Flora 271 (2020) 151685

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Editorial

Climate, landscape history and management drive Eurasian steppe biodiversity

A R T I C L E I N F O

Keywords
Grasslands
Phylogeography
Refuge areas
Grazing
Land-use change
Habitat loss and fragmentation

A B S T R A C T

Palaearctic steppes are among the largest continuous terrestrial natural habitats of the world with high biodiversity at multiple scales. Steppe grasslands and adjacent forest steppes are characteristic landscape elements from Central and Eastern Europe to Northern China across the whole temperate zone of Eurasia with some floristically similar regions in North Africa, Anatolia, and Iran. The origin and evolution of the landscape history of the Eurasian steppes started in the lower Miocene and passed through widening and diminishing of the steppe area. This history is mirrored by the phylogeography of typical steppe species. Today, the area of typical steppes is highly reduced by various activities of humans. Because steppes are often characterised by fertile soils, they are subjected to large-scale degradation and area loss by intensive crop production, or other forms of overuse especially in the Western part of their distribution zone. Steppes are among the most threatened and least protected habitats globally, and therefore, the conservation and restoration of steppe biodiversity, especially in agriculture-dominated landscapes, are key priorities for research and practice. Effective biodiversity conservation and restoration depend, however, on knowledge of ecological properties and processes that are responsible for the sustainment of crucial ecological functions and services in pristine steppes. In this special issue we aimed to give emphasis on the most recent and novel research in steppe biodiversity and ecology, highlighting the enormous levels of biodiversity at multiple scales shaped by a complex interaction of a long-term evolutionary history, macroclimate and local factors including disturbances such as overgrazing. Fine-tuned management, for example in a form of low-intensity and extensive grazing is urgently needed for maintaining and/or restoring steppe resistance and resilience to climate change extremities.

1. Introduction

Palaearctic steppes are among the largest continuous terrestrial natural habitats of the world, and have high biodiversity at multiple scales. Steppe grasslands and adjacent forest steppes are key elements of natural vegetation in vast landscapes from Central and Eastern Europe to Northern China (Figs. 1 and 2), spanning across the entire temperate zone of Eurasia and similar habitats in North Africa, Anatolia, and Iran (Wesche et al., 2016; Erdős et al., 2018). Steppes offer globally unique options for studies on biological patterns in a relatively homogeneous, yet spatially most extensive biome. The origin, expanding, fragmentation and shrinking of the Eurasian steppe has a long history over about 20 million years. This history is closely linked to climatic oscillations and these have been tremendous during the ice ages of the Pleistocene starting about 2.6 million years ago (reviewed in Hurka et al., 2019 and literature cited therein). A detailed analysis of steppe plant species mirrors this exciting history: diversification and hybridisation are common processes and happened at different time scales. Examples include evolution of biodiversity on a continental scale, effects of large climatic gradients on species performance, or ecosystem functioning under extreme and very variable conditions.

Steppe habitats were widely transformed into agricultural landscapes, while secondary steppe originated in Europe after opening of the dominating forests due to human influence. Extant steppe grasslands are typically grazed, and animal husbandry (herding) has been the traditional form of land use (Wang and Wesche, 2016; Török et al., 2016). Because typical steppes are characterised by fertile soils, they are subjected to large-scale degradation and area loss by intensive crop production or other forms of overuse especially in the Western part of their distribution zone (Deák et al., 2016), while overgrazing is a problem in several steppe regions elsewhere (Török and Dengler, 2018). Conservation and restoration of steppe biodiversity, especially in agriculture-driven landscapes, have key priority for research and practice, and a recent review summarised the growing literature on Eurasian steppes under globally changing land use and climate (Wesche et al., 2016). Effective and sustainable steppe management, however, depends on sound knowledge of the underlying history and evolution, and the ecological properties which are responsible for the sustainment of crucial ecosystem functions and services. In this special issue we aimed to give high emphasis on the most recent and novel research in steppe biodiversity, phylogeography and evolution. The special issue was initiated in the summer of 2018, and was supported and advertised by

This article is part of a special issue entitled: "Ecology and Evolution of Steppe Biodiversity" published at the journal Flora.

