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Is there a massive glacial–Holocene flora continuity in Central Europe?

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ABSTRACT

The prevailing paradigm about the Quaternary ecological and evolutionary history of Central European ecosystems is that they were repeatedly impoverished by regional extinctions of most species during the glacial periods, followed by massive recolonizations from southern and eastern refugia during interglacial periods. Recent literature partially contradicts this view and provides evidence to re-evaluate this Postglacial Recolonization Hypothesis and develop an alternative one. We examined the long-term history of the flora of the Carpathian (Pannonian) Basin by synthesising recent advances in ecological, phylogeographical, palaeoecological and palaeoclimatological research, and analysing the cold tolerance of the native flora of a test area (Hungary, the central part of the Carpathian Basin). We found that (1) many species have likely occurred there continuously since before the Last Glacial Maximum (LGM); (2) most of the present-day native flora (1404 species, about 80%) can occur in climates as cold as or colder than the LGM (mean annual temperature ≤+3.5°C); and (3) grasslands and forests can be species-rich under an LGM-like cold climate. These arguments support an alternative hypothesis, which we call the Flora Continuity Hypothesis. It states that long-term continuity of much of the flora in the Carpathian Basin is more plausible than regional extinctions during the LGM followed by massive postglacial recolonizations. The long-term continuity of the region's flora may have fundamental implications not only for understanding local biogeography and ecology (e.g. the temporal scale of processes), but also for conservation strategies focusing on protecting ancient species-rich ecosystems and local gene pools.

Key words: biodiversity conservation, Carpathian Basin, Last Glacial Maximum, paleoecology, Pleistocene, recolonization, refugia, vegetation history, phylogeography.

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I. INTRODUCTION

The protection of primary and species-rich ecosystems has long been among the key targets of nature conservation. Therefore, demonstrating long-term continuity of ecosystems is highly relevant for nature conservation policies and strategies (Médail & Diadema, 2009; Veldman *et al.*, 2015; Nerlekar *et al.*, 2022). Ecologists also frequently emphasise the importance of understanding long-term (e.g. millennial-scale) processes (e.g. Wardle *et al.*, 2009), long-term coexistence of species in certain ecosystems (Veldman *et al.*, 2015; Tsakalos *et al.*, 2018), and long-term co-evolution of plants and animals (e.g. Thomas & Schönrogge, 2019). Recent genetic and palaeoecological studies also highlight the need for increased recognition of ancient ecosystems (Feurdean *et al.*, 2018; Hájková *et al.*, 2011).

Rapidly developing methods of Quaternary palaeoecology allow for the reconstruction of ever more complex histories, often leading to a substantial re-evaluation of existing models, for example, of landscape-scale vegetation patterns (e.g. Magyari *et al.*, 2010; Binney *et al.*, 2017), and of the timing and causes of vegetation changes (Willis *et al.*, 1997; Sümegi *et al.*, 2022) and megaherbivore activity (Kerley, Kowalczyk & Cromsigt, 2012; Wooller *et al.*, 2021; Wang *et al.*, 2021). However, examples of evidence-based reconstruction of the entire past floras at regional scales are still rare due to methodological and financial constraints (Pardoe *et al.*, 2021).

During the Last Glacial Maximum [LGM, 26.5–19 thousand calendar years before present (ka cal BP); Clark *et al.*, 2009], Europe was divided into three major parts based on the extent of ice and permafrost: (*i*) Fennoscandia and its surroundings, which were covered with ice sheets (Hughes *et al.*, 2016); (*ii*) the Mediterranean, where permafrost was absent except in the mountains (Oliva *et al.*, 2018); and (*iii*) a middle part between these two, where permafrost was spatially discontinuous (Lindgren, Hugelius & Kuhry, 2018; Ruszkiczay-Rüdiger & Kern, 2016; Stadelmaier *et al.*, 2021) and the Alps were largely ice covered (Seguinot *et al.*, 2018). These three parts have strikingly different flora and vegetation histories: postglacial recolonization in the north (Hewitt, 1999; Brochmann *et al.*, 2003), Pleistocene–Holocene continuity in the south (Weiss & Ferrand, 2007; Médail & Diadema, 2009; González-Sampériz *et al.*, 2020), and a mix of postglacial recolonization and LGM survival in the middle part (Magri *et al.*, 2006; Birks & Willis, 2008; Varga, 2009; Magyari *et al.*, 2010; Schmitt & Varga, 2012; Chytrý *et al.*, 2017*a*; Postolache *et al.*, 2017; Kirschner *et al.*, 2020). There is as yet no information on the proportion of plant species that survived the LGM in the middle part, an area which includes our focal area, the Carpathian Basin (also called the Pannonian Basin or Carpatho-Pannonian Region; Csorba *et al.*, 2018).

In this review, we provide a perspective on flora continuity *versus* postglacial recolonization in the Carpathian Basin based on recent ecological, palaeoclimatic, palaeoecological and phylogeographical literature, and an analysis of the cold tolerance of the native flora in a test area (Hungary, the central part of the Carpathian Basin). We propose a new hypothesis, the Flora Continuity Hypothesis, which states that there was potentially massive long-term continuity of vascular flora in the Carpathian Basin during the Late Pleistocene and Holocene, from before the LGM to the present. While the Postglacial Recolonization Hypothesis assumes that most native plant species now present in the Carpathian Basin colonised the region after the LGM, our new hypothesis assumes the opposite: most of the native plant species were present in the region throughout the LGM, while only a limited number of species, far fewer than previously thought, colonised the region after the LGM.

