Hungarian University of Agriculture and Life Sciences
Doctoral School of Biological Sciences

DESCRIPTION OF THE FLORA CONTINUITY HYPOTHESIS AND THE HISTORICAL ECOLOGICAL STUDY OF THE PESZÉR FOREST

Thesis of doctoral (PhD) dissertation

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1. INTRODUCTION AND OBJECTIVES

In recent centuries, the Earth's ecological systems have undergone unprecedented transformations (IPBES 2019), a phenomenon also evident in Hungary (Báldi & Batáry 2011; Biró et al. 2018). Modern habitat loss and species extinctions are largely driven by human activities, either directly (e.g., land use) or indirectly (e.g., the spread of invasive species, climate change) (e.g., Pievani 2014).

Beyond its indispensability to humans, a fundamental tenet of modern nature conservation is that biodiversity possesses intrinsic value (Standovár & Primack 2001); thus, its preservation is among our foremost responsibilities and obligations.

The preservation of our natural assets, however, is fraught with numerous challenges (e.g., Rands et al. 2010); in certain cases, even the conservation of individual species can be particularly difficult (e.g., Haraszthy 2014; Gameiro et al. 2020), while the preservation of complex systems often proves to be an even more intricate task (e.g., Molnár 2014; Keith et al. 2015).

In practical nature conservation decision-making, it is often necessary to establish a priority order for the protection of habitats and species (Vadász 2015). For instance, in the case of a habitat, one must decide whether to preserve its current state (species composition and structure) or the successional processes themselves; in the case of species, it must be determined which species should be given priority for protection at a given locality, even if this comes at the expense of another valuable species (e.g., the case of the European roller preying on the Hungarian meadow viper).

The careful establishment of priorities requires data collected from multiple perspectives. For example, short-term knowledge of population dynamics (e.g., Pigniczki et al. 2019; Bódis et al. 2019) and habitat dynamics (e.g., Molnár et al. 2017; Demeter et al. 2021; Orbán et al. 2023) is of particular importance, as is understanding how species and habitats respond to management interventions (e.g., Vadász et al. 2016; Kun et al. 2021). Another crucial element in conservation prioritization is the knowledge of past events on both short and long timescales (Molnár & Biró 2010), at both general and specific levels. General knowledge may include, for instance, understanding major climatic changes and the resulting substantial vegetation transformations (e.g., Sümegi et al. 2012; Feurdean et al. 2014), or the historical mechanisms of their drivers (e.g., fires, herbivore fauna; see Pearce et al. 2023; Czyzewski et al., in press). Specific knowledge may involve, for example, the history of an individual species (e.g., Németh et al. 2024) or that of a particular habitat mosaic (e.g., Molnár & Biró 1996).

Historical ecological research is of great significance for the preservation of ecological systems, as knowledge of the past enables a better interpretation of the present state and, on this basis, allows for more reliable projections of potential future changes (Rackham 1986; Molnár & Biró 2010; Barnosky et al. 2017). Thinking on such long temporal scales can also help to establish conservation priorities with greater caution, as it allows us to perceive the issue as an ongoing process.

The historical component of nature conservation management concepts draws simultaneously on general, regional knowledge and specific, local insights. My doctoral dissertation is built upon such a pair of studies. The first investigates what proportion of the flora of the Carpathian Basin may have survived the Last Glacial Maximum (LGM) in situ, while the second examines the changes that have occurred over the past two and a half centuries in the Peszér Forest, wich located in the Northern Kiskunság and renowned for its unique species composition. From a conservation perspective, knowledge of the long-term continuity of our flora can greatly assist in determining local and regional conservation priorities, while a thorough understanding of the history of a given area helps to view the habitat mosaic as a dynamic process, thereby providing important information for defining future management directions.

1.1. Objectives of the description of the Flora Continuity Hypothesis

According to the prevailing paradigm concerning the Quaternary ecological and evolutionary history of Central European ecosystems, glacial periods repeatedly impoverished habitats through the regional extinction of most species, followed by mass recolonization from southern and eastern refugia during interglacial periods (Postglacial Recolonization Hypothesis) (e.g., Boros 1958; Járai-Komlódi 1995; Járai-Komlódi 2003; Borhidi 2004; Kun 2018). Recent literature, however, contradicts this view in several respects and raises the possibility of its reassessment. I have proposed a new, alternative hypothesis (Flora Continuity Hypothesis), which posits that the majority (approximately 75–85%) of the native vascular flora of the Carpathian Basin survived the Last Glacial Maximum (LGM) in situ. Thus, the long-term continuity of our present native vascular flora appears more probable than a scenario of substantial impoverishment during the LGM followed by postglacial recolonization.

I examine the theoretical plausibility of this new hypothesis through the following three questions:

1) What trends do the most recent paleoecological and phylogenetic studies reveal regarding the survival of native plant species in the Carpathian Basin during the LGM?
2) Based on the habitats of present-day landscapes with climates similar to that of the Carpathian Basin during the LGM, can it be assumed that LGM-period habitats in the Carpathian Basin were species-rich?
3) What proportion of Hungary’s current native flora occurs in areas with a mean annual temperature equal to or lower than that prevailing in Hungary during the LGM?

1.2. Objectives of the historical ecological analysis of the Peszér Forest

The Peszér Forest is one of Hungary’s most valuable sandy forest-steppe habitat complexes. In the 19th century, it served as a habitat for valuable species such as the Austrian dragonhead (*Dracocephalum austriacum*), the Hungarian marbled white butterfly (*Melanargia russiae clotho*), and the rough bush cricket (*Onconotus servillei*). Recent studies on vegetation dynamics and questions arising during conservation planning have created the need for a historical ecological analysis of the forest.

