphorus and heavy metals, which are common in industrial fertilizers (Lambers & Plaxton 2015, Hájek et al. 2017, Ali et al. 2019), v) disruption of mycorrhizae at elevated nutrient concentrations (Hart et al. 2003, Hájek et al. 2017), vi) reduced diversity of nutrient forms on fertilized soils, leading to the promotion of fewer species adapted to the available forms (Turner 2008, Olde Venterink 2011), vii) differences in species adaptations between nitrogen- and phosphorus-limited habitats and the resulting changes in fitness when limitation changes (Olde Venterink 2011), or viii) a larger pool of species adapted to phosphorus-limited habitats (Olde Venterink 2011, Hájek et al. 2017). Clearly, there is still much room for further research and testing of the hypotheses put forward.

The aforementioned moisture may play an important role, but we do not yet know enough about the mechanisms of its effects. A repeatedly discussed possibility is the strong seasonal variation in moisture. Clay soils, predominant in regions of *Brachypodio-Molinietum* meadows, are prone to becoming wet in precipitation-rich periods/summers and drying out in drier periods/summers. Some authors consider this **temporal environmental heterogeneity** as an important factor limiting competitive exclusion and promoting species coexistence in forest-steppe meadows (Semenova-Tyan-Shanskaya 1966, Klimeš 2008, Merunková et al. 2012). It is indeed noteworthy that the very factor that naturally varies over time (soil moisture reflecting variable annual precipitation) determines the distribution of the main vegetation types, and thus the main ecological groups of species, in many sites of extremely species-rich forest-steppe meadows (Roleček et al. 2019c). The mechanism that stabilizes the coexistence of species with different fitness under variable conditions (stabilizing mechanism; Chesson 2000, Wilson 2011) may be the **storage effect** (Chesson 1984, 2000) through alternated favouring and disfavouring of species with different habitat requirements (e.g. relatively moisture-demanding and drought-tolerant species). Thus, relatively favourable periods, when intraspecific competition dominates, alternate with relatively unfavourable periods, when interspecific competition dominates. On the other hand, the results of studies in which moisture was measured instrumentally (Hájek et al. 2017, Fajmonová et al. 2020) rather support the idea that these habitats are favourable, more or less mesic, and in some cases even less dry than the habitats of productive meadows of the *Arrhenatherion* alliance. This view is also supported by the fact that the highest species richness is usually recorded in higher elevations, on northern slopes or in shallow depressions, i.e. in places that are wetter and relatively more stable in terms of moisture than average. Similarly, the local deep clayey soils have a considerable capacity to retain moisture and buffer fluctuations caused by variable rainfall, although not all of the water bound in these soils is available to plants (Kolay 2008). In any case, moisture may rather promote coexistence through a **non-spatial mid-domain effect** (Letten et al. 2013), where moderately wet habitats offer conditions lying at the intersection of the largest number of species niches (Kubíková & Kučera 1999, Roleček et al. 2014). This mechanism is consistent with the results of studies highlighting the importance of subtle differences in moisture niches for species coexistence (Araya et al. 2011, Silvertown et al. 2015).

As an alternative or complement to stabilizing mechanisms, equalizing mechanisms (Chesson 2000, Wilson 2011, Song et al. 2019) promote coexistence by reducing interspecific differences in fitness. For example, regular **mowing associated with biomass removal**, typically in the form of hay, may be such a mechanism. This way of economic use of peri-Carpathian forest-steppe meadows is traditional (Procopianu-Procopovici 1892, Sillinger 1929, Kozłowska 1930, Soó 1949) and still practiced in many places. Mowing is sometimes seen as an **intermediate disturbance**, promoting greater diversity than disturbance of low or too high intensity (Connell 1978). Mowing usually leads only to damage, not to complete elimination of the individual plants present. Thus, along with colonization-extinction dynamics, long-term persistence plays an important role in meadows (Klimeš 1999, Rychtecká & Lepš 2020), increasing the number of species coexisting at any given time. The equalizing effect of mowing consists primarily in the periodic, spatially even removal of aboveground biomass, which is at the same time the main tool of plants in the asymmetric competition for light (Weiner 1990, DeMalach et al. 2017). Higher, potentially competitively superior species are penalized proportionally more in this process, as they lose a larger fraction of their biomass than lower species or species with leaf rosettes (Lepš 1999, Klimeš 2008). As a result, the predominance of competitively superior species and the subsequent successional development of the stand are blocked.

Grazing and burning are alternative or complementary sources of disturbance that may replace mowing and haymaking when these traditional forms of farming decline. In terms of maintaining extreme species richness, their effect is variable and still understudied. However, our experience to date shows that they may become suitable practices of replacement management, particularly in the case of abandoned sites, over a period of years or the first decades. Out-of-season burning (usually practiced in winter or early spring) is still common in the peri-Carpathian forest-steppe meadow sites in western Ukraine and less frequent in Romania; we have recorded it sporadically also in Hungary, Slovakia and the Czech Republic. Among other effects, burning prevents litter accumulation and thus hinders successional changes after the cessation of management, accompanied by a decline in species richness (Klimeš et al. 2013, Dmytrash-Vatseba & Shumska 2020). Thus, at the western Ukrainian site of Kasova hora near Bovshiv, in stands that were regularly burnt and otherwise unmanaged for a minimum of ten years, we still recorded up to 93 species per 16 m^2, including competitively inferior species such as *Dactylorhiza viridis*, *Gymnadenia conopsea*, *Phyteuma orbiculare* and *Ranunculus breyninus* (Roleček et al. 2019c, Hájek et al. 2020). Burning practiced in the growing season would probably have more negative consequences. Thus, a better understanding of the fire ecology of peri-Carpathian forest-steppe meadows is a research priority given the potential benefits of burning as a low-cost management tool.

Neither the effects of **grazing by large herbivores** on extreme species richness have been sufficiently studied yet. Grazing of domestic animals (most often sheep and cattle, rarely horses) is currently practiced at a large number of sites of peri-Carpathian forest-steppe meadows in Transylvania, less frequently elsewhere, sometimes in stands that used to be traditionally mown (Bădărău 2005, Dengler et al. 2012, Roleček et al. 2019a). From the point of view of plant diversity, grazing in these ecosystems is usually assessed as less desirable (Bădărău 2005, Bonari et al. 2017). Such an assessment is obvious in the case of overgrazing, which results in significant changes in the structure and species composition of vegetation (Bădărău 2005, Akeroyd & Page 2011); nowadays, it occurs mainly during intensive year-round sheep grazing. Low-intensity seasonal grazing of cattle, supplementary grazing on aftermaths and inter-annual alternation of mowing and grazing tend to be less controversial. In this context, it will be interesting to monitor the changes in species richness in our permanent plot with the world maximum number of species per 10 m^2 (Fânațele Clujului site). Traditionally it has been mown, but in the last ten years or so it has been grazed quite intensively by sheep and the number of plant species here seems to be increasing (Roleček et al. 2021b, see Chapter 3.1). Whether such a development is usual, what its long-term dynamics will be and how other stand characteristics will be affected is the subject of our further investigation.

Another interesting question is the effect of **pH and calcium content** on the diversity of peri-Carpathian forest-steppe meadows (for simplicity we will discuss these two related variables together). As is well known, the species pool of dry grasslands in Central Europe is richer at sites with higher pH/calcium content (Chytrý et al. 2003). This is probably influenced by its evolution during Pleistocene climatic oscillations, when calcareous substrates dominated both spatially and temporally (Pärtel 2002, Ewald 2003). However, at the stand level, the relationship of species richness to pH/calcium content may vary in Central European steppe grasslands, and a negative relationship has been repeatedly found in studies involving peri-Carpathian forest-steppe meadows (Dvořáková 2009, Merunková et al. 2012, Turtureanu et al. 2014). The causes of this phenomenon are probably complex. A proximate cause is the fact that the most species-rich stands belong to the *Brachypodio-Molinietum* association, which usually occurs on deep, superficially decalcified soils (Dvořáková 2009, Püntener et al. 2023). The soil reaction of the topsoil is therefore lower here than in shallower soils with species-poorer vegetation, where the properties of the soil-forming substrate, which is most often calcareous, are more pronounced. However, as suggested by Turtureanu et al. (2014), if the analysed gradients of pH/calcium content and species richness were longer and included dry grasslands on strongly acidic substrates that are generally species poor, the resulting relationship of these variables would be different. Assessing the importance of soil pH and calcium content is further complicated by the multifaceted nature of their effects on plants (White & Broadley 2003, Neina 2019) and their interdependence with other variables that affect species richness – particularly moisture and nutrient availability (Lapenis et al. 2008, Penn & Camberato 2019).

3.4. Which way forward

As can be seen, the causes of the extreme species richness of the peri-Carpathian forest-steppe meadows, this stunning example of coexistence, are still far from being elucidated. It is a complex phenomenon and the relationships between the different factors operating at different spatial scales are not easy to unravel. Much of the knowledge comes from descriptive and comparative vegetation studies where it has been obtained, *cum grano salis*, by the way. Focused research, using adequate methodological tools, can therefore yield novel insights. Here we try to summarize some of the most interesting topics.

At the landscape level (Fig. 29), it remains an open question how much local survival and how much immigration from surrounding areas contributed to the formation of the light-demanding species pool during the Holocene. And if survival was significant, then how much of it took place in open-canopy forests versus more or less open landscapes. Here, we expect a major contribution from palaeoecology, and we are pursuing the topic intensively, as discussed in the following Chapter 4. Genetic studies may provide further important insights, as suggested by a few existing papers (e.g. Těšitel et al. 2018, Černá 2020).

Another big unknown is the role of moisture, despite focused research. Is it really relatively stable and therefore supports a wide range of species of non-extreme habitats by creating optimal conditions for their survival (Fajmon et al. 2020)? Or is seasonal or inter-annual variation in moisture a source of environmental heterogeneity and thus one of the mechanisms balancing fitness of species with different habitat requirements and enabling their coexistence (Semenova-Tyan-Shanskaya 1966, Klimeš 2008, Merunková et al. 2012)? To answer these questions, long-term studies in permanent plots involving monitoring of the physiological response of individual species to changing moisture or experiments manipulating moisture directly in species-rich plots are likely to be necessary.

An important challenge for the conservation of the species-rich peri-Carpathian forest-steppe meadows is a better understanding of the effects of different management practices, especially mowing, grazing of different intensities and burning. Generously designed manipulative experiments with a full factorial design may contribute to finding a solution here. However, their long-term run is critical, as short-term effects may not correspond to the long-term ones (Lepš et al. 2019, Skálová et al. 2022). Also, the implementation of experimental interventions at the designed extent is challenging in terms of logistics, especially in the case of grazing and burning.

Coexistence in peri-Carpathian meadows may also be influenced by other, so far little studied factors, e.g. the effects of soil microorganisms (Ardestani et al. 2022, Těšitelová et al. 2022). The abundant occurrence of mycorrhizal species (e.g. *Orchidaceae*; Jongepier & Jongepierová 1995) supports this idea and one can, for example, think of nutrient redistribution through mycorrhizae as another possible equalizing mechanism promoting species coexistence. Therefore, the study of plant-soil feedback (Bever et al. 1997) is another promising research area. The analysis of plant functional traits will certainly also play a role, as many studies, especially in the last decade, convincingly show that variation in functional traits influences community assembly and species coexistence (Adler et al. 2013, Kraft et al. 2015).

4. Holocene history of peri-Carpathian forest-steppe meadows

We may consider two fundamentally different ways in which communities with similar species composition are formed in different places. Either they **arise *de novo***, for example when the same species competitively establish themselves during succession at different places with similar environmental conditions and species pool. In this case, species composition converges in similar habitats and diverges in dissimilar habitats. However, vegetation similarity may also **persist from the past**, while other stands change and diverge – for example through changes in management, the spread of invasive species or encroachment by woody plants. Similar habitats with different histories may then maintain different species composition even after a uniform disturbance regime has been established and reasons for the differences may not be apparent. This **inertia of species composition** may have different sources. Von Holle et al. (2003) suggest mechanisms that are i) environmental (habitat conditions are more favourable for the species present than for the species that may replace them), ii) biotic (in particular competition from the species present), iii) demographic (the species present have larger populations and richer diaspore production) and iv) biological (e.g. the survival of long-lived species in conditions under which they would not re-establish themselves). A general consequence of this **historicity of vegetation** is that the present-day vegetation mosaics are composed of a heterogeneous mixture of communities of different ages (Sádlo 2006, Roleček et al. 2015). Communities that are more archaic are often referred to as **relict**, as they may represent remnants of previously more widespread vegetation types (Roleček et al. 2015, Dítě et al. 2018).

As already mentioned, from the beginning of the research we worked with the hypothesis that the vegetation of peri-Carpathian forest-steppe meadows is deeply relict, despite the presence of various younger elements. We assume that its species composition is derived from open-canopy forests of the Early Holocene, whose modern analogue may be the hemiboreal forests of the Southern Urals and Southern Siberia (Roleček 2007, Hájková et al. 2011). Our hypothesis is not entirely new; similar considerations on the origin of forest-steppe meadows were independently developed, for example, by the Romanian geographer and botanist **A. S. Bădărău** in his dissertation thesis on the history of vegetation in Transylvania (Bădărău 2005): *The age of the forest-steppe "island" from the central-west part of the Transylvanian Basin is neither very recent nor miocenic / pliocenic. It dates back at the very beginning of the Holocene but we have to underline that some components of the former "periglacial" cold Weichselian forest-steppe continued their existence into the warmer but much restricted, insular forest-steppe environment of the Holocene in Transylvania.* And in another place: *As an outcome the* [human] *cultures that inhabited this space had here merely to maintain the extant proportion between forest and grassland and to preserve the open nature of the natural landscape by preventing the forest from occupying the areas covered by meadow-steppe grasslands.* After all, as discussed above (Chapter 2.6), peri-Carpathian forest-steppe meadows were considered to some extent relict by many old authors (e.g. Procopianu-Procopovici 1892, Podpěra 1930, Koczwara 1931, Szafer 1935).

Nevertheless, this hypothesis has remained controversial, especially because the idea of long-term survival of forest-steppe meadows contradicts the scheme of Holocene vegetation development in Central Europe accepted by many palaeobotanists and vegetation ecologists of the second half of the 20th century. According to this scheme, during the climatically favourable, precipitation-rich Middle Holocene, the lower and middle elevations of Central Europe were dominated by a more or less closed forest. Non-forest vegetation virtually disappeared from non-extreme habitats and could only be established after human deforestation. A clear idea of the discontinuity in the Holocene presence of non-forest communities was formulated, for example, in the textual part of the map of potential natural vegetation of the Czech Republic (Rybníčková & Rybníček 1998): *The first farmers began to settle the open-canopy mixed oak forests on loess substrates at the lowest elevations, where they cleared small spaces for Neolithic settlements and their farming facilities within the forest complexes. [...] Palynological research shows that Neolithic farmers, at least initially, disturbed the natural climax vegetation in our territory only slightly. [...] The overall opening of the landscape also caused mesoclimatic changes, including drying, and opportunities opened up for secondary migration of light-demanding, often xerothermic plants from formerly isolated extreme habitats. As a consequence, in warm areas, vegetation xerophytisation and the emergence of secondary xerothermic vegetation, which is often mistakenly referred to as steppe relicts, occurred.*[36]

Here we have an apple of discord, one of the key topics of Central and Eastern European palaeoecology: **the steppe question**. Before we get to its current treatment, it may be useful to look deeper into its rich history.

4.1. History of the steppe question in Central Europe

The origin of steppes in Central Europe has been addressed by various authors from different perspectives since the 19th century (e.g. Kerner 1863, Krause 1894, Borbás 1900, Podpěra 1906). Their primary interest was to clarify how and when steppe biota in Central Europe originated. We leave aside the steppe question focused in this way. Although the age of occurrence of individual steppe species is still largely unknown (Divíšek et al. 2022), we will consider the idea that steppes were widespread in our country during periods of dry climate in the Last Glacial period and Early Holocene to be unproblematic (Ložek 1973, Rybníčková & Rybníček 1998, Pokorný 2011, Janská et al. 2017). We will focus on the debate that considers the Middle Holocene, when shady forests reached their maximum distribution, as the critical period for steppe survival in Central Europe.