II. ENVIRONMENTAL CONDITIONS IN THE CARPATHIAN BASIN DURING THE LGM

During the LGM, the climate in 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 in the lowlands, between −3 and 1 °C in the hilly landscapes and low mountains, and between −10 and −3°C in the Carpathian mountains (throughout this review, climate data are derived from the Community Climate System model, CCSM4.0: https://www.cesm.ucar.edu/models/ccsm4.0/ccsm/). The corresponding temperature values for these three landscape types at present are between 9 and 12 °C, 5 and 9 °C, and −2 and 5 °C, respectively (CCSM4.0). Before the LGM, only in the Riss glaciation (300–130 ka cal BP) were periods as cold as (or slightly colder than) the LGM, and the Carpathian Basin was not ice covered at that time either (Ehlers, Gibbard & Hughes, 2011; Batchelor *et al.*, 2019). After the last interglacial (Riss–Würm: 130–115 ka cal BP; Dahl-Jensen *et al.*, 2013), the Würm glacial period was relatively cold, with the coldest phase being the LGM (Andrews, 2009).

Both during the LGM and today, a strong gradient of total annual precipitation existed between lowlands and mountains in the Carpathian Basin (LGM: 540–1000 mm,

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present: 500–1300 mm; CCSM4.0). Data are inconsistent, suggesting both arid climate (Fuhrmann *et al.*, 2019; Obreht *et al.*, 2019) and humid/mild climate (Ludwig *et al.*, 2021) in the Carpathian Basin during the LGM. Precipitation data from the CCSM4.0 model indicate a humid climate. It can be assumed that the climate was not uniform during the LGM, with different periods of either relatively humid or more arid conditions (Sümegi *et al.*, 2022). Local humidity and aridity were also affected by topography (e.g. dry south-facing slopes, wet valleys, wetlands on basin bottoms) and vegetation (e.g. shading by forest canopy). Consequently, most landscapes were likely to include a wide range of soil humidity levels, making it possible for species with a variety of moisture requirements to inhabit the region.

During the LGM, permafrost was continuous in high mountains, discontinuous in lower mountains and hilly landscapes, and largely absent from the lowlands (Ruszkiczay-Rüdiger & Kern, 2016; Velasquez *et al.*, 2021; Stadelmaier *et al.*, 2021; Fig. 1). Glaciers were restricted to small areas, occurring mostly in the Tatra mountains (Zasadni & Kłapyta, 2014) and the Southern Carpathians (Ehlers *et al.*, 2011).

In spite of rapid advances in palaeoclimate modelling, there are still considerable uncertainties in the CCSM4.0 model for the LGM in this region, which mostly concern precipitation rather than temperature (see e.g. Ludwig *et al.*, 2016). The spatial distribution of permafrost during the LGM suggests that the climate could not have been significantly colder than that predicted by the models (currently, continuous permafrost occurs below −8°C MAT, and discontinuous permafrost below −4°C MAT; Levavasseur *et al.*, 2011). Mean precipitation in the LGM predicted by the CCSM4.0 model appears to be too high, as palaeoecological (mainly malacological) studies of this region indicate much lower values (Ludwig *et al.*, 2021; Sümegi *et al.*, 2022).

III. FLORA AND VEGETATION OF THE CARPATHIAN BASIN DURING THE LGM

The current flora and vegetation of the Carpathian Basin is diverse (Ciocârlan, 2000; Doniță *et al.*, 2005; Jarolímek & Šibík, 2008; Bölöni, Molnár & Kun, 2011; Chytrý *et al.*, 2017*a*; Molnár *et al.*, 2018). While the composition and history of the flora and vegetation of the Carpathian mountains share many common characteristics with other European mountains, the central part of the Carpathian Basin (Pannonian biogeographical region) is a distinct biogeographical entity in Europe (Sundseth, 2010). This basin is rich in Continental, Pontic, (Sub-)Mediterranean and European flora elements (Rédei & Horváth, 1995; Ciocârlan, 2000; Chytrý *et al.*, 2022).

During the LGM, the lowlands, hilly landscapes and mountains of the Carpathian Basin were covered by grass steppes, meadow steppes, tundra and forests on loess, rocky, sandy and saline soils, forming mosaics with various wetland habitats (Feurdean *et al.*, 2014, 2015; Magyari *et al.*, 2014*a*; Janská *et al.*, 2017; Kuneš *et al.*, 2008; Sümegi *et al.*, 2022).

The prevailing view of the history of flora and vegetation during the LGM in the Carpathian Basin is based on the assumption that the flora was substantially impoverished (e.g. cold-resistant, species-poor mammoth steppe flora; see e.g. Járai-Komlódi, 2003), and that most of the present-day species (re)colonised the region from southern and eastern refugia during the Late Glacial and Holocene (e.g. Boros, 1958; Járai-Komlódi, 2003; Borhidi, 2004; Kun, 2018). However, this Postglacial Recolonization Hypothesis has never been well supported due to the lack of reconstructions of the entire flora. Moreover, it has been challenged for some groups by recent studies using novel approaches and techniques (e.g. Schmitt & Varga, 2012; Kajtoch *et al.*, 2016; Kirschner *et al.*, 2020; Willner *et al.*, 2021).

