

Biodiversity-rich European grasslands: ancient, forgotten ecosystems

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Abstract

Worldwide reforestation has been recommended as a landscape restoration strategy to mitigate climate change in areas where the climate can sustain forest. This approach may threaten grassland ecosystems of unique biodiversity as such policies are based on the false assumption that most grasslands are man-made. Here, we use multiple lines of evidence (palaeoecological, pedological, phylogenetic, palaeontological) from Central Eastern Europe and show that various types of grasslands have persisted in this area throughout postglacial i.e. the past 11,700 years. A warm and dry climate, frequent fires, herbivore pressure, and early Neolithic settlements kept forests open until widespread forest clearance beginning 4000-3000 years ago. Closed forest cover has been the exception for the past two million years. This long-term persistence has likely contributed to the high biodiversity of these grasslands. Consequently, we call for a more cautious prioritisation of the protection of what may be erroneously considered natural, i.e. forests, by many environmental specialists and managers. Instead we provide a new framework for a better understanding of the evolution and persistence of different grassland types and their biodiversity, so that grasslands can be better understood, valued and conserved.

Keywords: ancient grasslands, anthropogenic disturbance, climate change mitigation, fire, fossil records, herbivores

1. Introduction

46 The World Resources Institute (WRI) Atlas of Forest and Landscape Restoration was
47 designed to identify opportunities for landscape restoration worldwide, an initiative supported
48 by several international organisations concerned with land degradation, climate change
49 mitigation and biodiversity loss (WRI, 2015). It contrasts the potential extent of tree cover
50 based on climate conditions with the current distribution of forest globally. This map identifies
51 23 million km² of land worldwide suitable for tree planting, mostly being currently open
52 landscapes with grassland (<http://www.wri.org/applications/maps/flr-atlas>). However,
53 grassland experts oppose the offsetting of agricultural deforestation through the afforestation
54 of grassy ecosystems arguing that this approach ignores the unique biodiversity, cultural
55 significance and important ecosystem services provided by this ecosystem (Willis et al.,
56 2008; Parr et al., 2014; Veldman et al., 2015a,b; Bond et al., 2016; Joshi et al., 2018). Their
57 imperative is to map “old-growth” grasslands, where tree cover is naturally sparse and where
58 such afforestation would be detrimental. Another important debate is how to provide
59 strategies to reduce the impact of the ongoing abandonment of high biodiversity grasslands,
60 therefore preventing succession towards low biodiversity secondary shrub and forest
61 communities (Biró et al., 2010; Valkó et al., 2018a).

62 Here we go further and challenge the perception that treeless areas in temperate regions,
63 where the current climate would permit forest development, have all previously been forested
64 and therefore grasslands and open canopy woodlands are secondary habitat types in these
65 regions. This perception fails to consider the vital role of natural disturbances such as fire or
66 herbivores (Bond and Keeley, 2005). We illustrate this by analysing evidence from Central
67 Eastern Europe. The choice of this region is based on the following arguments: i) it hosts one
68 of the largest tracts of grasslands in Europe crucial for maintaining biodiversity in European
69 agricultural landscapes (Wilson et al., 2012); ii) has one of the highest small-scale species
70 diversities in the world (Dengler et al., 2014; Turtureanu et al., 2014; Chytrý et al., 2015); and
71 iii) is a transitional, complex region between closed forest and steppe biomes (Bohn et al.,
72 2003) and hence contains grasslands of diverse origin and history. Yet, despite these
73 features, grasslands are rarely highlighted as biodiversity hotspots. This is because the key
74 characteristics and ecological processes important for this classification, such as biodiversity
75 intactness and a lack of human disturbance, cannot be readily applied to them (Mittermeier
76 et al., 2011). Our goal is to better define grassland types based on their origin, age and the
77 drivers of their formation and maintenance so that grasslands can be better understood,
78 valued and conserved.

79

80 **2. A new framework for defining European grassland types**

81 Bohn et al. (2003) provided a geobotanical expert assessment, which maps Europe's
82 potential natural vegetation (PNV) i.e. the vegetation cover that would exist today in the
83 absence of human activity. It defines most areas that are currently covered by grasslands or
84 open woodlands in Central Eastern Europe as dominated by deciduous broadleaved forest
85 or mixed coniferous and broadleaved forest (Fig. 1). Open, or at least partly open vegetation
86 types, are only recognised in the lowlands of the Carpathian Basin. Fossil records show that
87 grasslands and open canopy woodlands covered extensive areas in Central Eastern Europe
88 during the Pleistocene (i.e., the past 2 million years) when cold and dry climate conditions
89 prevailed (Kuneš et al., 2008; Ellenberg and Leuschner, 2010; Feurdean et al., 2014;
90 Magyari et al., 2014). Warmer climate conditions during the Holocene (i.e. the last 11,700
91 years) then greatly reduced the potential distribution and/or extension of grasslands (Birks
92 and Willis, 2008). An especially critical period for grassland persistence was the mid
93 Holocene period (9000-4500 cal yr BP), when moister climatic conditions triggered forest
94 expansion (Roberts et al., 2018). Identification of warm/moist stage refugia for grasslands
95 (i.e. locations where they persisted) during the mid Holocene is therefore of crucial
96 importance for understanding ancient grasslands.