The German geographer and botanist **Robert Gradmann** (1865–1950) aptly formulated this steppe question at the beginning of the 20th century. He drew attention to the contradiction between the idea of the prehistoric landscape of Central Europe as a more or less continuous primeval forest and the findings of the archaeology and biogeography of the time. He presented his null hypothesis – the primeval forest – as follows (Gradmann 1901): *...what would the landscape*

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[36] Orig.: *První zemědělci začali osidlovat světlé smíšené doubravy na sprašových podkladech v nejnižších polohách, kde klučili uvnitř lesních komplexů nevelká prostranství pro neolitické osady a jejich hospodářské zázemí.* […] *Z palynologických výzkumů vyplývá, že neolitický zemědělec alespoň zpočátku na našem území narušoval přirozenou klimaxovou vegetaci jen nepatrně.* […] *Celkové prosvětlení krajiny způsobovalo i změny mezoklimatické, mj. i vysušení, a otevřely se možnosti pro druhotnou migraci světlomilných, často xerotermních rostlin z dřívějších ojedinělých extrémních stanovišť. V důsledku toho docházelo v teplých oblastech ke xerofytizaci vegetace a vzniku druhotných xerotermních porostů, které bývají mylně označovány jako stepní relikty.*

of Central Europe look like today if man had never intervened in its development? And there we have the picture of a coherent primeval forest stretching from the Alps to the North and Baltic Seas, from the Atlantic coast to the pustas of Hungary and the steppes of southern Russia, and continuing further north into the Siberian forest belt. Only a few gaps break through this primeval forest. There are the peaks of the Alps and the Carpathians as well as the more significant elevations of a few low mountain ranges, the Sudetes, the Harz, the Black Forest, the Vosges, the Swiss Jura, which rise bare-headed from the sea of forests. There are also the dunes and heaths, the salt marshes and moors of the North Sea coast, in the interior a few freshwater pools and larger moorland areas, otherwise only small gaps in rocky precipices and scree slopes, as well as the temporary gaps created by lightning, wind or snow damage, only to grow over again after a short time. Only on sunny steep slopes and, in very dry conditions, on flat terrain, such as the heaths of southern Bavaria (Garchinger Heide, Lechfeld) or certain limestone and loess hills of Central Germany, is it necessary to think of the tree growth as somewhat sparse; otherwise it is dense, closed primeval forest everywhere.[37] However, Gradmann does not accept this colourful picture and confronts it with contemporary archaeological knowledge about prehistoric human settlement: *All the landscapes that were settled in late Germanic* [i.e. Roman] *times were also inhabited in the Younger Stone Age, even if they were probably less densely populated. Even the Stone Age people were not forest dwellers or mere hunters or gatherers; as is known from the pile dwellings, they owned cattle, sheep and pigs, grew wheat, millet, barley and flax and must therefore already have had arable and pasture land at their disposal. One cannot avoid the conclusion: if the old cultivated areas of Central Europe, as they still served as the only and exclusive sites of settlement at the beginning of our era, were created, artificially deforested, by man at all, then this work could only have been accomplished by Neolithic man.*[38] However, he was not finished with this uncompromising reasoning, and as a botanist he combined it with his knowledge of the occurrence of steppe flora and fauna in Central Europe: *The only remaining assumption is* […] *that the first settlers in Central Europe found certain areas already free of forests.* […] *If one now compiles the old steppe districts of Central Europe on the basis of the characteristics given, one arrives at the certainly surprising result that those inland are identical, as far as the topography can be traced*

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[37] Orig. *...welchen Anblick würde die mitteleuropäische Landschaft heute darbieten, wenn nie der Mensch störend in ihre Entwicklung ein gegriffen hätte? Und da erhalten wir nun thatsächlich das Bild eines zusammenhängenden Urwalds, der sich von den Alpen bis zur Nord- und Ostsee, von der atlantischen Küste bis zu den Pussten Ungarns und den Steppen Südrusslands erstreckt und sich weiter im Norden in den sibirischen Waldgürtel fortsetzt. Nur von wenigen Lücken ist dieser Urwald durchbrochen. Da sind die Gipfel der Alpen und Karpaten sowie die bedeutenderen Erhebungen einiger weniger Mittelgebirge, der Sudeten, des Harzes, des Schwarzwalds, des Wasgenwalds, des Schweizer Jura, die kahlen Hauptes aus dem Wäldermeer emportauchen. Da sind ferner die Dünen und Heiden, die Salzwiesen und Moore des Nordseestrands, im Innern einige Süsswasserbecken und grössere Moorflächen; sonst bloss noch kleinere Lücken an Felsabstürzen und Geröllhalden, sowie die vorübergehenden Blössen, wie sie etwa durch den zündenden Blitzstrahl, durch Wind- oder Schneebruch entstehen, um nach kurzer Zeit wieder zu überwachsen. Nur an sonnigen Steilhängen und vielleicht bei sehr grosser Trockenheit auch auf ebenem Gelände, wie etwa den Heiden Südbayerns (Garchinger Heide, Lechfeld) oder gewissen Kalk- und Lösshügeln Mitteldeutschlands hat man sich den Baumwuchs etwas lichter zu denken, sonst überall dichten, geschlossenen Urwald.*

[38] Orig.: *Alle die Landschaften, die man in spätgermanischer Zeit besiedelt findet, waren auch zur jüngeren Steinzeit schon bewohnt, wenn auch wahrscheinlich weniger dicht. Und zwar sind schon die Steinzeitmenschen keine Waldmenschen, keine blossen Jäger oder Sammler gewesen; sie befassen, wie aus den Pfahlbaufunden bekannt ist, Rinder, Schafe und Schweine, bauten Weizen, Hirse, Gerste und Lein und müssen demnach auch schon über Acker- und Weideland verfügt haben. Man kann dem Schluss nicht ausweichen: sind die alten Kulturflächen Mitteleuropas, wie sie noch am Beginn unsrer Zeitrechnung als einzige und ausschliessliche Stätten der Besiedelung gedient haben, überhaupt vom Menschen geschaffen, künstlich entwaldet worden, so kann dies Werk nur der neolithische Mensch vollbracht haben.*

at all yet, with the sites of ancient settlement already known to us. Such steppe districts are, for example, in the North German lowlands the large diluvial river terraces, especially the lowlands of the Elbe and the Saale, the eastern edge of the Harz, in Southern Germany the Upper Rhine lowland, the lower Alpine foothills from Switzerland to Lower Austria, furthermore the high plains of the Swabian and Franconian Alb, the lowlands of the Main and Neckar regions, northern Bohemia.[39] The synthesis of these findings led him to the following conclusion, which he considered inevitable: *If an explanation is to be given that does justice to all the facts listed, it can only be as follows: the first population of Central Europe settled there at a time when the old steppe districts were still at least very sparsely wooded; they soon occupied these districts so densely that even under the climate, which later became more humid again, the forest growth there could never get out of hand, while the actual wooded areas remained uninhabited from the beginning. As each successive population took care of the non-forest areas and settled them alone, it was possible that the features of the old diluvial steppe landscape were preserved until the beginning of the Middle Ages, even under the later decisively forest climate. The pre-Roman inhabitants of Central Europe were not able to clear large areas of primeval forest, but they were able to permanently prevent the encroachment of forest growth on their pasture and arable land. As the present day shows, regular grazing on the land is enough to do this.*[40]

As can be seen, Gradmann thought about the landscape and the relationship between forest and open landscape in a quite modern way: he combined the findings of several disciplines, accounted for the dynamics of vegetation on different time scales and sought possible processes behind the observed phenomena. Some of his ideas, of course, need to be corrected at the current level of knowledge – first and foremost, that the Neolithic people inhabited Central Europe in a period of dry climate that kept the landscape open. We now know that this was at the beginning of the Middle Holocene, a relatively humid period when the expansion of mesophilous shady forests was taking place after the end of the drier and thermally more continental Early Holocene.

Gradmann's *Steppenheidetheorie*,[41] as the concept came to be called, was rejected by the German palaeobotanist **Karl Bertsch** (1878–1965) for this reason as well. His critique, based on a

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[39] Orig.: *Es bleibt nur die Annahme übrig,* […] *dass nämlich schon die ersten Besiedler Mitteleuropas bestimmte Gebiete bereits in waldfreiem Zustande vorgefunden haben.* […] *Stellt man nun auf Grund der angegebenen Merkmale die alten Steppenbezirke Mitteleuropas zusammen, so gelangt man zu dem gewiss überraschenden Ergebnis, dass diese im Binnenlande, soweit sich die Topographie überhaupt bis jetzt verfolgen lässt, mit den uns bereits bekannten Stätten uralter Besiedlung identisch sind. Solche Steppenbezirke sind z. B. im norddeutschen Tiefland die grossen diluvialen Stromterrassen, besonders die Niederungen der Elbe und der Saale, der Ostrand des Harzes, in Süddeutschland die oberrheinische Tiefebene, das untere Alpenvorland von der Schweiz bis nach Niederösterreich, ferner die Hochflächen der schwäbischen und fränkischen Alb, die Niederungen des Main- und Neckargebietes, das nördliche Böhmen.*

[40] Orig.: *Soll eine Erklärung gegeben werden, die allen den aufgezählten Thatsachen gerecht wird, so kann diese wohl nur so lauten: die erste Bevölkerung Mitteleuropas hat sich daselbst niedergelassen zu einer Zeit, als die alten Steppenbezirke mindestens noch sehr waldarm waren; sie hat diese Bezirke bald so dicht besetzt, dass auch unter dem später wieder feuchter werdenden Klima der Waldwuchs daselbst niemals überhandnehmen konnte, während die eigentlichen Waldgebiete von Anfang an unbewohnt blieben. Indem jede nachfolgende Bevölkerung sich der waldfreien Bezirke bemächtigte und sie allein besiedelte, konnte es geschehen, dass die Züge der alten Diluvialsteppenlandschaft auch unter dem späteren entschiedenen Waldklima bis zum Beginn des Mittelalters erhalten blieben. Die vorrömischen Bewohner Mitteleuropas waren zwar nicht im Stande, grosse Flächen Urwaldes zu roden, wohl aber konnten sie da, wo sie dem Waldwuchse gleichsam noch zuvorgekommen waren, dessen Eindringen in ihr Weide- und Ackerland dauernd verhindern. Wie der Augenschein noch in der Gegenwart lehrt, genügt dazu schon ein regelmässiges Beweiden des Landes.*

[41] Gradmann referred to the *Steppenheide* as a formation of dry grasslands and related non-forest habitats where, in his opinion, relict steppe elements were preserved (Gradmann 1898). The term *Steppenheidetheorie*, however, was not introduced by him (Gradmann 1933).

synthesis of pyloanalytical data from a number of Central European profiles (Bertsch 1928), was later often adopted (e.g. Tüxen 1931, https://de.wikipedia.org/wiki/Steppenheidetheorie). It is worth noting that in his critical study Bertsch quotes a long passage from the work of the aforementioned K. Rudolph, who in contrast was able to reconcile Gradmann's theory with the new findings (Rudolph 1928): *Also here the explanation already given for the colonisation of the steppe plants seems more probable to me, that the Neolithics also moved in before the final closure of the natural forest cover of Bohemia, not in a later steppe period* [i.e. the Subboreal, the early phase of the Late Holocene], *that he still found remnants of the indigenous forest-steppe in the dry and warm lowlands, which we can still consider quite probable for the hazel and mixed oak forest period* [i.e. the Middle Holocene]. *He was able to use them for his settlement without clearing and could, just in the spirit of Gradmann, have kept them free of forest through cultivation (grazing, etc.) even into the beech-fir period* [i.e. the Late Holocene]. *Gradmann's theory is thus only shifted to a certain extent without being affected in its basic features. It was not a steppe period that was inserted into the forest period, but the gradual transition from the steppe to the forest period that gave rise to the original settlement land.*[42] Rudolph's variation on Gradmann's theme is thus already close to some contemporary views (Chapter 4.2). Let us note as a sidelight that Bertsch omitted two places in his quotation where Rudolph explicitly subscribed to Gradmann.

Another influential critic of Gradmann's view of the origin of the Central European steppes was the eminent German phytosociologist **Reinhold Tüxen** (1899–1980). His polemic was multifaceted and in the field of palaeoecology was based on the opinions of Bertsch (Tüxen 1931). From our point of view, it is important that Tüxen contributed significantly not only to the rejection of *Steppenheidetheorie*, but also to a large extent to the setting of the debate on the appearance of past vegetation and landscape, as well as to views on what relevant answers might look like. Gradmann was an empiricist and his reconstruction sought to explain the observed patterns (particularly the spatial relationship between the occurrence of steppe plants and prehistoric settlement) as simply and consistently as possible. We have already seen a similar approach to palaeoecological reconstruction in the works of Sillinger, Podpěra and Szafer (Chapters 2.6.1 and 2.6.2); later a similar approach was taken e.g. by Ložek (1992). Tüxen, on the other hand, proposes that the starting point of the reconstruction should be a model of vegetation in a "primeval landscape" (*Urlandschaft*), developed on the basis of the known relationship of vegetation to key environmental factors (in particular climate, soil and relief), modified by the knowledge of pollen analysis about past vegetation composition. As Gradmann (1933) immediately recognized, Tüxen's seemingly more exact approach is in fact highly theoretical and places great emphasis on more advanced successional stages in reconstructing past vegetation. Disturbances are of secondary importance in this worldview, the forest naturally prevails over the steppe. Similar

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[42] Orig.: *Auch hier scheint mir die bereits für die Ansiedlung der Steppenpflanzen gegebene Erklärung wahrscheinlicher, dass auch der Neolithiker noch vor dem endgültigen Zusammenschluss der natürlichen Walddecke Böhmens eingezogen ist, nicht erst in einer späteren Steppenzeit, dass er in den trockenwarmen Niederungen noch Reste der ursprünglichen Waldsteppe vorfand, die wir für die Hasel- und die Eichenmischwaldzeit noch für durchaus wahrscheinlich halten können. Er kam eben noch zurecht, sie für seine Ansiedlung ohne Rodung auszunützen und hätte sie dann, ganz im Sinne Gradmanns, durch Kultur (Weide usw.) waldfrei erhalten auch in die Buchen-Tannenzeit hinein. Die Gradmannsche Theorie erfährt dadurch nur eine gewisse Verschiebung, ohne in ihren Grundzügen berührt zu werden. Nicht eine in die Waldzeit hineingeschobene Steppenzeit, sondern der allmähliche Übergang von der Steppe in die Waldzeit hat das ursprüngliche Siedlungsland gegeben.*

features can be found in the considerations of Klika and Moravec (Chapter 2.6.1). We may speculate that the concept of potential natural vegetation developed by Tüxen and later widely applied (Tüxen 1956, Bohn & Neuhäusl 2004), which was based on similar assumptions as his critique of *Steppenheidetheorie*, contributed significantly to the understanding of Central European xerothermic vegetation as secondary and fundamentally different from steppe. While the concept itself is a useful abstraction (Somodi et al. 2021), it can only be used in reconstructing past landscapes if its limitations and assumptions are considered.

Among the advocates of the hypothesis of the natural character of Central European dry grasslands and their understanding as a part of steppe vegetation was the already mentioned H. Meusel. He wrote the following about the origin of these communities (Meusel 1940): *The spread of grassland flora under the influence of man, the development of various types of semi-artificial dry grasslands during forest clearing and grazing, of sparse bushy woodland in the case of coppice and coppice-with-standards forestry, has often led to the view that all grassland vegetation in Central Europe is not indigenous. Thus, today sociologists describe almost all dry grasslands in our territory as semi-artificial formations. It must be pointed out, however, that in most districts of Central Europe the spatially much more extensive semi-artificial grasslands can be traced back to natural communities in the area of original forest clearings. In this case, human culture has mostly only changed the extent of the vegetation, it has not created new plant communities.*[43] Meusel therefore did not consider indigeneity at the level of a particular stand or landscape, but at the level of an abstract vegetation type – a community. He was also aware that the use of different criteria for defining steppe by different authors may be a source of misunderstanding. He himself advocated a definition based primarily on species composition: *While the so-called "true steppes" colonize deep chernozems, in the formation of which the vegetation plays a major role, in the area of the hill steppe one usually finds only undeveloped slope soil. But this is no reason to separate* [these] *floristically closely related phenomena. Here, too, it must be acknowledged that each vegetation type has a certain range of adaptation, that the individual environmental factors may replace each other in their effect in a certain way, and that a classification* [of steppes] *based primarily on environmental factors can therefore lead to quite unnatural results.*[44] According to Meusel, an indigenous community is one that is close in species composition to its natural precursor and at the same time has sufficient developmental continuity with it.

Many other Central European botanists have contributed significantly to the discussion of the steppe question (e.g. Soó 1929, Podpěra 1930, Zólyomi 1953, Wendelberger 1954); however,

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[43] Orig.: *Die vielfach zu beobachtende Ausbreitung der Grasheideflora unter dem Einfluss des Menschen, die Entwicklung von verschiedenartigen halbkünstlichen Trockenrasen bei Waldrodung und Beweidung, von lichten buschartigen Gehölzen bei Nieder- und Mittelwaldwirtschaft hat vielfach zu der Ansicht geführt, dass in Mitteleuropa die gesamte Grasheidevegetation nicht ursprünglich sei. So werden heute von den Soziologen fast alle Trockenrasen unseres Gebietes als halbkünstliche Bildungen bezeichnet. Es muss jedoch darauf hingewiesen werden, dass in den meisten Bezirken Mitteleuropas die räumlich zwar vielfach ausgedehnteren, halbkünstlichen Grasfluren auf natürliche Gesellschaften im Bereich ursprünglicher Waldlichtungen zurückzuführen sind. Die menschliche Kultur hat in diesem Fall die Vegetation meist nur in ihrer Ausdehnung verändert, nicht hat sie haben neue Pflanzenvereine geschaffen.*

[44] Orig.: *Während die sog. "echten Steppen" auf tiefgründiger Schwarzerde siedeln, an deren Zustandekommen die Vegetation wesentlich mit beteiligt ist, findet man im Bereich der Hügelsteppe meist nur unentwickelte Hangböden. Doch das ist durchaus kein Grund, floristisch nächst verwandten Erscheinungen zu trennen. Man wird auch hier erkennen müssen, dass jeder Vegetationstyp eine bestimmte Anpassungsbreite hat, dass sich die einzelnen Umweltfaktoren in bestimmter Art gegenseitig in ihrer Wirkung ersetzen können und demnach eine vorzüglich von der Umweltfaktoren geleitete Gliederung zu recht unnatürlichen Ergebnissen führen kann.*

the above fragment perhaps sufficiently illustrates the importance of this question and the controversy it has generated.

4.2. Modern discourse of the steppe question in Central Europe

If the relative proportion of forested and open landscape in the Middle Holocene was critical for the survival of the Central European steppe biota until the present day, palaeoecological reconstructions should provide crucial data for answering the steppe question. We have already seen that two of the leading representatives of Central European palaeobotany in the second half of the 20th century, **Eliška Rybníčková and Kamil Rybníček** (1932–2015 and 1933–2014, respectively), concluded, based on a lifelong experience, that there was a discontinuity between the steppe vegetation of the Early Holocene and the modern dry grasslands, filled by mixed oak forests (Rybníčková & Rybníček 1998). In the context of all that has been discussed above, it is hardly surprising that there was no consensus on such a view even in the Czech environment. Palaeoecologist and malacologist **Vojen Ložek** (1925–2020) outlined his view in a fundamental handbook on the Czech flora as follows (Ložek 1997): *Based on palaeoecological investigations in correlation with the development of biocenoses, it is clear that the preservation of chernozem districts up to the present time has been largely conditioned by human impact, which already in deep prehistory halted the spread of forest and kept some areas open. The existence of a number of true steppe elements in these areas is also related to this...*[45] He later elaborated his thoughts on the subject extensively (Ložek 2004).