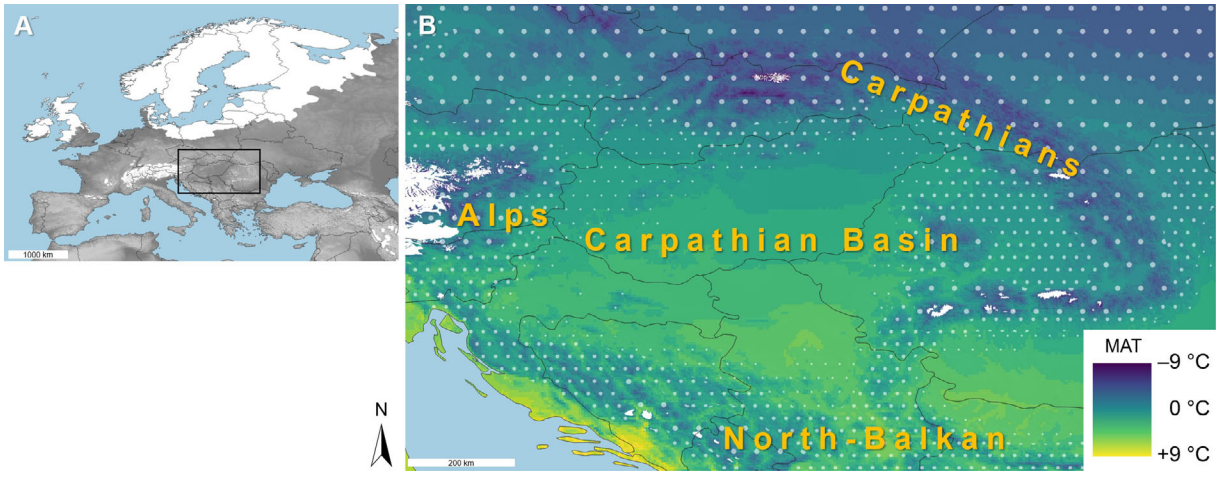

Fig. 1. Europe (A) and the Carpathian Basin (B) in the Last Glacial Maximum (26.5–19 ka cal BP). Mean annual temperature (MAT) ranged between +5°C in the southern lowlands and −10°C in northern mountains (data derived from CCSM4.0). The distribution of ice sheets (white areas) is based on Ehlers *et al.* (2011). In B, dots show the distribution of permafrost (large dots = continuous permafrost; middle-sized dots = discontinuous permafrost; small dots = sporadic permafrost). Areas with no dots had no permafrost present. The distribution of permafrost is based on Velasquez *et al.* (2021) and Stadelmaier *et al.* (2021).

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IV. ARGUMENTS SUPPORTING THE FLORA CONTINUITY HYPOTHESIS

(1) Palaeoecological and phylogeographical arguments for a pre-LGM origin of local plant populations

Recent palaeoecological and phylogeographical studies have demonstrated the survival of many plant (and animal) species during the LGM. There is increasing evidence for the survival during the LGM of not only typical cold-tolerant species like *Kraschenninnikovia ceratoides* (Seidl *et al.*, 2020, 2021) and *Scorzonera purpurea* (Kajtoch *et al.*, 2016; Meindl *et al.*, 2016). There is also evidence or assumption of occurrence of several tree species in climatic islands, which maintain favourable mesoclimatic conditions in contrast to the harsher conditions in the landscape matrix. Such so-called 'extra-Mediterranean cryptic refugia' (Stewart & Lister, 2001) have been identified in the Carpathian Basin, e.g. for *Quercus*, *Corylus*, *Fraxinus excelsior*-type, *Ulmus*, *Fagus*, and *Carpinus betulus* (Willis, Rudner & Sümegi, 2000; Willis & Van Andel, 2004; Tzedakis, Emerson & Hewitt, 2013; Feurdean *et al.*, 2014; Magyari *et al.*, 2014*b*). Phylogeographical studies have even provided evidence for the LGM survival of some forest-dwelling herbaceous plant species, e.g. *Erythronium dens-canis* (Bartha *et al.*, 2015) and *Hepatica transsilvanica* (Laczkó & Sramkó, 2020). Additionally, malacological data provide direct evidence for the existence of forest refugia in the Carpathians during the LGM (Juřičková, Horáčková & Ložek, 2014). The survival of many cold-tolerant and some thermophilous steppe species, at least at favourable microsites, during the LGM, was also proved or assumed by palynological (Willis *et al.*, 2000; Jankovská & Pokorný, 2008; Magyari *et al.*, 2010, 2014*a*), biogeographical (Varga, 2009; Chytrý *et al.*, 2017*b*), palaeodistribution modelling (Divíšek *et al.*, 2022) and phylogeographical studies (Cieślak, 2014; Kajtoch *et al.*, 2016; Kirschner *et al.*, 2020; Willner *et al.*, 2021, and references therein). Examples of these species include *Adonis vernalis* (Seidl *et al.*, 2022), *Adonis volgensis* (Kajtoch *et al.*, 2016), *Astragalus onobrychis* (Záveská *et al.*, 2019; Plenk *et al.*, 2020), *Atriplex tatarica* (Hodková *et al.*, 2019), *Cirsium pannonicum* (Cieślak, 2014), *Euphorbia seguieriana* (Frajman *et al.*, 2019), *Iris aphylla* (Wróblewska *et al.*, 2010; Kajtoch *et al.*, 2016), *Klasea lycopifolia* (Cieślak, 2013), *Kraschenninnikovia ceratoides* (Seidl *et al.*, 2020, 2021), *Linum flavum* (Cieślak, 2014; Kajtoch *et al.*, 2016; Plenk *et al.*, 2017), *Linum hirsutum* (Cieślak, 2014), *Pentanema ensifolium* (syn. *Inula ensifolia*) (Cieślak, 2014), *Scorzonera purpurea* (Kajtoch *et al.*, 2016; Meindl *et al.*, 2016) and *Stipa capillata* (Durka *et al.*, 2013). Thus, palaeoecological and phylogeographical evidence is accumulating for many species with diverse ecological requirements (i.e. steppe, meadow, forest and wetland species) that supports the Flora Continuity Hypothesis.

(2) Cold tolerance of the present-day native flora

One of the key questions is how many species of the native flora could have tolerated the cold climate of the LGM. We investigated the cold tolerance of species based on their present distribution. We chose Hungary as a test area that is sufficiently large and representative of the Carpathian Basin landscape. We investigated how many of the present-day native Hungarian vascular plant species occur today elsewhere under climates as cold as Hungary during the LGM or colder. All MAT values were derived from the CCSM4.0 model. For this comparison, we collected species occurrence data from regions of Eurasia with a MAT below +3.5°C (Fig. 2).