97 It is widely accepted that natural grasslands growing on rocky skeletal and other poor soils
98 with a permanent or seasonal moisture deficit, i.e. outcrops, steeper slopes, gravel
99 riverbanks, salt and sandy soils the so-called primary grasslands have survived continuously
100 in small pockets throughout the Holocene in their current locations (Lang, 1994; Poschlod
101 and WallisDeVries, 2002). Currently, the extent of these grassland types is limited, apart
102 from grasslands growing on salt and dry sandy soils, which are more common in the
103 Carpathian Basin (Molnár and Borhidi 2003; Deák et al., 2014). It is therefore highly
104 improbable that these small, isolated grassland areas were the only refugia of the
105 extraordinarily rich grassland flora of so-called “semi-natural” grasslands. The high genetic
106 diversity of some grassland plant species in this region (Turtureanu et al., 2014) and the
107 remarkable species richness and endemic plant and animal species typical for grasslands
108 (Chytrý et al., 2015) suggest a wider extent of primary grasslands during the Holocene.
109 In contrast to the primary grasslands, open canopy woodlands and grasslands currently
110 found in areas where climate and soils would allow forest growth, and which are only
111 extensively managed (i.e., no artificial fertiliser and pesticide application) are considered to
112 be semi-natural (Pärtel et al., 2005; Leuschner and Ellenberg, 2017). Here, we challenge the
113 view that most of these grasslands have replaced formerly naturally occurring forests within
114 recent centuries or millennia. We present multiple lines of evidence (palaeobotanical,
115 pedological, phylogenetic, palaeontological) from five countries in Central Eastern Europe, a
116 region with some of the highest-biodiversity grasslands of the world. Firstly, we review
117 published direct records of past grassland occurrence (pollen, plant macrofossils, charcoal)
118 from both natural (lakes, bogs) and archaeological archives, alongside other indirect fossil
119 (pedological, zoological) and recent genetic evidence from Central Eastern Europe.
120 Secondly, we review the characteristics of the environmental and disturbance factors
121 (climate, fire, herbivores and human impact) during the Holocene in this region. Finally, we
122 evaluate whether continuous grassland presence was possible under the Holocene climatic
123 conditions, fire and grazing regimes, and increasing anthropogenic impacts.
124 Based on their age and the drivers of their formation, we set out a new framework for three
125 types of grasslands in Central Eastern Europe: 1) Primary, natural grasslands on skeletal
126 and other poor soils, which have existed throughout the Holocene until the present; 2)
127 Primary, ancient grasslands on deeper soils, maintained by climate and disturbances during
128 the early Holocene and then predominantly by disturbances until the present; and 3) Semi-
129 natural grasslands, extensively managed grasslands, formed and maintained by
130 anthropogenic disturbances during the late Holocene (Table 1). We argue for the recognition
131 of the importance of previously overlooked ancient grasslands that have persisted throughout
132 the Holocene, maintained by natural and later also by anthropogenic disturbances.

134 **3. Multi-proxy evidence for grassland persistence during the Holocene**

135 **3.1 Fossil plant evidence**

136 Pollen and palaeobotanical records from natural archives (lakes and peatbogs) in currently
137 grassland-rich areas in Central Eastern Europe indicate the prevalence of a more open
138 landscape between 11,700 and 9000 cal yr BP and the maximum extent of forest cover
139 between 9000 and 4500 cal yr BP (Figs.1, 2; Table 2; Fig.S1). While these studies show a
140 reduction in grassland cover, especially of xerothermic and floodplain grasslands during the
141 mid Holocene, there is no evidence of their widespread disappearance. Rather, there is
142 strong support for their persistence, given the concurrent presence of many grasslands, i.e.
143 *Adonis* spp., *Artemisia* spp., *Centaurea* spp., *Festuca rubra*, *Festuca* spp., *Filipendula* spp.,
144 *Helianthemum* spp., *Potentilla erecta*, *Potentilla* spp., *Sanguisorba* spp., *Trifolium* spp.,
145 *Thymus* spp., and light-demanding tree and shrub taxa during this period (Fig. 1; Table 2).
146 Archaeobotanical reports from Hungary and Poland suggest an even greater proportion of
147 heliophilous taxa growing locally than pollen records indicate (Fig. 1; Table 2). Remains of
148 grassland species including steppe elements, i.e. *Asperula cynanchica*, *Phleum pratense*,

149 *Plantago media*, *Stipa pennata*, *Stipa* sp., *Silene vulgaris*, *Teucrium chamaedrys*, have been
150 reported from archaeobotanical records of early Neolithic sites from Germany (Fig. 1; Table
151 2) and Czech Republic (Archaeobotanical Database of the Czech Republic;
152 <http://www.arup.cas.cz>). Calcareous grasslands have also been identified in the Neolithic
153 lakeshore sites in the northern foothill of the Alps (Fig. 1; Table 2). The species found are
154 typical of closed xerophilous and mesophilous grasslands at sites where trees would have
155 been able to grow under the climatic conditions of the mid Holocene. Taken together, fossil
156 plant evidence from natural archives and archaeological sources suggest that grasslands
157 existed locally before the start of the Neolithic and therefore before marked human impacts.
158 These findings also demonstrate grassland persistence throughout the mid Holocene,
159 although archaeological records show the occurrence of higher grassland diversity than that
160 found in pollen records.

