# **Grasslands of Eastern Europe**

**Péter Török,** MTA-DE Lendület Functional and Restoration Ecology Research Group, Debrecen, Hungary **Iwona Dembicz,** Botanical Garden Center for Biological Diversity Conservation in Powsin, Polish Academy of Sciences, Warsaw, Poland; and Department of Plant Ecology and Environmental Conservation, Faculty of Biology, University of Warsaw, Warsaw, Poland

**Zora Dajić-Stevanović,** Department of Botany, Faculty of Agriculture, University of Belgrade, Belgrade, Republic of Serbia **Anna Kuzemko,** M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine

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# **Abstract**

Grasslands cover around 282,000 km<sup>2</sup>, corresponding to 14.6% of the total area in the countries of Eastern Europe, here defined as East Europe, Eastern Central-Europe, and the non-Mediterranean part of the Balkan Peninsula. Primary (steppes, alpine grasslands, azonal and extrazonal grasslands) and secondary grasslands (created mostly by forest cuts) provide a wide range of ecosystem services, such as biomass production and food for grazing animals and other herbivores, carbon storage and sequestration, home for pollinators as well as for migratory and breeding birds, water infiltration, purification and storage, erosion prevention and recreation. Both primary and secondary grasslands in Eastern Europe harbor a rich flora and fauna, but they are threatened by area loss, the twin threats of intensification and abandonment, invasive species encroachment, and climate change. Large areas of grasslands in the lowland regions have been converted to croplands, and the remaining grassland fragments are in general degraded by intensified use. Intensified use and application of tillage, drainage, intercropping, high intensity grazing or the use of pesticides, mineral and organic fertilizers have a detrimental effect on flora and fauna. In contrast, low accessible areas in mountains, foothills or other marginal areas, the traditional grassland management is abandoned. To recover or improve grassland biodiversity, in many countries, the re-introduction of traditional management regimes by mowing or grazing have been suggested. In case of completely destroyed grasslands, restoration of grassland vegetation and diversity by spontaneous succession and/or technical reclamation are necessary. While in large-scale restoration programs successes were often reported, it was also noted by the authors that the success of restoration was strongly influenced by the availability of high-quality grasslands in the landscape, acting as donor sites or spontaneous sources of propagules. High quality grassland fragments act as hotspots of biodiversity in landscapes dominated by agriculture; thus, their preservation should be prioritized in conservation actions.

# **Delimitation and Physiogeography**

Grasslands in Eastern Europe cover around 282,000 km<sup>2</sup>, approximately 14.6% of the total area of the countries in Eastern Europe, Eastern Central-Europe and the non-Mediterranean part of the Balkan Peninsula (Fig. 1). With high differences between countries or subregions, the proportion of high natural value grasslands can be up to 70% of permanent grassland area (Török and Dengler, 2018; Török et al., 2018).

The Eastern European region is characterized by a cool continental climate with an increasing Mediterranean influence in the south (Peel et al., 2007). The region clearly divides into two main subregions: Central European highlands and mountain chains (the Carpathians, Balkan- and Crimean Mountains) with their intermountain basins (e.g., Great Hungarian Plain) in the South and Southwest and Central and Eastern European Lowlands in the North and Northeast. While the landscape of the southern part of the region is related to the older (Paleozoic or Mezozoic) bedrock or Holocene alluvial deposits, the surface of the lowlands in the north was shaped mostly during the Pleistocene. Young glacial landscapes with lakes are only present in the northernmost part of the region; the vast areas more to the south were glaciated earlier and are covered with older, denudated and transformed tills or galacio-fluvial deposits. Moreover, south of the glaciation borders, a thick loess cover accumulated during the Pleistocene, dominating the landscape and masking older landforms. The region is characterized by the presence of many large rivers (e.g., Vistula, Danube, Dnieper, Dnister, Siverskyy Donets and tributaries), the valleys of which are environmentally rich and harbor valuable grassland sites.

Eastern Europe is the western border of the Eurasian steppe and forest steppe zones, primary steppe grasslands and forest-steppe mosaics historically covered large areas in Bulgaria, Hungary, Moldova and Ukraine (Wesche et al., 2016; Török et al., 2018). A considerable part of the region is situated in the zones of deciduous forests and forest-steppes, where the primary vegetation consists of deciduous and mixed forests or forest-steppe mosaics (Metzger et al., 2005; Erdős et al., 2018a). These areas are dominated mostly by secondary grasslands, created after forest cuts and maintained by regular mowing and/or livestock grazing (Dengler et al., 2014).

# **Origin and Biodiversity of Grasslands**

The grass family appeared almost 90 million years ago, but its diversification and the development of grassland ecosystems happened much later (Gibson, 2009). Grassland ecosystems in South America appeared about 34 million years before present (BP), whereas in Europe the steppe-like grasslands occurred probably 5 million years BP. Natural grasslands have existed continuously since the Pleistocene (2.4 million years BP), and during glacial periods they covered the majority of the European continent in form of steppe-tundra in the north and xerothermic grasslands in the south. It is assumed that present steppes and steppe grasslands in the forest steppe zone (i.e., primary grasslands) originated in the Holocene from the near glacial steppe-tundra (also called "tundra-steppe" or "mammoth steppe"), which dominated the landscape of the region in cold periods of the Pleistocene (Binney et al., 2017; Chytrý et al., 2017). In Ukraine, the steppe range was slightly changing after the last glaciation according to climate

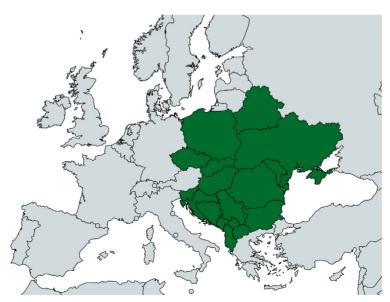


Fig. 1 The Eastern European region. The region covers countries of East Europe, Eastern Central-Europe, and the non-Mediterranean part of the Balkan Peninsula. The map was created by Map Chart (https://mapchart.net/).

fluctuations, being more mesophilous during the relatively warm and humid Holocene Climate Optimum (9000 to 5000 BP; Kremenetski, 1995). Simultaneously, the migration of species from Mediterranean and Asian glacial refugia enriched the steppe species pool during the Holocene, leading to the development of the current European steppe (Korotchenko and Peregrym, 2012). Recent paleoecological research has revealed that, during the climatic optimum, when the large-scale expansion of dense, deciduous forests occurred in the region, patches of natural grassland ecosystems survived in favorable locations even outside of what is traditionally regarded as steppe and forest-steppe zone (Moskal-del Hoyo et al., 2018; Pokorný et al., 2015). Those isolated refugia, as well as the continuous steppe zone, served as important sources of species for many types of semi-natural grasslands created by humans in the forest zone (Kajtoch et al., 2016).

In the north of the region the biodiversity of the more humid semi-natural grasslands probably originates from both the open forests and from wetlands (mostly fens and floodplains). It is believed that the large ungulates which lived there, including the aurochs and wisent, had a potential to create gaps or maintain openings in the forest resulting from natural disturbances such as windthrows or flooding. Moreover, beaver activity could create treeless areas around watercourses (Hejcman et al., 2013). Noticeably, there is a large number of grassland species with distributions related primarily to the forest zone of Eurasia, indicating the existence of open habitats long before the Neolithic revolution (Pärtel et al., 2005). Such species include *Iris sibirica*, *Gladiolus imbricatus*, *Maculinea teleius*, and *Maculinea alcon*. During interglacial periods their areas decreased because of forests spreading (Pärtel et al., 2007). During the last glaciations in the Holocene, 7500–6800 years BP, neolithic people developed agricultural practices, mainly by introducing grazing, which resulted in the alteration of forests towards semi-natural grasslands (Hejcman et al., 2013).