https://doi.org/10.1016/j.flora.2020.151685

Available online 15 August 2020
0367-2530/

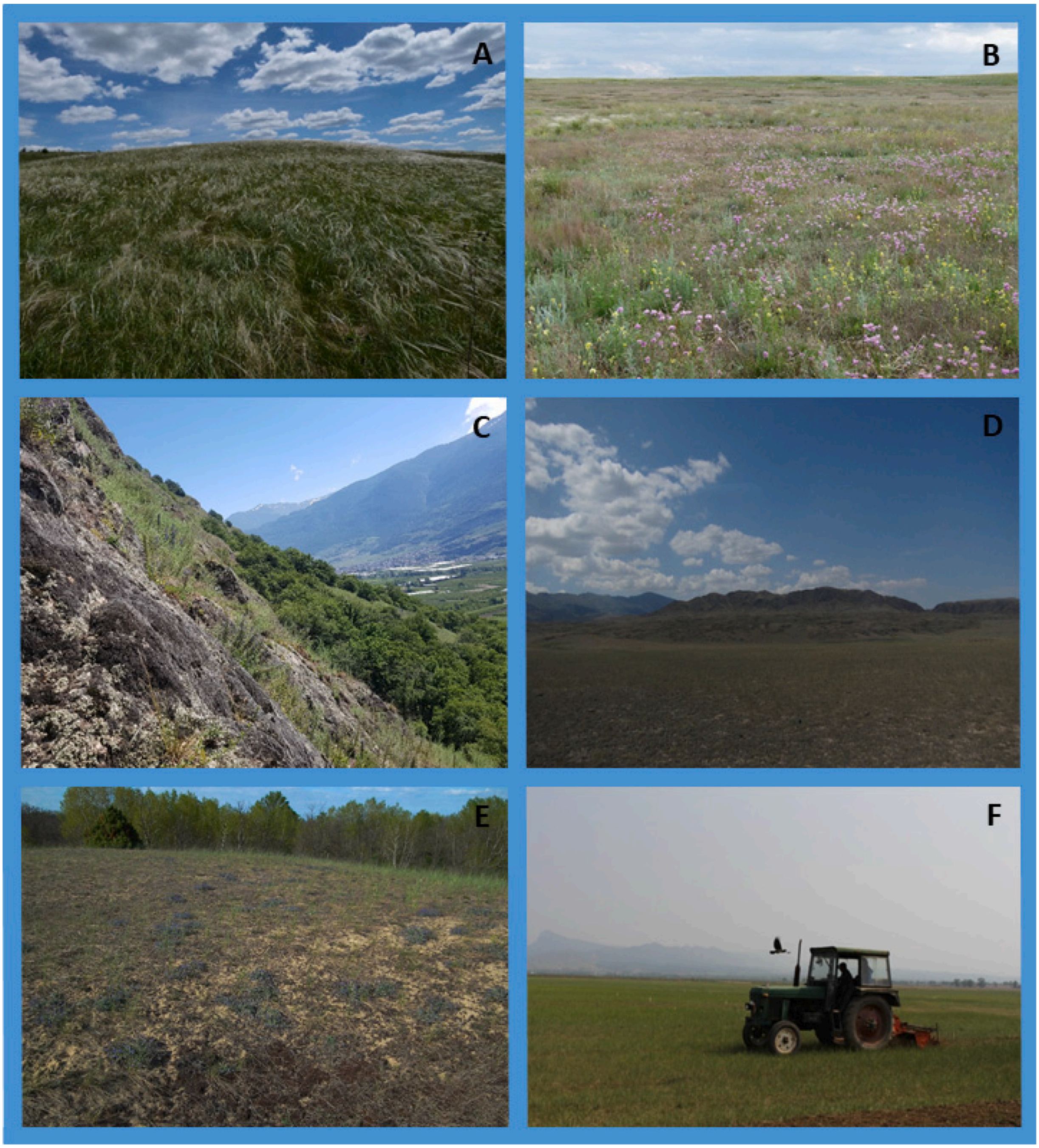

Fig. 1. Steppe diversity in Eurasia. (A) Steppe grassland rich in feather grasses in the Voronezh-Don region, Russia (photo by B. Neuffer); (B) Forb-rich steppe grassland in Northwestern Kazakhstan (photo by B. Neuffer); (C) Steppe-like grassland in the Canton of Valais, Switzerland (photo by S. Boch); (D) Desert steppe in the Urzhar District in Eastern Kazakhstan (photo by A. Seidl); (E) Open sand steppe near to Fülöpháza, Central Hungary (photo by P. Török); (F) Steppe ploughing in Inner Mongolia, China (Photo by W. He).