161

162 **3.2. Zoological evidence**

163 Indirect evidence for the persistence of open, or partly open landscapes throughout the mid
164 Holocene comes from the palaeontological remains of animal species restricted to extensive,
165 open habitats (Fig. 1). Results from the Carpathian Basin (Hungary and Romania) show that
166 several species typical of steppic environments e.g. *Asinus hydruntinus* (European Wild
167 Ass), *Equus ferus* subsp. *gmelini* (Eastern European Wild Horse), *Microtus gregalis* (Narrow
168 Headed Vole), *Ochotona pusilla* (Steppe Pika), *Otis tarda* (Great Bustard) and *Vipera ursinii*
169 subsp. *rakosiensis* (Meadow Adder) were abundant during the early Holocene (Németh et
170 al., 2017). They became discontinuously present from 8000 cal yr BP and several of these
171 species disappeared between 5000 and 4000 cal yr BP at a time of increased anthropogenic
172 pressure, but in a grassland landscape. Fossil malacological records in currently grassland-
173 rich landscapes reveal a similar picture (Fig. 1); a continuous Holocene presence of strictly
174 open habitat molluscs (*Chondrula tridens*, *Helicopsis striata*, and *Vallonia pulchella*) unable
175 to survive in closed forests (Ložek, 2005; Horsák et al., 2009; Moskal-del Hoyo et al., 2018).
176 Overall, while there is evidence that many open habitat mollusc species contracted their
177 range during mid Holocene forest expansion, there is also robust support for their local long-
178 term persistence, and consequently also for the continuity of grassy ecosystems.

179

180 **3.3 Phylogeographic evidence**

181 Phylogeographic analysis represents a further source of data facilitating the interpretation of
182 the distribution of past grasslands. A pattern of genetic diversity decline from core
183 populations in southern Siberia towards the range periphery of smaller populations in
184 western Europe has been confirmed for several grassland plant species including *Adonis*
185 *vernalis* (Hirsch et al., 2015), *Iris aphylla* (Wroblewska 2008), *Stipa capillata* (Wagner et al.,
186 2011) and *Stipa pennata* (Wagner et al., 2012). These studies have also revealed a
187 surprisingly low genetic differentiation between central and peripheral intermediate
188 populations, or a complete lack of private alleles among peripheral populations (e.g. Wagner
189 et al. 2011; Hirsch et al., 2015), which may reflect the absence of any long-standing isolation
190 of these populations. This implies that these species must have had a more continuous past
191 distribution in Central and Eastern Europe allowing gene flow and interbreeding. Rapid
192 progress in the field of DNA analysis, especially environmental DNA, may shed further light
193 on the origin and past range distribution of grasslands (Thomsen and Willerslev, 2015)

194

195 **3.4 Pedological evidence**

196 A further line of evidence used in the interpretation of former vegetation distributions comes
197 from soil types (IUSS WRB 2006). In Central Eastern Europe, dark soils (chernozems) from
198 steppe and forest steppe zones are considered to have developed before the spread of
199 forests and to have persisted under open or semi-open vegetation (Pokorný et al., 2015).

200 Others, however, view these soils as having survived under forest development (Eckmeier et
201 al., 2007). A palaeo-pedological analysis from the Transylvanian Basin (Romania) shows the
202 occurrence of islands of dark soils of Pleistocene age (20,000-14,000 cal yr BP), which, in
203 drier areas, persisted until the present (Pendea et al., 2002) suggesting grassland
204 persistence throughout the Holocene. However, in other areas of the Transylvanian Basin,
205 dark soils were overlain by Luvisols, typical of nemoral forests, about 5000 cal yr BP (Timar
206 et al., 2010) when wetter climatic conditions prevailed, whilst the current vegetation is
207 predominantly grassland. Grassland occurrence on soils typically favouring forests may be
208 explained by the prevalence of open woodlands throughout the Holocene, allowing the long-
209 term persistence of dark soil, rather than the post-deforestation formation of this soil type.
210 Forest soils occur extremely rarely on chernozems developed on loess substrates in the
211 Hungarian Plain therefore suggesting the long-term existence of steppe grasslands (Máté
212 1957, Molnár 2010). Indeed, the continuous dominance of grasslands from the Late
213 Pleistocene on loess deposits in the southern Carpathian Basin has been recently
214 demonstrated on the basis of n-alkane biomarkers (Marković et al., 2018). Thus, pedological
215 evidence from chernozems, including those developed on loess, shows that chernozems
216 existence under open or semi-open vegetation.

217

218 **4. Drivers of grassland persistence during the Holocene**

219 **4.1 Climate conditions**

220 Proxy-based and climate simulations indicate warmer-than-present summer temperatures,
221 lower precipitation and soil moisture, and greater seasonality in the early Holocene (11700-
222 9000 cal yr BP) in Central and Eastern Europe at the time of maximum grassland extent
223 (Feurdean et al., 2013; 2014; Heiri et al., 2014). Palaeoclimatological records show a decline
224 in temperatures in this region from approximately 9000 to 4500 cal yr BP (Heiri et al., 2015;
225 Tóth et al., 2015; Hajkova et al., 2016). Climate simulations are consistent with this pattern of
226 mid Holocene cooling, but also marked precipitation and soil moisture increases in the mid
227 latitudes in Europe (Feurdean et al., 2013). Palaeoecological reconstructions show that
228 significant forest expansion occurred in response to cool and moist conditions in Central
229 Eastern Europe (Magyari et al., 2010; Feurdean et al., 2015; Kuneš et al., 2015; Novenko et
230 al., 2016; Pokorný et al. 2015; Jamrichová et al., 2017; Moskal-del Hoyo et al., 2018).
231 Therefore, both proxy and modelled palaeoclimatic and palaeoecological evidence from the
232 lowlands of Central Eastern Europe clearly show that grasslands were most extensive during
233 the warm and dry climatic conditions, with prolonged droughts, of the early Holocene
234 (11,700-9000 cal yr BP) and became restricted under wetter conditions during the mid
235 Holocene (9000-4500 cal yr BP; Fig. 2). This illustrates the stronger competitive advantage
236 of grasslands over trees when resources are limited i.e., lower moisture availability and
237 prolonged droughts.