Have we made any progress since then? Does Central European palaeoecology have a clearer answer to the steppe question today? The discussion, so far rather academic, has been significantly advanced by the book *Grazing ecology and forest history* of the Dutch ecologist **Frans Vera** (Vera 2000), whose main concern was to appreciate the influence of wild large herbivores on Holocene forest and open landscape dynamics in Western and Central Europe. However, his **wood-pasture hypothesis** has appealed to a wide professional audience, probably also due to its emphasis on the consequences of forest versus non-forest development for biodiversity and conservation. Although Vera's theses have not been unequivocally accepted in palaeoecology (e.g. Birks 2005, Mitchell 2005, Soepboer & Lotter 2009, Whitehouse & Smith 2010, Sandom et al. 2014a), grazing by wild large herbivores is now considered one of the main mechanisms that may have maintained landscapes in pre-agricultural times open. Thus, reference to Vera's work can be found in almost every new paper dealing with the Holocene continuity of open landscapes in Central Europe. Perhaps influenced by these discussions, the steppe question has been asked by a number of Central European palaeoecologists in the past decade, and a series of modern multi-proxy palaeoecological studies situated in important Central European forest-steppe regions (Fig. 30) have emerged.

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[45] Orig.: *Z paleopedologických výzkumů v korelaci s vývojem biocenóz je zřejmé, že uchování černozemních okrsků až do současné doby bylo do značné míry podmíněno lidským zásahem, který již v hlubokém pravěku zastavil šíření lesa a udržel některé oblasti volné. S tím souvisí i existence řady pravých stepních prvků v těchto územích…*

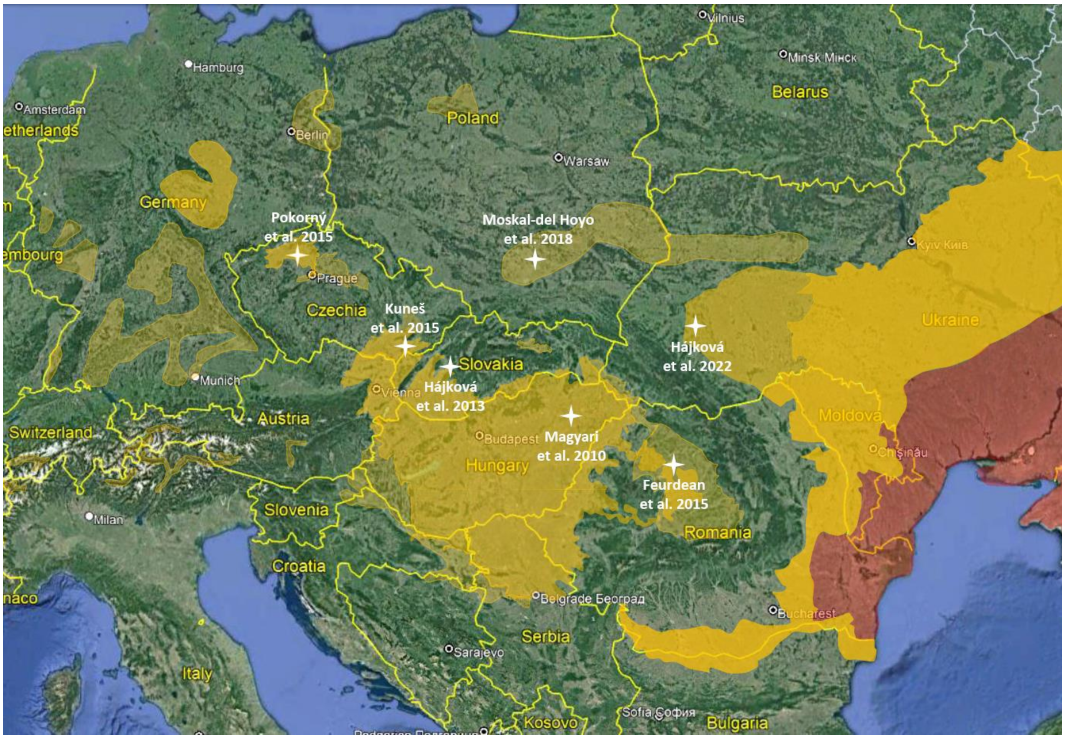

Fig. 30. Sites of modern multi-proxy palaeoecological studies discussed in the text (white asterisk), the results of which support the hypothesis of Holocene continuity of non-forest habitats in important Central European forest-steppe regions (orange). The three levels of orange saturation roughly reflect the abundance of continental steppe elements. The steppe zone of Eastern Europe is marked in red. The delineation of the regions is simplified and based on a compilation of various sources (Braun-Blanquet 1961, Šmarda 1961, Skalický 1988, Molnár & Kun 2000, Bohn & Neuhäusl 2004, Chytrý 2012, Petrov & Terekhina 2013, Fekete et al. 2016, Kajtoch et al. 2016; https://atlas-roslin.pl, https://geomap.land.kiev.ua, http://wdc.org.ua/atlas, https://www.floraweb.de/webkarten). Map background taken from GoogleEarth.

The first of these focused on the postglacial vegetation development of the **Great Danube Plain** in Hungary, a region of the renowned pustas with diverse steppe vegetation (Magyari et al. 2010). According to the authors, the results of fossil pollen and microcharcoal analyses support the hypothesis of the survival of a forest-steppe mosaic in this region throughout the Holocene. However, the authors highlighted the importance of unfavourable (e.g. saline) habitats for the preservation of non-forest vegetation and considered the deforestation of formerly forested areas by Neolithic farmers, so their idea of continuity is not too far from what, for example, the Rybníčeks considered discontinuity. On the other hand, the authors highlighted the role of fires, which they regarded as an important natural factor maintaining open habitats, especially during the Early Holocene. Their microcharcoal data indicate increased fire activity from the beginning of the Holocene until about 6000 cal BP, i.e. well into the Neolithic.

A study dealing with Holocene continuity of open landscape was soon carried out also on the northern margin of the **Little Danube Plain** in Slovakia (Hájková et al. 2013). It was based on analyses of fossil pollen and non-pollen palynomorphs (e.g. fungal spores), microcharcoal, plant macrofossils and mollusc shells. The authors concluded that vegetation in the Middle Holocene was predominantly composed of open-canopy forests, with dry climate, edaphic factors (soil, nutrient availability, relief), disturbance by wild herbivores, natural fires and human activities since the Mesolithic contributing to their open character. They based their interpretations on the abundance of microcharcoal (especially during the Early Holocene and from the Iron Age onwards) and the presence of spores of coprophilous fungi. They assumed the survival of steppe vegetation mainly on loess loams on the slopes above the Upper Nitra valley and evidenced it with continuous curves of open landscape pollen types and the regular presence of steppe and semi-dry grassland indicators (e.g. *Artemisia*, *Chenopodiaceae*, *Centaurea scabiosa* type, *Plantago media*/*major*). Bottlenecks for the survival of light-demanding species were identified around 7500 and 3700 cal BP.

In the **Transylvanian Basin** in Romania, a similar study was carried out a few years later (Feurdean et al. 2015). The authors analysed a similarly broad range of proxies, including fossil pollen and non-pollen palynomorphs, plant macro- and microcharcoal, and archaeological data on prehistoric settlement. They concluded that until about 5700 cal BP the area was dominated by extensive forests. However, these were not completely closed due to drought, repeated fires and human influence, so they did not hinder the survival of species-rich grasslands throughout the Holocene. Using the REVEALS modelling technique (Sugita 2007), the authors estimated the proportion of non-forest habitats in the critical period of the Middle Holocene to be about 35%. They also mentioned the possible influence of large herbivores on vegetation, noting that the abundance of spores of coprophilous fungi, which may indicate their activity, is low in the analysed record (except perhaps the Late Holocene).

In the same year, a study from the opposite edge of the Pannonian Basin system, the **Vienna Basin** in southern Moravia, was published (Kuneš et al. 2015). In addition to fossil pollen and non-pollen palynomorphs, the authors analysed detailed archaeological data and, as in the previous study, used the REVEALS model to reconstruct the representation of forest and non-forest habitats. They concluded that their results indicate Holocene continuity of open habitats in the landscape. According to them, grasslands and open-canopy forests were supported by a dry climate that hindered the spread of deciduous forests. Because clear evidence of human activity in the fossil record was not identified until about 4000 cal BP, the authors concluded that Neolithic farmers (who appeared in the area about 7500 cal BP) colonised the open habitats surviving from the Early Holocene and so their activities did not significantly alter the landscape. The low abundance of coprophilous fungal spores was interpreted as evidence that large herbivores did not play a major role here, as in Transylvania. However, regarding the assumed climatic limitation of the local ecosystems, we have to mention that the authors worked with the MCM climate model (Bryson & Bryson 1997), which reconstructed a dry climate for the Middle Holocene. However, more recent models (e.g. Divíšek 2021, Arthur et al. 2023), as well as the geographically closest modern climate reconstruction based on proxy data (Dabkowski et al. 2019), show the Middle Holocene as relatively humid.

The steppe question was obviously resonating in palaeoecological circles at that time, as in the same year another similar study was published, this time from a **forest-steppe island in**

northwestern Bohemia (Pokorný et al. 2015). It was based on analyses of fossil pollen, microcharcoal and mollusc shells. The authors concluded that although forest spread was the dominant ecological process in the Middle Holocene, their data demonstrate the continuous occurrence of steppe grasslands. They suggested that at the time of the onset of Neolithic agriculture, the study area was covered by a forest-steppe with open-canopy birch-pine forests analogous to the present-day forest-steppe landscapes of southwestern Siberia. In their opinion, the decline of light-demanding species with the expansion of mesophilous tree species was prevented by deforestation and cattle grazing by Neolithic farmers, who created a semi-natural steppe that was a direct continuation of the Late Pleistocene and Early Holocene natural steppe. They explicitly supported the central thesis of Gradmann's *Steppenheidetheorie* that Neolithic agriculture first appeared in Central Europe in those areas that were not completely forested and contained remnants of natural steppe.

The question of the appearance of the landscape in the early days of agriculture has also been addressed by a series of papers from the **chernozem region of southeastern Poland** (Moskal-del Hoyo et al. 2017, 2018, Moskal-del Hoyo 2021), an area that is known for the occurrence of some characteristic forest-steppe species. Due to the origin of most of the analysed material (plant macrofossils, macrocharcoal, mollusc shells, to a lesser extent osteological material and fossil pollen) from archaeological contexts, the results are only partly indicative of the landscape appearance before the onset of human settlement. Nevertheless, the authors conclude that the dominant vegetation at the beginning of the Neolithic (the younger half of the 8th millennium BP) was open-canopy oak and oak-pine forests, perhaps with islands of persisting steppe vegetation. The occurrence of steppes is evidenced by feather grass caryopses and awns and the shells of steppe snails. However, the authors' conclusions regarding the Holocene continuity of non-forest habitats are somewhat more reserved than in the above studies.

From the adjacent forest-steppe region of the **Ukrainian Western Podillia**, we brought the latest contribution to the discussion of the steppe question in a study focused on the origin of peri-Carpathian forest-steppe meadows (Hájková et al. 2022). We analysed a wide range of proxies, including fossil pollen, plant macrofossils, mollusk shells, macro- and microcharcoal, elemental composition of fen sediments and archaeological data on prehistoric settlement. We concluded that all the studied proxies support the hypothesis of the persistence of an open or semi-open landscape in the Western Podillia throughout the Holocene. The characteristic features of the studied sediments included the complete absence of wood remains, the continuous occurrence of light-demanding fen specialists, the continuous presence of pollen of light-demanding herbs (albeit in relatively small quantities), the marked predominance of pollen of light-demanding tree species over shade-tolerant ones (Fig. 31) and the stable concentration of geochemical indicators of erosion. The continuous presence of great amount of herbaceous microcharcoal suggests the importance of fires in maintaining open habitats, and archaeological data provide evidence of human presence in the vicinity of the study sites throughout the Holocene. Comparison with modern pollen spectra also suggested that the landscape was probably more forested in the past than today, but rather with light-demanding tree species.

It is clear from the above that palaeoecologists in the last two decades have been inclined towards the idea of Holocene continuity of non-forest habitats in Central Europe. In addition to the new data and results brought about by the use of modern methods, the ambition to reconcile palaeoecological interpretations with the observed patterns of biodiversity also seems to have guided them. That is the empirical approach that we have already pointed out by Sillinger (Chapter 2.6.1) and Gradmann (Chapter 4.1). From a logical point of view, such reasoning may appear problematic (Hempel & Oppenheim 1948): the high diversity of non-forest species (*explanandum*) that we have tried to explain by the hypothesis of Holocene continuity of open landscapes (*explanans*) turns here into an argument that we use to support the hypothesis itself. To avoid falling into the trap of the logical circle, we can no longer explain diversity by continuity... Personally, however, I believe that the logic of palaeoecological reconstruction is different: above all, the proposed model of past development must be consistent with as many pieces of evidence as possible while minimizing the complexity of the model itself. The idea of discontinuity seems to fall short in this respect, and at the same time there is no reason to consider it a less complex (parsimonious) model.

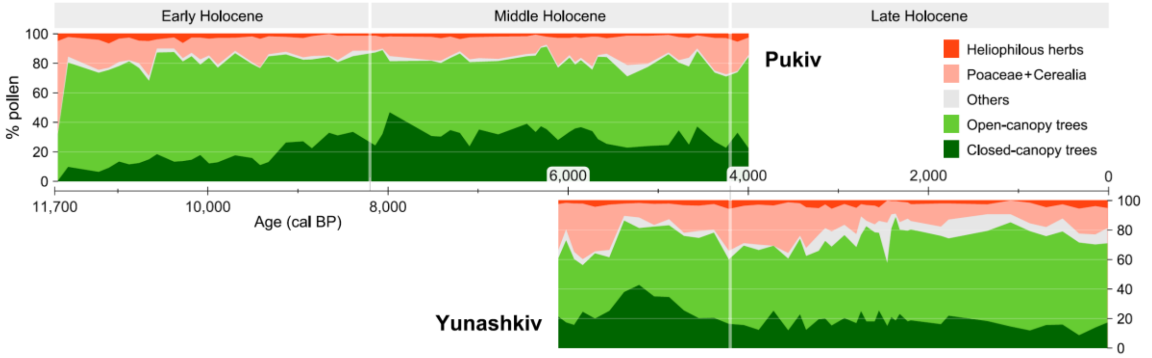

Fig. 31. Summary pollen diagrams of profiles from the forest-steppe region of Western Podillia, Ukraine, analysed in our research (Hájková et al. 2022). The diagrams illustrate significant representation of light-demanding herbs, grasses and trees of open-canopy forests throughout the Holocene. In the vicinity of the analysed profiles (Pukiv and Yunashkiv sites) there are vegetation complexes including species-rich peri-Carpathian forest-steppe meadows.

In addition, the alternative hypothesis of continuity also receives support from studies using other methods. In particular, the results of genetic analyses of steppe species are consistent with the idea of their Holocene persistence in Central Europe (Cieślak 2014, Kajtoch et al. 2016, Kirschner et al. 2020, Willner et al. 2021). Also, reconstructions of Holocene dynamics of plant diversity based on the synthesis of large amounts of palynological data show that the increase in diversity associated with the emergence of cultural landscapes during the Middle Holocene was not preceded in forest-steppe regions by a general decline in diversity caused by forest expansion (Roleček et al. 2021a) – in contrast to, for example, northern Europe (Giesecke et al. 2019). In another synthetic study, Jamrichová et al. (2017) found that in the critical period before the beginning of the Neolithic (8500–7500 cal BP), pollen spectra in Central Europe showed a large variation in the abundance of pollen types characteristic of forest versus non-forest habitats. The non-forest indicators were most abundant in the forest-steppe regions on the periphery of the Carpathians and in the continental Spiš Basin in Slovakia, where steppe species and other relict light-demanding elements are significantly represented today (Šmarda 1961, Hájková et al. 2015). A follow-up study (Divíšek et al. 2020) then compared these pollen data with data on the species richness of recent vegetation and showed that differences in vegetation development during the Middle Holocene significantly contribute to explaining the current regional differences in species richness of dry grasslands and open-canopy forests. Thus, the reconstructed continuity of open landscapes may also serve as an explanatory variable in the studies of biodiversity patterns at biogeographical scale.

I believe that it will not do any harm to finally relativize this inevitably subjective overview of arguments with an excerpt from the book *Landscape and Revolution*, which is a fount of original reflections on the Holocene development of the Central European landscape (Sádlo et al. 2005): *It is obvious that the correct interpretation of the landscape's past lies somewhere between the idea of a vast steppe and a dark forest. This ambiguity leads to the extension of the steppe question to other habitat types assumed to be relict – the "steppe question" is also a question of salt marshes, fens, sands, alpine zone. There is an increased understanding of the importance of the reading frame (over how large an area and for how long it took place?), local differences (what applies to Lower Backwoods may not be relevant in Upper Backwoods) and how important is the way questions are asked. The steppe question evolves through its many reformulations. It has become a tree on which the scientific community sharpens its claws. Its purpose is not to ask about a problem and solve it, but to keep asking about it and solving it.*[46]

4.3. The origin of peri-Carpathian forest-steppe meadows

Even if we accept the Holocene continuity of non-forest habitats in the forest-steppe regions of Central Europe, this does not fully explain the origin of the peri-Carpathian forest-steppe meadows. Why? Primarily because of the strong affinity of this vegetation to climatically relatively humid regions (Chapter 2.2), which were historically more prone to the spread of closed forests; and in drier regions, where the climate favoured the survival of steppe grasslands on sunny slopes, because of the link of forest-steppe meadows to mesic habitats (northern slopes, foothills; Chapter 2.2), which also were prone to encroachment by woody plants. Thus, although we find evidence of continuity of the non-forest habitats in the palaeoecological record, it is uncertain whether the peri-Carpathian forest-steppe meadows, or their contemporary precursors, were part of these. Their sites could simply have been occupied by forests even in diverse forest-steppe mosaics. To reconstruct their development, we therefore need to descend from the landscape to the local level.