We analysed the native vascular flora (Tracheophyta) from our test area (Horváth *et al.*, 1995; Király *et al.*, 2009) excluding hybrids, archaeophytes and neophytes (Csiky *et al.*, 2023), but including recently extinct native species (Horváth *et al.*, 1995). We extracted species occurrence data from the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org/) for 18 reference areas in Europe and Northern Eurasia (Fig. 2C; see online Supporting Information, Appendix S1 for details). Reference areas were selected to avoid larger cities and botanical gardens (see https://tools.bgci.org/map.php). For several of these reference areas, we only used occurrence data from above a certain elevation: above 1700 m above sea level (a.s.l.) in the Alps (Austria and Switzerland), above 1200 m a.s.l. in the Western Carpathians (Slovakia and Poland) and Sudetes (Poland and the Czech Republic), above 700 m a.s.l. in Fennoscandia (Norway and Sweden), and above 2200 m a.s.l. in the Greater Caucasus (Russia, Georgia, Azerbaijan). For the Mongolian reference area, we used flora lists (Gubanov, 1996; Urgamal *et al.*, 2014) from regions colder than +3.5°C MAT. Plant names follow the GBIF database (Page, 2016).

The collated flora lists of the reference areas were combined and compared with our list of native Hungarian flora, and the percentage overlap between these two lists was calculated (see Appendix S3; see Appendix S2 for a discussion of uncertainties in our analysis). We found that of the 1748 native species that occur in Hungary today, 1404 species (80.3%) are also found elsewhere under climates as cold as in Hungary during the LGM (Table 1, Appendix S3).

Since the LGM was the coldest climatic period of the Late Pleistocene, and given uncertainties regarding modelling of precipitation and other bioclimatic parameters (e.g. summer and winter temperatures) in this region during the LGM, we focused on MAT (see Appendix S2 for further details). However, we provide a map of mean annual precipitation (MAP) in Appendix S2. Of the 18 reference areas, 12 had precipitation equal to (535–850 mm) or lower (sometimes much lower) than Hungary in the LGM (reference areas 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18; see Fig. S1). These reference areas contained 1089 (62.3%) of the species present in the Hungarian native flora.

Six of the reference areas are relatively distant biogeographically, which increases the uncertainty of taxonomic identity. Therefore, we calculated the overlap value using only those 11 reference areas (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11) that are not further from Hungary than the Ural mountains.

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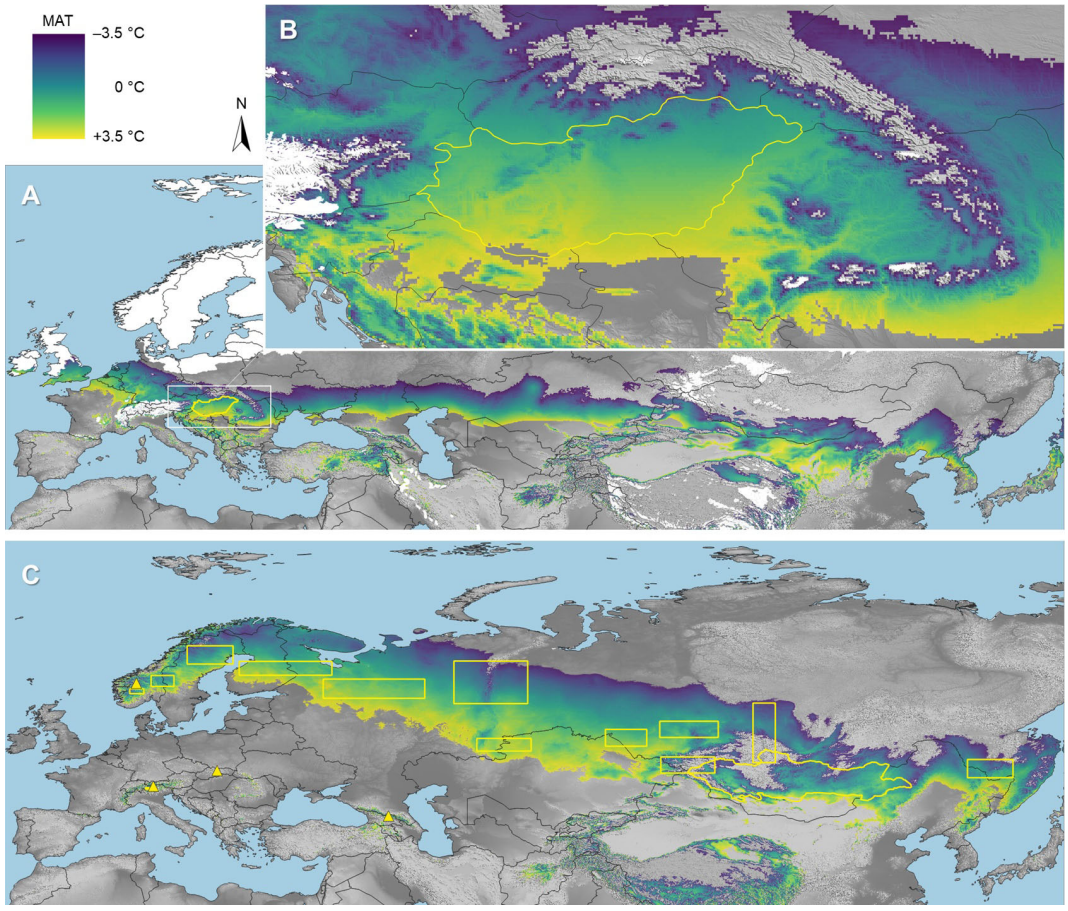

Fig. 2. Zones of similar mean annual temperature (MAT) in Eurasia: (A) Areas in Eurasia with MAT in the Last Glacial Maximum (LGM) similar to that in the test area in the LGM (Hungary, yellow outlined area in white boxed region; MAT between +3.5 and −3.5°C, based on CCSM4.0). (B) A close-up of the white boxed area in A showing MAT of the test area in the LGM. (C) Areas with current MAT similar to MAT in the test area during the LGM. To assess the cold tolerance of the native flora in the test area to conditions in the LGM, we collated lists of vascular plants from 18 reference areas with a present-day MAT that is as cold as or colder than the LGM MAT of the test area. These reference areas are shown by the 13 yellow rectangles (note small box in the Alps), four additional mountainous areas (yellow triangles) and a large reference area in Mongolia (yellow outlined region; Gubanov, 1996).