The aim of my study is to uncover the ecological history of the Peszér Forest over the past 250 years in order to better understand the causes behind the extinction of valuable species and to identify the key factors for the future survival of the remaining species. The practical objective of the research is to support conservation management planning for the Peszér Forest with historical information.

I address the above questions through the following more detailed objectives:

1) What was the vegetation character of the Peszér Forest prior to forestry modifications, and how has it changed since then?
2) How has land use affected the forest stands and grasslands over the past 250 years, and what impacts might this have had on the valuable species?
3) What factors may have caused the extinction of some valuable species, and what might support the long-term conservation of the remaining species?

2. MATERIALS AND METHODS

2.1. Flora Continuity Hypothesis

During the Last Glacial Maximum (LGM), the climate of the Carpathian Basin was cold continental (Obreht et al. 2019; Sümegi et al. 2022). The mean annual temperature (MAT) ranged between +1 and +5 °C on the plains, between −3 and +1 °C in hilly and mid-mountain regions, and between −10 and −3 °C in the Carpathians (CCSM4.0, http1). The coldest climatic periods in the Carpathian Basin during the Pleistocene (2.6 million–11.7 thousand years ago; Cohen et al., 2013) occurred during the Last Glacial Maximum (LGM) and the Riss glaciation (400–150 thousand years ago; Lauer et al., 2018) (Andrews, 2009).

During the LGM, the vegetation matrix of the Carpathian Basin was likely dominated by treeless habitats, which developed under loess, rocky, sandy, and saline edaphic conditions. Most of these open habitats were probably dry, with steppe or meadow-steppe character, while tundra-like vegetation may have occurred only in higher mountain areas (Magyari et al., 2014; Feurdean et al., 2015; Janská et al., 2017; Sümegi et al., 2022). Forest components may have been present along rivers and in sandy lowland areas (Sümegi et al., 2011a, 2011b; Sümegi et al., 2015), while in mountainous regions they may have formed more or less continuous zones (Kuneš et al., 2008; Feurdean et al., 2014; Magyari et al., 2014; Janská et al., 2017).

As justification for formulating the Flora Continuity Hypothesis, I present three arguments. These do not aim to prove the hypothesis but rather serve to explain the basis on which the new hypothesis was proposed alongside the traditional one. The first argument summarizes paleoecological and phylogenetic findings; the second concerns the potential species richness of habitats under LGM climatic conditions; and the third is an analysis examining the cold tolerance of native vascular plant species in a test area (Hungary), based on contemporary occurrences in regions with mean annual temperatures equal to or lower than those prevailing in the test area during the LGM.

The development of the paleoecological and phylogenetic argument was conducted through a synthesis of relevant publications on the topic. The articles were compiled into a database, which was populated through systematic searches (e.g., keyword searches conducted during the preparation of Molnár et al. 2023 and the present doctoral dissertation), as well as ad hoc methods and snowball sampling (identifying additional publications via references).

My experience with species richness under mean annual temperatures comparable to those of the LGM-era Carpathian Basin is based on personal field observations from the Ural region and Mongolia. Although I compiled species lists, I did not conduct systematic phytosociological sampling; therefore, to support the second argument for the new hypothesis, I sought species count data published for these regions. Species richness data for the Carpathian Basin were similarly sourced from the literature.

One of the key questions during hypothesis generation was whether there is even a theoretical possibility that the majority of the local flora could potentially have tolerated the cold climate of the LGM in situ. The analysis serving as the third argument sought to address this theoretical possibility by examining how many of Hungary's current native vascular plant species are presently found in regions with climates as cold as, or colder than, those prevailing in Hungary during the LGM. Cold tolerance was assessed based on the current distribution of the species. Using the GBIF database (http2), I retrieved species lists from Eurasian regions where the mean annual temperature is below +3.5 °C (Figure 1). Although my primary aim was to assess the cold tolerance of the flora, I also performed a restricted analysis incorporating precipitation data and regions considered biogeographically close. For both present and past climate determinations, I used the CCSM4.0 model.