Palaecological studies validated that some semi-natural grasslands in Eastern Europe already existed between 8500 and 6000 BP (Price, 2000; Barczi et al., 2006), but most of the grasslands of secondary origin were established much later, in the Middle Ages. These secondary grasslands were mostly created by clear-cutting of various types of forests, and reached their largest extent during the last 200 years (Török et al., 2018). For example, it is thought that mesophilous meadows of the *Arrenatherion elatioris* have developed after medieval times (Poschlod et al., 2009; Hejcman et al., 2013); however, they are among the most widespread meadows today. Pastures are in general older than mown meadows as in most regions the scythe appeared much later than the livestock grazing systems. Also, the age of grasslands is increasing from the North to the South, because regions with drier and warmer climate favoring grassland vegetation are more frequent in the Southern part of the region, while in the North spontaneous shrub and tree encroachment highly suppressed grassland vegetation (Török et al., 2018).

As the steppes and forest-steppes of Eastern Europe constitute the western border of these biomes, many species of the steppe fauna have their distribution limits in the region, like the bobak marmot (Marmota bobak), the great jerboa (Allactaga major), the thick-tailed three-toed jerboa (Stylodipus telum), the gray dwarf hamster (Cricetulus migratorius), the steppe lemming (Lagurus lagurus), the greater mole-rat (Spalax microphthalmus), the northern mole vole (Ellobius talpinus), the steppe polecat (Mustela eversmanii), the marbled polecat (Vormela peregusna), and the steppe ratsnake (Elaphe dione) (Akimov and Radchenko, 2009; IUCN, 2019). However, the ranges of some species are limited to Eastern European steppes and semi-natural grasslands, e.g., that of the Podolsk mole-rat (Spalax zemni), the sandy mole rat (S. arenarius), the Balkan mole-rat (S. graecus), and the European ground squirrel (Spermophilus citellus; the range of this species extends to Austria). For the speckled ground squirrel (Spermophilus suslicus) Eastern Europe together with the European part of Russia constitute the whole distribution range of the species. Especially rich in endemic species, mostly invertebrates, are the steppes of the Crimean Peninsula (Akimov and Radchenko, 2009).

The natural and the semi-natural grassland flora of the lowlands in the region is dominated by species with wide Euro-Siberian distribution. However, there is a group of species, also referred to as Pannonian species, which have most of their range within the described region. They include such important grassland specialists as *Rhinanthus borbasii*, *Festuca vaginata*, *F. wagneri*, *Colchicum arenarium*, *Dianthus diutinus*, *Iris arenaria*, *Pulsatilla pratensis* ssp. *hungarica*, and *Linum hirsutum*. Much more species with limited distributions are related to the mountain ranges in the south of the region, especially those of the Balkan Peninsula, e.g., in Central Serbia and Kosovo (41% of the total number of 490 Balkan endemic plants were recorded in the class Festuco-Brometea (Aćić et al., 2015)).

Like in other parts of Europe, the flora and fauna of semi-natural grasslands contribute much to the overall biodiversity of the region. However, the diversity of these ecosystems is strongly shaped by management regime and human-controlled landscape factors (e.g., a large proportion of grasslands in the surrounding landscape supports the biodiversity of the given grassland area; Janišová et al., 2014). The oligo- to mesotrophic, traditionally managed, semi-natural, temperate grasslands of Eastern and Central Europe hold world-records for vascular plant diversity at small spatial scales (Vassilev et al., 2011; Wilson et al., 2012; Chytrý et al., 2015).

In Romania, 43 species were recorded in a plot of 0.1 m<sup>2</sup>, and 98 within a 10-m<sup>2</sup> plot (Dengler et al., 2009), while in the White Carpathians, a mountain range on the border between the Czech Republic and Slovakia, there were 67, 88 and 131 vascular plant species in plots of 1, 4 and 49 m<sup>2</sup>, respectively (Merunková et al., 2012). Semi-natural grasslands are important not only for plant biodiversity but also for other organisms. It is, for example, estimated that around 74% of European grasshopper species depend on open habitats (Hochkirch et al., 2016). Semi-natural grasslands seem to be equally important for butterflies (Skórka et al., 2007) and birds (Hoste-Danyłow et al., 2010). Despite recently observed negative trends, eastern European semi-natural grasslands are still hosting higher biodiversity when compared to their western counterparts (Batáry et al., 2010; Żmihorski et al., 2016).

# **Typology of Grasslands**

Grasslands in Eastern Europe can be classified as primary (natural) and secondary (semi-natural) grasslands. Primary grasslands cover sites that are in general unfavorable for the establishment of trees. The most important types are the following:

#### Steppes and Steppe Grasslands in Forest Steppe Mosaics

Steppes are primary climatogenic grasslands on dry habitats, which are not suitable for the establishment of trees in hilly regions, foothills, and lowlands (Fig. 2A). Steppes are very diverse and mosaic-like habitats characterized by perennial graminoids of *Bromus, Elymus, Agropyron, Festuca,* and *Stipa* species. They are in general rich in forbs, the most frequent genera being *Achillea, Artemisia, Aster, Astragalus, Centaurea, Inula, Linum,* and *Salvia*. There is an early spring aspect characterized by several early flowering species from the genera *Adonis, Gagea, Ornithogalum, Pulsatilla,* and *Tulipa*. Steppe grasslands in Eastern Europe are the westernmost localities of their Eurasian distribution. (Wesche et al., 2016; Török et al., 2016a). In the steppe zone, historically extended steppe grasslands were typical for loess deposits, mostly on chernozemic soils. In the forest-steppe zone, steppe grasslands are components of forest-grassland complexes (Fig. 2B, Erdős et al., 2014; Erdős et al., 2018a,b). In the region, remaining stands of this grassland type are typical in the Czech Republic, Hungary, Moldova, Poland, Romania, Ukraine, and the countries of the Northern Balkan. Based on recent estimates, the overall extent of this type of grasslands in the region is around 1.1 million hectares (Török and Dengler, 2018).

### **Alpine Grasslands**

Alpine grasslands are climatogenic grasslands occurring in regions that are too cold for the establishment of trees. Based on a recent estimate, there are 500,000 ha of these grasslands in the Eastern European region (Török and Dengler, 2018), but this grassland type is not discussed in detail in this article.