238

239 **4.2 Fire**

240 The role of fire as one of the main drivers of the rise in grassy ecosystem during the Miocene
241 has been advocated (Osborne and Behling, 2006; Strömberg, 2011) and confirmed by
242 fossil records from C₄ dominated grasslands in Africa (Hoetzel et al., 2013). This is not
243 surprising as dominant grassland species have fine fuels with rapid curing and fast regrowth
244 rates as well as perennating buds near or below the soil surface; adaptations that ensure
245 regeneration after disturbances that damage the above-ground parts of the plant (He and
246 Lamont, 2018). Thus, whilst grass and herbs can withstand frequent fire, this shift in fire
247 regime may have harmed previously dominant tree species adapted to infrequent fire (He
248 and Lamont, 2018). Although, short-term, field-based burning experiments in Hungary found
249 conflicting results about the effect of fire on grassland biodiversity (Valkó et al., 2014, 2018b),
250 controlled laboratory and small-scale field experiments examining the effect of fire on seeds
251 found a predominantly negative effect of fire on seed germination in grassland species,

252 however, some positive effects (Fabaceae) also emerged (Ruprecht et al., 2013; 2015).
253 Disturbances by fire have recently been considered essential for increased grassland
254 competitive advantage over trees during the Holocene in Central Eastern Europe (Magyari et
255 al., 2010; Feurdean et al., 2015). For example, a positive effect of frequent fires on the
256 competitive advantage of grasses over trees and, by this means, on the extent of grassland
257 in Transylvania, Romania, has been inferred from sedimentary charcoal particles and pollen
258 (Feurdean et al., 2013). On the contrary, the decline in fire frequency during the mid
259 Holocene has been shown to be detrimental for grassland extent. The significance of global
260 fire activity in grassy biomes during the early and late Holocene, based on charcoal datasets,
261 has recently been emphasised by Leys et al (2018). Taken together, neo- and
262 palaeoecological evidence indicate that fire may have had a more important role in the shifts
263 between forest and grassland, and in grassland maintenance, than previously thought.
264 Exploring to what extent temperate grasslands are associated with frequent fires and which
265 grassland species/communities are most resilient or benefit mostly from fire could be useful
266 for the enhancement of management practices, i.e., preventing excessive dominance by
267 competitor grass species as well as the succession towards shrublands and forests.

268

269 **4.3 Herbivores**

270 Large herbivorous mammals influence the physiology and growth of plants and are
271 considered ecological keystones in maintaining tree–grass coexistence (Crawley, 1983;
272 Sankaran et al., 2005). Released from megaherbivore pressure and with a change in climate
273 at the Pleistocene-Holocene boundary, European lowlands witnessed substantial forest
274 regeneration and a reduction in vegetation openness (Vera, 2000; Svenning, 2002).
275 Megaherbivore extinction may also have had a cascading effect on the population size and
276 diversity of small mammals dependent on vegetation openness and indirectly on the fire
277 regime (Gill et al., 2014). However, comparatively, little attention has been given to the effect
278 of the declining population size or extinction of wild herbivores, or the subsequent role of
279 livestock, on landscape structure during the mid to late Holocene. We know from
280 palaeontological and archaeozoological records in the Carpathian Basin that several large
281 herbivores i.e., *Alces alces* (Eurasian Elk), *Bison bonasus* (European Bison), *Dama dama*
282 (Eurasian Fallow Deer), *Equus ferus* subsp. *gmelini* (Wild Horse) and *Equus hemionus*
283 (Asiatic Wild Ass) became discontinuously present from the mid Holocene, i.e. 8000 cal yr
284 BP and that many became extinct by 4000 cal yr BP (Németh et al., 2017; Bejenaru et al.,
285 2018). In contrast, livestock numbers increased from 6500 cal yr BP (Schumacher et al.,
286 2016). Domestic livestock could prevent forest encroachment in the absence or with a low
287 density of wild herbivores. Domestic animals can replace wild herbivores as dispersal agents
288 (Bruun and Fritzboeger, 2002; Cosyns et al., 2005), however, their movement is limited by
289 agricultural practices. Combined fossil records of fauna, pollen and coprophilous fungi that
290 reproduce exclusively on animal dung (*Sporormiella* spp., *Sordaria* spp., *Podospora* spp.)
291 can provide means of assessing the effects of herbivores on grassland dynamics and also
292 the timing of the shift in influence from grazing by wild herbivores to livestock grazing (Gill et
293 al., 2009). Such records are still scant in Europe, but the existing studies generally show the
294 increasing effects of grazing by domestic livestock from 5000 cal yr BP (Schumacher et al.,
295 2016). Understanding the responses of grasslands to different grazing animals (body size,
296 grazing intensity and height, foraging strategy and forage selectivity) will be essential in the
297 development of future grassland management strategies as various forms of livestock
298 grazing have been proposed to simulate the effects of grazing and browsing by wild
299 herbivores (Poschlod and WallisDeVries, 2002; Bakker et al., 2004; Tóth et al., 2016;
300 Poschlod, 2017).