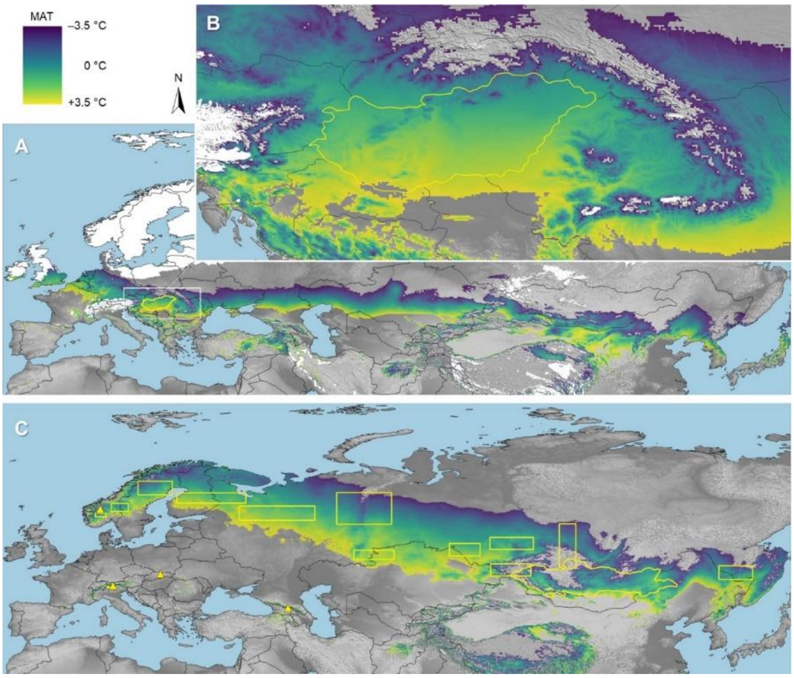

Figure 1. Zones of equal mean annual temperature (MAT) in Eurasia: (A) Eurasian regions where the MAT during the LGM was similar to that of the study area (Hungary, yellow outlined region; MAT between +3.5 °C and −3.5 °C, based on CCSM4.0). (B) Enlarged view of the white-framed section in panel A, showing the MAT of the study area during the LGM. (C) Areas where the current MAT matches the LGM MAT of the study area; reference sites are indicated [normal landscape reference sites: yellow rectangles, 13 in total (one small site in the Alps is less visible); mountainous reference sites: yellow triangles, 4 in total; Mongolian reference site: affected regions outlined in yellow].

2.2. Peszér Forest

The Peszér Forest is located in the Northern Kiskunság, northeast of the village of Kunpeszér. The study area is a 1,152 ha forest block forming the larger part of the Peszér Forest Special Area of Conservation (HUKN20002). In the region, the mean annual temperature is 12.2 °C (1993–2022; http3), the mean annual precipitation ranges between 530 and 570 mm, and the prevailing wind direction is northwesterly (Kocsis 2018).

The historical analysis of vegetation change in the Peszér Forest was preceded by a current vegetation dynamics study of the forest (see Molnár et al. 2017) and a historical ecological analysis of the surrounding landscape (see Molnár 2019a). For the historical analysis of the Peszér Forest, I conducted an extensive collection of source materials.

Keyword searches were conducted in the following major databases (keywords: Peszér Forest, Peszér, Kunpeszér, names of surrounding settlements, place names, etc.). Search results were reviewed systematically: Arcanum Digital Science Library (1,228 records); Hungaricana Library (962 records); The Biodiversity Heritage Library (224 records); Electronic Periodicals Archive and Database (529 records); Archaeological Database of the Hungarian National Museum (28 records); and the Photographic Collection of the Hungarian Museum of Ethnography (several hundred records).

A comprehensive literature review was conducted in the following thematic areas: botanical, entomological, soil science, and forestry publications related to the Peszér Forest; local history studies of surrounding settlements; late medieval charters mentioning nearby settlements; and records of *Pinus sylvestris* occurrences in the Peszér area. In addition, 18 of the 34 archival boxes of the Ráckeve estate forestry records were reviewed (Hungarian National Archives, National Archives); references to the Peszér area were extracted from Anton Kerner's 102 floristic articles (Kerner 1869–1879); excerpts relating to the Kunpeszér area were collected and digitized from the diary of Ádám Boros (Boros 1915–1972); and herbarium specimens from settlements in the vicinity of Kunpeszér were retrieved from national digitized herbarium collection databases (Hungarian Natural History Museum, University of Debrecen).

Between 2018 and 2021, I conducted semi-structured interviews with nine individuals concerning historical events of the second half of the 20th century, following the methodology of Newing et al. (2011).

To collect and process the information obtainable from maps, I used the following sources: manuscript maps (Cultural Heritage Portal, MNL), military surveys and 19th-century cadastral maps (Arcanum Maps), archival and recent aerial photographs and maps (Fentről.hu, Geoshop.hu Portal, Erdőtérkép Portal, Google Earth Pro); the vegetation-biotic database of the Kiskunság National Park Directorate for the Peszér Forest, and the digital elevation model of the area (LIDAR survey).

Prior to and during the historical investigation, I conducted field studies which, in addition to vegetation dynamic analyses (Molnár 2017), included microtopography analyses (Molnár 2021) and the registration of species occurrences, with the aim of enabling a more reliable interpretation of the historical data. For organizing GIS-compatible layers, I used the QGIS software package. The textual sources were organized in Microsoft Word, resulting in a 942-page compilation containing original excerpts and interviews (Molnár 2022).

3. RESULTS

3.1. Flora Continuity Hypothesis

3.1.1. Paleoecological and phylogenetic arguments for the pre-LGM origin of local populations

Recent paleoecological and phylogenetic research suggests that numerous plant species may have survived the LGM period within the Carpathian Basin. Increasing evidence indicates that not only typically cold-tolerant species persisted locally, but many other taxa as well. Based on paleoecological and phylogenetic studies, there are data supporting the local survival of marsh and fen species (e.g., *Filipendula ulmaria*, *Potentilla palustris*), thermophilous deciduous woody taxa (e.g., *Quercus*, *Corylus*, Tilia), forest herbaceous species (e.g., *Erythronium dens-canis*, *Hepatica transsilvanica*), as well as both thermophilous and cold-tolerant steppe–forest-steppe species (e.g., *Astragalus onobrychis*, *Linum hirsutum*, *Stipa capillata*) (see Table 1).

Table 1. Taxa that locally survived the LGM period according to paleoecological and phylogenetic studies. Bold: paleoecological evidence; italics: phylogenetic evidence; *: woody species.