We found 76.8% overlap (1343 species) with the native flora of the test area.

(3) Species richness of cold-climate ecosystems

Previously, most botanists and biogeographers believed that a cold and dry LGM climate led to species impoverishment in the Carpathian Basin (see Section I). Recent data and observations from Central Asia do not support this view. The high species richness of grasslands (Mühlenberg *et al.*, 2000; Makunina & Parshutina, 2017; Chytrý *et al.*, 2019; Sabatini *et al.*, 2022) and forests (Chytrý *et al.*, 2007, 2008, 2012; Sabatini *et al.*, 2022) of southern Siberia, where the current climate is similar to that of the Carpathian Basin in the LGM, suggests there could have been a similar species richness of grasslands and forests during the LGM in the Carpathian Basin (see Table 2, Fig. 3). Local palynological evidence also exists for higher-than-expected species richness of vegetation mosaics in the Eastern Carpathians during the LGM (Magyari *et al.*, 2014*b*). Nevertheless, the analogues from southern Siberia suggest that mountain regions with harsher climates may have been species-poor relative to regions at lower altitudes (Chytrý *et al.*, 2017*a*). Thus, based on recent analogues for the climate in Hungary during the LGM, we argue that it is unlikely that most Carpathian Basin ecosystems in the LGM were species-poor.

In conclusion, we argue that the three arguments presented above strongly support – although of course cannot prove – the Flora Continuity Hypothesis, which states that long-term extensive flora continuity may be a more plausible scenario than a large-scale LGM extinction of regional flora and subsequent massive postglacial recolonization in the Carpathian Basin.

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Table 1. Examples of vascular plant species of the native flora of Hungary that also occur in present-day reference areas that are as cold as or colder than the climate in Hungary during the Last Glacial Maximum (LGM). Numbers indicate the total number of reference areas (maximum 18) in which the species is present today (scaled by colour, with lowest values in green and highest values in red). See Appendix S3 for the full list of species. Habitat preferences are according to Horváth *et al.* (1995). Scientific 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*

V. BIOGEOGRAPHICAL AND ECOLOGICAL IMPLICATIONS OF THE FLORA CONTINUITY HYPOTHESIS

If our hypothesis is correct, there are fundamental consequences for our understanding of the biogeography and ecology of the Carpathian Basin. If the majority of the flora of this region survived throughout the LGM, Late Glacial and the Holocene, despite likely substantial changes in population sizes and spatial distribution of many plant species, there is no need to invoke the dynamic recolonization of the region as previously assumed.

Our hypothesis implies that impoverishment and recolonization of the flora of the Carpathian Basin may have been less dynamic at a regional scale than previously believed. Given the known micro- and mesoclimatic diversity of the Carpathian Basin landscapes during and after the LGM (e.g. Gábris *et al.*, 2018) and the co-existence of wet and dry, shady and sunny habitats (Janská *et al.*, 2017), we cannot exclude a similar level of flora continuity across all subregions of the Carpathian Basin below 1800 m a.s.l. Although Soó (1964) and Borhidi (2004) suggested that the floristic differences between subregions of the Carpathian Basin are of Holocene origin, many of these differences may actually be older [see Cieślak (2014) and Kajtoch *et al.* (2016) for grasslands]. Endemic species such as *Hepatica transsilvanica* (Laczkó & Sramkó, 2020), *Linum dolomiticum* (Dobolyi, 2003) and *Ferula sadleriana* (Lendvay & Kalapos, 2014), as well as endemic subspecies or local variants, may also pre-date the LGM.

Models based on simulations of past climates and current climate envelopes of species suggest that most suitable habitats in the LGM for current Central European steppe species were located south of the Carpathian Basin, namely in the Adriatic region, the Balkan Peninsula and near the Black Sea (Divíšek *et al.*, 2022). These models, however, are based on macroclimate rather than topoclimate and microclimate. Therefore, while they indicate overall suitability of larger

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Table 2. Maximum numbers of vascular plant species in selected species-rich grasslands and forests in cold climates in present-day northern Eurasia, compared to those found in habitats in the Carpathian Basin and the Carpathian Mountains.

Climate	Region	Habitat type	Sampling area	Maximum number of species	Reference
Similar MAT (+5°C to −10°C) to the climate of the Carpathian Basin in the LGM	Southern Urals	Grassland	100 m^2	109	Palpurina *et al.* (2017)
	Southern Altai-Sayan	Grassland	100 m^2	90	Palpurina *et al.* (2017)
	Northern Altai-Sayan	Grassland	100 m^2	88	Palpurina *et al.* (2017)
	Northern Khakassia	Grassland	100 m^2	94	Polyakova *et al.* (2016)
	Western Sayan	Forest	100 m^2	69	Chytrý *et al.* (2007)
	Northern Altai	Forest	100 m^2	114	Chytrý *et al.* (2012)
Present-day climate (MAT: +12°C to −2°C) of the Carpathians and the Carpathian Basin	Western Carpathians	Grassland	100 m^2	133	Chytrý *et al.* (2015)
	Eastern Carpathians	Grassland	16 m^2	82	Babai & Molnár (2014)
	Transylvanian Basin	Grassland	100 m^2	127	Dengler *et al.* (2012)
	Great Hungarian Plain	Grassland	20 m^2	60	Horváth (2010)
	Western Carpathians	Forest	100 m^2	100	Chytrý *et al.* (2015)

LGM, Last Glacial Maximum; MAT, mean annual temperature.

areas that may have supported abundant populations of these species in the LGM, they do not provide information on small patches of suitable habitats in less-suitable landscape matrices. They also cannot identify areas with climate that differs from the current species climatic envelope but is still within the tolerance limits of the species. We agree with Magyari *et al.* (2010) that the substantial immigration of many Pontic steppe species from the east or the south in the Holocene assumed by Boros (1958), Soó (1973) and Járai-Komlódi (2003) is unlikely, although some cold-sensitive species may have migrated north in the postglacial period. Similarly, the postglacial colonisation of the Pannonian lowlands from the surrounding low mountains (Kerner, 1863; Borbás, 1900; Willner *et al.*, 2021) or migration in the opposite direction (Borhidi, 2004) may have been less pronounced: species that survived the LGM in these regions could also have survived in most landscapes in Hungary.