301

302 **4.4. Early human impact counteracted the encroachment of forest onto primary** 303 **grasslands**

304 As the increase in forest cover from 8000 cal yr BP coincided with the spread of Neolithic
305 culture across South Eastern Europe (Bogaard et al., 2004; Kreuz 2008), a critical question
306 in respect to grassland extent is whether anthropogenic impacts could have counteracted the
307 climate-driven development of a closed forest (Pokorný et al., 2015). Archaeological datasets
308 from this part of Europe indicate that Neolithic settlements tended to be established in open
309 landscapes and that field sizes were small (Moskal-del Hoyo et al., 2013; Chapman, 2017;
310 Marinova and Ntinou, 2017). As people first settled in naturally open landscapes, this
311 tendency could explain the apparent lack of major deforestation at this time in the pollen
312 records from Central Eastern Europe (Fig. 2). Fire activity was naturally high during the early
313 Holocene (Magyari et al., 2010; Feurdean et al., 2013), and humans may have taken
314 advantage of wildfires to extend their agro-pastoral activities into freshly burned habitats. In
315 agreement with Pokorný et al. (2015) we hypothesise that early anthropogenic land
316 management may have slowed, or partially arrested, the development of closed forest
317 favoured by the wetter climatic conditions of the mid Holocene at locations with low biomass
318 productivity, contributing to the maintenance of landscape openness.

320 **4.5. Semi-natural grasslands replacing forests: when and how?**

321 Individual pollen records, as well as large-scale quantitative vegetation reconstructions from
322 Central Eastern Europe, show that the level of anthropogenic impact on forest remained low
323 until about 6000-5000 cal yr BP (Magyari et al., 2010; Feurdean et al., 2015; Kuneš et al.,
324 2015; Jamrichová et al., 2017; Fig. 2). Modelled vegetation and land use (arable and pasture
325 cover) changes across Europe suggest that open areas expanded gradually from previously
326 cleared forest after ca. 6000 cal yr BP (Kaplan et al., 2017). A noticeable increase in the
327 abundance and richness of grassland along with the decline in total forest cover but increase
328 for *Quercus*, a tree taxon typical for woodland and woody pasture, in Central Eastern Europe
329 occurred from 4700-3500 cal yr BP onwards (Jamrichová et al., 2017). This demonstrates a
330 growing anthropogenic role in the extension of grasslands and the formation of open
331 woodlands. These grasslands belong to the so-called semi-natural grasslands that
332 developed from forests and are maintained by land management (Pärtel et al., 2007; Pereira
333 et al., 2017). Technological advances in agriculture and the expansion of urban centres and
334 farms from the Late Bronze Age and Iron Age (3500 cal yr BP) have led to both an extension
335 and intensification of the land use in Central Europe (Poschold, 2015; Rösch et al., 2016). It
336 is therefore not surprising that from this time onwards, the richness and extent of grassland
337 has been found to correlate closely with prehistoric settlement density and land management
338 (Poschold and WallisDeVries, 2002; Pärtel et al., 2005; Hajkova et al., 2011; Hejcman et al.,
339 2013; Poschold, 2017). Later on i.e. from the 15th to 20th centuries, grassland expansion is
340 strongly linked to sheep flock migration. Livestock acted as dispersal vectors and their
341 mobility may be one of the reasons that ancient and older semi-natural grasslands may have
342 similar species diversity (Poschold and WallisDeVries, 2002; Molnár et al. 2012; Poschold,
343 2017). The sowing of hayseed and mowing may also have promoted grassland expansion in
344 many parts of Europe (Babai and Molnár, 2014). In summary, semi-natural grasslands
345 expanded into formerly forested sites and have subsequently been maintained by a variety of
346 land management practices including grazing, burning and mowing.

348 **5. A new framework for Holocene grassland persistence; conservation consequences**

349 We provide a new framework distinguishing three types of biodiversity-rich grasslands in
350 Central Eastern Europe. These are: primary grasslands on skeletal and other poor soils
351 (primary grasslands I), ancient grasslands maintained by natural and anthropogenic
352 disturbances (primary grasslands II), and semi-natural grasslands developed as a result of
353 human activities replacing forests (Fig. 3; Table 1). We have identified the reasons for the

354 continuous presence of primary grasslands during the Holocene including both natural i.e.
355 climate conditions and soils (primary I), climate and disturbance factors i.e. fire and grazing
356 (primary grasslands II). Neolithic people may have first settled in naturally open areas such
357 as grasslands or grassland-woodland mosaics arresting the development of a full forest
358 cover when the climate became wetter (mid Holocene), indirectly favouring the preservation
359 and expansion of grasslands. The intensification of human impact from 4700-3500 cal yr BP
360 onwards subsequently lead to considerable extension of semi-natural grassland on formerly
361 forested sites. A succession from grassland to forest after the cessation of land management
362 (e.g. grazing or burning) is not necessarily a proof against the primary or ancient aspect of
363 grasslands, but may indicate the lack of disturbances. Livestock grazing in the late Holocene
364 has replaced ancient grazing by megaherbivores prevailing until the early Holocene and that
365 by large herbivores throughout the mid Holocene.

366 Our findings also reveal misconceptions about the origin of Central Eastern European
367 grasslands and open canopy woodlands. The concept of a previously continuous, closed
368 forest in extant grassland-rich landscapes where climatic conditions are favourable for forest
369 fails to hold true, as grasslands are likely to have been continuously present throughout the
370 Holocene. The long-term persistence of grasslands at these locations is probably an
371 important reason for one of the highest small-scale species richness, many endemic,
372 worldwide in these habitats. Such species-rich plant communities can require millennia to
373 develop and only well-connected grassland patches can support genetically diverse plant
374 populations. These findings challenge the commonly held view that conservation activities
375 should primarily focus on the protection of forests in many areas of Central Eastern Europe.