the Eurasian Dry Grassland Group (EDGG; Box 1). The present special issue contains 12 papers with 75 authors from 13 countries. We invited both basic research as well as applied studies, and the present papers thus address (i) steppe biodiversity and phylogeography, and (ii) land use effects and grazing. All share an overarching interest in understanding steppe biodiversity, with the former dealing with long, evolutionary timescales and the latter with a focus on current processes. For both, interactions with climate are key topics. Climate history but also current climate conditions differ between regions within the vast Eurasian steppe belt. How this has affected phylogeography of a given steppe region, and how local climate interacts with modified local land use impact, still is to be explored.

2. Steppe biodiversity and phylogeography

Origin and evolution of steppe flora has puzzled biogeographers and botanists for a long time, though it is clear that species originated from very different regions, each having its own history. In spite of a large body of literature (recently reviewed in Hurka et al., 2019), detailed knowledge about temporal and spatial patterns in the origin of the Eurasian steppe flora still is limited. Immigration from external areas during the long history of the steppe, geographic position of refugia during cold and warm phases, *in situ* survival and immigration from *ex situ* refugia, as well as biotic effects including grazing and competition have definitely influenced steppe florogenesis.

New tools such as molecular phylogeographic studies, dated phylogenies, ancestral area reconstructions and correlation with climate/landscape history at the species and population level now help to understand the evolution of the steppe flora. They allow to explore whether and how paleoclimate oscillations and landscape evolution influence phylogenies and genetic subdivisions across species ranges, and how molecular signals in present-day genomes mirror the biogeographic dynamics and colonization history of steppe habitats in space and time.

Six original research papers in the present issue address these aspects. The study objects comprise different plant families and address a range of levels from the genus down to species and populations. Some studies cover the entire distribution area of the respective taxa, others concentrate on specific parts of distribution ranges. What they all have in common is their focus on the relationship between dated molecular phylogenetic and phylogeographic analyses and the evolutionary history of the steppe. The possible role of steppe refuge areas during the cold and warm phases of the Pleistocene for the evolutionary history of the respective taxon is a special focus. The study objects were *Adonis vernalis*, Ranunculaceae (Kropf et al.), *Allium* Section *Rhizomatosa*, Amaryllidaceae (Friesen et al., 2020a), *Astragalus onobrychis*, Fabaceae (Plenk et al.), the genus *Camelina*, Brassicaceae (Žerdoner Čalasan et al.), *Krascheninnikovia ceratoides*, Chenopodiaceae (Seidl et al.), and *Schivereckia podolica*, Brassicaceae (Friesen et al., 2020b).

Not all species presently occur over the entire biome. The *Allium* study has its main area in Central Asia (*Allium*), others focus on the more western European part (*Adonis, Astragalus*, and *Schivereckia*). Some studies cover the entire steppe belt (*Camelina* and *Krascheninnikovia*), which was only possible due to very comprehensive sampling. Molecular

Box 1
The Eurasian Dry Grassland Group (EDGG).

The Eurasian Dry Grassland Group (EDGG) is an official working group of the International Association for Vegetation Science (IAVS), founded in 2008 (http://www.edgg.org). With a membership free of any charge, the EDGG coordinates transnational policy actions and research focusing on the biodiversity, ecology and conservation of all natural and semi-natural grasslands in the Palaearctic. The EDGG facilitates the communication between members by using its mailing list and the quarterly published open-access editorial peer-reviewed electronic journal *Palaearctic Grasslands*. Each year, the EDGG organizes the Eurasian Grassland Conference as well as Field Workshops to which all EDGG members are eligible to join. The EDGG facilitates establishment of national databases on grassland biodiversity, and started a transnational database called GrassPlot with the aim of combining standardised multi-scale datasets collected during the field workshops with comparable datasets from other projects to support grassland research and macroecological studies in grassland biodiversity. The EDGG is very actively organising and publishing thematic issues and special features in and with internationally recognised journals and publishers.

eDGG Grassland research and conservation

Fig. 2. Map of the Eurasian steppe biome. Map is based on re-classification of the Global 200, for further details of the method see Wesche et al. (2016), Olson et Dinerstein's (1998).

marker systems allowed to apply a molecular clock, and intraspecific differentiations could be traced back to the geological history of the landscape. Landscape history has also been subjected to heavy fluctuations during the late Miocene and Pliocene of the quarternary ice ages.