We also suggest that the floras of certain ecosystems (e.g. rock and loess grasslands) and vegetation mosaics (e.g. foothills, floodplains) may have been relatively stable over long time periods. Certain ecosystems could have been species-rich during the LGM (see Section IV.3, Fig. 4), as shown by palynological evidence for local species richness of palaeovegetation mosaics (Magyari *et al.*, 2014*b*). Furthermore, the Flora Continuity Hypothesis implies that past and present floras may overlap more than previously expected. We also suggest that an important factor in the species richness of many Central European grasslands (Roleček, Čornej & Tokarjuk, 2014; Biurrun *et al.*, 2021; Roleček *et al.*, 2021) may be the long-term (sub)regional continuity of their flora (Feurdean *et al.*, 2015; for the Holocene see Hájková *et al.*, 2011; Hájek *et al.*, 2016). Individual grassland stands may be of more recent origin (Horváth *et al.*, 2011) but at the landscape scale the flora may be of a substantially older age.

The extent to which habitat preferences of plant species change or remain stable across glacial cycles is little known, and may be species specific. For example, shade-tolerant species of beech forests and other broad-leaved deciduous forests in Central Europe also occur today in the Ural region, Siberia and Mongolia in open birch–poplar or larch forests, e.g. *Adoxa moschatellina*, *Maianthemum bifolium*, *Paris quadrifolia* (Ermakov, Dring & Rodwell, 2000; Chytrý *et al.*, 2008; Á.P. Molnár, personal observations). Chytrý *et al.* (2010) suggested that light-demanding species survived in the herb layers of open forests in Central Europe during the Late Glacial and Early Holocene periods, assuming that the degree of canopy shading (and not the species of the shading tree) was the primary limiting factor for these species. In addition, some species occur in different habitats under different climates. For example, *Lilium martagon* inhabits grasslands in Mongolia (Makunina & Parshutina, 2017; Á.P. Molnár, personal observations) and similarly cold subalpine grasslands in the Carpathians, but is restricted to shady forests at lower elevations in the Carpathian Basin (Király *et al.*, 2009). *Sanguisorba officinalis* occurs in diverse open habitats, including dry and rocky steppic grasslands in Siberia and Mongolia (Á.P. Molnár, personal observations), but is only found in wet meadows in the Carpathian Basin (Király *et al.*, 2009).

On the other hand, some species have very similar habitat preferences under different climates. For example, *Ligularia sibirica* occurs in fens both in the Carpathian Basin (Király *et al.*, 2009; Ciocârlan, 2000) and Siberia and Mongolia (Horsák *et al.*, 2015; Á.P. Molnár, personal observations). *Koenigia islandica* was present in the Carpathian Basin during the LGM and was regarded as a tundra indicator based on its present European distribution and habitat preferences (Járai-Komlódi, 2003). However, in the present-day Mongolian forest-steppe zone (−2°C MAT), it is found in spring fens and in muddy parts of floodplain wetlands (Á.P. Molnár, personal observations), making its habitat uncertain during the LGM in the Carpathian Basin, and suggesting caution regarding its status as a tundra indicator.

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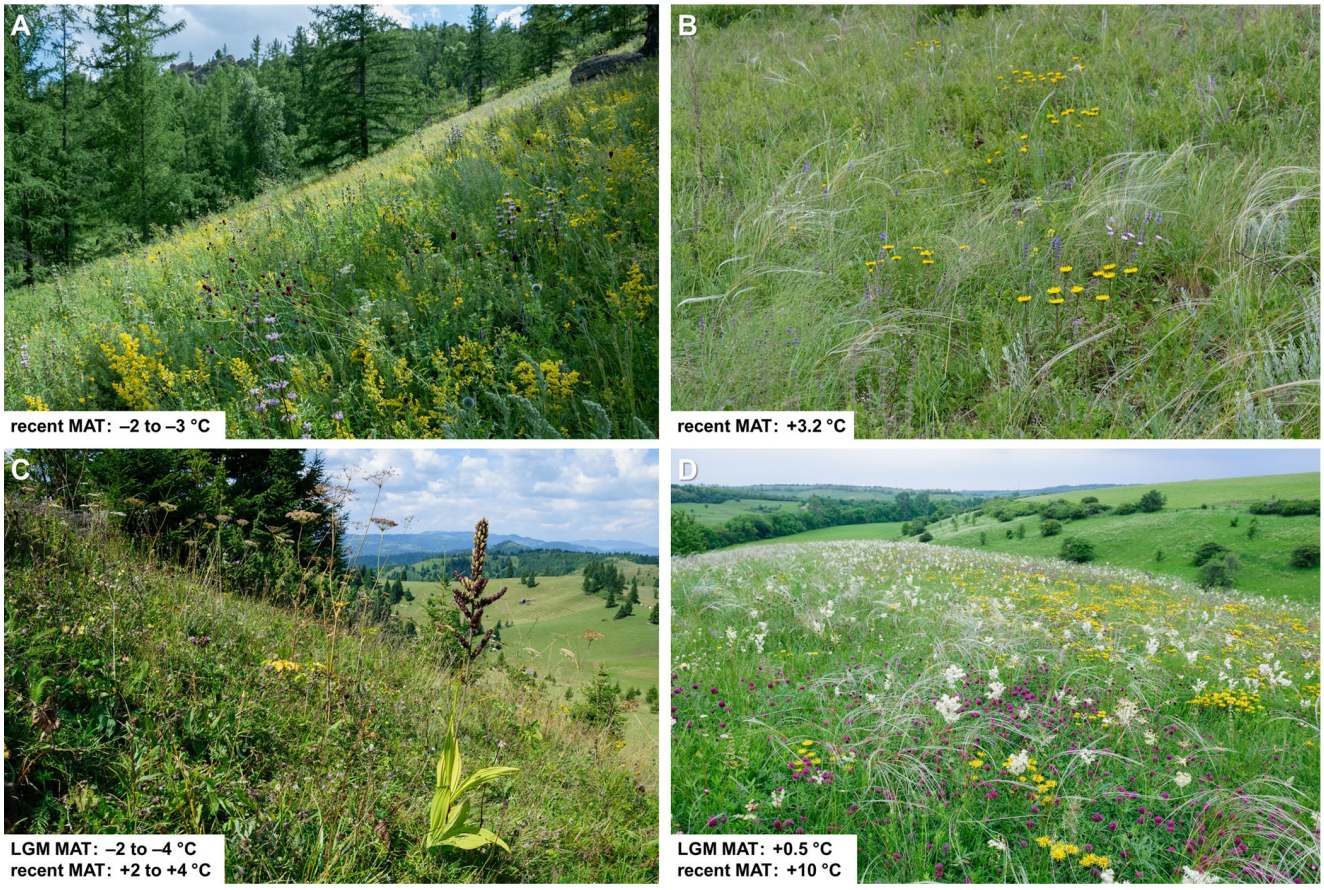