376 Anthropogenic impacts tend to focus on forest clearance, but this perspective paper
377 highlights that conservationists and land managers need to carefully consider that, in many
378 cases, it is not primary forests that hold the highest biodiversity. Further, human-made, or
379 managed environments, such as extensively managed grasslands, are long-term landscape
380 features, contain unique plant and animal communities, and provide important ecosystems
381 services. Our findings support the recent wider acceptance of the notion that people and
382 nature should not be separated in the societal discourse of environmental science (Mace
383 2014). Finally, we advocate the need for a more detailed understanding of the role of
384 disturbances in grassland-forest dynamics, to avoid the overly simplistic assumption that
385 sparse tree cover is evidence of past deforestation. Fossil records provide such data and the
386 routine incorporation of palaeoecological investigations into environmental management is a
387 key step in developing science-based evidence for the conservation of the biodiversity of
388 grasslands. Thus, our regional case study supports the advocacy of Willis et al. (2010),
389 Barnosky et al. (2017) and Whitlock et al. (2018) for merging palaeobiology and conservation
390 biology as well as an appreciation of the dynamic history of species and ecosystems,
391 including the role of humans.

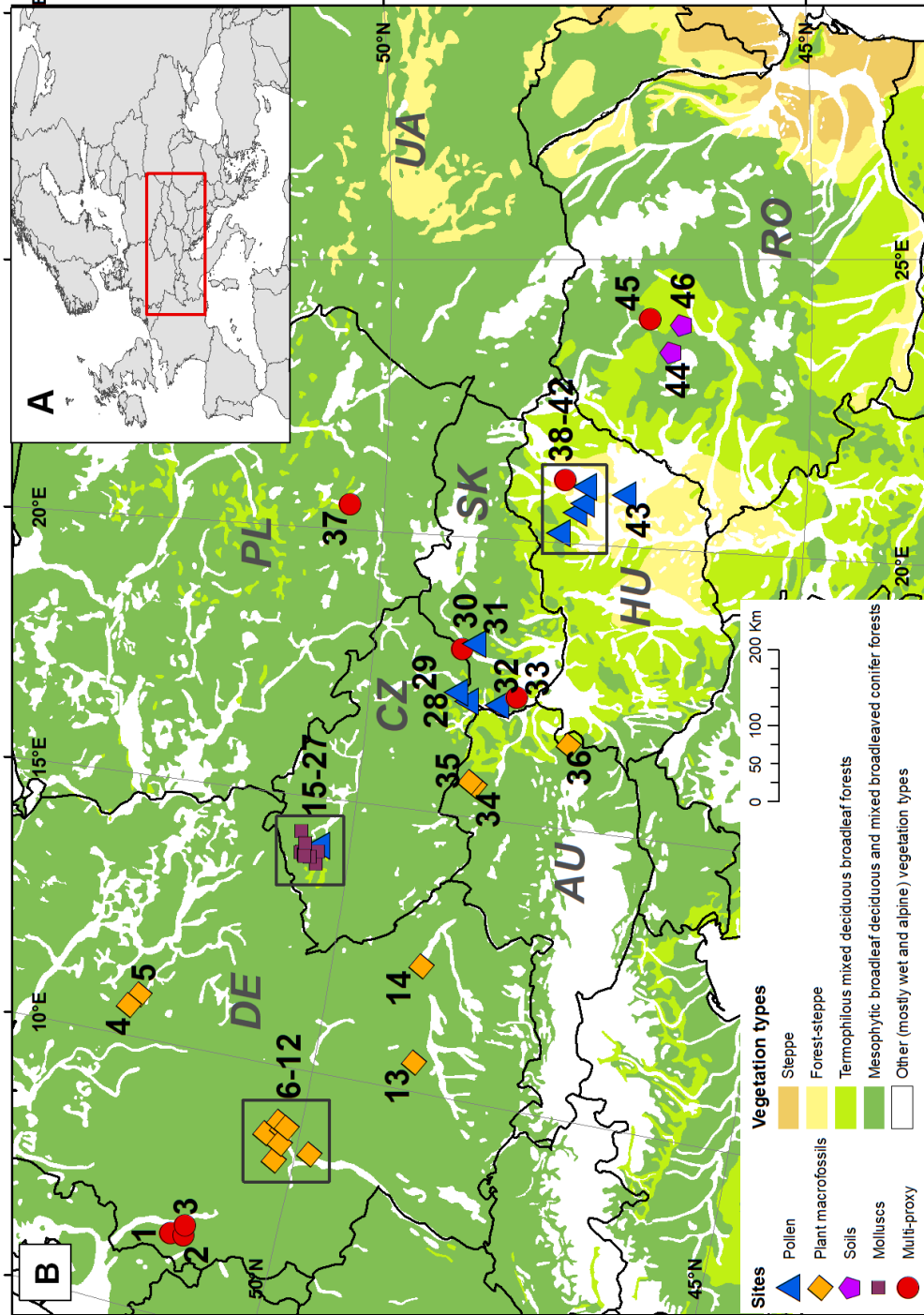
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393 **Figures captions**