The study on *Camelina* by Žerdoner Čalasan et al. provides a dated molecular phylogeny and ancestral area reconstruction covering all species of the genus *Camelina* elucidating its evolutionary and biogeographical history. These species occur in several different ploidy levels and the taxonomic status was unclear, identifications often were wrong. The authors succeeded in the design of a molecular marker system which now allows to obtain a reliable picture. Sister to *Camelina* is *Neslia*, and the two clades split up during the Pliocene. Diversification of *Camelina* started in the Middle East around the transition from Pliocene to Pleistocene (3–2 mya). Several genetically distinct inter- and intraspecific lineages evolved, which appear to correlate geographically. More important, the calibrated time estimation resulted in the interpretation of the influence of climatic shifts and paleogeographic events on the distribution patterns of the *Camelina* species in time and space. Thus, differentiation and range evolution in *Camelina* mirror the climate/-landscape dynamics of the steppe biome.

Species in the genus *Allium* are among the most characteristic elements of the steppe flora, and *Allium* is among the largest genera of all vascular plants. Friesen et al. (2020a) studied section *Rhizomatosa* (including section *Caespitosoprason)*, which is confined to Central Asian steppe habitats. Species relationships within this section were largely unresolved, and the authors therefore provided molecular phylogenies for most taxa of the section and distribution maps of its species. Estimates of divergence time of the species belonging to section *Rhizomatosa* and their distribution are in agreement with the origin and climate/-landscape history of Central Asian steppe since the lower Miocene. The Katun Valley in the Russian Altai is probably a hitherto unrecognized interglacial (warm stage) refugium not only for *Allium bellulum* but also for other Pleistocene cold steppe plants.

Draba and its allies form another large species group, and Friesen et al. (2020b) provide a species-level study on *Schivereckia podolica* (= *Draba podolica*), an enigmatic eastern European species with disjunct distribution in Russia, Ukraine, and Podolian-Galician outposts. A comprehensive molecular analysis (cpDNA and nuclear DNA) revealed that *Schivereckia* is nested within a highly supported clade of central Asian, Caucasian and North American *Draba* species. Time divergence estimation and ancestral area reconstruction support the interpretation of this species assembly as periglacial relics. Results argue for continuous persistence of certain steppe plants since the Pleistocene and support the view that the flora of the modern steppes of Europe has originated partly from Pleistocene glacial steppes.

Close relationships between North-America and Eurasia are also shown in a study by Seidl et al. on *Krascheninnikovia ceratoides*, one of the most characteristic steppe plants. Based on molecular dating, the authors argue for divergence of *Krascheninnikovia* from its sister clade *Ceratocarpus* at the end of the Oligocene/beginning of the Miocene, the time of the origin of the steppe biome in Eurasia. Diversification within *Krascheninnikovia* is probably of Pleistocene age. Molecular data indicate that the species spread from the Altai mountain region to the east and to the west. Diploids migrated via eastern Asia to North America (subsp. *lanata*), and diploids and tetraploids to western Asia and Europe (subsp. *ceratoides*). The molecular analysis revealed that the spread of the main lineages is likely related to major phases of steppe and semi-desert expansions during glacial periods of the Pleistocene.

Two studies took a population level approach with a closer focus on the western part of the Eurasian steppe biome. Kropf et al. compared *Adonis vernalis* populations across a geographical transect from eastern Romania (Dobruja) towards their westernmost range edge, including disjunct peripheral populations and westernmost isolated exclaves. They used cpDNA sequence analysis and AFLP fingerprinting, and detected varying genetic variability over the regions partly contradicting theoretical expectations. The abundance-centre-hypothesis predicts increasing between-population differentiation and declining genetic diversity within populations towards the range edge. Whereas AFLP data opposed these expectations, cpDNA data were in line with the peripheral transect prediction. The study showed that analysing different molecular markers may lead to different conclusions about genetic diversity patterns within and between peripheral populations.

