How climate, topography, soils, herbivores, and fire control forest–grassland coexistence in the Eurasian forest-steppe

László Erdős[1,2,*,†], Péter Török[2,3,4,†], Joseph W. Veldman[5], Zoltán Bátori[6], Ákos Bede-Fazekas[1,7], Martin Magnes[8], György Kröel-Dulay[1] and Csaba Tölgyesi[9]

[1]*Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány utca 2-4, 2163 Vácrátót, Hungary*

[2]*MTA-DE Lendület Functional and Restoration Ecology Research Group, Egyetem tér 1, 4032 Debrecen, Hungary*

[3]*Department of Ecology, University of Debrecen, Egyetem tér 1, 4032 Debrecen, Hungary*

[4]*Botanical Garden – Center for Biological Diversity Conservation in Powsin, Polish Academy of Sciences, Prawdziwka street 2, 02-973 Warszawa, Poland*

[5]*Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX 77843-2258, USA*

[6]*Department of Ecology, University of Szeged, Közép fasor 52, 6726 Szeged, Hungary*

[7]*Department of Environmental and Landscape Geography, Eötvös Loránd University, Pázmány Péter sétány 1/C, 1117 Budapest, Hungary*

[8]*Institute of Biology, University of Graz, Holteigasse 6, 8010 Graz, Austria*

[9]*MTA-SZTE 'Momentum' Applied Ecology Research Group, Közép fasor 52, 6726 Szeged, Hungary*

[*] Author for correspondence (Tel.:+36304995142; E-mail: erdos.laszlo@ecolres.hu).

[†] Joint first authors; these authors contributed equally to this work.

ABSTRACT

Recent advances in ecology and biogeography demonstrate the importance of fire and large herbivores – and challenge the primacy of climate – to our understanding of the distribution, stability, and antiquity of forests and grasslands. Among grassland ecologists, particularly those working in savannas of the seasonally dry tropics, an emerging fire–herbivore paradigm is generally accepted to explain grass dominance in climates and on soils that would otherwise permit development of closed-canopy forests. By contrast, adherents of the climate–soil paradigm, particularly foresters working in the humid tropics or temperate latitudes, tend to view fire and herbivores as disturbances, often human-caused, which damage forests and reset succession. Towards integration of these two paradigms, we developed a series of conceptual models to explain the existence of an extensive temperate forest–grassland mosaic that occurs within a 4.7 million km^2 belt spanning from central Europe through eastern Asia. The Eurasian forest-steppe is reminiscent of many regions globally where forests and grasslands occur side-by-side with stark boundaries. Our conceptual models illustrate that if mean climate was the only factor, forests should dominate in humid continental regions and grasslands should prevail in semi-arid regions, but that extensive mosaics would not occur. By contrast, conceptual models that also integrate climate variability, soils, topography, herbivores, and fire depict how these factors collectively expand suitable conditions for forests and grasslands, such that grasslands may occur in more humid regions and forests in more arid regions than predicted by mean climate alone. Furthermore, boundaries between forests and grasslands are reinforced by vegetation–fire, vegetation–herbivore, and vegetation–microclimate feedbacks, which limit tree establishment in grasslands and promote tree survival in forests. Such feedbacks suggest that forests and grasslands of the Eurasian forest-steppe are governed by ecological dynamics that are similar to those hypothesised to maintain boundaries between tropical forests and savannas. Unfortunately, the grasslands of the Eurasian forest-steppe are sometimes misinterpreted as deforested or otherwise degraded vegetation. In fact, the grasslands of this region provide valuable ecosystem services, support a high diversity of plants and animals, and offer critical habitat for endangered large herbivores. We suggest that a better understanding of the fundamental ecological controls that permit forest–grassland coexistence could help us prioritise conservation and restoration of the Eurasian forest-steppe for biodiversity, climate adaptation, and pastoral livelihoods. Currently, these goals are being undermined by tree-planting campaigns that view the open grasslands as opportunities for afforestation. Improved understanding of the interactive roles of climate variability, soils, topography, fire, and herbivores will help scientists and policymakers recognise the antiquity of the grasslands of the Eurasian forest-steppe.