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[46] Orig.: *Zřejmé je, že správná výpověď o minulosti krajiny leží kdesi mezi představou širé stepi a temného lesa. Tato nejednoznačnost vede k rozšíření stepní otázky i na jiné typy stanovišť s předpokladem reliktnosti – „stepní otázka" je také otázkou slanisk, slatin, písčin, alpinského pásma. Vzrostlo porozumění tomu, jak důležitý je při hledání odpovědi čtecí rámec (na jak velkých plochách a jak dlouho se to odehrávalo?), lokální rozdíly (to, co platí pro Dolní Lhotu, nemusí mít v Horní Lhotě význam) a jak důležitý je způsob kladení otázek. Stepní otázka se vyvíjí svými četnými reformulacemi. Stala se stromem, na němž si vědecká obec brousí drápy. Jejím smyslem není zeptat se na problém a vyřešit jej, ale ptát se po něm a řešit jej.*

Here, however, we encounter the problem of the limited availability of palaeoecological data and sources of such data, because stratified sediments, suitable, for example, for the analysis of fossil pollen or mollusc shells, are far from being available at every site. Thus, unless we are extremely lucky, we must be content with less representative palaeoecological data in reconstructing the Holocene development, or use other possible sources of information on the history of these sites and ecosystems. In our research, we focused on three regions rich in peri-Carpathian forest-steppe meadows, which we identified above as hotspots of extreme species richness (Chapter 3.1) and for which we also have at least partial palaeoecological data: the White Carpathians in the Czech Republic, the wider surroundings of the Fânațele Clujului site in Romanian Transylvania and the wider surroundings of the Dzyurkach and Kasova hora sites in western Ukraine. What is their Holocene history?

4.3.1. White Carpathians

In the White Carpathians, the first attempt to reconstruct the history of forest-steppe meadows using palaeoecological methods was made by the aforementioned V. Ložek. He summarised his view in the monograph *Protected Landscape Area Biele/Bílé Karpaty* as follows (Ložek 1992): *Special mention should be made of the steppe meadows and pastures in the southwestern part of the mountains on the Moravian side, known for the richness of steppe elements growing also on deeper soils. These communities probably have a direct link to the chernozem steppes of the Early Holocene, the afforestation of which was prevented by the arrival of Neolithic farmers and pastoralists.* [...] *However, the herb-rich meadows of the higher elevations were mostly created in the Middle Ages, although some may be older, as suggested by findings from other parts of the Carpathians.*[47] Ložek therefore understood the local forest-steppe meadows as relict, but he thought of them in a differentiated way and considered humans as the main driver of the Holocene dynamics of forest and open habitats in the region. He based his conclusions mainly on the results of analyses of mollusc shells in the calcareous tufa sediments, which he later summarized in his book *The mirror of the past* (Ložek 2007). There he also mentioned the possible influence of large herbivores: *Since there are no habitats inaccessible to the forest, it must be assumed that these* [open] *areas were maintained by selective grazing, in earlier times by wild, later by domesticated large herbivores.*[48]

Palaeoecological research of tufa-forming springs in this area was also carried out by other authors. Horsák & Hájková (2005) did not comment on the origin of the local forest-steppe meadows, as they had only a single young profile from the area of their occurrence. They then summarized the results of the analyses of macrofossils aimed at reconstructing the history of the springs as follows: *As documented by both palaeomalacological and palaeobotanical results, the*

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[47] Orig.: *Zvláštní zmínku zasluhují stepní louky a pastviny v jihozápadní části pohoří na moravské straně, známé bohatstvím stepních prvků rostoucích i na hlubších půdách. Tato společenstva mají patrně přímou návaznost na černozemní stepi staršího holocénu, jejichž zalesnění zabránil příchod neolitických rolníků a pastevců.* […] *Květnaté louky vyšších poloh však vznikly většinou až ve středověku, i když některé mohou být staršího data, jak nasvědčují nálezy z jiných částí Karpat.*

[48] Orig.: *Vzhledem k tomu, že zde nejsou stanoviště nepřístupná lesu, nutno předpokládat, že tyto* [otevřené] *plošky byly udržovány selektivní pastvou, ve starších dobách divokých, později pak domestikovaných velkých býložravců.*

open meadow state of the studied habitats is quite young. It is the result of human activities, mainly extensive deforestation during the largest Wallachian colonisation (in progress 700–600 years ago). We are convinced that also the majority of other similar habitats and their unique communities are artificial in the region. The Rybníčeks went further in their conclusions and interpreted the entire pre-medieval landscape of the White Carpathians as forested one. They associated the appearance of non-forest habitats with medieval colonisation, in contrast to the adjacent lowlands (Rybníček & Rybníčková 2008): *Although* […] *archaeologists have documented the continuous prehistoric settlement along the river Váh (Slovakia) and along the valley of the river Morava (Moravia—Czech Republic), the colonisation of the foothills and valleys of the Bílé Karpaty on both sides of the borderland started first in the early medieval period some 800 years B.P. The first historical data refer to the towns and villages of Uherský Brod A.D. 1131, Velká nad Veličkou A.D. 1220, Nové Mesto nad Váhom A.D. 1253, Čachtice A.D. 1276 and Strání A.D. 1357. The mountains began to be settled first some 600 years ago* […] *or a little later, bringing forest grazing, local deforestation, formation of meadows and pastures, building of farms, etc.* At this point, we will not go into the methodological details of the individual studies, which contributed to the striking disagreement of the above conclusions. In any case, it is obvious that in order to find a consensus on the historical development of the White Carpathian meadows, it was necessary to come up with something new – be it palaeoecological data, methodological approach or theoretical concept.

In this situation, we entered the discussion with a study in which we attempted to offer all of the mentioned elements (Hájková et al. 2011). We took advantage of a unique find of organic sediment in the core area of the forest-steppe meadows near Velká nad Veličkou, whose multi-proxy analysis suggested that a diverse cultural landscape including meadows existed here about two thousand years ago – i.e. that the meadows are older than medieval (assuming that their existence was uninterrupted). At the same time, we summarized biogeographical data on the occurrence of rare plant species with disjunct distributions, which are strikingly concentrated in the region (Roleček 2007, Grulich 2008; Fig. 32) and may be of relict origin. If they are indeed relicts (and not the products of later immigration), these species are living proofs of the continuity of open habitats even on mesic sites, as some of them are relatively moisture-demanding and could not survive in drier sites (e.g. *Gentiana acaulis*, *Pedicularis exaltata*, *Thalictrum simplex* subsp. *galioides*). We also carried out a detailed survey of the archaeological data and showed that Neolithic settlement extended into the core area of the forest-steppe meadows and the area was relatively densely populated also in the younger periods of prehistory (Fig. 33). Thus, we can assume that humans were involved in maintaining habitats suitable for forest-steppe meadow species for a long time, and their influence extends back to the critical period of the Middle Holocene. At the same time, we repeated here the previously formulated idea (Roleček 2007) that the species composition of forest-steppe meadows may be derived from Early Holocene birch-pine forests, whose contemporary analogue is the hemiboreal forests of southwestern Siberia. We later elaborated this concept and applied it also to other regions (Roleček et al. 2014, 2015; Section 5.4).

Fig. 32. Biogeographically significant species of the peri-Carpathian forest-steppe meadows: a – *Pedicularis exaltata* (CZ, UA); b – *Adonis volgensis* (RO; photo D. Borovyk); c – *Klasea lycopifolia* (CZ, SK, RO, UA); d – *Ranunculus breyninus* (RO, UA); e – *Ligularia glauca* (RO, UA; photo V. Budzhak); f – *Veronica spuria* (CZ, HU, UA); g – *Veratrum nigrum* (CZ, RO, UA); h – *Mercurialis ovata* (RO, UA); i – *Dracocephalum ruyschiana* (HU); j – *Thalictrum simplex* subsp. *galioides* (CZ); k – *Serratula coronata* (RO, UA; photo A. Tokaryuk); l – *Adenophora liliifolia* (SK, HU, RO, UA); m – *Anemonastrum narcissiflorum* (UA); n – *Crepis sibirica* (UA); o – *Lathyrus pisiformis* (UA); p – *Danthonia alpina* (CZ, SK, HU, RO). These species are largely linked to the *Brachypodio-Molinietum* association (and similar stands of the *Geranion sanguinei* alliance) at the forest-steppe sites, while their range is disjunct or reaches its limit in Central Europe. Abbreviations in brackets indicate the countries where the species occur in this vegetation.

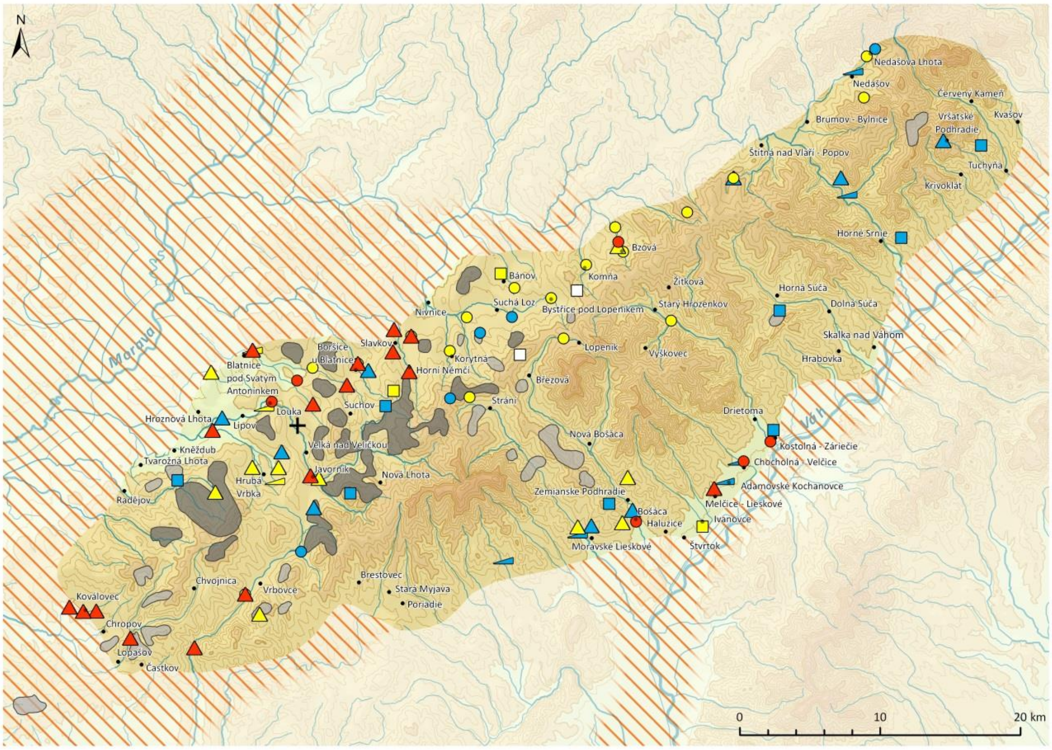

Fig. 33. A detailed distribution map of *Brachypodio pinnati-Molinietum arundinaceae* grasslands (grey segments) and prehistoric archeological records from the Neolithic to Bronze Age (various symbols) in the White Carpathians, published by Hájková et al. (2011). Distribution of *Brachypodio-Molinietum* grasslands is based on both historical data (Sillinger 1929) and the analysis of relevés from the Czech National Phytosociological Database. Darker grey colour of the segments indicates the presence of at least one plant species with a disjunct distribution. Archaeological data are classified into four categories of settlement type using different symbols and three categories of age using different coloured symbols. Settlement type: square – fortified hilltop settlement; triangle – other settlement; scalene triangle – burial place; small circle – fragmentary record. Age: red – Neolithic; yellow – Eneolithic; blue – Bronze Age; white – exact age unknown. When archaeological sites provide evidence for various periods, only the oldest record was mapped. Only the territories of the Bílé Karpaty geological unit and the klippen belt were mapped. Hatching indicates neighbouring lowlands along the Morava, Olšava, Myjava and Váh rivers with well-documented intense prehistoric settlement. Black cross indicates location of the analyzed sediment.

This study raised a considerable interest, but also new questions, so we focused on the search for new sediments whose palaeoecological analysis would provide even more convincing evidence of the historical development of the local meadows, especially during the critical period of the Middle Holocene. Unfortunately, such an old sediment was found only in the northeastern part of the White Carpathians, which has a more humid climate, species-rich forest-steppe meadows are almost absent there, and the forest played an important role in the Holocene development of the local vegetation (Hájek et al. 2016). The other sedimentary profiles covered only one or two last millennia, so we used them at least to test the hypothesis that even the turbulent development during the Migration period and the High Middle Ages has not resulted in the complete depopulation and disappearance of the local open habitats (Hájková et al. 2018). Our investigations, which also examined some previously analysed sites, also yielded the finding that the occurrence of steppe mollusc shells in strata corresponding to the Middle Holocene, interpreted by Ložek (2007) as evidence of the continuity of non-forest habitats, is caused by the imperfect stratification of the analysed sediments. Radiocarbon dating (Pavézková 2019, M. Horsák et al., unpublished) has shown that the occurrence of steppe molluscs falls into either an earlier period (i.e. Early Holocene, when local forest-steppes may have been climatically determined) or a younger period (Middle Ages).

In order to advance our investigations, we had to expand our methodological repertoire to include a palaeoecological proxy that is independent of specific sedimentary environment and is indicative of development at average sites. One such proxy is soil charcoal, i.e. the macroscopic remains of burned wood of local origin preserved in the soil. An analysis of 13 soil profiles covering almost the entire altitudinal gradient of the White Carpathians (Novák et al. 2019) showed that while soils in the middle and higher elevations show clear traces of the forest phase with a representation of shade-tolerant trees (mainly *Fagus*), chernozem-like soils at the foothills contain mostly or exclusively charcoal of light-demanding trees (*Pinus*, *Betula*, *Quercus*). In the mid-elevations we also repeatedly observed layers with large amounts of charcoal, which may indicate deforestation events using fire (burning). At the foothills, such layers were absent and charcoal was generally scarce, indicating a more continuous development and supporting the idea that a relatively open forest-steppe mosaic was maintained here throughout the Holocene. At the same time, communities with relatively mesophilous species typical of forest-steppe meadows may have survived on the deep soils here. On the other hand, these results suggest that the most species-rich meadows in the middle elevations of the White Carpathians (e.g. at Porážky site) were formed after deforestation, most probably between the Bronze Age and the Early Middle Ages. However, numerous forest-steppe species contributing to their formation may have survived the forest phase in the adjacent forest-steppe foothills. Thus, we can say that the pedoanthracological data support a reconstruction of Holocene development close to the above-mentioned ideas of Sillinger and Ložek (Chapter 2.6.1).

The question remains what kept the local forest-steppe open when the climate was sufficiently humid (Dabkowski et al. 2019, Divíšek 2021) for closed forest growth on deep soils during the critical period of the Middle Holocene. The regular presence of soil charcoal suggests that fire may have played a role. Were these fires natural or human-ignited? We do not know. In the drier climates of the Early Holocene they may have been natural, whereas since the Neolithic they may have been man-made. We can only speculate about the influence of Mesolithic hunter-gatherers, as we have no evidence of their presence in the White Carpathians (Kertész 2002, Oliva 2018). Also considerations about the influence of wild large herbivores (Ložek 2007) are not yet supported by data. We do not neglect the explanation of the survival of rare light-demanding species due to the effects of landslides and springs either (Ambrozek 1989, Grulich 2008); however, we consider these characteristic landforms rather as complementary sources of habitat heterogeneity, because they are also frequent in other parts of the Carpathians, where characteristic species of forest-steppe meadows are absent.

Our recent research on soil memory also brings back into play the question of the historical role of trees in the White Carpathian forest-steppe. While soil charcoal indicates a limited presence of trees on chernozem-like soils, pedological analyses revealed their traces (funnels under former trees, root channels, indications of upheavals) in five out of six analysed White Carpathian profiles (P. Šamonil et al., unpublished). Further study of this topic is therefore necessary and we are intensively working on it. We also use other less common methodological tools such as the analysis of soil phytoliths (K. Hošková et al., unpublished) and chemical biomarkers (M. T. Karimi Nezhad et al., unpublished).

4.3.2. Transylvania

Since 2020, we have also focused on soil memory research at forest-steppe meadow sites in Transylvania. The most important results are still only partially published and are based on soil age assessment and soil charcoal analysis. Both have yielded findings that deepen our insights into the history of peri-Carpathian forest-steppe meadows and provide valuable evidence for testing previously formulated hypotheses.

The age of the chernozem-like soils (specifically the Chernic Luvic Phaeozems), determined on the basis of the meteoric ^{10}Be content, was estimated at 20 to 25 thousand years in two profiles at the Fânațele Clujului site near Cluj and at 53 to 65 thousand years in the profile on Gorgan Hill near Valea Florilor (Püntener et al. 2023). Thus, in the first case the estimated origin of the soils dates back to the Last Glacial Maximum, in the second even to the middle part of the Last Glacial period. This unexpectedly large estimated age requires further investigation, however, a pre-Holocene origin of the local chernozem-like soils has been suggested before based on the results of radiocarbon dating of pedogenic carbonates (14,320–14,700 cal BP; Pendea et al. 2002) and OSL dating of the buried mollic horizon (9200–13,400 years old; Timar Gabor et al. 2010). Most importantly, such a large age is also consistent with the results of our soil charcoal analyses. During our first investigations in the White Carpathians, we collected samples for pedoanthracological analysis mostly from the depths of up to 100 cm, and the vast majority of soil charcoals were thus found to be of Holocene age (Novák et al. 2019). In contrast, in Transylvania, we identified the transition to the soil substrate at depths exceeding 150 cm at a larger number of sites, providing a more complete charcoal record extending deeper into history. It turned out that at least at some sites, the charcoal assemblages from greater depths have a specific taxonomic composition (J. Novák et al., unpublished) and their radiocarbon ages fall almost exclusively into the Late Glacial, sometimes even the Full Glacial (Table 7). They are completely dominated by conifers, mainly *Pinus*, *Juniperus*, and occasionally the difficult-to-distinguish *Larix*/*Picea*. In our opinion, these results support the idea that during the Late Glacial and at least some periods of the Full Glacial (the oldest charcoal was dated to 43,660 cal BP), open-canopy forests with taiga tree species grew on the sites of the present-day peri-Carpathian forest-steppe meadows in Transylvania. Although we do not know much about the composition of their herb layer yet, in accordance with our initial hypothesis we assume that it was close to the present-day hemiboreal forests of southwestern Siberia, classified within the *Brachypodio-Betuletea* and *Rhytidio-Laricetea* classes (Ermakov et al. 2000; Chapter 5.4).