#### **Azonal and Extrazonal Grasslands**

Pedogenic or topogenic grasslands, where special habitat properties prevent the establishment of trees. The extent of this grassland type is estimated to be about 400,000 ha in Eastern Europe (Török and Dengler, 2018). There are several subtypes within this grassland type:

# Coastal and inland saline grasslands

Pedogenic grasslands in lowland regions, where the astatic water availability and high salt content of the soil prevents the establishment of trees (Fig. 2C and D). These grassland types are the most well-preserved in Eastern Europe, as their soil is unsuitable for agricultural production and can be utilized only with extensive pasture management. The most typical inland saline vegetation occurs in large extents in Hungary and Ukraine, but small fragments are present in all countries with dry lowland regions like Slovakia, Serbia, Bulgaria or Macedonia (Eliáš et al., 2013). These types of grasslands are characterized by a high cover of tussockforming fescue species (*F. pseudovina*, *F. rupicola*, *F. regeliana*), and several *Puccinellia* and *Juncus* species are also typical, especially in wet places at slightly lower elevations. Characteristic forbs are halophytes or other salt-tolerant species in the genera *Artemisia*, *Aster, Limonium, Plantago, Podospermum, Salicornia, Salsola, Spergularia*, and *Suaeda*.

## Sand steppes and coastal sand grasslands

These pedogenic grasslands cover acidic to calcareous sands which are in general unsuitable to sustain trees (Fig. 2E). Their vegetation is characterized by tussock-forming grasses, including fescues (Festuca vaginata, F. pseudovina, F. psammophila, F. polesica, F. beckeri), Corynephorus canescens, Koeleria glauca, Stipa capillata, and S. borysthenica. Also, several small clonally spreading Carex species are typical (e.g., C. stenophylla, C. praecox, C. supina, and C. colchica). Many short-lived forbs are characteristic in the spring, including the genera Arenaria, Cerastium, Draba, Erophila, and Veronica. Cryptogamic species (mosses and lichens) can reach considerable cover in this type of grasslands. Sand grasslands occurring in the lowlands of the Eastern European region are typical in the countries of Belarus, Croatia, the Czech Republic, Hungary, Poland, Serbia, Slovakia, Slovenia, and Ukraine.

#### Grasslands on shallow rocky substrates

Because of the steep slopes, high erosion enables only the development of shallow and rocky soils (skeletal soils), which is in general unsuitable for the establishment of trees. This topogenic grassland type typically occurs in small patches near the top of hills and middle mountains (Fig. 2F). The species composition is characterized by xerophytes, and the species composition and richness is strongly influenced by the type of the bedrock (the most species rich grasslands are on limestone or dolomite bedrock; grasslands formed on volcanic or metamorphic bedrock are less species rich). Typical graminoids are *Festuca, Bromus, Poa,* and *Stipa* species. Frequent forb genera are *Campanula, Cerastium, Inula, Potentilla, Spergula,* and *Veronica*. In addition, many species of the Brassicaceae family, as well as several succulent species from the genera *Jovibarba, Saxifraga, Sedum,* and *Sempervivum* occur in these grasslands.



Fig. 2 Grassland types of the region: (A) steppe grassland on chalk outcrops, Dvorichansky National Nature park, Kharkiv oblast, Ukraine; (B) steppe grassland patch in a forest-steppe of Northern Hungary; (C) inland saline grassland, Oril river floodplain, Poltava oblast, Ukraine; (D) coastal halophyte vegetation, Dzharylhach Island, Kherson oblast, Ukraine; (E) sand steppe, Oleshkivsky Sands National Nature park, Kherson oblast, Ukraine; (F) rocky grassland, Svydovets ridge, Carpathian Mountains, Ukraine; (G) dry secondary grassland on limestone, Bükk Mountains, Hungary; (H) mesic secondary grassland, Lower Dnieper floodplain, Kherson oblast, Ukraine. Photos by Anna Kuzemko (A, C, D, E and H), Roman Kish (F), and Péter Török (B and G).

### Secondary grasslands

Secondary grasslands were created by the anthropogenic suppression of phanerophytes and are sustained by regular management—mostly mowing and/or livestock grazing. They can be formed on various substrates from fine alluvial deposits to solid bedrock. Their secondary origin does not necessarily mean that they are less important in biodiversity conservation. In many cases, they are valuable and species rich habitats, sustained by several hundreds of years of extensive management. Secondary grasslands can be classified into the following subtypes:

### **Dry and Semi-Dry Grasslands**

The most valuable meso-xerophytic secondary grassland types, which occur on shallow to deep soils, formed mostly on calcareous or volcanic bedrocks in the whole region, from lowlands to mountains (Fig. 2G). Especially the calcareous types harbor many steppe elements and are extremely species-rich habitats, threatened in many countries by woody encroachment (Elias et al., 2018). Dry grasslands are also characterized by high cryptogam diversity. Characteristic graminoids are tussock-forming and rhizomatous species like *Brachypodium pinnatum*, *Elymus hispidus*, *Bromus erectus*, *Danthonia alpina*, *Sieglingia decumbens*, *Avenula pubescens*, *Nardus stricta*, *Festuca ovina*, *Melica altissima*, *M. transsylvanica*, *Carex caryophyllea*, and *C. montana*. Characteristic forbs are in the genera *Allium*, *Campanula*, *Centaurea*, *Clinopodium*, *Cirsium*, *Geranium*, *Inula*, *Lathyrus*, *Origanum*, *Peucedanum*, *Salvia*, *Thymus*, *Trifolium*, *Verbascum*, and *Vicia*.

#### Mesic to Wet Grasslands

These types of secondary grasslands are the most common in the region from lowlands to mountain areas. In general they cover medium to deep, in most cases nutrient-rich mesic to wet soils (Fig. 2H). Most characteristic species are generalist graminoids and forbs. Typical tussock forming and rhizomatous graminoids include Arrhenatherum elatius, Alopecurus pratensis, Agrostis tenuis, Anthoxanthum odoratum, Briza media, Bromus inermis, Cynosurus cristatus, Festuca pratensis, F. rubra, F. arundinacea, and Poa pratensis. Small-growing Carex species like C. pallescens, C. panicea, and C. tomentosa are also important. More moist types harbor A. stolonifera, Molinia arundinacea, Deschampsia caespitosa, Poa trivialis, further Carex species including C. nigra, C. flava, and C. flacca, and Juncus species (e.g., J. conglomeratus, J. effusus). They harbor several forb species from the genera Achillea, Chrysanthemum, Dactylorchiza, Gentiana, Leontodon, Lychnis, Medicago, Mentha, Orchis s.l., Ranunculus, Rhinanthus, Stellaria, Trifolium, and Veronica.

# **Ecology and Biodiversity Patterns**

As it was mentioned earlier, natural grasslands of the region are usually climatogenic (steppes, steppe grasslands in forest steppe mosaics, and alpine grasslands), pedogenic (sand steppes and coastal sand grasslands), or topogenic (grasslands on shallow rocky substrates). However, besides the crucial role of climate and extreme habitat conditions which prevent woody encroachment, the maintenance of ecosystem functioning, high biodiversity and typical species composition of natural grasslands can also be driven by other factors. For example, in the steppe ecosystem large mammal herbivores and fires are consumers of vegetation, preventing steppe ecosystems from reaching their climatic potential, and thus preventing the accumulation of litter and subsequent changes towards more mesophilous grasslands or shrublands. Many steppe nature reserves face the risk of losing biodiversity due to the implementation of fire prevention measures and the lack of important wild ungulates such as horses and saiga (the latter of which became locally extinct because of hunting and habitat fragmentation) (Havrylenko, 2011).