Glacial survival and post-glacial expansion of *Astragalus onobrychis* is the focus of the contribution by Plenk et al., who reported on genetic diversity and biogeographical history within different subregions of the species' European distribution. They argued for the Hungarian plain as a small-scale refugium. Haplotype clusters correlated with different ploidy levels. Data indicated a long-term – probably glacial – persistence of diploid populations in the southern Pannonian subregion, areas along the Black Sea coast, the northern Balkan Peninsula and the central Pontic subregion. An octoploid lineage likely originated more to the east and expanded to western Pontic areas and the Pannonian Basin probably already during the Pleistocene.

A local perspective is finally taken by Treiber et al., 2020, who tested how larger scale distribution ranges relate to local occurrences of biogeographical elements along a mountain range in southern Mongolia. The authors used random vegetation sampling and related this to available but also newly compiled global distribution data of the recorded species. They introduced fourth-corner analysis to statistics in biogeography, a method that had gained popularity in studies on plant functional traits. Analyses demonstrated that Central Asian elements as representatives of the locally prevailing flora have no clear-cut preferences along the elevation gradients, while all other phytogeographical groups showed distinct zonation and thus special niches. The data provide support for Walter's law of relative habitat constancy, and also show how different distribution and colonization patterns underlie composition of a given local vegetation.

3. Land use changes and grazing

Grazing by large mammals has been a key evolutionary driving force in most temperate grasslands, and the traditional and prevailing land use by animal husbandry is based on the grazing tolerance of most steppe species and the communities they build (Diaz et al., 2001). Eurasia still hosts one of the finest examples of traditional grazing systems, yet increasing livestock numbers coupled with reduced mobility have resulted in intensified grazing pressure, and presumably degradation (Addison et al., 2012; Wang et al., 2008). One key lesson of available studies is that grazing effects and consequences for ecosystem health differ vastly between different parts of the Eurasian steppe belt (Wesche et al., 2016), therefore studies focused on specific conditions are still highly needed. Moreover, consequences of land use on facets of biodiversity other than species richness and composition are poorly known. This special issue comprises five papers on the effects of land use. They share the key features of concentrating on a particular, biogeographically rather homogenous part of the biome, and most compare several sites within this part, thus arriving at a comprehensive picture with respect to local differences.

Three studies originated from Central Asian steppes of Mongolia and northern China. The study by Oyundelger et al. assesses effects of land use under a genetical perspective: they studied the effects of grazing on the genetic structure of a keystone steppe species. *Stipa glareosa* is a dominant feather grass of dry Mongolian steppes and desert steppes, and of high importance ecologically but also economically in terms of forage provision. The authors studied grazing effects by comparing grazing hotspots at wells and camps and less intensively grazed sites several km apart. Microsatellite markers were customised for the specific species, and comparisons of sites differing in grazing intensity were repeated along a large-scale climate gradient. In line with high levels of selfing in *S. glareosa*, genetic diversity was overall low. Populations differed with respect to genetic similarity along the climate gradient, but there were also significant effects of grazing, and evidence for certain phenotypes being associated with intense grazing. This points to microscale evolutionary processes shaping genetic structure in response to both grazing and climate.

Also working along a large-scale climate gradient, Qin et al. assessed grazing effects in meadow steppes, typical steppes and desert steppes of Inner Mongolia. Sampling was also conducted along local grazing gradients, in this case recording plant community composition and biomass. Authors used innovative structural equation modelling to assess effects of grazing on community stability, mediated by stability of specific groups as well as overall richness and composition. Unlike richness that was largely invariant to grazing in dry conditions, community stability was negatively affected in all steppe types as a consequence of grazing reducing species synchrony. Effects did, however, differ between key functional groups, demonstrating that adapted grazing management must consider both local abiotic and biotic conditions.