	Grassland and open forest species	**Closed forest species**	**Wetland species**	**Not assignable**
Documented or Phylogenetically Inferred Local Survival	__Aconitum__ _Adenophora liliifolia_ _Adonis vernalis_ _Adonis volgensis_ _Allium marginatum_ __Artemisia__ _Astragalus onobrychis_ _Atriplex tatarica_ _Cirsium pannonicum_ __Convolvulus__ __Ephedra__ _Euphorbia seguieriana_ __Helianthemum__ *__Hippophae__ _Inula ensifolia_ _Iris aphylla_ *__Juniperus communis__ _Klasea lycopifolia_ *_Krascheninnikovia ceratoides_ _Linum flavum_ _Linum hirsutum_ __Plantago major–media__ __Polygonum viviparum__ __Sanguisorba__ _Scorzonera purpurea_ __Sedum__ __Solanum__ _Stipa capillata_	__Acer__ _Aposeris foetida_ _Cardamine trifolia_ *___Carpinus betulus___ *__Carpinus orientalis/Ostrya__ *__Corylus (C. avellana)__ _Erythronium dens-canis_ _Euphorbia carniolica_ *__Fagus (F. sylvatica)__ *__Fraxinus excelsior-típus__ *__Fraxinus ornus__ _Hacquetia epipactis_ _Helleborus niger_ _Hepatica transsilvanica_ *__Juglans__ *__Larix__ *__Lonicera nigra-típus__ *__Picea (P. abies)__ *__Pinus (Diploxylon-típus)__ *__Quercus__ *__Ribes alpinum-típus__ *__Sambucus__ *__Sorbus__ *__Tilia__ *__Ulmus__	*__Alnus__ *__Betula nana__ *__Betula pubescens__ __Drosera__ __Filipendula ulmaria__ __Galium palustre__ __Lemna__ __Myriophyllum__ __Polygonum bistorta__ __Potamogeton__ __Potentilla palustris__ __Rhynchospora__ *__Salix__ __Saxifraga hirculus-típus__ __Scutellaria galericulata__ __Sparganium__ __Sphagnum__ __Typha angustifolia/Sparganium__ __Typha minima__	__Botrychium__ __Cerastium__ __Chrysosplenium__ __Equisetum__ __Euphorbia__ __Filipendula__ __Galium__ __Ranunculus__ __Rumex__ __Saxifraga__ __Selaginella__ __Selaginella selaginoides__ __Thalictrum__ __Urtica__
Documented or Phylogenetically Inferred Presumed (Re)colonization	_Atriplex tatarica_ _Corynephorus canescens_ _Hippocrepis comosa_ _Sanguisorba minor_	*_Carpinus betulus_ *_Fagus sylvatica_		

Among the taxa that survived the LGM locally, as evidenced by paleoecological or phylogenetic data, there is a wide range of ecological requirements (e.g., grassland vs. forest, cold- vs. warm-adapted, herbaceous vs. woody), suggesting that the entire flora persisting in situ during the LGM likely comprised species with diverse ecological preferences.

3.1.2. Species-rich habitats under cold climates

Earlier studies, primarily based on palynological data, have suggested that the cold and dry climate of the LGM led to substantial species loss in the Carpathian Basin (see Járai-Komlódi 2003). However, more recent data and observations from Central Asia do not support this view. Under climatic conditions comparable to those of the LGM Carpathian Basin, both grasslands (Mühlenberg et al. 2000; Polyakova et al. 2016; Makunina & Parshutina 2017; Palpurina et al. 2017; Chytrý et al. 2019; Sabatini et al. 2022) and forests (Chytrý et al. 2007, 2008, 2012; Sabatini et al. 2022) in southern Siberia can be species-rich (114–69 species per 100 m²). This suggests that similarly species-rich grasslands and forests could have existed in the Carpathian Basin during the LGM (see Figure 2).

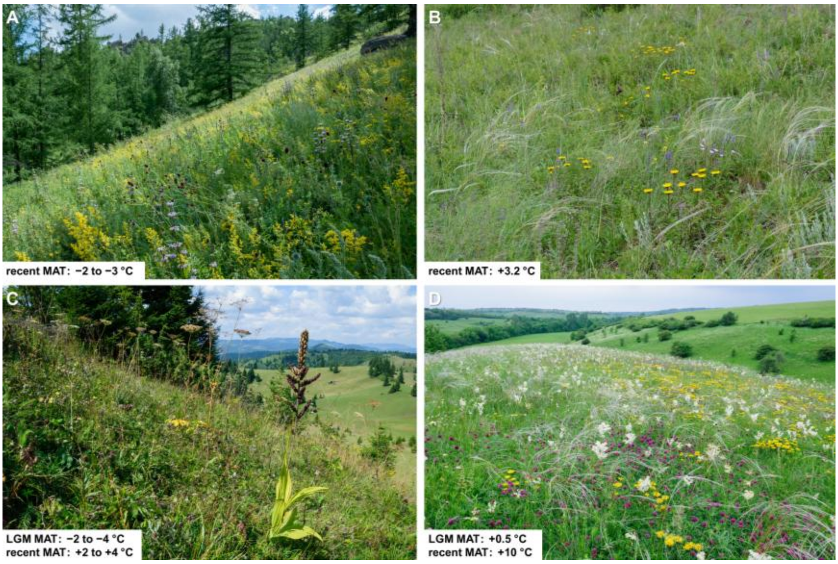

Figure 2. Species-rich meadow steppes occurring under different climatic conditions. Based on the occurrence of species-rich grasslands under climatic conditions similar to those of the LGM in the Carpathian Basin, it can be inferred that LGM habitats in the region were unlikely to be species-poor, and a species richness comparable to present-day levels is plausible. (A) 1650 m a.s.l., east of Ulaanbaatar, Khentii Mountains, Northern Mongolia; (B) 260 m a.s.l., near Severnoye, Southern Ural, Orenburg Region, Russia; (C) 1300 m a.s.l., Eastern Carpathians, Transylvania, Romania; (D) 150 m a.s.l., Tard, foreland of the Bükk Mountains, Hungary. (Climate data: CCSM4.0; photographs: Á. P. Molnár)