Microclimatic gradients are important for both natural and semi-natural grasslands. Vegetation typical for more northern zones or more mesophilous sites are occupying northern exposition, while more xerophytic grasslands occupy south-facing slopes (Sudnik-Wójcikowska and Moysiyenko, 2008; Sutcliffe et al., 2016). Soil and bedrock gradients are also important in both natural and semi-natural grasslands. The main drivers of species composition are soil pH (e.g., Nardus dominated grasslands occur on acidic bedrock), soil depth (e.g., Festuca pallens grasslands occur on rock outcrops), and soil texture (sand grasslands on coarse sediments and more steppe-like grasslands on loess). Moisture gradient is important predominantly in semi-natural grasslands, but its role can also be recorded in natural steppes, with depressions being occupied by more mesic vegetation or being prone to salinization. Besides the amount of available moisture, its seasonal variation is also important (e.g., the inundation time or its temporal fluctuations).

However, the most crucial driver of species composition in semi-natural grasslands is the management regime. Mowing promotes graminoids, while grazing usually suppresses them. Furthermore, grazing allows more forb species to develop and replenish (small disturbances and open soil surfaces created by trampling are crucial for the germination of many grassland species). The type of grazing livestock can also be an important factor. Cattle and horses eat the taller grasses while sheep prefer forbs and short grasses (Tóth et al., 2018). Goats, which are browsers, can reduce shrub encroachment into the grassland (Elias et al., 2018). Mowing regime can also influence species composition; for example, early mowing favors early-flowering species. The importance of the fertility gradient should also be emphasized. It is especially important in semi-natural grassland types as natural primary productivity is controlled by moisture deficit. Recent studies point out the role of limiting nutrients in shaping the species composition of grasslands, with different species adapted to N and P limitation (Roeling et al., 2018).

Biodiversity patterns (especially of plants) can be controlled by the same gradients as the species composition of grasslands. In general, the biodiversity of various groups of organisms inhabiting grasslands (especially drier, more xerothermic types of grasslands) is decreasing from south to north in the region, mostly due to the climate and the geological history (glaciation and later the expansion of forests), as well as the mountain ranges forming a barrier for the migration of species from the south (like the Sudety and the Carpathian Mts). However, at regional scales, the patterns can be opposite. For example, in natural steppes in Ukraine plant diversity decreases from the forest-steppe zone to the south, along with the drought stress becoming more intensive. Management type is another important driver of species richness in grasslands, in particular in semi-natural ones. Traditional

management usually supports biodiversity, while too intensive management leads to its decline (Cremene et al., 2005). The highest fine-scale richness of vascular plants occurs in semi-natural mown grasslands (Turtureanu et al., 2014), but grazing and small disturbances created by animals can also be important for the diversity of this taxonomic group (Enyedi et al., 2009). It is worth mentioning that the plant richness of natural grasslands, like steppes, is enhanced by grazing and fires (Kuzemko et al., 2016).

Typically, the relationship of pH with fine-scale plant diversity in the region seems to be hump-shaped, with the highest richness occurring under neutral or slightly basic conditions, although under drier conditions the relationship may be negative or non-existent/non-detectable (Palpurina et al., 2017). Well known is the hump-shaped relationship between primary productivity and plant species richness (Fraser et al., 2015). As it was mentioned before, in natural grasslands primary productivity is controlled by climate (with the resulting pattern of richness in steppe), but in semi-natural grasslands it depends on fertility. Limiting nutrients can influence the richness or the richness-productivity pattern (Palpurina et al., 2019).

The relationship between biodiversity and productivity in grassland ecosystems was much studied (e.g., Grime, 2001; Kelemen et al., 2013; Cerabolini et al., 2016; Sonkoly et al. 2019). The most important factors affecting the productivity of grassland communities are water and nutrient availability, which influence the biodiversity of the community. High values of phosphorus, nitrogen and potassium decrease the biodiversity of grasslands (Merunková and Chytrý, 2012). Bernhardt et al. (2010) reported some data on grassland productivity from different parts of the EU. The regions with the lowest productivity are located in the Mediterranean, with annual yields limited to 1.5 t per ha or even less; slightly higher yields are obtained for mountain areas, which are more mesic, e.g., the Pyrenees and the mountains of the Balkan Peninsula. The Central EU countries (Poland, the Czech Republic and Slovakia) reach fairly high yields, around 4 t per ha, while in the steppe conditions of Hungary, Bulgaria and other southeast European countries, the yields are much lower—about 1.5 t per ha, because of unfavorable water regime and drought.

# **Ecosystem Services and Threats**

Natural and semi-natural grasslands provide a wide range of ecosystem services, such as biomass production and food for grazing animals and herbivores, carbon storage and sequestration, home for pollinators as well as for migratory and breeding birds, resources for flood reduction, water infiltration, purification and storage, erosion prevention and recreation (Peciña et al., 2019). The conversion of grassland into arable land decreases soil carbon because of the reduced carbon input from litter and the loss of carbon by tillage (Jones and Donnelly, 2004). Plant diversity and soil organic carbon pools are thought to be the major factors for the provision of several ecosystem services, mainly pollination, herbs for traditional medicinal use, nutrient cycling, nutrient retention and biomass production (Peciña et al., 2019). In addition to cultural and aesthetic values, grasslands play an important role in nutrient cycling, balancing of the local climate and soil erosion, and sustaining pollinators and biological control agents (e.g., Fantinato et al., 2018). Grassland ecosystems have also attracted substantial scientific and policy interest because of their potential role as sinks or sources for atmospheric carbon dioxide. Conversion of arable land into permanent grassland is one measure that is believed to have a considerable carbon sequestration potential (Ammann et al., 2007). The supply of multiple ecosystem services is decreasing significantly worldwide because of pressures of climate change and other anthropogenic factors, including overgrazing, intensive agricultural production, deforestation, and urbanization (Costanza et al., 2014). Both climate change and grazing exert great influence on the supply and interrelation of ecosystem services (Hao and Yu, 2018). However, modern agricultural practices, mainly referring to intensive agriculture, as well as fragmentation and land-use abandonment in recent decades, have caused a biodiversity loss and consequent conservational concerns, due to negative effects of value and provision of grassland ecosystem services.

#### **Area Loss**

The most alarming threat for most of the natural communities including grasslands is area loss. Important causes of area loss are the (i) conversion to croplands and other agricultural areas, (ii) afforestation, establishment of tree plantations and spontaneous forest succession, (iii) and urbanization. The most threatened grasslands are in the lowlands, embedded into intensively managed croplands. Recent estimates suggest that in the last 200 years at least 50% of all grassland area has vanished in the Eastern European region (Török and Dengler, 2018). The area loss is strongly variable between grassland types and/or regions. Bíró et al. (2018) summarized the area loss of 8 natural and semi-natural grassland types in Hungary. They found that the lowest decrease in area occurred in saline grasslands (39%), which are unsuitable for agricultural production, while other grassland types displayed 85–98% decrease in area. A similarly high decrease was reported for the western part of steppes and forest steppes (Deák et al., 2016; Wesche et al., 2016; Erdős et al., 2018b).

One of the consequences of habitat loss is high fragmentation and the isolation of remaining grassland patches, which are exceptionally severe in Eastern European steppes. For example, in the Lugansk region (Ukraine) the formerly continuous steppe vegetation has survived in 2000 fragments that are mostly surrounded by intensive agricultural landscapes (Parnikoza and Vasiluk, 2011). The increasing fragmentation and isolation of semi-natural grasslands is a serious threat for grassland biodiversity in many other countries in the region. Isolation can lead to local extinctions (while immigration from other patches has low probability) and can negatively influence the genetic structure of the populations, as was found in steppe enclaves of southern Ukraine (Dembicz et al., 2016; Wódkiewicz et al., 2016).