Key words: biome transition, old-growth grassland, spatiotemporal heterogeneity, tree-grass coexistence, topography, soil, herbivory, fire.

CONTENTS

I. INTRODUCTION

Grasslands (including savannas) cover approximately 40% of the terrestrial biosphere (White, Murray & Rohweder, 2000), support high biodiversity (Myers *et al.*, 2000; Murphy, Andersen & Parr, 2016), provide habitat for native animals and domestic livestock, and supply a variety of other ecosystem services, including belowground carbon storage (Alkemade *et al.*, 2013; Dass *et al.*, 2018; Erdős *et al.*, 2018*a*). Despite their importance, grasslands are often overlooked in conservation planning, undervalued because they lack dense tree cover, and misinterpreted as degraded vegetation in need of reforestation (Parr *et al.*, 2014; Tölgyesi *et al.*, 2022). This confusion over the conservation value of grasslands is acute in places where the climate can support the development of forests (Veldman, 2016). Indeed, much of the research on the determinants of grassland distributions is framed to answer the question of why they exist at all, particularly in places where successional theory suggests there ought to be forests (Sarmiento, 1984; Bond, 2008).

To answer why grasslands exist in climates that can support forests, there are two prevailing views among ecologists. The first view, the climate–soil paradigm, has long considered climate to be the principal control over biome distributions (e.g. Holdridge, 1967), while recognising that certain soils can limit tree growth, thus permitting grasslands to exist (e.g. Beard, 1953). In the climate–soil paradigm, grasslands that are not on special soils, and depend upon fire and large herbivores for their maintenance, are typically considered to be degraded ecosystems, deforested by humans, and in a stage of arrested succession (Veldman *et al.*, 2015). The second view, the emerging fire–herbivore paradigm (e.g. Pausas & Bond, 2019), views climate and soils as insufficient to explain the distribution of biomes, and emphasises the relationships among vegetation, fire, and herbivores (Murphy & Bowman, 2012). At first glance, the growing popularity of the fire–herbivore paradigm can appear to be supplanting the idea that climate and soils matter at all (e.g. Veenendaal *et al.*, 2018). But rather than viewing these two paradigms as mutually exclusive, we suggest that recent work to understand the role of fire and herbivores in shaping grassland and forest distributions does not replace, but adds nuance, specificity, and mechanistic detail, where the climate–soil paradigm falls short. Indeed, proponents of the fire–herbivore paradigm study these forces in addition to and in relation to soils (e.g. Hoffmann *et al.*, 2012; Staver, Botha & Hedin, 2017) and climate (Higgins Bond & Trollope, 2000; Staver, Archibald & Levin, 2011; Lehmann *et al.*, 2011, 2014; Hempson, Archibald & Bond, 2015).

While progress on the ecological importance of fire and herbivores has advanced for tropical and subtropical savanna ecosystems (Scholes & Archer, 1997; Sankaran, Ratnam & Hanan, 2004; Bond, 2008; Baudena, D'Andrea & Provenzale, 2010; Hoffmann *et al.*, 2012; Ratajczak, D'Odorico & Yu, 2017), temperate grasslands of Eurasia continue to be viewed largely through the lens of the climate–soil paradigm. To understand better the ecological controls over grasslands and forests and to improve their respective conservation and restoration in the face of climate and land-use change, we reviewed the literature on the Eurasian forest-steppe. We developed a series of conceptual models of forest–grassland coexistence to depict purported drivers visually in a hierarchical manner, beginning with macroclimate (henceforth 'climate'). Because mean climate alone is clearly inadequate for explaining the existence of the forest-steppe, we draw on our literature review to add climate variability, topography, soils, herbivory, fire and feedback mechanisms to successive models in the hierarchy. Collectively these models illustrate how it is possible for the Eurasian forest-steppe to occupy such broad geographic and climatic ranges. We hope that our conceptual models will help ecologists, environmental policymakers, and land managers recognise the multiple drivers of forest–grassland coexistence across Eurasia, and help explain why herbivores and fire need to be considered, in addition to climate and soils.