Conversion of steppes to arable fields or sown pastures is a key topic across the entire biome, and the paper by Yang et al. gives a particularly detailed study on effects of ploughing, seeding and fertilizing on a steppe site in Inner Mongolia. All three measures are currently applied in the degraded steppes of the regions, yet the current study is novel in subjecting them to a direct comparison. Authors recorded effects on plant species richness and turnover, and also distinguished different functional groups. All three treatments had clear effects on plant community composition, yet in contrast to their widespread application in restoration, effects were often detrimental. In particular, perennial species often responded negatively to management interventions, resulting in overall reduced biomass. This is in line with commonly observed low recovery rates in long-lived species, which typically dominate in intact steppes. This showed that restoration measures must be carefully designed.

In contrast to Central Asia, most grasslands in the European parts of the steppe biome depend on regular management for persistence (Fischer and Wipf, 2002; Hejcman et al., 2013). Boch et al. give a detailed account of diversity and composition of steppes in the dry valleys of Switzerland. These are considered of national importance, and are thus monitored and typically managed. Authors selected typical steppe plots from a very large national vegetation database, and assessed effects of local abiotic conditions and grazing on species richness and composition. Harvesting from available trait databases, authors derived indicator values for productivity, and found that richness showed a unimodal relationship to productivity. While richness was largely unaffected by grazing alone, it showed clear responses to tree and shrub cover. Modest management thus worked best to maintain local steppe diversity. This highlights that management for controlling encroachment of woody perennials is crucial, especially in regions that are climatically suitable for growth of forests.

The second study on Central European steppes was contributed by Kertész et al., who studied effects of moderate land use in six characteristic steppe types of the Pannonic basin. They sampled pairs of used and unmanaged sites in the six habitat complexes that reflect the main edaphic and climatic conditions. Land use depended on these, and ranged from pasturing to mowing and timber harvesting, yet was moderate in all cases. Authors also built on a large vegetation data base, and the applied sampling scheme allowed to compare diversity from gamma to beta and alpha level, applying novel bootstrap statistics. Gamma diversity surprisingly was found as the most sensitive indicator of naturalness. Analyses showed that three of the surveyed habitat complexes require relatively strict protection, while moderate land use is in agreement with conservation goals for the other three. This reflects the transitory character of the region's grassland, with some requiring management to remain intact, while others owe their existence to abiotic conditions.

4. Conclusions and outlook

The papers in the special issue clearly pointed out that the steppes are characterised by high levels of plant biodiversity and a complex and mosaic pattern of richness and habitats at multiple scales. This complex pattern has originated and is sustained via the interaction of macroclimate and local patterns of abiotic factors and small-scale disturbances. We can conclude that the macroclimate and landscape history of the Eurasian steppe belt have an effect on species phylogenies, genetic subdivisions across species ranges and fine-scale distribution patterns. Thus, molecular signals and plant community composition may mirror biogeographic dynamics and colonization of steppe habitats from different source areas.

Current biodiversity patterns are strongly shaped by increased levels of human influence. Drastic area loss and fragmentation of steppes and subsequent land-use changes mostly in the form of overgrazing or other forms of overuse threaten not only steppe biodiversity at the species level, but also negatively affect the functional and phylogenetic diversity of steppe plant communities and also decrease their stability and thus, their resistance and resilience to climatic extremities predicted by reliable models of climate change. It was stressed that the different types of steppe habitats even at the small scale need special and fine-tuned management mostly in form of livestock grazing and/or mowing. Temperate grasslands are among the least protected habitats worldwide. The area loss and fragmentation of steppe biodiversity are especially alarming taking also into consideration that only a very small proportion of steppes is under nature protection.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The editors thank the editorial board for inviting the special feature to Flora. The editors are thankful to the author teams and all reviewers for their contributions and input to this special issue. The authors were supported by NKFIH [K 119225, KH 129483 to PT], the Momentum Program [Hungarian Academy of Sciences, PT] and the BioTip Program [Federal German Ministry of Science and Education] during the preparation of the special issue. The editors dedicate this issue to Emeritus Professor Herbert Hurka on the occasion of his 80th birthday, with deep appreciation for his more than 50 years of active and innovative research on biogeography, evolutionary history and plant phylogeny of steppes.

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