# **Changes in Management: Intensification and Abandonment**

Management changes can be considered the most important threats for grassland biodiversity in the Eastern European region. The cessation of former management became typical in the last 50 years in Eastern Europe affecting mostly grasslands in mountainous areas, foothills and other areas with low accessibility (Török and Dengler, 2018). Land abandonment in these regions resulted in the decrease of grassland biodiversity and increased woody encroachment (Valkó et al., 2011, 2012). Land abandonment was especially intensive in the 1960s, when traditional herding management was replaced in many places by the intensive forms of animal husbandry. A second wave of abandonment happened after the fall of the Socialist regimes and the collapse of collective farms. However, land abandonment also result in a slight increase of grassland areas in lowlands because of the spontaneous recovery of grasslands following cropland abandonment (Ramankutty and Foley, 1999). The access of EU subsidies in countries such as the Czech Republic, Slovakia, Romania and Hungary, impacted grassland biodiversity controversially. In some foothill regions shrub encroachment was suppressed and many grassland sites were cleared from shrubs, which affected grassland biodiversity positively. In other grasslands, subsidies enabled the farmers to improve the management of grasslands and provided a source for intensification, which resulted in the decrease of farmland biodiversity (Sutcliffe et al., 2015). For example, in Romania the subsidies increased the amount of grazing livestock, which, in most cases, meant an increased sheep grazing in high diversity grasslands historically maintained by low-intensity cattle grazing and/or mowing. The process proved detrimental to grassland biodiversity (Roman et al., 2019).

### **Invasive Species Encroachment**

Grasslands were considered in a recent evaluation of invasion threat by Pyšek et al. (2010) as habitats characterized with intermediate levels of invasion and low invasion risk. However, grassland habitats are subjected to highly different levels of invasion and invasion risk. Botta-Dukát (2008) found that there are grassland types that can be characterized by low levels of invasion (e.g., rocky grasslands and saline grasslands), while others like sand grasslands are highly invaded. Plant invasions are strongly associated with the management changes of grasslands. In general, the overuse of grasslands (e.g., overgrazing or improper management) can create many establishment gaps in the vegetation and can facilitate the invasion. Climate change can also interact with this process, e.g., extreme weather events can create bare-soil patches in the vegetation, and increased frequency of droughts and fire favor the establishment of fire-adapted and drought-tolerant C4 grasses (Walther et al., 2009; Török and Aradi, 2017).

#### **Climate Change**

An emerging future threat is climate change, which can considerably affect grassland biodiversity in the forthcoming decades. According to the last predictions, (1) the yearly mean temperature will rise by about 1–3 °C, (2) precipitation patterns will be reshaped, as winter precipitation is expected to increase at the expense of summer precipitation, (3) the frequency of extreme weather events (e.g., extreme droughts, wildfires, extreme frosts, heavy rains) will increase in the future (Anders et al., 2014; Wesche et al., 2016). These effects jointly reshape the composition of grasslands by favoring drought-tolerants and ephemerous species, and increasing the proportion of Mediterranean species in the southern and central part of the region (Thuiller et al., 2005).

#### Some Further Drivers of Grassland Biodiversity

In many countries in Europe, grasslands assigned to the military are well-preserved and sustained because of the limited access and other restrictions in management (Elias et al., 2018). However, recent military conflicts (e.g., in Ukraine) had devastating impact on the subjected regions and embedded grasslands (e.g., uncontrolled fires by explosives, demolition by artillery fires, armored vehicle maneuvers, Vasyliuk et al., 2017). In Western Europe, among the most important threats are nitrogen deposition and aerial eutrophication (Dengler and Tischew, 2018). In the Eastern European region this threat can be considered to be of much lower importance. It was found that the nutrient enrichment of nutrient-limited grassland types (e.g., dry grassland types on shallow soils) can facilitate the increase in the cover of generalist graminoids and, due to their increased biomass production, can also decrease the beneficial effects of management on the grassland biodiversity (Kelemen et al., 2014; Habel et al., 2013).

# **Conservation, Sustainable Management and Restoration**

# Conservation

The most valuable grassland habitats can be found in protected areas, most cases in national parks and other nature reserves (e.g., Askania-Nova Biosphere Reserve, Carpathian Biosphere Reserve, Ukrainian Steppe Reserve, Oleshkivski Sands National Nature Park, Slovenský Raj National Park). In general, the active protection of semi-natural grasslands only began in the late 20th century when the approach of nature conservation shifted from absolute non-intervention to active conservation. Until then, the emphasis was mainly placed on species conservation, sometimes not even considering or misunderstanding habitat ecology and the requirements of the species. While due to the non-intervention approach, although there were a very few grasslands in protected nature areas preserved, it made possible to save particularly valuable virgin steppes from plowing (extensive stands were destroyed in the so called "virgin steppe" campaign in the 50s).

One of the main legislative instruments that regulates the protection of grassland ecosystems in Europe, is the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), which principal aims are to ensure conservation of wild plant and animal species and their natural habitats. This Convention provides the basis for development of the Emerald network of areas of special conservation interest. In EU Member States, this type of network is called Natura 2000. Natura 2000 is based on two directives: the Birds Directive and the Habitats Directive. There are more than 4000 Natura 2000 sites, in which there is a noticeable cover of grasslands. Within the Natura 2000 and the Emerald network, management plans are fine-tuned to take into account the environmental requirements of certain habitat types of certain rare or endangered species.

# **Sustainable Grassland Management and Restoration**

In the Eastern European region several grasslands were created and later sustained by extensive forms of management mostly by mowing or grazing (Dengler et al., 2014). Large areas of grasslands in the lowland regions has been converted to croplands, and the remaining grassland fragments are in general degraded by intensified use. Intensified use and application of tillage, drainage, intercropping, high intensity grazing or the use of pesticides, mineral and organic fertilizers have a detrimental effect on flora and fauna (McLaughlin and Minneau, 1995). In contrast, low accessible areas in mountains, foothills or other marginal areas, the traditional grassland management is abandoned (van Dijk et al., 2005). In lowland regions of Eastern Europe, natural and semi-natural grasslands are embedded as small islands in the sea of intensified landscape. These patches also often key elements of High Nature Value (HNV) farmland systems, which are low-input farming systems in terms of biodiversity and management practices. The sustainable management of species-rich grasslands in EU countries of Eastern Europe is made achievable under the Common Agricultural Policy (Oppermann et al., 2012). In Eastern Europe, a high proportion of extensively managed remnants of the traditional rural areas are present (Oppermann et al., 2012). In many countries, the re-introduction of traditional management by mowing or grazing as a restoration tool has been suggested (Török et al. 2016b, Galvánek and Lepš, 2008; Valkó et al., 2011, 2012). Low intensity grazing by herded livestock (local breeds) or free grazing (by wild horses and cattle) are often recommended (Török et al., 2016b,c; Tóth et al., 2018). In many regions the re-introduction of traditional management is not feasible or sustainable; thus, conservation authorities and site managers are seeking substitute management practices (e.g., prescribed burning during the dormant season, Valkó et al. 2014). Instead of a single type of management by mowing or grazing adopting a whole scheme of traditional land use may be required for many grasslands to sustain the extraordinary grassland diversity in a particular region (Babai and Molnár, 2014).