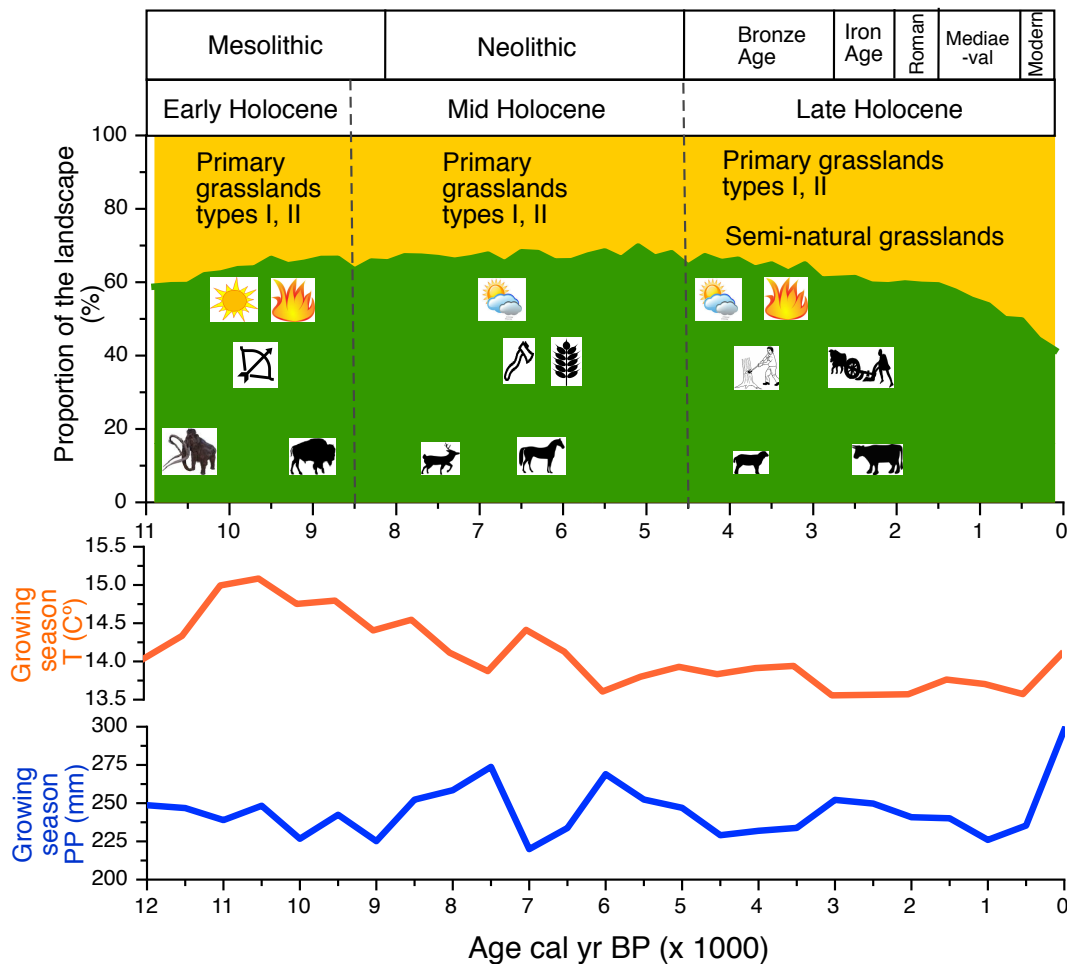
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395 **Figure 1.** Location of the study area in Europe (A) and the distribution of the main vegetation
396 types in Central Eastern Europe based on the potential natural vegetation map of Europe (B;
397 Bohn et al., 2003). Colour symbols show location of various types of fossil records extracted
398 from literature (Table 2 and S1) indicating either continuous grassland presence throughout
399 the Holocene or during the afforestation phases of the mid Holocene (9000-4000 cal yr BP).
400 These fossil records reveal that grasslands were continuously present throughout the
401 Holocene in places where potential natural vegetation has been assumed to be forest.

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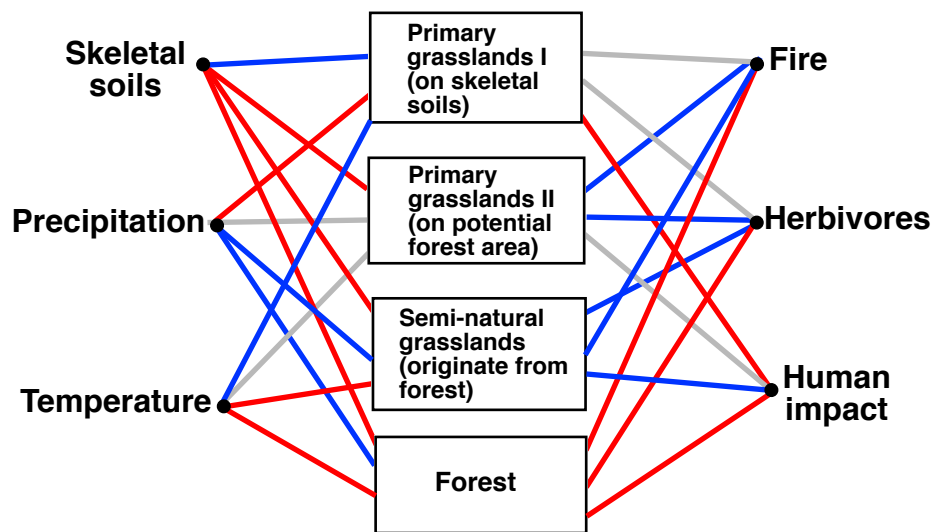


403 **Figure 2.** Pollen based reconstruction of forest (green) versus open land cover (yellow) from
 404 Central Eastern Europe during the Holocene using the pseudobiomisation method (Fyfe et
 405 al., 2015). Cumulative land cover record was constructed by spatially aggregating 96 pollen
 406 records extracted from the Pangaea Database and distributed across the region shown in
 407 Fig.1 and Fig. S1. Forest cover includes both broadleaf and conifer trees, whereas open land
 408 cover includes pastures/natural grasslands, and arable/disturbed land. Geological and
 409 archaeological periods as well as the predominance of each grassland type throughout the
 410 Holocene are also highlighted. Trends in simulated growing season temperature and
 411 precipitation for Lake Stiucii, Romania after Feurdean et al. (2015).