Fig. 3. Species-rich meadow steppes under diverse climates. (A) Forest steppe in Mongolia with a mean annual temperature (MAT) between −2 and −3°C MAT, which is similar to the climate of higher parts of the Carpathian Basin during the Last Glacial Maximum (LGM). Hillside at 1650 m above sea level (a.s.l.) east of Ulaanbaatar, Khentii Mountains, northern Mongolia. (B) Meadow steppe near the south-western Ural Mountains with a MAT of +3.2°C, which is similar to the lowlands of the Carpathian Basin during the LGM. Hillside at 260 m a.s.l. near Severnoye, Southern Urals, Orenburg Region, Russia. (C) Landscape in Gyimes (Eastern Carpathians) at 1300 m a.s.l., MAT in the LGM between −2 and −4°C, present-day MAT between +2 and +4°C), with a diverse mosaic of mountain meadow steppes managed as hay meadows and open and closed coniferous and mixed forests. (D) Species-rich meadow-steppe on loess at 150 m a.s.l. near Tard village, NE Hungary, at the northern edge of the Great Hungarian Plain, MAT in the LGM +0.5°C, present-day MAT +10°C. Species-rich grasslands (compare with A, B and see Table 1) in climates as cold as or colder than the climate of the Carpathian Basin during the LGM suggest that the grasslands of these landscapes may also have been species-rich during the LGM. Climate data: CCSM4.0. Photographs: Á.P. Molnár.

We suggest that our Flora Continuity Hypothesis may be extended to animal groups, which is consistent with previous discussions of extra-Mediterranean refugia (Schmitt, 2007; Stewart *et al.*, 2009; Varga, 2009; Schmitt & Varga, 2012; Kirschner *et al.*, 2020; Sümegi *et al.*, 2022). Continuity was proved for some species that were not expected to survive the LGM, such as *Parnassius mnemosyne* (Pecsenye *et al.*, 2016), *Salamandra salamandra* (Vörös *et al.*, 2016) and *Nannospalax* spp. (Németh *et al.*, 2020).

The Flora Continuity Hypothesis may be more widely applicable to other Central European regions – especially north and east of the Carpathians (e.g. Romania, Moldova, central and western Ukraine, and southern Poland) and dry areas in the Czech Republic and central and southern Germany, which also had discontinuous permafrost and relatively high MAT values during the LGM (Stadelmaier *et al.*, 2021; Fig. 1).

We hope that the Flora Continuity Hypothesis will stimulate future research. Our knowledge of ecosystem species richness during the LGM could be significantly enhanced by more detailed studies of climatically similar regions and by further palaeoecological studies. It is conceivable that by refining palaeoclimate models and using the most biologically appropriate parameters in these models (see Brun *et al.*, 2022), more accurate estimates of the distribution ranges of species that potentially survived the LGM can be obtained. However, climate-based models will always be limited in their accuracy because (*i*) species distribution ranges are not accurately predicted by macroclimate alone (e.g. Ludwig *et al.*, 2019;

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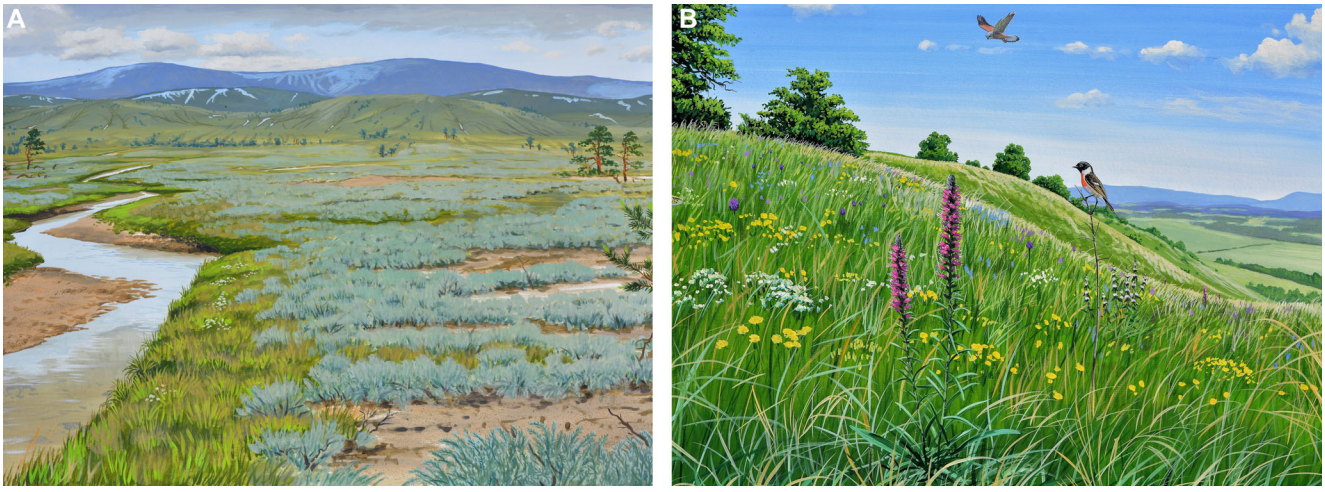