In degraded grasslands, the decrease of management intensity is often recommended, but in case of completely destroyed grasslands (e.g., converted grassland areas), restoration of grassland vegetation and diversity by spontaneous succession and/or technical reclamation are necessary. There were several large-scale grassland restoration programs in Eastern Europe. Most publications were related to grassland restorations in the Czech Republic and lowland regions of Hungary (Halassy et al., 2016; Kövendi-Jakó et al., 2019; Török et al., 2011; Prach et al., 2014; Lengyel et al., 2012). While in large-scale restoration programs successes were often reported, it was also noted by the authors that the success of restoration was strongly influenced by the availability of high-quality grasslands in the landscape, acting as donor sites or spontaneous sources of propagules. These facts underline that the preservation of natural and semi-natural high-quality grassland fragments should be prioritized in conservation actions (Török and Helm, 2017).

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#### References

Acić, S., Šilc, U., Petrović, M., Tomović, G., Stevanović, Z.D., 2015. Classification, ecology and biodiversity of Central Balkan dry grasslands. TUEXENIA 35, 329–353. Akimov, I.A., Radchenko, V., 2009. Red data book of Ukraine. Animals. Global Consulting, Kiev.

Ammann, C., Flechard, C.R., Leifeld, J., Neftel, A., Fuhrer, J., 2007. The carbon budget of newly established temperate grassland depends on management intensity. Agriculture, Ecosystems and Environment 121, 5–20.

Anders, İ., Stagl, J., Auer, I., Pavlik, D., 2014. Climate change in central and Eastern Europe. In: Rannow, S., Neubert, M. (Eds.), Managing protected areas in central and Eastern Europe under climate change. Advances in global change research, vol. 58. Springer, Dordrecht, pp. 17–30.

Babai, D., Molnár, Z., 2014. Small-scale traditional management of highly species-rich grasslands in the Carpathians. Agriculture, Ecosystems and Environment 182, 123–130. Barczi, A., Tóth, T.M., Csanádi, A., Sümegi, P., Czinkota, I., 2006. Reconstruction of the paleo-environment and soil evolution of the Csípőhalom kurgan, Hungary. Quaternary International 156-157, 49–59.

Batáry, P., Báldi, A., Sárospataki, M., et al., 2010. Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. Agriculture, Ecosystems & Environment 136, 35–39.

Bernhardt, K.G., Lapin, K., Werschonig, E., 2010. The future of plant diversity in grassland farming vegetation—A review of diversity in a strongly transformed agricultural landscape, Biotechnology in Animal Husbandry. In: XII International Symposium on Forage Crops of Republic of Serbia —Forage Crops Basis of Sustainable Animal Husbandry Development, pp. 205–217. Kruševac.

Binney, H., Edwards, M., Macias-Fauria, M., et al., 2017. Vegetation of Eurasia from the last glacial maximum to present: Key biogeographic patterns. Quaternary Science Reviews 157, 80–97.

Bíró, M., Bölöni, J., Molnár, Z., 2018. Use of long-term data to evaluate loss and endangerment status of Natura 2000 habitats and effects of protected areas. Conservation Biology 32, 660–671.

Botta-Dukát, Z., 2008. Invasion of alien species to Hungarian (semi-)natural habitats. Acta Botanica Hungarica 50 (Suppl), 219–227.

Cerabolini, B.E.L., Pierce, S., Verginella, A., et al., 2016. Why are many anthropogenic agroecosystems particularly species-rich? Plant Biosystems 150, 550-557.

Chytrý, M., Dražil, T., Hájek, M., et al., 2015. The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). Preslia 87, 217-278.

Chytrý, M., Horsák, M., Syrovátka, V., et al., 2017. Refugial ecosystems in Central Asia as indicators of biodiversity change during the Pleistocene–Holocene transition. Ecological Indicators 77, 357–367.

Costanza, R., de Groot, R., Sutton, P., et al., 2014. Changes in the global value of ecosystem services. Global Environmental Change 26, 152-158.

Cremene, C., Groza, G., Rakosy, L., et al., 2005. Alterations of steppe-like grasslands in Eastern Europe: A threat to regional biodiversity hotspots. Conservation Biology 19, 1606–1618

Deák, B., Tóthmérész, B., Valkó, O., et al., 2016. Cultural monuments and nature conservation: The role of kurgans in maintaining steppe vegetation. Biodiversity and Conservation 25. 2473–2490.

Dembicz, I., Moysiyenko, I.I., Shaposhnikova, A., et al., 2016. Isolation and patch size drive specialist plant species density within steppe islands: A case study of kurgans in southern Ukraine. Biodiversity and Conservation 25, 2289–2307.

Dengler, J., Tischew, S., 2018. Grasslands of Western and northern Europe—Between intensification and abandonment. In: Squires, V.R., Dengler, J., Feng, H., Hua, L. (Eds.), Grasslands of the world: Diversity, management and conservation. CRC Press, Boca Raton, pp. 27–63.

Dengler, J., Ruprecht, E., Szabó, A., et al., 2009. EDGG cooperation on syntaxonomy and biodiversity of Festuco-Brometea communities in Transylvania (Romania): Report and preliminary results. Bulletin of the European Dry Grassland Group 4, 13–19.

Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palaearctic grasslands: A synthesis. Agriculture, Ecosystems & Environment 182, 1-14.

Eliáš, P., Sopotlieva, D., Dítě, D., et al., 2013. Vegetation diversity of salt-rich grasslands in Southeast Europe. Applied Vegetation Science 16, 521-537.

Elias, D., Hölzel, N., Tischew, S., 2018. Goat paddock grazing improves the conservation status of shrub-encroached dry grasslands. TUEXENIA 38, 215-233.

Enyedi, Z.M., Ruprecht, E., Deák, M., 2009. Long-term effects of the abandonment of grazing on steppe-like grasslands. Applied Vegetation Science 11, 55-62.

Erdős, L., Tölgyesi, Cs, Horzse, M., Tolnay, D., Hurton, Á., Schulcz, N., Körmöczi, L., Lengyel, A., Bátori, Z., 2014. Habitat complexity of the Pannonian forest-steppe zone and its nature conservation implications. Ecological Complexity 17, 107–118. https://doi.org/10.1016/j.ecocom.2013.11.004.

Erdős, L., Kröl-Dulay, Gy, Bátori, Z., Kovács, B., Németh, Cs, Kíss, P.J., Tölgyesi, Cs, 2018a. Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics. Biological Conservation 226. 72–80.

Erdős, L., Ambarlı, D., Bátori, Z., et al., 2018b. The edge of two worlds: Eurasian forest-steppes in dynamic transition. Applied Vegetation Science 21, 345-362.

Fantinato, E., Del Vecchio, S., Giovanetti, M., Acosta, A.T.R., Buffa, G., 2018. New insights into plants coexistence in species-rich communities: The pollination interaction perspective. Journal of Vegetation Science 29, 6–14.

Fraser, L.H., Pither, J., Jentsch, A., et al., 2015. Worldwide evidence of a unimodal relationship between productivity and plant species richness. Science 349, 302-305.

Galvánek, M., Lepš, J., 2008. Changes of species richness pattern in mountain grasslands: Abandonment vs. restoration. Biodiversity and Conservation 17, 3241-3253.