II. ECOLOGY, BIOGEOGRAPHY, AND CONSERVATION OF THE EURASIAN FOREST-STEPPE

Positioned between temperate forests to the north, and mostly treeless continental steppes to the south, the Eurasian forest-steppe occupies a 9000 km long and, on average, 430 km wide belt from central Europe to far eastern Asia (Fig. 1A) (Erdős *et al.*, 2018*a*). Forest-steppes are the natural vegetation in large parts of Hungary, Serbia, Romania, Bulgaria, Moldova, Ukraine, Russia, Kazakhstan, Mongolia, and China, occurring within a belt of roughly 4.7 million km^2 (Erdős *et al.*, 2018*a*). We consider forest-steppes to be landscape mosaics composed of forests (dense communities of trees and shrubs, >2 m tall) intermixed with open grasslands of herbaceous plants. Proportions of forest and grassland vary, with forests typically occupying 10–70% of the mosaic landscape. Although extensive areas of forest-steppe have been destroyed in Europe, large tracts remain intact across Asia (Zlotin, 2002; Smelansky & Tishkov, 2012). The extensive geographic range of the forest-steppe encompasses a wide range of climatic conditions, including mean annual temperatures from 1 to 14 °C and mean annual precipitation from 210 to 600 mm (Erdős *et al.*, 2018*a*).

Forest-steppes form mosaic landscapes of two ecosystem states: forest and grassland (Fig. 1B, C) (Erdős *et al.*, 2018*a*). The forest state is dominated by deciduous and/or evergreen trees, including *Betula pendula* Roth (species nomenclature according to the Catalogue of Life, catalogueoflife.org), *B. pubescens* Ehrh. (Betulaceae), *Larix gemilinii*

(Rupr.) Kuzen., *L. sibirica* Ledeb., *Pinus sylvestris* L. (Pinaceae), *Populus neimongolica* Doweld, *P. tremula* L. (Salicaceae), and *Quercus robur* L. (Fagaceae), whereas the grassland state is typically composed of perennial C_3 grasses, primarily species in the genera *Festuca* and *Stipa* (Poaceae). Boundaries between forests and grassland are typically stark and support a rich community of forbs and deciduous shrubs. In addition to many plant species that are common in the neighbouring temperate forest or steppe biomes, forest-steppes also have their own characteristic taxa that primarily occur in mosaics. These include the trees *Acer tataricum* L. (Sapindaceae) and *Quercus robur* (subspecies *pedunculiflora*; Fagaceae), the shrubs *Prunus fruticosa* Pall. (Rosaceae) (Fig. 1D), *Ribes diacanthum* Pall. (Grossulariaceae) and *Spiraea aquilegifolia* Pall. (Rosaceae), the perennial C_3 grasses (Poaceae) *Brachypodium pinnatum* (L.) P. Beauv., *Helictochloa hookeri* (Scribn.) Romero Zarco, and *Melica altissima* L., the sedges (Cyperaceae) *Carex humilis* Leyss. and *C. michelii* Host, and numerous forbs, including *Artemisia latifolia* Ledeb. (Asteraceae), *Anemone sylvestris* L. (Ranunculaceae), *Cervaria rivini* Gaertn. (Apiacea), *Iris ruthenica* Ker Gawl. and *Iris variegata* L. (Fig. 1E) (Iridaceae), *Pulsatilla patens* (L.) Mill. (Ranunculaceae), *Ranunculus polyanthemos* L. (Ranunculaceae), and *Trifolium montanum* L. (Fabaceae). The forest-steppe is home to several endemics, including *Colchicum arenarium* Waldst. & Kit. (Colchicaceae) (Fig. 1F) and *Dianthus diutinus* Schult. (Caryophyllaceae) for the Carpathian Basin and *Leymus tuvinicus* Peschkova (Poaceae) and *Pilosella tjumentzevii* (Serg. & Üksip) Tupitz. (Asteraceae) for the South Siberian mountains (Jakucs, 1961; Walter & Breckle, 1989; Simon, 2000; Peshkova, 2001; Korotchenko & Peregrym, 2012; Rachkovskaya & Bragina, 2012; Smelansky & Tishkov, 2012; Makunina, 2017; Hongyan Liu, personal communication).