Table 7. Species composition of the oldest soil charcoals at the sites of peri-Carpathian forest-steppe meadows. Charcoals older than Neolithic are shown, the age is rounded to decades. The selection of dated charcoals does not necessarily reflect the representation of species in a given period, as species of interpretive significance were dated preferentially (see Novák et al. 2019).

Taxon	Age [cal BP]	Site	Country	Depth [cm]
Pinus	8120	Miliovy	CZ	90
Juniperus	8350	Valea Florilor	RO	100
Juniperus	8560	Chortova hora	UA	90
Pinus	8850	Kasova hora	UA	130
Tilia	9290	Machová	CZ	60
Quercus	10660	Hájová	CZ	110
Juniperus	10940	Valea Lui Craiu	RO	100
Pinus* + *Tilia	12590	Búrová	CZ	120
Betula	12790	Búrová	CZ	160
Juniperus	13030	Chortova hora	UA	110
Juniperus	13240	Valea Calda	RO	140
Juniperus	13380	Sălicea	RO	180
Pinus	13460	Miliovy	CZ	135
Juniperus	13520	Valea Florilor	RO	180
Juniperus	13700	Valea Lui Craiu	RO	80
Juniperus	14060	Boj-Cătun	RO	60
Juniperus	14070	Boj-Cătun	RO	90
Juniperus	14870	Boj-Cătun	RO	120
Juniperus	17690	Valea Calda	RO	120
Juniperus	23030	Boj-Cătun	RO	160
Quercus	41500	Hájová	CZ	30
Larix/Picea	43660	Valea Florilor	RO	160

A distinctive feature of the local soil charcoal assemblages is the regular occurrence of *Juniperus*. This light-demanding shrub is considered an indicator of grazing, or rather successional stages after the retreat of intensive grazing (it favours a combination of soil disturbance and release of grazing pressure; Fitter & Jennings 1975, Broome et al. 2017), while tolerating less intense fires (Fitter & Jennings 1975, Diotte & Bergeron 1989). It is almost absent in present-day peri-Carpathian forest-steppe meadows (one of the exceptions is Nagy-mező in the Hungarian Bükk Mts), probably due to both unsuitable management (mowing) and a preference for cooler and more humid regions (it is a typical species of pastures in the middle elevations). Nevertheless, it is a useful species in terms of palaeoecological reconstruction, as it can be identified in both the charcoal and pollen records. For example, in a classic pyloanalytical study of glacial-interglacial cycles from the Massif Central in France (Reille et al. 2000), *Juniperus* was identified as the first woody species to spread during interglacial warmings, shortly before or simultaneously with the expansion of *Betula* and *Pinus*. In

Transylvania, numerous charcoals of *Juniperus* were found e.g. in a high-quality pedoanthracological profile from the Gorgan site near Valea Florilor (J. Novák et al., unpublished). Here, in addition to the Late Glacial (13,520 cal BP), we documented its occurrence at the end of the Early Holocene (8350 cal BP), at the end of the Middle Holocene (4520 cal BP) and in the Late Medieval (600 cal BP). At the same time, the overall taxonomic composition of soil charcoal shifts from an assemblage corresponding to hemiboreal forest with *Pinus*, *Larix*/*Picea*, *Betula* and *Juniperus* to a species-poor assemblage dominated by *Juniperus* and some other non-forest elements (*Stipa*, *Poaceae*, *Prunus*), more or less corresponding to the current vegetation of the site (steppe meadow of the *Stipetum tirsae* association with scatters shrubs including typical forest-steppe species *Prunus tenella*). We believe that this is the most convincing evidence to date of the local continuity of open habitats of mesophilous steppe vegetation in the peri-Carpathian region.

Although the charcoal record may not capture all the twists and turns of Holocene development (we simply do not have information from the periods without fires), our conclusions are supported also by other results. First of all, by the similar, though not so distinct, record of non-forest development at the other analysed sites of species-rich forest-steppe meadows in Transylvania. At the Valea Lui Craiu site in the Fânațele Clujului meadow complex, from where the current world maximum of species richness per 10 m^2 area originates, we also have not detected any tree species in the charcoal assemblages, and *Juniperus* was recorded in the Early (10,940 cal BP) and Middle (4690 cal BP) Holocene, in addition to the Late Glacial (13,700 cal BP). Only slightly different is the record from the neighbouring site of Valea Calda, where only a small amount of *Fraxinus* dated to the Roman period was recorded among the tree charcoal (1720 cal BP), along with regularly represented charcoal of grasses and light-demanding shrubs. *Juniperus* was also present here in the Middle Holocene (5400 cal BP). At the Boj-Cătun site, we then recorded *Juniperus* over a wide time range from the Last Glacial Maximum (23,030 cal BP), through the Late Glacial (more dates) to the Middle Holocene (6000 cal BP). The record is again dominated by light-demanding elements (including *Poaceae* and *Stipa*), with occasional forest trees (*Quercus*, *Ulmus*). However, the representation of tree species is even lower than in profiles at the foothills of the White Carpathians, of which Miliovy louky meadows near Blatnička have the most similar charcoal composition (including *Juniperus* and *Pinus* near the base; Novák et al. 2019). The important role of *Juniperus* in the core area of the Transylvanian forest-steppe is also supported by the results of pollen analysis. While in profiles from other parts of Transylvania, *Juniperus* is either absent or only sporadically represented during the Holocene (Diaconeasa & Mitroescu 1987, Tantau et al. 2006, Feurdean et al. 2007), it forms an almost continuous curve in the pollen diagram from the forest-steppe meadow area between the cities of Cluj and Dej (Feurdean et al. 2015).

Comparison with the charcoal profiles of species-poorer meadows in the more forested area southwest of Cluj (Lita and Sălicea sites) shows a contrasting development. In this area, the forest phase was well represented during the Holocene landscape development, which is well captured by soil charcoal. Particularly instructive is the profile from the vicinity of Sălicea village, which has a similar taxonomic composition at the base to that of Gorgan Hill (*Pinus*, *Juniperus*, *Larix*/*Picea*, date 13,380 cal BP), but during the Holocene we observe a dynamic development towards forest vegetation with a diverse representation of tree species (e.g. *Fraxinus*, *Quercus*, *Corylus*, *Fagus*, *Abies*). The observed differences cannot be fully explained by the different climatic conditions and altitude, since, for example, the Valea Lui Craiu forest-steppe site lies less than 20 km away at an altitude still favourable for mesophilous forests (550 m a.s.l.). The fact that we did not record any oak charcoals (with the exception of a single sample), otherwise characteristic of forest-steppe sites, is taken as an indication of a long-term disturbance regime preventing the expansion of trees. Indeed, even today the entire surrounding landscape is conspicuously treeless. Further traces of woody plants in soil profiles (Püntener et al. 2023) need to be investigated in more detail, also with regard to their possible origin in the vegetation of glacial forests.

Similarly to the White Carpathians, the hypothesis of Holocene continuity of non-forest vegetation on mesic sites in Transylvania is also supported by the concentrated occurrence of rare, relatively moisture- and light-demanding species that could not have persisted at extreme sites of dry steppe grasslands. These species include e.g. *Adenophora liliifolia*, *Adonis volgensis*, *Colchicum bulbocodium*, *Paeonia tenuifolia* and *Serratula coronata* (Bădărău 2005). In our opinion, by linking the results of soil memory analyses with palaeoecological data on landscape development and biogeographical knowledge on the distribution of forest-steppe species, a convincing picture of the persistence of grassland habitats in Transylvania emerges, and the hypothesis of a direct link between the present-day communities and Late Glacial hemiboreal forests gains further support.

4.3.3. Western Ukraine

In order to examine whether a similar continuity of peri-Carpathian forest-steppe meadows can be expected in western Ukraine, we have recently analysed several components of soil memory in this region at six sites of species-rich forest-steppe meadows. Three sites were located in the borderland between the Pokutian-Bessarabian Upland and the Prut-Siret Interfluve near the town of Chernivtsi (including the Dzyurkach site near the village of Spaska, from where the current world maximum of species richness per 16 m^2 originates). The other three sites are located in the Western Podillia between the towns of Burshtyn and Halych (including the site of Kasova hora with many isolated occurrences of rare light-demanding species).

The results are still being processed and we have not yet succeeded in transporting some samples from the Ukraine. Nevertheless, the first results of pedoanthracological analyses (J. Novák et al., unpublished) show that while only charcoals of light-demanding species (including *Quercus*) are represented at the forest-steppe sites in the Western Podillia, charcoals of mesophilous deciduous trees (*Fraxinus*, *Corylus*, *Fagus*, *Abies*) are predominant at the Dzyurkach site situated higher up (420 m a.s.l.) in the Prut-Siret Interfluve. Therefore, it is likely that the latter site, similarly to Porážky in the White Carpathians, has undergone a forest phase. However, radiocarbon data suggest that its deforestation occurred quite early, perhaps between the Eneolithic and the Early Bronze Age (4570–3860 cal BP), so there was sufficient time for the immigration of forest-steppe species from the adjacent forest-steppe foothills. In contrast, the light-demanding conifers

Pinus and *Juniperus* grew at the forest-steppe sites of Kasova hora and Chortova hora even at the end of the Early Holocene (8860 and 8560 cal BP) and in the middle Holocene (5600 cal BP), i.e. the periods of maximum forest cover in the landscape. These partial results thus support the idea of Holocene continuity of grasslands or open-canopy forests in Western Podillia, which is consistent with the results of our multi-proxy palaeoecological reconstruction at the landscape level (Hájková et al. 2022).

4.4. Summary

Palaeoecological research to date supports the Ložek's idea of Holocene continuity of open habitats at least at some sites of the peri-Carpathian forest-steppe meadows. The most convincing evidence comes from the northwestern Transylvania and Western Podillia, and within the White Carpathians from the southwestern foothills. That is, from areas that have been inhabited by man since the Neolithic at the latest. Thus, humans may have been the principal factor in maintaining the landscape open. Further attention should be paid to the role of natural factors (fire, grazing) and their interaction with humans, the spatial variation of development (dynamic mosaics versus long-term spatially stable open habitats) and the role of trees, which seem to be variable not only among regions but also among sites. The application of less common palaeoecological methods such as soil phytolith analysis, chemical biomarker analysis and soil organic matter dating may provide new evidence.

5. Peri-Carpathian forest-steppe

Scattered across our planet's forest biomes are specific ecosystems whose biodiversity is far beyond what is common in their range. They have one more common feature: they are non-forest, mainly grassland formations growing in areas where forests could grow given favourable climatic conditions (Jeník 1969, Weigl & Knowles 2013, Pausas & Bond 2020). Besides some African and Asian savannas (Backéus 1992), these include grass balds in Queensland, Australia (Webb 1964, Moravek et al. 2012), and in the Appalachian Mountains in the eastern USA (Weigl & Knowles 2013), Garry oak meadows in the northwestern USA and southwestern Canada (McCune et al. 2013, Pellatt et al. 2015), dry grasslands in Swabian Alb, Germany (Gradmann 1898, Wilmanns 2003), Baltic wooded meadows (Kukk & Kull 1997) or wonderglades in the Leningrad region of northwestern Russia (Khaare 1979, Sennikov 2009).

When the occurrence of grassland formations is associated with extreme habitat conditions, e.g. shallow soils as in the case of Central European rocky steppes (Willner et al. 2017), Siberian stepoids in the forest zone (Sizykh 2009, Namzalov 2020) and North American bedrock meadows (Pätsch et al. 2022), the explanation for their otherness is usually trivial (although even here the effects of different factors may combine). However, when they grow in favourable, productive habitats, there is often no simple ecological explanation and their origin may be unclear. Sometimes it is even referred to as mysterious or miraculous (Khaare 1979, Moravek et al. 2012). However, the results of historical and palaeoecological studies increasingly show that what unites these phenomena and distinguishes them from their surroundings is their **specific history**: a long-term, centuries- to millennia-long **continuity of open, non-forest character** (Moravek et al. 2012, Weigl & Knowles 2013, Pellatt et al. 2015, Pausas & Bond 2020). This has allowed the accumulation of large numbers of non-forest species, or their survival from past periods when non-forest ecosystems were more widespread. A documented, assumed, but sometimes overlooked or questioned cause of continuity here is **periodic disturbance**; particularly human activities, grazing by large herbivores or fire.

Based on the facts presented in the previous chapters, we believe that the peri-Carpathian forest-steppe meadows belong to this group of phenomena. They are also confined to productive habitats that have the potential for the growth of mesophilous forests (Chapters 2.1 and 3.3.3). They are also dependent on regular disturbances (mowing, grazing, fire; Chapters 2.2, 3.3.3 and 4). They too have survived continuously on their sites for centuries or millennia and in some cases appear to have a direct link to Early Holocene non-forest and open-canopy forest habitats (Chapter 4). They are also hotspots of extraordinary biodiversity, and in the case of vascular plants even the highest worldwide on the scale of metres to tens of square metres (Chapters 2.2 and 3). Analogous ecosystems are known from some other regions of Central and Eastern Europe, mainly the peripheries of forest-steppe regions (Chapter 2.5, Feurdean et al. 2018). The best-known examples include the Central Russian forest-steppes around Kursk, comparable in small-scale species richness to the peri-Carpathian grasslands (Chapter 2.5), or the Krasnoufimsk and Mesyagutovo forest-steppe islands in the Ural foothills (Nikonova et al. 2012, Zolotareva et al. 2019). Due to their specific biodiversity and relatively humid climate, they have long been recognized as specific phenomena, different from more southerly forest-steppes (Alyekhin 1934, Gorchakovskiy 1967). Because of their relatedness, we also consider vegetation complexes including peri-Carpathian forest-steppe meadows as a type of forest-steppe, which we call **peri-Carpathian forest-steppe**.

5.1. The beginnings of the debate on the historicity of forest-steppes

The **contingent, historical development of vegetation** of the northern forest-steppes was emphasised as early as the end of the 19th century by **S. I. Korzhinskiy** (1861–1900), one of the best experts on the Russian steppes before they were transformed by modern agriculture. He wrote about the relationship between forest and non-forest areas in his study region between the Volga and the Urals (Korzhinskiy 1891): *I do not want to deny that, in general, steppes are more characteristic of a dry and hot climate and forests are more temperate and humid. That is indisputable. But I assert that in the steppe borderland studied by me, both steppe and forest vegetation can develop equally everywhere; that wherever forest and steppe formations meet, the former, being stronger and more mature, displaces the latter; thus, the steppe flora is maintained only in places where the forests have not yet penetrated or where their development is hampered by unfavourable external conditions. Thus, the division of forest and steppe spaces is determined not by climatic factors but by the conditions of the struggle for existence between forests and steppes on the one hand and the historical phase of this struggle on the other. So I repeat that the distribution of forest and steppe formations in our zone depends neither directly on climate, nor on the topographical character of the area, nor on the nature and properties of the substratum, but only on the conditions and course of the struggle for existence.*[49]

Such a view may seem somewhat exaggerated (Milkov 1950, Kleopov 1990) and influenced by contemporary Darwinian considerations of competition as one of the main vital forces. Nevertheless, it provides a useful counterbalance to the **ecological determinism** that has influenced the early debate on the relationship between forest and non-forest habitats and has made its way into textbooks. Among its most influential representatives was one of the founders of modern pedology, **V. V. Dokuchayev** (1846–1903), who expressed his opinion on the origin of the forest-steppe mosaics in 1892 (Dokuchayev 1936): *Thus the insular nature of the forests in the Little Russian* [i.e. Ukrainian] *pre-steppe, in other words the distinctiveness of the forest-steppe itself, is a completely natural phenomenon, existing since ages and not accidental and temporary, so its causes can and must be rooted only in the permanent physical features of the country and its*

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[49] Orig.: *Я не хочу отрицать, что въ общемъ степи свойственны болѣе сухому и жаркому климату, а лѣса болѣе умѣренному и влажному. Это безспорно. Но я утверждаю, что въ той пограничной степной полосѣ, изслѣдованной мною, повсюду можетъ развиваться одинаково и степная и лѣсная растительность; что всюду, гдѣ соприкасаются лѣсныя и степныя формаціи, первыя, какъ болѣе мощныя и совершенныя, вытѣсняютъ вторыя; что въ силу этого степная флора сохраняется лишь тамъ, куда лѣса еще не успѣли проникнуть, или гдѣ развитіе этихъ послѣднихъ встрѣчаетъ препятствіе въ неблагопріятныхъ внѣшнихъ условіяхъ. Такимъ образомъ распредѣленіе лѣсныхъ и степныхъ пространствъ обусловливается не климатическими факторами, но съ одной стороны условіями борьбы за существованіе между лѣсомъ и степью, а съ другой — историческимъ моментомъ хода этой борьбы. Итакъ я повторяю, что въ нашей полосѣ распредѣленіе лѣсныхъ и степныхъ формацій не зависитъ непосредственно ни отъ климата, ни отъ топографическаго характера мѣстности, ни отъ природы и свойствъ субстрата, но только отъ условій и хода взаимной борьбы за существованіе.*

geological past…[50] Dokuchayev particularly emphasized macroclimatic and soil conditions, and there is no doubt that these play an important role in the distribution of forest and non-forest habitats in forest-steppe regions, as shown also by recent studies (Chytrý et al. 2022). However, their importance is inevitably limited in areas with mild terrain and higher rainfall. Then, we observe in some researchers a wishful effort to find the environmental conditions responsible for the occurrence of open steppe habitats, or they even label the entire ecosystem is secondary and young (Chapter 2.6).