Gibson, D.J., 2009. Grasses and grassland ecology. Oxford University Press, Oxford.

Grime, J.P., 2001. Plant strategies, vegetation processes, and ecosystem properties. Wiley, New York.

Habel, J.C., Török, P., Dengler, J., et al., 2013. European grasslands: A threatened ecosystem biodiversity hotspot. Biodiversity and Conservation 22, 2131–2138.

Halassy, M., Singh, A.N., Szabó, R., et al., 2016. The application of a filter-based assembly model to develop best practices for Pannonian sand grassland restoration. Journal of Applied Ecology 53, 765–773.

Hao, R., Yu, D., 2018. Optimization schemes for grassland ecosystem services under climate change. Ecological Indicators 85, 1158-1169.

Havrylenko, V.S., 2011. The biosphere reserve Askania Nova is a good model for tracking of the ecosystem processes in the protected steppes of Eurasia. Ecology and Noosphaerology 22, 90–97.

Hejcman, M., Hejcmanová, P., Pavlů, V., Beneš, J., 2013. Origin and history of grasslands in Central Europe—A review. Grass and Forage Science 68, 345-363.

Hochkirch, A., Nieto, A., García Criado, M., et al., 2016. European red list of grasshoppers. In: Crickets and bush-crickets. Publications Office of the European Union, Luxembourg. Hoste-Danylow, A., Romanowski, J., Żmihorski, M., 2010. Effects of management on invertebrates and birds in extensively used grassland of Poland. Agriculture, Ecosystems & Environment 139, 129–133.

IUCN, 2019. The IUCN Red List of Threatened Species. Version 2019-1. http://www.iucnredlist.org. Downloaded on 30 June 2019.

Janišová, M., Michalcová, D., Bacaro, G., Ghisla, A., 2014. Landscape effects on diversity of semi-natural grasslands. Agriculture, Ecosystems & Environment 182, 47–58.

Jones, M.B., Donnelly, A., 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO<sub>2</sub>. New Phytologist 164, 423–439.

Kajtoch, Ł., Cieślak, E., Varga, Z., Paul, W., Mazur, M.A., Sramkó, G., Kubisz, D., 2016. Phylogeographic patterns of steppe species in Eastern Central Europe: A review and the implications for conservation. Biodiversity and Conservation 25, 2309–2339. https://doi.org/10.1007/s10531-016-1065-2.

Kelemen, A., Török, P., Valkó, O., Miglécz, T., Tóthmérész, B., 2013. Mechanisms shaping plant biomass and species richness: Plant strategies and litter effect in alkali and loess grasslands. Journal of Vegetation Science 24, 1195–1203.

Kelemen, A., Török, P., Valkó, O., et al., 2014. Sustaining recovered grasslands is not likely without proper management: Vegetation changes after cessation of mowing. Biodiversity and Conservation 23, 741–751.

Korotchenko, I., Peregrym, M., 2012. Ukrainian Steppes in the past, at present and in the future. In: Werger, M.J.A., van Staalduinen, M.A. (Eds.), Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World, Plant and Vegetation. Springer Netherlands, Dordrecht, pp. 173–196.

Kövendi-Jakó, A., Halassy, M., Csecserits, A., et al., 2019. Three years of vegetation development worth 30 years of secondary succession in urban-industrial grassland restoration. Applied Vegetation Science 22, 138–149.

Kremenetski, C.V., 1995. Holocene vegetation and climate history of southwestern Ukraine. Review of Palaeobotany and Palynology 85, 289-301.

Kuzemko, A.A., Steinbauer, M.J., Becker, T., et al., 2016. Patterns and drivers of phytodiversity in steppe grasslands of Central Podolia (Ukraine). Biodiversity and Conservation 25, 2233–2250.

Lengyel, S., Varga, K., Kosztyi, B., et al., 2012. Grassland restoration to conserve landscape-level biodiversity: A synthesis of early results from a large-scale project. Applied Vegetation Science 15, 264–276.

McLaughlin, A., Minneau, P., 1995. The impact of agricultural practices on biodiversity. Agriculture, Ecosystems and Environment 55, 201-212.

Merunková, K., Chytrý, M., 2012. Environmental control of species richness and composition in upland grasslands of the southern Czech Republic. Plant Ecology 213, 591–602.

Merunková, K., Preislerová, Z., Chytrý, M., 2012. White Carpathian grasslands: Can local ecological factors explain their extraordinary species richness? Preslía 84, 311–325.

Metzger, M.J., Bunce, G.H., Jongman, R.H.G., Mücher, C.A., Watkins, J.W., 2005. A climatic stratification of the environment of Europe. Global Ecology and Biogeography 14, 549–563. Moskal-del Hoyo, M., Wacnik, A., Alexandrowicz, W.P., et al., 2018. Open country species persisted in loess regions during the Atlantic and early subboreal phases: New multidisciplinary data from southern Poland. Review of Palaeobotany and Palynology 253, 49–69.

Oppermann, R., Beaufoy, G., Jones, G. (Eds.), 2012. High nature value farming in Europe. Verlag Regionalkultur, Ubstadt-Weiher.

Palpurina, S., Wagner, V., von Wehrden, H., et al., 2017. The relationship between plant species richness and soil pH vanishes with increasing aridity across Eurasian dry grasslands: Plant species richness, soil pH and precipitation. Global Ecology and Biogeography 26, 425–434.

Palpurina, S., Chytrý, M., Hölzel, N., et al., 2019. The type of nutrient limitation affects the plant species richness–productivity relationship: Evidence from dry grasslands across Eurasia. Journal of Ecology 107, 1038–1050.