3.1.3. Cold tolerance of the contemporary native flora

Based on the comparison of species lists from the reference regions with the native flora of Hungary (http4), 1,404 out of the 1,748 native vascular plant species currently occurring in Hungary (80.3%) are found today under climatic conditions with the same or lower mean annual temperatures as those experienced in Hungary during the LGM (examples are given in Table 2).

Table 2. Examples of native plant species currently occurring in Hungary that are found today under climates with mean annual temperatures comparable to those in Hungary during the LGM. The numbers indicate in how many reference sites the species has been recorded (maximum 18); the lowest values are highlighted in green, and the highest in red. Habitat preferences of the species were determined following Horváth et al. (1995). Species names follow the Global Biodiversity Information Facility (GBIF) database (Page 2016).

	Grassland and open forest species		**Closed forest species**		**Wetland species**
9	*Achillea nobilis*	12	*Actaea spicata*	14	*Alisma plantago-aquatica*
8	*Adonis vernalis*	14	*Aegopodium podagraria*	11	*Butomus umbellatus*
4	*Anacamptis morio*	8	*Anemone nemorosa*	18	*Callitriche palustris*
12	*Anemone sylvestris*	6	*Asarum europaeum*	7	*Carex elata*
12	*Artemisia campestris*	5	*Brachypodium sylvaticum*	12	*Catabrosa aquatica*
4	*Aster amellus*	2	*Cardamine trifolia*	14	*Cicuta virosa*
13	*Brachypodium pinnatum*	7	*Carex sylvatica*	16	*Eleocharis acicularis*
18	*Campanula glomerata*	5	*Circaea lutetiana*	9	*Glyceria fluitans*
15	*Centaurea scabiosa*	13	*Convallaria majalis*	10	*Glyceria maxima*
4	*Colchicum autumnale*	7	*Corylus avellana*	8	*Hydrocharis morsus-ranae*
2	*Dictamnus albus*	16	*Elymus caninus*	7	*Iris pseudacorus*
3	*Echinops ritro*	3	*Euonymus europaeus*	13	*Lathyrus palustris*
6	*Festuca rupicola*	4	*Fagus sylvatica*	12	*Lemna minor*
9	*Filipendula vulgaris*	8	*Fragaria moschata*	2	*Lindernia procumbens*
9	*Fragaria viridis*	6	*Fraxinus excelsior*	15	*Menyanthes trifoliata*
2	*Iris pumila*	7	*Hepatica nobilis*	13	*Nuphar lutea*
10	*Koeleria macrantha*	10	*Lapsana communis*	9	*Nymphaea alba*
2	*Linum flavum*	3	*Lathyrus niger*	16	*Phalaris arundinacea*
3	*Melica ciliata*	17	*Maianthemum bifolium*	17	*Phragmites australis*
2	*Orlaya grandiflora*	7	*Mycelis muralis*	12	*Potamogeton lucens*
9	*Oxytropis pilosa*	15	*Paris quadrifolia*	15	*Ranunculus trichophyllus*
16	*Plantago media*	18	*Poa nemoralis*	8	*Sagittaria sagittifolia*
4	*Potentilla recta*	17	*Populus tremula*	13	*Schoenoplectus lacustris*
9	*Pulmonaria mollis*	3	*Primula acaulis*	5	*Scrophularia umbrosa*
3	*Rosa gallica*	4	*Pulmonaria officinalis*	2	*Sium sisaroideum*
2	*Salvia nutans*	5	*Rhamnus cathartica*	6	*Stratiotes aloides*
3	*Stachys recta*	3	*Rumex sanguineus*	10	*Thelypteris palustris*
10	*Stipa pennata*	11	*Stachys sylvatica*	10	*Typha angustifolia*
2	*Teucrium chamaedrys*	2	*Ulmus minor*	11	*Typha latifolia*
5	*Veronica austriaca*	4	*Viola odorata*	15	*Utricularia vulgaris*

Of the 18 reference sites, the 12 sites where the mean annual precipitation was equal to (535–850 mm) or lower (sometimes substantially lower) than that of Hungary during the LGM encompass 1,089 native Hungarian vascular plant species (62.3%).

When excluding biogeographically more distant reference sites, i.e., considering only the 11 sites located west of the Ural Mountains (biogeographically closer), 76.8% of the native Hungarian flora (1,343 species) are represented.

Despite the uncertainties inherent in the analysis, these results clearly indicate the orders of magnitude involved, suggesting that local survival of most species was theoretically possible. Even when accounting for precipitation and excluding biogeographically distant sites, the estimated survival rate remains high (62.3% and 76.8%, respectively).