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427 **Figure 3.** The effect of climate, soils and disturbances by fire, herbivores and humans on the
 428 three types of grasslands and forest. Blue line denote a positive effect, red line a negative
 429 effect and grey both effects.
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431
 432 Acknowledgements
 433 Gabriela Florescu is acknowledged for drawing Figure 1.
 434

435 **Role of the funding source**

436 This work was supported by the German Research Foundation [FE-1096/4-1]. E.R. was
 437 supported by the János Bolyai Research Scholarship of the Hungarian Academy of
 438 Sciences. Z.M. was supported by the National Research, Development and Innovation Office
 439 (GINOP-2.3.2-15-2016-00019 project). Funding sources had no involvement in study design;
 440 in the collection, analysis and interpretation of data; in the writing of the report; and in the
 441 decision to submit the article for publication.

442 **Conflict of Interest**

443 There is no conflict of interest with any other people or organizations.
 444

445
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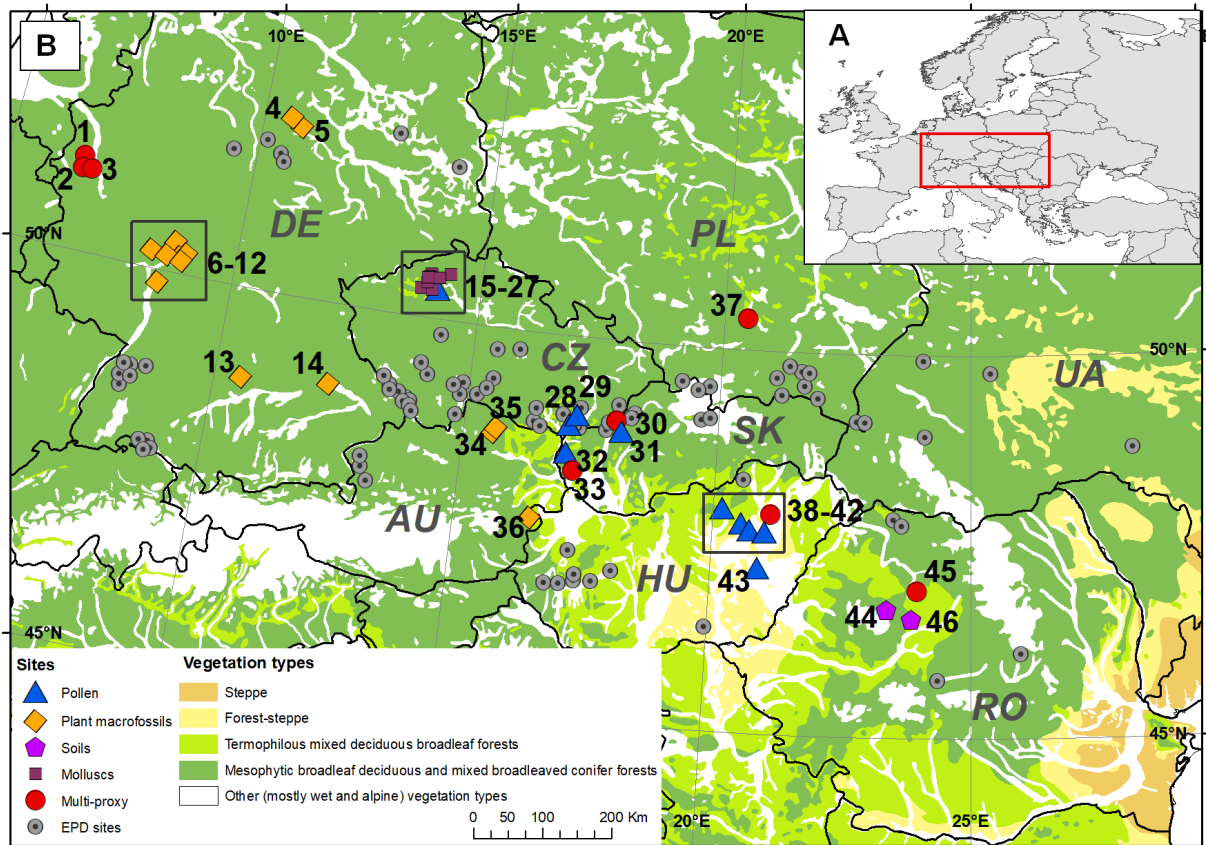
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707 **Supplementary Material**

708 **Figure S1** Location of sites extracted from the European Pollen Database (EPD) and used to
709 construct Figure 2.
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713 **Table S1.** Location of sites extracted from the literature and used to construct Figure 1.

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715 **Table 1.** Species-rich grassland types

716	Grassland type	Characteristics
717	Primary grassland I	Natural grasslands on skeletal and other poor soils with moisture deficit
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719		
720	Primary grassland II	Ancient grasslands formed and maintained mainly by climate conditions and natural fires, herbivores and, later, also influenced by anthropogenic disturbances
721		
722		
723		
724	Semi-natural grassland	Secondary grasslands formed and maintained by anthropogenic disturbances (deforestation, livestock grazing, cultivation, use of fire) in areas suitable for forests during the late Holocene
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