Against such considerations, however, has always stood the view that the essential element of the functioning of forest-steppes is their dynamics, especially exogenous dynamics driven by disturbances. The previous debate on this topic was summarized by the Ukrainian researcher **E. M. Lavrenko** (1900–1987) in the compendium *Vegetation of the USSR* (Lavrenko 1940): *Of course, at present no one would defend the "forest-destroying" hypothesis of steppe deforestation in the orthodox form in which it was proposed by V. I. Taliyev. However, the great merit of Taliyev is that he has shown with his numerous works that the forests within the steppe region have become considerably steppified under the influence of human activities (deforestation, cattle grazing, etc.). The human being is an agent of victory of steppe over forest. In the past, steppe fires, consciously practised by man as a way to improve the growth of steppe grasses, seem to have played a major role in this regard. Man has thus slowed down the conquest of the steppe by the forest (within the forest-steppe) and, in places, may have steered the process in the opposite direction.*[51] This view has gained ground over time, as evidenced by the modern textbook *Zonal types of biomes in Russia* (Petrov 2003): *The settlement of the forest-steppe and steppe zones by humans occurred long ago, almost simultaneously with the development of the broad-leaved forest zone. The entire post-glacial history of the steppes is at the same time the history of the relationship between man and nature.* […] *At the end of the Holocene, there was a significant reduction in the area of forests. Meadow steppe vegetation began to occupy an increasingly larger area among the forest massifs.*[52]

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[50] Orig.: *Таким образом, островной характер лесов в малороссийском предстепье, иначе говоря, своеобразный характер самой лесостепи есть явление вполне естественное, от века существующее, и не случайное и временное, почему и причину его могут и должны корениться только в постоянно действующих физических особенностях страны и ее геологическом прошлом…*

[51] Orig.: *Конечно, в настоящий момент вряд ли кто-либо будет защищать "лесоистребительную" гипотезу безлесия степей в этом ортодоксальном выражении, в каком она была предложена В. И. Талиевым. Одноко большой заслугой Талиева является то обстоятельство, что своими многочисленными работами он показал что под влиянием деятельности человека (вырубка лесов, пастьба скота и т. д.) происходит значительное остепнение лесов в пределах степной области. Человек является агентом, благоприятствующим победе степи над лесом. В прошлом большую роль в этом отношении сыграли, видимо, степные пожары или "палы", сознательно практиковавшиеся человеком как способ улучшить рост степных трав. Человек, таким образом, замедлил завоевание степи лесом (в пределах лесостепи), а местами, возможно, направлял процесс в противоположную сторону.*

[52] Orig.: *Заселение лесостепной и степной зон произошло очень давно, почти одновременно с освоением зоны широколиственных лесов. Вся послеледниковая история степей – это в то же время история отношений между человеком и природой.* […] *В конце голоцена произошло значительное сокращение площади лесов. Между лесными массивами все большую площадь стала занимать лугово-степная растительность.*

5.2. Non-equilibrium character of the peri-Carpathian forest-steppe

It is clear that although the relative importance of environmental conditions and disturbances in shaping mosaics of forest and non-forest habitats in forest-steppe regions has always been disputed, we need to integrate both into our considerations and concepts. Pausas & Bond (2020) have recently suggested that in climatically favourable areas we can view forests on the one hand and grasslands maintained by grazing, burning or mowing on the other as **alternative biome states**. This concept is an application of the theory of alternative stable states (Lewontin 1969, Beisner et al. 2003) at the biogeographical scale. Alternative biome states describe a situation where ecosystems dominated by different growth forms, and thus differing in biomass, leaf area, shade tolerance or community structure, may exist in the same environment. One of these states (typically forest or non-forest) persists in an area for generations. The authors highlight the presence/absence of biomass consumers, primarily herbivorous vertebrates and fire, as the main feedback mechanism maintaining the biome in a given state. The peri-Carpathian forest-steppe appears to be a good example of an alternative state of the temperate deciduous forest biome, e.g. due to the contrast between the structure and species composition of the forest and non-forest state, the peculiar species composition repeated over a wide geographical area, the high species saturation or the dependence on periodic disturbances.

Of course, it is questionable whether it is appropriate to consider a disturbance-dependent state as stable, even if it lasts for a long time. Indeed, there are theoretical frameworks that treat disturbances differently. In the concept of **non-equilibrium species coexistence** (Pickett 1980), disturbance is considered as a factor that prevents the achievement of competitive equilibrium in a community and the prevalence of competitively superior species during succession. In our case, these competitors are shade-tolerant tree species. In this concept, the peri-Carpathian forest-steppe is a **non-equilibrium forest-steppe**, whose counterparts are equilibrium forest-steppes in drier areas and/or more rugged terrains (Fig. 34). The latter are determined by the joint effects of climate, relief and soil conditions (also denoted exposure or orographic forest-steppes; Namzalov et al. 2012, Chytrý et al. 2022) and the forest-steppe mosaic here remains stable even in the absence of disturbances. Because in the real world, forest-steppe mosaics are usually influenced by a complex of factors (Erdős et al. 2022, Chytrý et al. 2022) and habitat conditions may be as variable over time as disturbances (e.g., climate-driven soil moisture; Ónodi et al. 2014, Fischer et al. 2020), a perfectly equilibrial forest-steppe is only a theoretical construct. Nevertheless, we find the above concept useful for considering the spectrum of options of forest-steppe functioning.

Another alternative to the theory of alternative stable states is the concept of **alternative transient states** (Fukami & Nakajima 2011), in which the disturbance-dependent state is not considered stable. Transient states, although they may be maintained over the long term, may prove unstable over time (Hastings 2004). Generally, the assessment of ecosystem stability depends largely on the spatial and temporal scale and also on the understanding of disturbances as external interventions versus inherent components of the system (Sprugel 1991, Mori 2011). It is therefore to some extent a conceptual, not a factual difference.

Regardless of how we conceptualize disturbances, they are one of the keys to understanding the peri-Carpathian forest-steppe. The presence or absence of disturbances, their frequency and character (mowing, grazing, burning) significantly influence the non-equilibrium peri-Carpathian forest-steppe not only today, but have been equally important throughout its Holocene history for the survival of a rich pool of non-forest species. The latter is at the same time one of the defining characteristics of this ecosystem. While the present-day appearance of the non-forest habitats of the peri-Carpathian forest-steppe is shaped primarily by mowing, and to a lesser extent by domestic animal grazing and intentional burning (chap. 3.3.3), the spectrum of disturbance was different in the past (chap. 4.3), and clarifying the role of different types of disturbance remains an important task for further research.

5.3. Relict character of the peri-Carpathian forest-steppe

While the disturbance-driven persistence of non-forest habitats in climatically favourable regions may be understood as contingent, the similar species composition of the islands of the peri-Carpathian forest-steppe spread over an area of at least 200,000 km^2 clearly indicates the effects of ecological rules stabilizing the species composition. In the light of the concept described in the introduction to Chapter 4, we believe that both convergent development under similar natural conditions and the persistence of past similarity play an important role here. The starting point for this development is the inherited species pool of hemiboreal forests and forest-steppes, widespread in the habitats of the present-day peri-Carpathian forest-steppes at the end of the Last Glacial and the beginning of the Holocene (Chapter 4.3, Fig. 34). The peri-Carpathian forest-steppe is therefore a **relict forest-steppe**, not only in the sense that species more widespread in the past (i.e. relict) contribute significantly to its species composition, but also because relict survival from the past is the essence of its existence. As the results of our palaeoecological analyses suggest, the reason for this is that if it had ever been completely overgrown by forest in the past and its light-demanding species pool had not been preserved even at landscape level (which is theoretically well possible in at least some regions), the characteristic forest-steppe vegetation types would not be present in these places today and other communities, less species-rich and more widespread in today's landscape, would grow in the **secondary open habitats** created later by man.

This developmental dichotomy also answers the question of whether we should consider every mosaic of forest and non-forest habitats including dry grasslands in Central Europe as a forest-steppe. We believe this is not an advisable approach. Central European cultural landscapes in the lower elevations are commonly made up of a mosaic of forest and open habitats including various types of semi-dry grassland. However, the peri-Carpathian forest-steppe (as well as some other Central European forest-steppes, e.g. Pannonian, North Bohemian or Central German; Fig. 30) has two other key attributes that we believe warrant this designation: i) its significant component are species-rich (sub)continental dry grasslands (*Cirsio-Brachypodion pinnati*, *Festucion valesiacae*) and ii) the origin of these grasslands is relict at least at some sites, and if secondary (following deforestation), we can assume a direct migration link to relict sites in the same landscape. In contrast, we do not consider secondary mosaics of forest and open habitats dominated by species of mesophilous and wet grasslands, acidophilous grasslands and species-poor semi-dry grasslands (especially if suboceanic or (pre)-Alpine elements are significantly represented) that lack temporal or spatial continuity with sources of (sub)continental species to be forest-steppe. Admittedly, the distinction between the two landscape types is not a sharp one.

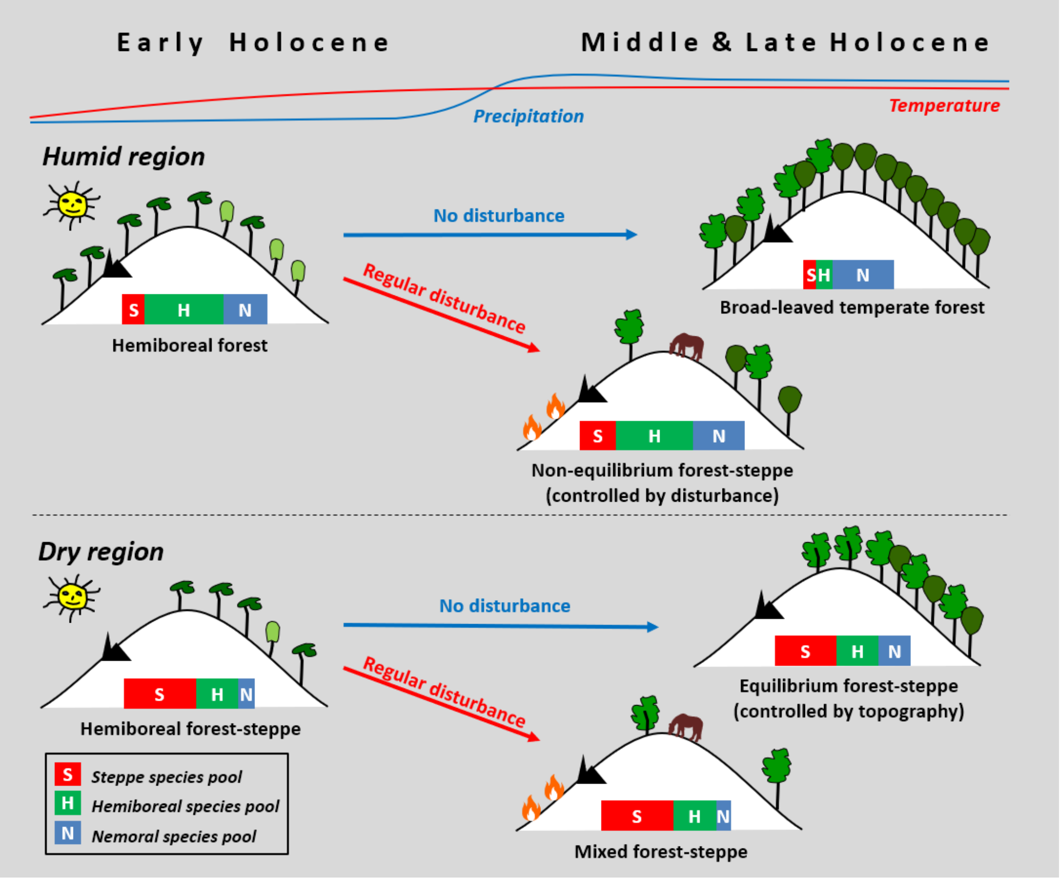

Fig. 34. Scheme of possible developmental trajectories of the peri-Carpathian forest-steppe during the Holocene. The proportion of hemiboreal forest to steppe during the Early Holocene is uncertain and probably changed with increasing temperatures and subsequent spread of trees, unless this process was limited by drought. Natural disturbances during the Early Holocene are not considered for simplicity.

5.4. Relationship to South Siberian hemiboreal forests

Since we have repeatedly pointed out the possible continuity of the peri-Carpathian forest-steppe meadows with the hemiboreal forests and forest-steppes, we should now characterize their common features more closely. In our opinion, the inherited species pool of Late Glacial and Early Holocene vegetation is an important attractor which, in the areas where it has survived, brings together the species composition of forest-steppe communities, including peri-Carpathian forest-steppe meadows. Unfortunately, the species composition of Late Glacial and Early Holocene forest-steppes is not well known. However, thanks to the analyses of fossil pollen and soil charcoal, we know that *Pinus*, *Betula* and *Juniperus* played a significant role in their tree and shrub layer (Reille et al. 2000, Chytrý et al. 2010, Pokorný et al. 2015; Table 7). Given that in the Early Holocene natural conditions were already relatively close to those of today, we assume that birch-pine forests of that time may have had a species composition similar to that found today in the vegetation of birch-pine forests beyond the eastern limit of the distribution of European shady broad-leaved forests (i.e. those communities that have competitively suppressed birch forests in most of Central and Eastern Europe over the last eight millennia). To the east of the Southern Urals, where shady broad-leaved forests are almost absent due to severe winters, their habitats are dominated by open-canopy hemiboreal forests dominated by hardy conifers and small-leaved deciduous trees, mainly *Pinus sylvestris* and *Betula pendula*, partly also by *Larix sibirica* and *Populus tremula* (Ermakov et al. 2000, Chytrý et al. 2010; Figs. 35 and 36). In their understorey, thanks to the sufficient light penetrating the open canopies, a number of light-demanding and semi-shade species in Europe mainly associated with open habitats, are present. In phytosociological classifications, these forests are largely classified in the *Brachypodio pinnati-Betuletea pendulae* class (Yermakov et al. 1991, Ermakov et al. 2000), while the more drought- and cold-tolerant ones in the *Rhytidio rugosi-Laricetea sibiricae* class (Korotkov & Ermakov 1999, Ermakov et al. 2000, Chytrý et al. 2008).

Although the parallel between the vegetation of the forest-steppe meadows of central Europe and the forests of southwestern Siberia may seem too distant, biogeographical analyses show that in fact their species composition is strikingly similar. Nimis et al. (1994) pointed out the dominance of Eurasian and Eurosiberian temperate taxa in the South Siberian hemiboreal forests dominated by birch (Fig. 37), which they even designated as the easternmost reaches of the European deciduous forest belt. According to them, the marginal status of South Siberian birch forests is reflected in the persistence of plants that are "ecologically marginal" relative to true forest vegetation. Based on an analysis of their habitat requirements, they concluded that in Europe these species are typical of forest meadows and fringes. This is a very interesting perspective for our study: Nimis et al. (1994) view the South Siberian hemiboreal forests, as well as European forest meadows and fringes (among which peri-Carpathian forest-steppe meadows can certainly be included), as refugia for Eurasian light-demanding flora that has been displaced by broad-leaved forests. Thus, from a different starting point, they came to similar conclusions as we did.

Corresponding ideas were developed as early as 1941 by the Ukrainian researcher Yu. D. Kleopov (1902–1943) in his posthumously published doctoral dissertation (Kleopov 1990): *The fact of ubiquitous contact of broad-leaved forests with fragments of periglacial steppes is very interesting; usually in these refugia of the most ancient steppe formations, a concentration of South Siberian meadow and birch-woodland species is also observed. ...it is impossible not to conclude that in the territories of the present distribution of broad-leaved forests of the European part of the USSR, a South Siberian birch-herb-rich-meadow landscape and in drier habitats a steppe (of the periglacial type) landscape was developed...*[53]

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[53] Orig.: *Весьма интересным является факт повсеместного контакта широколиственных лесов с обрывками перигляциальных степей, обычно в этих убежищах наиболее древних степных формаций наблюдается концентрация и южносибирских луговых и березняковых видов. ...нельзя не прийти к выводу, што на территориях нынешнего распространения широколиственных лесов европейской части СССР был развит южносибирский березово-разнотравно-луговой и по более сухим местообитаниям степной (типа перигляциальных степей) ландшафт...*

Fig. 35. South Siberian hemiboreal forest-steppe in the foothills of Eastern Sayan Mts. Dry *Artemisia* steppe on the sunny slope in the foreground, hemiboreal birch forest on the northern slope in the background, extensively managed wetland in the middle.

Fig. 36. A stand of mesophilous hemiboreal forest on the Zilair Plateau of the Southern Urals in the vicinity of the Relevé 3 below. The tree canopy is alternately dominated by *Pinus sylvestris*, *Larix sibirica* and *Betula pendula*, with *Brachypodium pinnatum*, *Calamagrostis arundinacea* and *Rubus saxatilis* in the understorey.