3.2. Peszér Forest

According to the earliest sources (18th–19th centuries), the Peszér Forest was a forest-patch network with a grassland-dominated matrix prior to forestry transformations (e.g., Anonymus ~1787; Blahausch 1846; Figure 3). The forest component was characterized by birch and poplar stands in the southern and northern parts, and oak stands in the central part (Blahausch 1846). Moving sand dunes occurred exclusively in the northern section (e.g., First and Second Military Surveys). The areas between the forest patches were characterized by moister inter-dune meadows and drier sandy grasslands on the dunes. (Landbeck 1843; Blahausch 1846; Frivaldszky 1859).

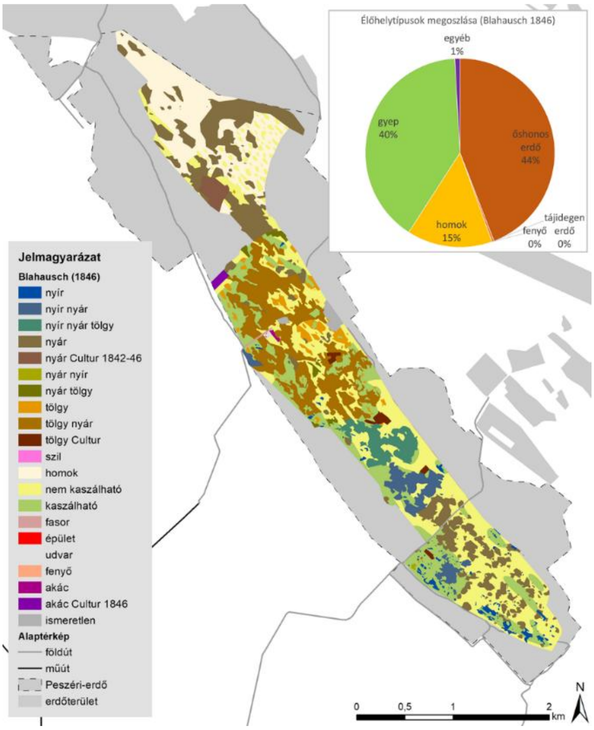

Figure 3. Processed version of the first (original) layer of Blahausch's (1846) map, and the proportions of habitat groups.

The primary (i.e., naturally established, non-planted) forest stands of the Peszér Forest (oak, poplar, and birch patches) were managed in the 18th–19th centuries using multi-decade rotation cycles (e.g., Blahausch 1846; Ballabár 1835). Afforestation began in the mid-19th century, initially focusing on converting clearings into forest (Blahausch 1846), and gradually extended to areas where timber had been harvested, establishing plantations: "*Between 1922 and 1936, for economic reasons, approximately 100 ha of Kunpeszér's oak-poplar stands were converted into monoculture Robinia pseudoacacia plantations*" (Babos 1958).

In the 18th century, the clearings were only partially mown, while most were grazed (e.g., Anonymus ~1787). From the 19th century, there is clear evidence of grazing in the northern and southern parts of the forest (Cadastral Map 1880), whereas the central part was presumably grazed much less, or not at all. There are no specific records of mowing from the 19th century. In the 20th century, grazing mostly occurred only along the edges, while in the inner clearings it may have taken place only for short periods (István Gengelicki, ex verb. 2021; Józsefné Kajdácsi, ex verb. 2021). Some of the inner clearings were manually mown until the late 1960s (Jánosné Kovács, ex verb. 2021; István Gengelicki, ex verb. 2021). Throughout the 18th–20th centuries, the intensity of grassland use in the estate forest's clearings cannot be precisely reconstructed, but scattered data suggest that it was likely less intensive than in the surrounding landscape, at least in the central part of the forest. This lower intensity of use may have had a beneficial effect on species composition and contributed to the survival of certain species.

The decline in the area of clearings began already in the mid-19th century (Frivaldszky 1859). The grasslands were gradually afforested (e.g., Blahausch 1846; Véssey 1881; Kolossváry 1961), and in the remaining clearings, intensive shrub encroachment has occurred in recent decades (aerial and satellite imagery). As a result, the grassland component, which still accounted for 40% of the area in the mid-19th century (Blahausch 1846), has decreased to 2.8% today (Erdélyi & Hartdégen 2022). Alongside this drastic decline of the grassland component, the extent of edge habitats has also significantly diminished. The ecologically most valuable edges – those between forests composed of native tree species and grasslands – measured 88.9 km in 1846, while in 2015 they measured only 6.8 km, representing a 92.4% decrease between the two time points (see Figure 4).