Fig. 4. It was previously assumed that all LGM landscapes in the Carpathian Basin were species-poor during the Last Glacial Maximum (LGM), and that most species of the present-day native flora recolonized the region after the LGM. Impressions of Central European landscapes during the LGM often imply low-diversity ecosystems (A), while recent landscapes are shown as species-rich (B). The Flora Continuity Hypothesis argues for potential massive long-term continuity of the vascular flora of the Carpathian Basin during the Late Pleistocene–Holocene, from before the LGM until the present, with the image shown in B also representative of the ecoysystems present during the LGM. Paintings by Márton Zsoldos (A: 2016, B: 2022).

Germain & Lutz, 2020; Hellegers *et al.*, 2020), and (*ii*) we do not have reliable modern analogues of climate and community composition for the LGM in the Carpathian Basin (Magyari *et al.*, 2014*a*; Varga, 2009), particularly because of much lower CO_2 levels at that time (Jouzel *et al.*, 1993).

Support for the Flora Continuity Hypothesis will require further palaeoecological and phylogeographical evidence, therefore we strongly support these research directions. For future phylogeographical studies, the list of species included in our cold tolerance analysis (Appendix S3) may be useful. For example, some species that were not verified by our analysis as potential survivors of the LGM may have actually survived (e.g. fen species, such as *Hottonia palustris* and *Urtica kioviensis*, or predominantly lowland/colline species that also occur in colder montane/subalpine grasslands, such as *Asyneuma canescens*, *Carex michelii*, *Iris graminea* and *Pulsatilla pratensis*, or species with very poor dispersal ability, such as *Ajuga laxmannii*, *Satureja montana* and *Sternbergia colchiciflora*). We may have failed to identify some species as cold tolerant because they are Pannonian endemics (e.g. *Ferula sadleriana*, *Linum dolomiticum*), meaning they are not present in our reference areas with LGM-like temperatures. A small range does not necessarily imply that the species cannot tolerate cold climates. Species with a small range are regional endemics that have likely evolved in the region and survived there, over very different climatic periods.

By contrast, our list contains some species whose survival through the LGM seems ecologically less probable (e.g. thermophilous or Atlantic species, including *Asphodelus albus*, *Cotinus coggygria* and *Hedera helix*). Further genetic studies and the development of novel research technologies (e.g. electron-microscopic and genetic studies of palaeopollen, metagenomics) may add many species to the flora of the LGM of the Carpathian Basin. However, we acknowledge that many species are difficult to detect using palynological methods (Meltsov *et al.*, 2011), and it is expensive and time-consuming to analyse the genetic patterns of whole floras. Consequently, there is much work remaining before we can reliably document the entire flora of the LGM in the Carpathian Basin.

VI. NATURE CONSERVATION IMPLICATIONS OF THE FLORA CONTINUITY HYPOTHESIS

Thorough testing of the Flora Continuity Hypothesis may take decades. In the meantime, we recommend greater caution in conservation decisions. If the flora of the Carpathian Basin exhibits long-term continuity since pre-LGM times, the natural heritage of the region may be much older than previously thought. We argue that strengthening the protection of ecosystems with high proportions of potential LGM flora may be highly relevant for saving our natural heritage. For example, the last surviving, highly isolated, small fragments of species-rich grasslands may need greater protection from encroachment of shrublands or colonisation by invasive species. We might risk losing populations that have inhabited the area for dozens of millennia.

Some species, often rare and protected ones, have recently shown unexpectedly low colonisation success (Molnár & Botta-Dukát, 1998; Hermy *et al.*, 1999). A possible explanation for their low mobility could be their long-term local persistence, i.e. they have not undergone selection for efficient dispersal in the Holocene. We argue that ecological restoration should help these species recolonize areas where they are now extinct. The recently delineated seed transfer zones (Durka *et al.*, 2017;

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Cevallos *et al.*, 2021) may be too large to protect ancient local gene pools. Instead, we advocate the principle of using local populations for seed transfer (Molnár, 2020).

VII. CONCLUSIONS

(1) We re-evaluated the Postglacial Recolonization Hypothesis on the origin of Carpathian Basin flora by reviewing and synthesising recent advances in ecological, phylogeographical, palaeoecological and palaeoclimatological research and by analysing the cold tolerance of the flora in a test area (Hungary).
(2) We propose an alternative, the Flora Continuity Hypothesis, which assumes a massive long-term continuity (*ca.* 80%) of the vascular flora of the Carpathian Basin across the Late Pleistocene and Holocene, from before the Last Glacial Maximum to the present.
(3) The Flora Continuity Hypothesis highlights the need to reconsider the temporal scale and speed of some ecological processes in this region, including species migration, colonisation and co-existence.
(4) National and European nature conservation strategies may also need to be adjusted, as regional floras may be much older than previously thought.
(5) We argue that the null hypothesis about the status of a species should be that it survived the LGM in the Carpathian Basin. This hypothesis could be rejected by research proving that the species has immigrated, and should be preferred to the reverse approach commonly used so far, in which the default scenario is assumed to be species extinction during the LGM and postglacial recolonisation.
(6) Much research is still needed to document fully the flora of the LGM in European areas lying between the LGM ice sheet in the north and the Mediterranean region in the south.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Details of the reference areas used in the analysis of cold tolerance of present-day native species from Hungary.
Appendix S2. Additional information on the methods used to assess the cold tolerance of the present-day native flora of our study area.
Fig. S1. Zones of similar mean annual precipitation (MAP) in Eurasia.
Appendix S3. Occurrence data for a comparison of present-day native flora of the test area (Hungary) with 18 reference areas (see Appendix S1 for list of reference areas).

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