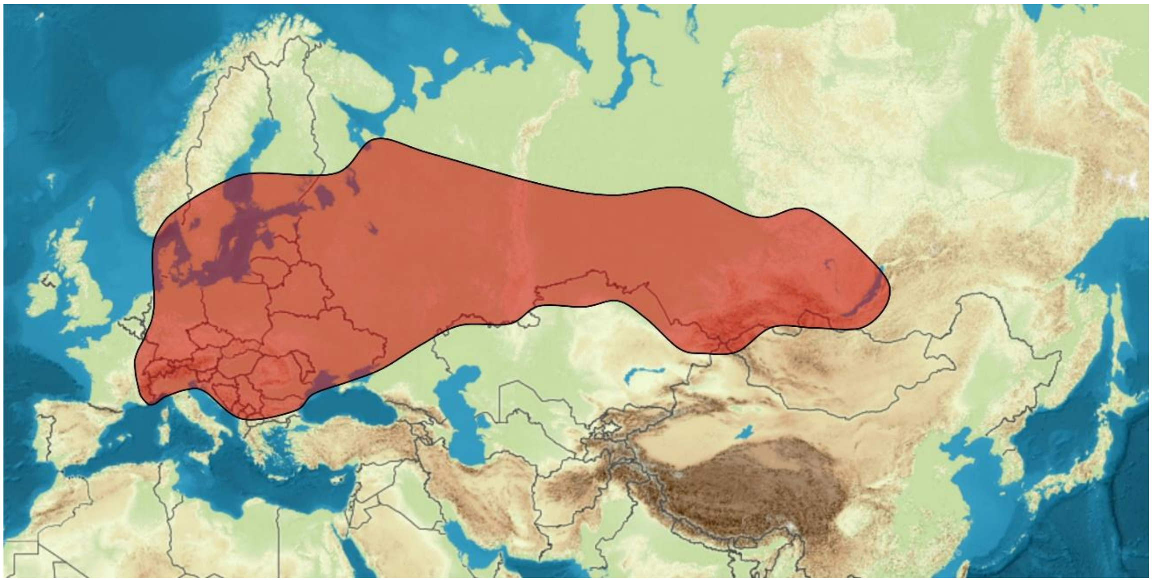

Fig. 37. Range intersection of 60% of species typical of hemiboreal forests of southwestern Siberia (adapted from Nimis et al. 1994). Shape corresponds to the Eurosiberian (north-)continental range. Map background taken from Mapy.cz.

Kleopov therefore, besides the results of the classic analysis of species ranges, placed great emphasis on the identification of areas where rare species with disjunct ranges occur in greater abundance. Like us (Chapter 4), he considered these areas as possible refugia of previously widespread flora and vegetation, the analysis of which may contribute to the reconstruction of the origin of the species composition of the current vegetation. Among these areas he included the Western Ukrainian Podillia and Pokutia, where peri-Carpathian forest-steppe meadows now occur, or the Central Russian Upland, where their closest eastern analogues grow (Chapter 2.5). Because Kleopov emphasized the importance of birch for this vegetation, he referred to the entire archaic flora of these stands as “betuletal”. At the same time, he pointed out its difference from the more xerophilous flora of the climatically determined steppes, which he considered to be developmentally younger within the forest-steppe regions; its modernisation, in his opinion, took place mainly in the xerothermic postglacial period. This remarkable reasoning thus leads to the seemingly paradoxical prediction that forest-steppe meadows, which were undoubtedly also modernized during later development (for example, during the spread of mesophilous species of man-made pastures and meadows), may contain a greater number of relict elements than the steppes of xerothermic habitats. This may be due to the fact that their habitat conditions are not as extreme, and therefore there is not as strong a filter of environmental conditions as in the case of climatically, topographically or edaphically determined dry steppes. At the same time, due to mesic conditions, they may have accumulated a number of ecologically and biogeographically heterogeneous species over time, which today contribute to their extreme species richness. On the other hand, in extreme habitats we can rather expect species turnover and colonization-extinction dynamics, because the habitat conditions change over time (van der Maarel & Sykes 1993, Fischer et al. 2020).

Table 8: Frequencies of the most frequent species of peri-Carpathian forest-steppe meadows ($f_{B\text{-}M}$; *Brachypodio-Molinietum* sensu Willner et al. 2019) and South Siberian hemiboreal forests ($f_{B\text{-}B}$; *Brachypodio-Betuletea* sensu Ermakov et al. 1991). Species are ranked by shared frequency (the lower of the two frequency values). Consensus diagnostic species of the *Brachypodio-Molinietum* association (Table 1) are indicated by an asterisk. Closely related vicariant species are separated by a slash.

Species	$f_{B\text{-}M}$	$f_{B\text{-}B}$
Brachypodium pinnatum s.lat.*	82	79
Achillea millefolium aggr.	79	33
Dactylis glomerata	62	31
Vicia cracca s.lat.*	30	43
*Inula salicina**	29	33
Poa pratensis s.lat.	44	29
*Viola hirta**	55	29
Cruciata glabra/krylovii*	26	25
*Avenula pubescens**	31	21
*Filipendula vulgaris**	63	19

Species	$f_{B\text{-}M}$	$f_{B\text{-}B}$
Galium boreale	19	82
*Hypochaeris maculata**	19	27
*Campanula glomerata**	33	18
Galium verum	67	18
Pulmonaria mollis s.lat.*	18	71
Fragaria viridis	37	16
Origanum vulgare	16	25
*Primula veris**	38	16
Trifolium pratense	23	16
Sanguisorba officinalis	15	57

What is then the species composition of South Siberian hemiboreal forests and how similar is it to peri-Carpathian forest-steppe meadows? The species with the highest values of shared frequencies in these communities are summarized in Table 8. A detailed quantitative comparison has been presented previously (Roleček et al. 2015) and its results show that among all vegetation types occurring in the Czech Republic, the peri-Carpathian forest-steppe meadows of the *Brachypodio-Molinietum* association are among the three communities most similar to the South Siberian hemiboreal forests, both in terms of their overall species composition and the representation of diagnostic species of hemiboreal forests. Other similar communities include the vegetation of the intermittently wet meadows of the Pannonian region classified in the association *Gentiano pneumonanthis-Molinietum litoralis*, the vegetation of the mountain tall-grass communities of the *Bupleuro longifoliae-Calamagrostietum arundinaceae* association and the vegetation of the open-canopy oak forests of mesic or semi-dry habitats, classified in the *Carici fritschii-Quercetum roboris* association or the *Brachypodium pinnatum-Quercus robur* community (the source of the nomenclature and syntaxonomy here is Moravec (1995)). In general, these are species-rich vegetation types distinguished by the abundance of rare light-demanding and semi-shade mesophilous species, indicating the long-term continuity of open habitats or open-canopy forests on their sites, under otherwise favourable habitat conditions. These are precisely the circumstances under which we may assume the persistence of the species pool of Early Holocene birch-pine forests.

South Siberian hemiboreal forests also include species with disjunct distribution, which have isolated sites in Central Europe in the vegetation complexes of the peri-Carpathian forest-steppe. These include e.g. *Adenophora liliifolia*, *Crepis sibirica*, *Dracocephalum ruyschiana*, *Iris ruthenica*, *Ligularia glauca*, *Serratula coronata*, *Thalictrum simplex*, *Trifolium lupinaster*, *Veratrum nigrum*, *Veronica spuria* and species from the *Actaea cimicifuga* group. As mentioned above, the occurrence of these species, especially when concentrated over a small area, may indicate Holocene continuity of open or semi-shade habitats at the site or in its vicinity. The occurrence of these species in the vegetation of the *Brachypodio-Betuletea* class at the western limit of its distribution is illustrated by the following relevé (Relevé 3):

Relevé 3: Russia, Bashkortostan, Southern Urals, Zilair Plateau, Zilair river valley near the village of Annovka, open-canopy pine-larch forest on a shady slope; 52.07639°N, 57.46083°E (WGS-84); 470 m a.s.l.; 13 July 2011; area 100 m^2; slope 25°; slope orientation 360°; tree cover 45%, herb cover 45%. Recorded by J. Roleček.

E_3: *Larix sibirica* 3, *Pinus sylvestris* 2b.
E_1: *Calamagrostis arundinacea* 2b, *Brachypodium pinnatum* 2a, *Rubus saxatilis* 2a, *Adenophora liliifolia* 1, *Carex pediformis* subsp. *rhizodes* 1, *Fragaria vesca* 1, *Galium boreale* 1, *Lathyrus vernus* 1, *Poa nemoralis* 1, *Primula veris* subsp. *macrocalyx* 1, *Aegopodium podagraria* +, *Bupleurum longifolium* +, *Carex digitata* +, *Corydalis solida* +, *Euphorbia esula* +, *Geranium pseudosibiricum* +, *Hieracium virosum* +, *Lathyrus pisiformis* +, *Pulmonaria mollis* +, *Silene nutans* +, *Stellaria holostea* +, *Thalictrum simplex* subsp. *simplex* +, *Trifolium medium* +, *Vicia tenuifolia* +, *Viola collina* +, *Asperula tinctoria* r, *Carex muricata* s.lat. r, *Crepis sibirica* r, *Galium aparine* r, *Heracleum sphondylium* subsp. *sibiricum* r, *Hieracium umbellatum* r, *Lilium martagon* var. *pilosiusculum* r, *Polygonatum odoratum* r, *Veronica chamaedrys* r, *V. spuria* r; *Rosa majalis* +.

This is a distinctly mesophilous hemiboreal forest growing at mid-elevation on the northern slope (Fig. 36). Its mesophilous character is manifested by the presence of nemoral species (e.g. *Carex digitata*, *Lathyrus vernus*, *Poa nemoralis*, *Stellaria holostea*), as well as light-demanding and semi-shade species of mesic habitats, including some nutrient-demanding species. Thus, the overall composition is close to the *Bupleuro longifoliae-Pinetum sylvestris* association (Martynenko et al. 2005).

Another remarkable common feature of peri-Carpathian forest-steppe meadows and South Siberian hemiboreal forests is the extraordinary species richness of vascular plants. Chytrý et al. (2012) recorded up to 82 species per 10 m^2 and 114 species per 100 m^2 in a hemiboreal forest in the forest-steppe region of the Northern Altai. These are probably the highest known species numbers for a given plot size in forests of the Palearctic biogeographic region. The species pool of forest-steppe meadows, inherited from these communities, seems to be predisposed for coexistence. Adaptive evolution and species co-adaptation (Thorpe et al. 2011, Schmutz & Schöb 2023) due to long-term interactions are thus another possible mechanism contributing to the extreme species richness of peri-Carpathian forest-steppe meadows.

The evolutionary perspective here encourages the search for specific species traits enabling coexistence, but such an analysis would go beyond the scope of this synthesis. Even so, the available evidence suggests that heliosciophilia, i.e. a certain tolerance of light-demanding species to shade, may be one of the key traits. In forest vegetation its contribution is clear, but even in forest-steppe meadows, which reach considerable stand height and cover, such a trait may certainly be an advantage. Analyses of the ecological spectra of constant species (Fig. 1), consensus indicator species (Table 1) and species shared among the richest relevés of the *Brachypodio-Molinietum* association (Chapter 3.1) show that the so-called fringe species are abundantly represented here. After all, of the 59 indicator species of peri-Carpathian forest-steppe meadows, 35 (i.e. almost

60%) are included in the EuroVegChecklist (Mucina et al. 2016) among diagnostic species of some type of forest vegetation (classes *Quercetea pubescentis*, *Quercetea robori-petraeae*, *Brachypodio-Betuletea* and *Carpino-Fagetea*) or vegetation of thermophilous forest fringes and tall herb-rich vegetation (*Trifolio-Geranietea* class). Hopefully it is not too trivial to conclude that shade tolerance of forest and fringe species is inherently an adaptation for coexistence and that this trait clearly contributes to the coexistence of species in peri-Carpathian forest-steppe meadows and to their extreme species richness.

5.5. Legacy of a lost world?

If the peri-Carpathian forest-steppe is an alternative biome state of Central European temperate forests, maintained in a non-forest state by regular disturbance, we can think of even deeper roots of its specific species composition. It is well known that Quaternary glacial-interglacial climatic cycles brought profound changes in conditions for species survival (Iversen 1958, Elias & Mock 2013). On the one hand, they created opportunities for speciation (Morales-Barbero et al. 2018, Kadereit & Abbott 2021), but were also a major cause of extinctions (Huntley 1993, Koenigswald 2003, Kurtén 2017, Magri et al. 2017). As a result of the pace of climatic cycles in the Middle and Late Pleistocene (long glacials, short interglacials), conditions in Central Europe were mostly favourable for non-forest ecosystems (cold steppes, tundra) and open-canopy forests with hardy conifers and small-leaved deciduous trees (Reille et al. 2000, Müller & Sánchez Goñi 2007, Helmens 2014). In shorter climatically favourable periods, shady forests composed of broadleaved deciduous trees have indeed spread, but disturbance by large herbivores may have contributed to the persistence of light-demanding species (Reille et al. 2000, Sandom et al. 2014a). The pre-Holocene faunas of this prominent group of organisms were species-rich and included key species capable of modifying the ecosystem structure, such as mammoths and rhinoceroses, in some areas also elephants, hippos and buffalo (Mostecki 1966, van Kolfschoten 2000, Tyráček et al. 2004, Kurtén 2017).

The conditions for the survival of light-demanding species in Central Europe changed fundamentally during the last glacial-interglacial cycle, when many large herbivores – whether preferring glacial or interglacial conditions – became extinct and the populations and ranges of others declined significantly. The causes of this collapse are a source of controversy, with the main dispute being over the relative contribution of natural and human factors (Stuart 1991, 2021, Lorenzen et al. 2011, Sandom et al. 2014b, Pavelková Řičánková et al. 2018). In any case, the future of light-demanding species, communities and ecosystems, especially those tied to favourable, productive habitats exposed to competition from woody plants, became increasingly uncertain and dependent on the activities of humans, whose population and impact on ecosystems have simultaneously increased (Mellars & French 2011, Tallavaara et al. 2015).

Many species of today's peri-Carpathian forest-steppe meadows were certainly part of this endangered group. We must admit that we still do not know enough about the extent to which changes in the disturbance regime and natural conditions (in addition to climate warming e.g. the rise in carbon dioxide concentrations; Harrison & Prentice 2003, Gerhart & Ward 2010, Da et al.

2019) at the end of the Pleistocene have been reflected in the species composition of individual communities, and thus how similar the current vegetation of forest-steppe meadows may be to its Pleistocene precursors (Kuneš et al. 2008, Magyari et al. 2014, Chytrý et al. 2019). Nevertheless, we may perhaps accept the idea of some analogy, also in view of the above findings on the Holocene continuity of this ecosystem. This opens up a fascinating perspective: by suppressing the development of shady temperate forests during the Holocene, man the farmer has created a precious refugium for light-demanding species; in this refugium survives a part of the diversity of the lost world of Pleistocene open and sparsely forested ecosystems maintained by disturbances, to whose demise man as a hunter-gatherer had previously contributed.

6. Conclusions

We started this study by quoting Josef Podpěra, a classic of Czech forest-steppe research, who referred to the White Carpathian forest-steppe meadows as unique in Central Europe. Podpěra was certainly right in that the meadows in the White Carpathians are a biologically valuable ecosystem, and it is justified that they are now protected within a UNESCO Biosphere Reserve. We also subscribe to his understanding of these communities as (forest-)steppe meadows, i.e. the relatively mesophilous continental steppe grasslands. However, our results clearly show that they are not unique in a geographical sense. The core of their species composition is the broadly conceived *Brachypodio pinnati-Molinietum arundinaceae* association, whose distribution we documented on the periphery of the entire Western and Eastern Carpathians and in some adjacent regions. Nevertheless, they are not a common vegetation type; on the contrary, they absent in large areas and rare or present in impoverished derivatives elsewhere. Thus, the close relationship of the stands in the different regions was overlooked for a long time, and when some authors drew attention to it, their observations did not become widely known.

Given the area of distribution, we refer to these communities as peri-Carpathian forest-steppe meadows. We consider the term “forest-steppe meadows”, which is not widely used in the Czech context, to be suitable, both because it refers to the close relationship of these meadows to some types of forest vegetation (open-canopy oak forests, hemiboreal forests) and because it corresponds to their occurrence in forest-steppe regions. Their most characteristic species throughout the range include *Brachypodium pinnatum*, *Carex montana*, *Crepis praemorsa*, *Potentilla alba* and *Pulmonaria mollis* s.lat. Analogous stands are also found in other parts of Central, South-Eastern and Eastern Europe. The variability of peri-Carpathian forest-steppe meadows is considerable and further data on the variability of similar vegetation are needed to validate their current classification within a single association.

The results of our field research and other studies published in the last decade confirm that the forest-steppe meadows of the *Brachypodio-Molinietum* association are the most species-rich vegetation known on areas of 10–16 m^2 (up to 119 vascular plant species per 16 m^2 in western Ukraine, up to 115 species per 10 m^2 in Transylvania, Romania, and up to 113 species per 16 m^2 in the White Carpathians, Czech Republic). The causes of their extreme species richness are not yet resolved, but it is clear that they are complex and that factors operating at different spatial and temporal scales are involved. We have developed a hierarchical model of these relationships linking a large landscape pool of light-demanding species (supported e.g. by biogeographical heterogeneity, large areas of grasslands and long-term continuity of open habitats) with a large local pool of light-demanding species (contributed e.g. by heterogeneous micro-relief, a mosaic of forest and non-forest habitats and haymaking), which then allows extreme numbers of species to coexist at the stand level. This can be modified by a number of other local factors, including the disturbance regime, moisture, nutrient availability and other soil properties, which determine, among other things, the high productivity of the peri-Carpathian forest-steppe grassland sites. Adaptive evolution and co-adaptation of species in this and analogous vegetation may also play a role, resulting from long-term interactions.

At the landscape and biogeographical level, peri-Carpathian forest-steppe meadows are part of habitat mosaics, which we refer to as peri-Carpathian forest-steppe. In addition to extreme species richness, its characteristic features include non-equilibrium and at the same time relict character. Non-equilibrium character implies that it is successionally unstable: the potential vegetation on its sites is forest due to favourable climatic and soil conditions, and it is maintained in a non-forest state by a regular disturbance regime. The relict character of the forest-steppe implies that, thanks to these disturbances, light-demanding species have persisted here for a long time, at some sites probably throughout the Holocene, since the time of broad distribution of heliophilous species of hemiboreal forest-steppe. If non-forest habitats appeared secondarily after deforestation, then there were places in the same landscape from which the distinctive light-demanding species might have spread. Where Holocene continuity has not been preserved, non-forest vegetation is less species-rich and belongs to other vegetation types. Human activities have probably played an important role in the maintenance of open habitats since the beginning of the Neolithic at the latest, but we still do not know enough about the relative importance of natural factors (fire, grazing) and their interactions with humans.