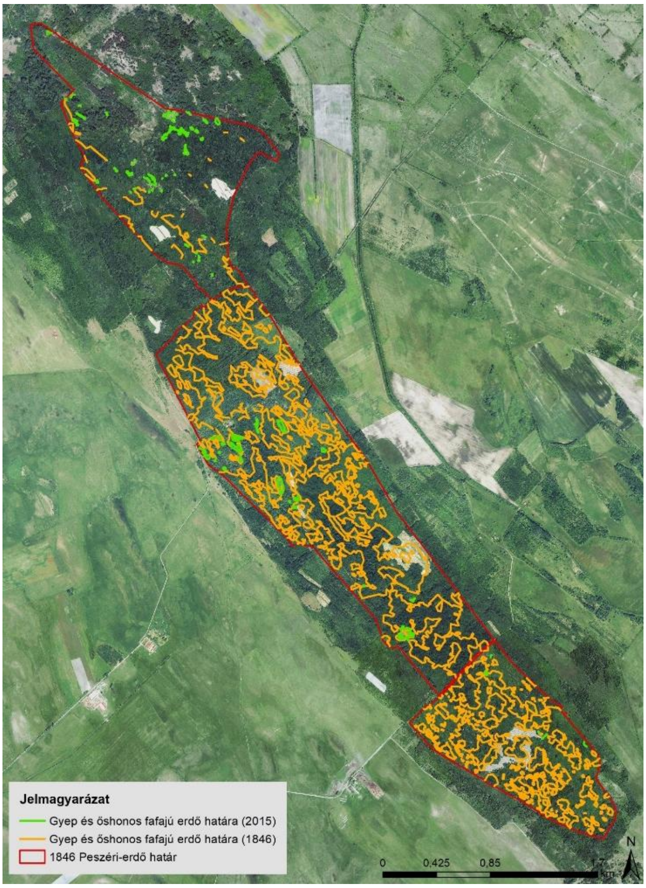

Figure 4. Change in ecologically valuable edge habitats (i.e., the boundaries between forests of native tree species and grasslands) between 1846 (Blahausch 1846; orange line) and 2015 (own digitization from 2015 aerial imagery; green line).

The unique species assemblage of the Peszér Forest known from the 19th century was likely maintained by the combination of heterogeneous habitats, a mosaic of grasslands and forests, and low-intensity grassland use. The last records of *Melanargia russiae* originate from surveys in 1912 (Frohawk & Rothschild 1912; Frohawk & Rothschild 1913; Gurney 1913), *Onconotus servillei* was last recorded in 1879 (Vángel 1885), and *Dracocephalum austriacum* in 1902 (Abafi-Aigner 1902). The extinction of these valuable grassland species was almost certainly driven by the afforestation of the clearings.

4. CONCLUSIONS AND RECOMMENDATIONS

One of the primary goals of nature conservation is the long-term conservation of ecological systems and their constituent species (Standovár & Primack 2001). Historical ecological research provides information that supports long-term thinking in the development of conservation strategies and the prioritization of actions. Strategies and concepts grounded in robust, comprehensive knowledge can significantly enhance the effectiveness of preserving our natural heritage.

The hypothesis casts new light on certain biogeographical and ecological issues that also have conservation relevance. For instance, if the impoverishment and subsequent recolonization of the flora of the Carpathian Basin could not have been as dynamic at the regional scale as previously assumed (see e.g. Borbás 1900; Rapaics 1918; Soó 1964; Zólyomi 1942; Debreczy 1981; Hendrych 1996; Borhidi 2004; Willner et al. 2021), it cannot be ruled out that the flora of certain landscapes (below 1800 m a.s.l.) may have been largely continuous from before the LGM, through the LGM, and up to the present day (Figure 5; for grasslands see: Cieślak 2014; Kajtoch et al. 2016).

Figure 5. According to the Flora Continuity Hypothesis, during the LGM the Carpathian Basin may have harbored species-rich habitats containing the vast majority of today's native plant species. The illustration depicts the southern foreland of the Mátra Mountains at a mid-summer timepoint during the LGM. The species shown in the foreground were selected from the present-day flora of the landscape based on the cold-tolerance analysis and phylogenetic evidence. The depiction of vegetation patterns and fauna is based on relevant paleoecological and archaeozoological studies (Illustration by Márton Zsoldos, 2023).

The hypothesis also raises the possibility that among various species assemblages, combinations with a very long local history (both plant–plant and animal–plant) may be common. This highlights the need to devote particular attention, from both conservation and ecological perspectives, to species-rich, well-structured, near-natural habitats (Rakonczay 2002; Illyés & Bölöni 2007; Molnár et al., in press).

The key message of the Flora Continuity Hypothesis for nature conservation is that the regional floras we aim to protect may have been present in our landscapes for much longer than previously assumed when major conservation strategies were developed in recent decades. The potential for long-term local persistence highlights the greater evolutionary distances both within and between populations across landscapes. This has two conservation implications: 1) in habitat restoration programs involving species translocations, greater caution is needed when determining dispersal distances, as inter-landscape propagule transfer may carry significant introgression risks; 2) when habitats are altered or lost (e.g., through shrub encroachment, afforestation, plowing, or urbanization), preventing local extinctions should be prioritized, because such events may lead to the loss of populations representing evolutionary lineages that have persisted locally for tens of thousands of years, for which no replacement is possible.

The hypothesis also raises the possibility that among different species assemblages, combinations with very long local histories – both plant–plant and plant–animal – may be common. This highlights the conservation importance of species-rich, well-structured, near-natural habitats, which deserve particular attention in management and protection strategies (Rakonczay 2002; Molnár et al., in press).

When prioritizing species, the hypothesis conveys two key messages: 1) it is particularly important to conserve species that have potentially persisted in our landscapes for longer periods, as their local populations may represent older, landscape-specific evolutionary lineages; 2) species that likely survived the LGM in situ are also more likely to endure a potential future glacial period, meaning that the conservation of their local populations is relevant not only for the remainder of the current interglacial but also for a much longer timescale.

Overall, the main message of the hypothesis is that the preservation of native populations and their genetic integrity –even for relatively common species – deserves greater emphasis, as these populations may represent very ancient evolutionary lineages that have long been present in the landscape.

Based on the historical-ecological analysis of the Peszér Forest, it can be concluded that in the 19th century the forest consisted of a fine-grained mosaic of grasslands and woodlands, which likely played a key role in sustaining a species composition that is unique at the landscape level.