- Parnikoza, I., Vasiluk, A., 2011. Ukrainian steppes: Current state and perspectives for protection. Annales Universitatis Mariae Curie-Skłodowska LXVI, 23-37.
- Pärtel, M., Bruun, H.H., Sammul, M., 2005. Biodiversity in temperate European grasslands: Origin and conservation: 13th international occasional symposium of the European grassland federation. In: Integrating efficient grassland farming and biodiversity: Proceedings of the 13th international occasional symposium of the European grassland federation, pp. 1–14.
- Pärtel, M., Helm, A., Reitalu, T., Liira, J., Zobel, M., 2007. Grassland diversity related to the late Iron age human population density. Journal of Ecology 95, 574-582.
- Peciña, M.V., Ward, R.D., Bunce, R.G.H., et al., 2019. Country-scale mapping of ecosystem services, provided by semi-natural grasslands. Science of the Total Environment 661, 212–225.
- Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11, 1633-1644.
- Pokorný, P., Chytrý, M., Juříčková, L., Sádlo, J., Novák, J., Ložek, V., 2015. Mid-Holocene bottleneck for central European dry grasslands: Did steppe survive the forest optimum in northern Bohemia, Czech Republic? The Holocene 25, 716–726. https://doi.org/10.1177/0959683614566218.
- Poschlod, P., Baumann, A., Karlik, P., 2009. Origin and development of grasslands in Central Europe. In: Veen, P., Jefferson, R., de Smidt, J., van der Straaten, J. (Eds.), Grasslands in Europe of high nature value. KNNV Publishing, the Netherlands, pp. 15–25.
- Prach, K., Jongepierová, I., Řehounková, K., Fajmon, K., 2014. Restoration of grasslands on ex-arable land using regional and commercial seed mixtures and spontaneous succession: Successional trajectories and changes in species richness. Agriculture, Ecosystems & Environment 182, 131–136.
- Price, D. (Ed.), 2000. Europe's first farmers. Cambridge University Press, Cambridge.
- Pyšek, P., Chytrý, M., Jarošík, V., 2010. Habitats and land use as determinants of plant invasions in the temperate zone of Europe. In: Perrings, C., Mooney, H., Williamson, M. (Eds.), Bioinvasions and globalization. Ecology, economics, management, and policy. Oxford University Press, Oxford, pp. 66–79.
- Ramankutty, N., Foley, J.A., 1999. Estimating historical changes in global land cover. Croplands from 1700 to 1992. Global Biogeochemical Cycles 13, 997-1027.
- Roeling, I.S., Ozinga, W.A., van Dijk, J., Eppinga, M.B., Wassen, M.J., 2018. Plant species occurrence patterns in Eurasian grasslands reflect adaptation to nutrient ratios. Oecologia 186, 1055–1067.
- Roman, A., Ursu, T.-M., Onţel, I., et al., 2019. Deviation from Grazing optimum in the grassland habitats of Romania within and outside the Natura 2000 network. In: Musarella, C.M., Ortiz, A.C., Ricardo, Q.C. (Eds.), Habitats of the World (Working title). IntechOpen Limited, London, p. 19. https://doi.org/10.5772/intechopen.85734.
- Skórka, P., Settele, J., Woyciechowski, M., 2007. Effects of management cessation on grassland butterflies in southern Poland. Agriculture, Ecosystems & Environment 121, 319–324.
- Sonkoly, J., Kelemen, A., Valkó, O., et al., 2019. Both mass ratio effects and community diversity drive biomass production in a grassland experiment. Scientific Reports 9, 1848. Sudnik-Wójcikowska, B., Moysiyenko, I.I., 2008. The floristic differentiation of microhabitats within kurgans in the desert steppe zone of southern Ukraine. Acta Societatis Botanicorum Poloniae 77, 139–147.
- Sutcliffe, L.M.E., Batáry, P., Kormann, U., et al., 2015. Harnessing the biodiversity value of central and eastern European farmland. Diversity and Distributions 21, 722–730.
- Sutcliffe, L.M.E., Germany, M., Becker, U., Becker, T., 2016. How does size and isolation affect patches of steppe-like vegetation on slumping hills in Transylvania, Romania? Biodiversity and Conservation 25, 2275–2288.
- Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America 102, 8245–8250.
- Török, P., Aradi, E., 2017. A new potentially invasive grass, sand dropseed (*Sporobolus cryptandrus*) discovered in sandy areas of Hungary—A call for information on new localities. Palaearctic Grasslands 35, 24–25.
- Török, P., Dengler, J., 2018. Palaearctic grasslands in transition: Overarching patterns and future prospects. In: Squires, V.R., Dengler, J., Feng, H., Hua, L. (Eds.), Grasslands of the world: Diversity, management and conservation. CRC Press, Boca Raton, pp. 15–25.
- Török, P., Helm, A., 2017. Ecological theory provides strong support for habitat restoration. Biological Conservation 206, 85-91.
- Török, P., Vida, E., Deák, B., Lengyel, S., Tóthmérész, B., 2011. Grassland restoration on former croplands in Europe: An assessment of applicability of techniques and costs. Biodiversity and Conservation 20, 2311–2332.
- Török, P., Wesche, K., Ambarli, D., Kamp, J., Dengler, J., 2016a. Step(pe) up! Raising the profile of the Palaearctic natural grasslands. Biodiversity and Conservation 25, 2187–2195.
- Török, P., Hölzel, N., van Diggelen, R., Tischew, S., 2016b. Grazing in European open landscapes: How to reconcile sustainable land management and biodiversity conservation? Agriculture, Ecosystems & Environment 234, 1–4.
- Török, P., Valkó, O., Deák, B., et al., 2016c. Managing for species composition or diversity? Pastoral and free grazing systems of alkali grasslands. Agriculture, Ecosystems & Environment 234, 23–30.
- Török, P., Janišová, M., Kuzemko, A., Rūsiṇa, S., Dajić Stevanović, Z., 2018. Grasslands, their threats and management in Eastern Europe. In: Squires, V.R., Dengler, J., Feng, H., Hua, L. (Eds.), Grasslands of the world: Diversity, management and conservation. CRC Press, Boca Raton, pp. 64–88.
- Tóth, E., Deák, B., Valkó, O., et al., 2018. Livestock type is more crucial than grazing intensity: Traditional cattle and sheep grazing in short-grass steppes. Land Degradation & Development 29, 231–239.
- Turtureanu, P.D., Palpurina, S., Becker, T., et al., 2014. Scale- and taxon-dependent biodiversity patterns of dry grassland vegetation in Transylvania. Agriculture, Ecosystems & Environment 182. 15–24.
- Valkó, O., Török, P., Tóthmérész, B., Matus, G., 2011. Restoration potential in seed banks of acidic fen and dry-mesophilous meadows: Can restoration be based on local seed banks? Restoration Ecology 19, 9–15.
- Valkó, O., Török, P., Matus, G., Tóthmérész, B., 2012. Is regular mowing the most appropriate and cost-effective management maintaining diversity and biomass of target forbs in mountain hay meadows? Flora 207, 303–309.
- Valkó, O., Török, P., Deák, B., Tóthmérész, B., 2014. Review: Prospects and limitations of prescribed burning as a management tool in European grasslands. Basic and Applied Ecology 15, 26–33.
- van Dijk, G., Zdanowicz, A., Blokzijl, R., 2005. Land abandonment and biodiversity. In: Relation to the 1st and 2nd Pillars of the EU's Common Agricultural Policy. Outcome of an international seminar in Sigulda, Latvia, 7–8 October, 2004. DLG, Utrecht: Government Service for Land and Water Management.
- Vassilev, K., Pedashenko, H., Nikolov, S.C., Apostolova, I., Dengler, J., 2011. Effect of land abandonment on the vegetation of upland semi-natural grasslands in the Western Balkan Mts., Bulgaria. Plant Biosystems 145, 654–665.
- Vasyliuk, O., Shyriaieva, D., Kolomytsev, G., Spinova, J., 2017. Steppe protected areas on the territory of Ukraine in the context of the armed conflict in the Donbas region and Russian annexation of the Crimean peninsula. Bulletin of the Eurasian Dry Grassland Group (33), 15–23.
- Watther, G.-R., Roques, A., Hulme, P.E., et al., 2009. Alien species in a warmer world: Risks and opportunities. Trends in Ecology & Evolution 24, 686-693.
- Wesche, K., Ambarli, D., Kamp, J., et al., 2016. The Palaearctic steppe biome: A new synthesis. Biodiversity and Conservation 25, 2197-2231.
- Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: The world records. Journal of Vegetation Science 23, 796-802.
- Wódkiewicz, M., Dembicz, I., Moysiyenko, I.I., 2016. The value of small habitat islands for the conservation of genetic variability in a steppe grass species. Acta Oecologica 76, 22–30.
- Żmihorski, M., Kotowska, D., Berg, Å., Pärt, T., 2016. Evaluating conservation tools in polish grasslands: The occurrence of birds in relation to Agri-environment schemes and Natura 2000 areas. Biological Conservation 194, 150–157.