Our results place the peri-Carpathian forest-steppe into a group of specific non-forest ecosystems that are scattered across the planet and whose rich biodiversity is beyond what is common in their range. At the same time, these mostly grassland formations are located in regions where forests predominate, or might predominate given favourable climatic conditions. Whether its genesis is understood as deterministic or contingent, we may think of the peri-Carpathian forest-steppe as an alternative state of the temperate deciduous forest biome, maintained in a non-forest state by regular disturbance. Among its precursors were probably the Late Glacial and Early Holocene birch-pine forests, whose inherited species pool contributes to the current species richness of forest-steppe meadows and to the similarity of their species composition at individual, often distant sites. The understanding of the peri-Carpathian forest-steppe as an alternative biome state also allows its loose analogy with collapsed open Pleistocene ecosystems maintained by grazing of wild large herbivores and fire.

7. Methods

Most of the results presented in this study are based on the cited literature and our own published work, the methodology of which is described in the published papers included below. Here we provide methodological details of the original analyses presented in Chapters 2 and 5, the purpose of which is largely illustrative. Analyses of vegetation data were mainly performed in Juice 7.1 (Tichý 2002). The source of nomenclature throughout this study is Euro+Med PlantBase (Euro+Med 2006+); the exceptions are *Brachypodium pinnatum* s.lat. (= *B. pinnatum* + *B. rupestre*), *Campanula moravica* (Spitzn.) Kovanda, *Carex muricata* s.lat. (= *C. muricata* group sensu Chater 1980), *Cytisus virescens* (Kovács ex Neilr.) A.Kern., *Festuca valesiaca* s.lat. (= *F. valesiaca* + *F. stricta* subsp. *sulcata*), *Ligularia glauca* (L.) O. Hoffm., *Lotus corniculatus* s.lat. (= *L. corniculatus* + *L. borbasii*), *Molinia caerulea* s.lat. (= *M. caerulea* + *M. arundinacea*), *Pimpinella saxifraga* s.lat. (= *P. saxifraga* + *P. nigra*), *Poa pratensis* s.lat. (= *P. angustifolia* + *P. pratensis*), *Pulmonaria mollis* s.lat. (= *P. mollis* + *P. dacica*), *Rumex acetosa* s.lat. (= *R. acetosa* + *R. thyrsiflorus*), *Veronica chamadrys* s.lat. (= *V. chamaedrys* + *V. vindobonensis*) and *Vicia cracca* s.lat. (= *V. cracca* + *V. tenuifolia*).

In Chaper 2.1, we created a list of consensus indicator species of peri-Carpathian forest-steppe meadows by combining lists of diagnostic species of the *Brachypodio-Molinetum* association published in seven different regional and national studies from Central Europe, namely the Czech Republic (Chytrý 2007a), Slovakia (Janišová & Uhliarová 2008, Hegedüšová Vantarová & Škodová 2014), Hungary (Lengyel et al. 2016), Romania (Dengler et al. 2012) and Ukraine (Roleček et al. 2019c; two different regions). Indicator species for the entire distribution area (phi > 0.1; Chytrý et al. 2002) calculated based on frequency data, published in Willner et al. (2019), were also included.

In the same chapter we compared the associations with species composition most similar to the *Brachypodio-Molinetum* association based on patterns of co-occurrence of constant species (Chytrý 2007a). Species were divided into 16 groups, subjectively interpreted in terms of ecology based on the results of cluster analysis (beta-flexible method, parameter beta = –0. 25, Bray-Curtis dissimilarity) of 994 species with at least 30 occurrences in a stratified dataset of 15,432 relevés. These relevés originated from the selection from the Czech National Phytosociological Database (Chytrý & Rafajová 2003), which was used to prepare the current version of the expert system for formalized vegetation classification of the Czech Republic (Chytrý et al. 2020). The similarity of associations was quantified using the Euclidean distance between frequency columns of associations defined on the basis of this expert system (Chytrý et al. 2020).

In Chapter 2.2, using NMDS ordination analysis, relevés classified into the *Brachypodio-Molinietum* association in the study by Willner et al. (2019) while reaching a sum of consensus indicator species values of at least 50 were compared with relevés originating from the Alps that were classified by their authors into the *Euphorbio verrucosae-Caricetum montanae* association while meeting the definition of the *Brachypodio-Molinietum* association by Willner et al. (2019).

In Chapter 2.3, from the initial set of 264 relevés assigned to the *Brachypodio-Molinietum* association by Willner et al. (2019), we removed relevés with a sum of consensus indicator species values of less than 50 and added relevés from more recent field studies by our team and the team of Monika Janišová (Janišová et al. 2021) meeting identical classification criteria. We subsequently geographically stratified this dataset (leaving a maximum of three relevés per grid cell of 0.75 min latitude and 1.25 min longitude, i.e. approximately 1.5 × 1.5 km), while excluding three relevés from the Alps, which we classified as the *Euphorbio verrucosae-Caricetum montanae* association based on the analysis in Chapter 2.2. We thus obtained a set of 110 relevés, which we classified using a modified Twinspan algorithm (Roleček et al. 2009) into three subtypes. We identified the indicator species of the subtypes using the phi coefficient standardized to group size (Tichý & Chytrý 2006).

In Chapter 5.4, we compared the frequencies of the most frequent common species of the *Brachypodio-Molinietum* association, reported in Willner et al. 2019, and the species of the South Siberian hemiboreal forests of the *Brachypodio-Betuletea* class, reported in Ermakov et al. 1991. We randomly selected eight relevés per association (i.e. the number of relevés in the least represented association) from the hemiboreal forest dataset to increase representativeness, resulting in a dataset of 136 relevés in 17 associations.

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List of included papers, their relevance to the topic of the habilitation thesis and the candidate's contribution

Variability of steppe vegetation

i) **Roleček J.**, Hájek M., Dřevojan P., Prokešová H., Fajmon K., Těšitel J., ... & Chorney I. I. 2019: Gradients, species richness and biogeographical links of steppe grasslands in Western Podolia (Ukraine). *Phytocoenologia* 49: 349–367.

> Relevance: Peri-Carpathian forest-steppe meadows are part of steppe grassland mosaics in a forest-steppe region of Western Podolia. They are largely confined to northern slopes. Their species richness may be extremely high and has a unimodal relationship with estimated productivity; it peaks in places with high evenness of species abundances.
>
> Contribution: First and corresponding author, lead conceptualization, methodology design, data analysis, interpretation of the results, manuscript writing and editing, contributed to data acquisition. Total contribution approximately 60%.

ii) Willner W., **Roleček J.**, Korolyuk A., Dengler J., Chytrý M., Janišová M., ... & Yamalov S. 2019: Formalized classification of semi-dry grasslands in central and eastern Europe. *Preslia* 91: 25–49.

> Relevance: The position of peri-Carpathian forest-steppe meadows within the variability of semi-dry grasslands of Central and Eastern Europe was established based on the analysis of a large amount of relevé data. Formal definition of the *Brachypodio-Molinietum* association was provided. The results show that meadow steppes in the forest-steppe zone of Eastern Europe are very similar to semi-dry grasslands of Central Europe.
>
> Contribution: Second author, contributed to data acquisition, data analysis, interpretation of the results and manuscript writing. Total contribution approximately 20%.

iii) **Roleček J.**, Dřevojan P., Iakushenko D. & Hájek M. 2022: Tall herb-rich steppe in the peri-Carpathian region of Ukraine and Romania. *Phytocoenologia* 51: 95–109.

> Relevance: This study showed that tall herb-rich vegetation of the *Geranion sanguinei* alliance is a regular component of the vegetation mosaics of the peri-Carpathian forest-steppe, particularly in the relatively moist and nutrient-rich depressions on the northern slopes. The stands may be very species rich and include species with disjunct distribution ranges, suggesting their ancient origin similar to *Brachypodio-Molinietum* forest-steppe meadows.

Contribution: First and corresponding author, lead conceptualization, methodology design, data analysis, interpretation of the results, manuscript writing and editing, contributed to data acquisition, project administration and funding acquisition. Total contribution approximately 60%.

Extreme species richness

iv) **Roleček J.**, Čornej I. I. & Tokarjuk A. I. 2014: Understanding the extreme species richness of semi-dry grasslands in east-central Europe: a comparative approach. *Preslia* 86: 5–27.

Relevance: This study reported new sites of extremely species-rich forest-steppe meadows from the foothills of the Eastern Carpathians in the southwestern Ukraine and compared them with similar sites in the peri-Carpathian region and beyond. We found many similarities and suggested that continuity on the Pleistocene-Holocene time scale and regularly practiced management reducing asymmetry in competition may be the crucial factors responsible for the extremely high local species richness of these grasslands.

Contribution: First and corresponding author, lead conceptualization, methodology design, data analysis, interpretation of the results, manuscript writing and editing and funding acquisition, contributed to data acquisition. Total contribution approximately 80%.

v) **Roleček J.**, Dřevojan P., Hájková P., & Hájek M. 2019: Report of new maxima of fine-scale vascular plant species richness recorded in East-Central European semi-dry grasslands. *Tuexenia* 39: 423–431.

Relevance: New maxima of vascular plant species richness ever recorded at 10 m^2 and 16 m^2 plots were reported from peri-Carpathian forest-steppe meadows in Transylvania and Western Ukraine, respectively. The results support the view that extreme species richness is a temporally stable feature of managed East-Central European semi-dry grasslands and suggest that low to moderate intensity grazing may support species-rich vegetation similarly to mowing.

Contribution: First and corresponding author, lead data analysis, interpretation of the results, manuscript writing and editing, co-lead conceptualization and methodology design, contributed to data acquisition. Total contribution approximately 40%.

vi) Hájek M., Hájková P. & **Roleček J.** 2020: A novel dataset of permanent plots in extremely species-rich temperate grasslands. *Folia Geobotanica* 55: 257–268.

Relevance: In this paper a network of 40 permanent plots established in the extremely species-rich peri-Carpathian forest-steppe meadows and related communities was reported. The network allows the long-term dynamics of the species richness and composition of these grasslands to be monitored.

Contribution: Senior author, co-lead conceptualization, methodology design and funding acquisition, contributed to data acquisition, manuscript writing and editing. Total contribution approximately 15%.

vii) Biurrun I., Pielech R., Dembicz I., Gillet F., Kozub Ł., Marcenò C., ... **Roleček J.**, ... & Dengler J. 2021: Benchmarking plant diversity of Palaearctic grasslands and other open habitats. *Journal of Vegetation Science* 32: e13050.

Relevance: Establishment of international database of species richness in Palaearctic grasslands was reported. Its first analyses confirmed that the peri-Carpathian forest-steppe meadows are the richest known grasslands on area of 10 m^2 in the Palearctic region.

Contribution: Co-author of a multi-authored paper, contributed to data acquisition, manuscript writing and funding acquisition. Total contribution approximately 1%.

viii) **Roleček J.**, Dřevojan P., Hájková P., Goia I. & Hájek M. 2021: Update on maxima of fine-scale vascular plant species richness in a Transylvanian steppe meadow. *Tuexenia* 41: 459–466.

Relevance: The maximum of vascular plant species richness at 10 m^2 plot was updated after revisiting of a permanent plot established in a peri-Carpathian forest-steppe meadow in Transylvania. The results suggest an increase in species richness following moderate-intensity grazing of the previously mown stand.

Contribution: First and corresponding author, lead data analysis, manuscript writing and editing, co-lead conceptualization, methodology design and interpretation of the results, contributed to data acquisition. Total contribution approximately 35%.

History and palaeoecology of the Central European forest-steppe

ix) Hájková P., **Roleček J.**, Hájek M., Horsák M., Fajmon K., Polák M. & Jamrichová E. 2011: Prehistoric origin of the extremely species-rich semi-dry grasslands in the Bílé Karpaty Mts (Czech Republic and Slovakia). *Preslia* 83: 185–204.

Relevance: A review of the available information on the history of forest-steppe meadows in the White Carpathians including an analytical part bringing new evidence of their prehistoric origin. Their Holocene continuity was hypothesized and the role of ancient human activities was put forward.

Contribution: Second author, co-lead conceptualization, interpretation of the results, manuscript writing and editing, contributed to data acquisition. Total contribution approximately 30%.

x) **Roleček J.**, Hájek M., Karlík P. & Novák J. 2015: Reliktní vegetace na mezických stanovištích [Relict vegetation on mesic sites]. *Zprávy České botanické společnosti* 50: 201–245.

Relevance: This comprehensive synthetic study focused on relict vegetation on mesic sites at lower elevations of the Czech Republic. We proposed that most of the relict vegetation types on mesic sites originate from communities widespread before the mid-Holocene, mainly from open-canopy hemiboreal forests. Several other hypothetical ancestral vegetation types have been discussed. The study is written in Czech, but the extensive abstract and captions of figures and tables in English make it accessible to an international audience.

Contribution: First and corresponding author, lead manuscript writing and editing, co-lead conceptualization, methodology design, data analysis, interpretation of the results, contributed to data acquisition. Total contribution approximately 50%.

xi) Hájek M., Dudová L., Hájková P., **Roleček J.**, Moutelíková J., Jamrichová E. & Horsák M. 2016: Contrasting Holocene environmental histories may explain patterns of species richness and rarity in a Central European landscape. *Quaternary Science Reviews* 133: 48–61.

Relevance: Using the White Carpathians as an example, this study shows how differences in Holocene landscape development may have contributed to present-day patterns of grassland species composition and richness.

Contribution: Co-author, co-lead conceptualization, contributed to interpretation of the results, manuscript writing and editing. Total contribution approximately 15%.

xii) Těšitel J., Vratislavská M., Novák P., Chorney I. I. & **Roleček J.** 2018: Merging of *Pedicularis exaltata* and *P. hacquetii* in the Carpathians: from local history to regional phylogeography based on complex evidence. *Folia Geobotanica* 53: 301–315.

Relevance: This genetic study brought evidence for the ancient origin of the isolated population of *Pedicularis exaltata* in the White Carpathians and thus provided partial support for the hypothesis of Holocene continuity of the peri-Carpathian forest-steppe meadows.

Contribution: Senior author, contributed to conceptualization, methodology design, data acquisition, data analysis, interpretation of the results, manuscript writing and editing. Total contribution approximately 25%.

xiii) Novák J., **Roleček J.**, Dresler P. & Hájek M. 2019: Soil charcoal elucidates the role of humans in the development of landscape of extreme biodiversity. *Land Degradation & Development* 30: 1607–1619.

Relevance: This pedoanthracological study provided support for the hypothesis of Holocene continuity open to semi-open landscape in lower elevations of the White Carpathians, whereas middle and higher elevations experienced a forested period. It suggested that humans and fire have played an important role in the local landscape development.

Contribution: Second and corresponding author, lead manuscript writing and editing, co-lead conceptualization, data analysis, interpretation of the results, contributed to data acquisition. Total contribution approximately 30%.

xiv) **Roleček J.**, Dřevojan P. & Šmarda P. 2019: First record of *Festuca amethystina* L. from the Transylvanian Basin (Romania). *Contributii Botanice* 54: 91–97.

Relevance: The first find of a rare light-demanding species *Festuca amethystina* in the Transylvanian Basin provided support for the long-term continuity of the local tall herb-rich vegetation of the *Geranion sanguinei* alliance, which is a characteristic component of the Transylvanian forest-steppes.

Contribution: First and corresponding author, lead conceptualization, manuscript writing and editing, co-lead methodology design, data analysis, interpretation of the results, contributed to data acquisition. Total contribution approximately 50%.

xv) **Roleček J.**, Abraham V., Vild O., Svobodová-Svitavská H., Jamrichová E., Plesková Z., ... & Kuneš P. 2021: Holocene plant diversity dynamics show a distinct biogeographical pattern in temperate Europe. *Journal of Biogeography* 48*:* 1366–1376.

Relevance: This reconstruction of Holocene plant diversity dynamics, based on the synthesis of a large amount of palynological data, shows that the increase in plant diversity associated with the emergence of cultural landscapes during the Middle Holocene was not preceded in forest-steppe regions of Central Europe by a general decline in diversity caused by forest expansion. This contrasts with the stagnation or decline in diversity at higher elevations and supports the hypothesis of Holocene continuity of open habitats in the forest-steppe regions.

Contribution: First and corresponding author, lead manuscript writing and editing, co-lead conceptualization, methodology design, data analysis, interpretation of the results and funding acquisition, contributed to data acquisition. Total contribution approximately 35%.

xvi) Willner W., Moser D., Plenk K., Aćić S., Demina O. N., Höhn M., ... **Roleček J.** ... & Kropf M. 2021: Long-term continuity of steppe grasslands in eastern Central Europe: Evidence from species distribution patterns and chloroplast haplotypes. *Journal of Biogeography* 48: 3104–3117.

Relevance: This study showed that genetic and biogeographical data are inconsistent with the scenario of Late Holocene immigration of steppe species from outside the Pannonian Basin. Rather, they support a Holocene continuity of steppe grasslands in East-Central Europe.

Contribution: Co-author, contributed to conceptualization, data acquisition, interpretation of the results, writing and funding acquisition. Total contribution approximately 10%.

xvii) Hájková P., Petr L., Horsák M., Jamrichová E. & **Roleček J.** 2022: Holocene history of the landscape at the biogeographical and cultural crossroads between Central and Eastern Europe (Western Podillia, Ukraine). *Quaternary Science Reviews* 288: 107610.

Relevance: All proxy data evaluated in this palaeoecological study support the hypothesis that an open or semi-open landscape existed in the forest-steppe region of Western Podillia during the Holocene. Local forest-steppe grasslands may have been maintained through the interplay of a relatively humid climate, fire and long-term human activities.

Contribution: Senior author, lead funding acquisition, co-lead conceptualization, methodology design, interpretation of the results, manuscript writing and editing, contributed to data acquisition and analysis. Total contribution approximately 30%.