With the reduction of grasslands, numerous valuable species became locally extinct, and most of the remaining species are today confined to forest edges and clearings. The main message of the historical investigation is therefore that the fine-grained grassland–forest mosaic is crucial for the conservation of the Peszér Forest's unique species assemblage. In recent years – partly as a result of this study – several clearings have been created, and grassland reconstruction suitable for the site has been initiated using propagules sourced from the surrounding landscape (OAKEYLIFE project).

The historical investigation also helps local conservation decision-making to view the Peszér Forest in a historical context, rather than relying solely on knowledge derived from interpreting its current state.

It is well known from numerous cases that the conservation of ecological systems is not a simple task, and the development and implementation of a well-founded management strategy requires knowledge at general, regional, and specifically local scales. Under current conditions, the preservation of habitats and species appears to be an increasingly difficult challenge. However, the scientific toolkit is now far broader than in previous periods (e.g., digital databases, accessible international literature, and opportunities for project-based funding). Therefore, we advocate for even stronger support of foundational research to inform regional and local conservation planning.

5. NEW SCIENTIFIC RESULTS

5.1. Flora Continuity Hypothesis

(1.1) I demonstrated that, based on paleoecological and phylogenetic evidence, species that survived the Last Glacial Maximum (LGM) in situ exhibit highly diverse ecological preferences (e.g., grassland vs. forest, cold- vs. warm-adapted, herbaceous vs. woody), suggesting that the entire flora surviving the LGM locally may have consisted of species with a wide range of ecological niches.

(1.2) In present-day landscapes with climates similar to that of the Carpathian Basin during the LGM, both grasslands and forests can be species-rich, suggesting that, contrary to previous views, the habitats of the Carpathian Basin may also have been characterized by high species richness during the LGM.

(1.3) Analysis of the climate tolerance of Hungary's current native flora indicates that 80.3% of species presently occur in areas with mean annual temperatures equal to or lower than those in Hungary during the LGM. Even when accounting for precipitation and excluding biogeographically distant regions, the proportion of climate-tolerant species remains high (62.3%; 76.8%). These results suggest that the majority of Hungary's present-day native vascular flora would have been potentially capable of tolerating the LGM climate of the region.

(1.4) Based on a reassessment of previous views on the origin of the Carpathian Basin's current native vascular flora (the Postglacial Recolonization Hypothesis), I proposed a new, alternative hypothesis – the Flora Continuity Hypothesis. According to this hypothesis, the majority of the region's native vascular flora (approximately 75–85%) survived the LGM in situ, indicating that most of Hungary's native species may have been continuously present in the region throughout the Late Pleistocene and Holocene.

5.2. Peszér Forest

(2.1) I conducted a historical ecological investigation of the Peszér Forest over the past 250 years, analyzing land-use practices and vegetation changes in the area. According to the earliest sources (18th–19th centuries), the Peszér Forest was a network of forest patches embedded in a grassland-dominated matrix prior to forestry modifications. The reduction of open grassland areas began already by the mid-19th century. The grasslands were gradually afforested, and on the remaining clearings, intensive shrub encroachment has occurred in recent decades. As a result, the grassland component, which still accounted for 40% in the mid-19th century, has decreased to 2.8%, while the forest–grassland edges have shrunk from 88.9 km to 6.8 km.

(2.2) During the 18th–20th centuries, it is not possible to reconstruct precisely the intensity of grassland use on the clearings within the manorial forest, but scattered data suggest that these areas – at least the central part of the forest – were likely used less intensively than the surrounding grasslands. This reduced use may have had a favorable effect on the species composition of the grasslands and could have contributed to the survival of certain species.

(2.3) The primary (i.e., non-planted) forest stands of the Peszér Forest (oak, poplar, and birch patches) were managed in the 18th–19th centuries with relatively short cutting cycles. While these short rotations may have contributed to the persistence of the clearings, they also indicate intensive utilization of the forest stands.

(2.4) The unique species assemblage of the Peszér Forest known from the 19th century was likely maintained by the combination of heterogeneous habitats, a mosaic of grasslands and forests, and low-intensity grassland use. The extinction of grassland species last recorded at the end of the 19th and beginning of the 20th century was most likely caused by the afforestation of the clearings (e.g., *Melanargia russiae*, *Onconotus servillei*, *Dracocephalum austriacum*).

6. LIST OF PUBLICATIONS RELATED TO THE DISSERTATION TOPIC

6.1. In English

Molnár, Á. P., Demeter, L., Biró, M., Chytrý, M., Bartha, S., Gantuya, B. & Molnár, Zs. (2023): Is there a massive glacial–Holocene flora continuity in Central Europe? Biological Reviews 98(6): 2307–2319.

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Varga A., Molnár Zs., Biró M., Demeter L., Gellény K., Miókovics E., Molnár Á., Molnár K., Ujházy N., Ulicsni V. & Babai D. (2016): Changing year-round habitat use by extensively herded cattle, sheep and pigs in East-Central Europe between 1940 and 2014: Consequences for conservation management. Agriculture Ecosystems & Environment 234: 142–153.

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6.2. In Hungarian

Molnár Á. P., Máté K. és Bánfi P.: „Nagyvizites módszertan” – Ökológiai koncepcióra, közös tudásalkotásra és visszatérő terepi egyeztetésekre épülő természetvédelmi élőhelykezelési gyakorlat a Körös Maros Nemzeti Parkban. Természetvédelmi Közlemények 31. (in press)

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