In addition to their high biodiversity, forest-steppes are important for the ecosystem services they provide. Some of these services depend on the simultaneous availability of resources from the two ecosystem states (i.e. forest and grassland). For example, forest-steppes have been used as pastures for millennia, and still provide livelihoods for rural people throughout Eurasia (e.g. Rachkovskaya & Bragina, 2012; Smelansky & Tishkov, 2012). While grasslands are the main source of forage, forests provide wild fruits and acorns (Varga *et al.*, 2020) and offer shelter for animals during extreme hot and cold weather (Gantuya *et al.*, 2019). Moreover, forest edges (i.e. the contact zones between the two states) themselves are regarded as highly valuable pastures in Mongolia (Gantuya *et al.*, 2019). Forests are also utilised for fuelwood collection and occasional selective logging (Hauck *et al.*, 2012; Lkhagvadorj *et al.*, 2013).

While there is growing consensus that forest and grassland ecosystem states can co-occur across a wide range of tropical and subtropical climates and soil conditions (Lehmann *et al.*, 2011; Staver *et al.*, 2011), due to the interplay of herbivory, fire, and vegetation feedbacks (Sankaran *et al.*, 2005; Hoffmann *et al.*, 2012; Murphy & Bowman, 2012), such a consensus regarding the interactive roles of climate and disturbance is lacking for the forest-steppe. We believe this lack of consensus is due to the historical emphasis on climate and soils in European vegetation ecology. Indeed, the distributions of the temperate forest biome and the temperate steppe biome are strongly predicted by climate across Eurasia (e.g. Schultz, 2005; Wang, Prentice & Ni, 2013; Evans & Brown, 2017). But now, after two decades of case studies in Eastern Central Europe (e.g. Bátori *et al.*, 2018; Erdős *et al.*, 2014*a*, 2018*b*, 2019*a*, 2021; Tölgyesi *et al.*, 2020), Kazakhstan (e.g. Bátori *et al.*, 2018; Tölgyesi *et al.*, 2018), Mongolia (e.g. Dulamsuren *et al.*, 2008*a*; Dulamsuren, Hauck & Mühlenberg, 2008*b*; Dulamsuren, Hauck & Leuschner, 2013; Hauck, Dulamsuren & Heimes, 2008; Khishigjargal *et al.*, 2013; Ishikawa *et al.*, 2018; Takatsuki, Sato & Morinaga, 2018), Russia (Anenkhonov *et al.*, 2015; Makunina, 2016, 2017), and China (e.g. Liu *et al.*, 2000, 2012, 2015), we have a substantial body of literature that enables a comprehensive overview of how climate, topography, soils, herbivores, and fire control forest–grassland coexistence in the Eurasian forest-steppe.

Such a synthetic approach to the ecology of the Eurasian forest-steppe is needed to inform environmental policy and land-management decisions, particularly in light of global calls to restore ecosystems for biodiversity and to plant trees to mitigate climate change. Tree planting is currently the primary emphasis of nature-based climate initiatives (Cook-Patton *et al.*, 2020; Baker, 2021), with ecosystems comprised of a mixture of forests and grasslands among the target areas (Veldman *et al.*, 2019; Holl & Brancalion, 2020). There is a growing concern that afforestation programmes will compromise grassland biodiversity and ecosystem services in the short term, and by failing to consider climate–vegetation–fire–herbivore relationships, will fail to maintain carbon in planted trees over the long term (Parr *et al.*, 2014; Bond *et al.*, 2019). For example, the widespread pine plantations in forest-steppes are unreliable stores of carbon due to high flammability (Cseresnyés, Szécsy & Csontos, 2011). The high water demand of forest-steppe trees compared to grasses can also lead to tree dieback in drought periods of the ongoing climate change (Kharuk *et al.*, 2017; Mátyás *et al.*, 2018), and the high water consumption of trees can desiccate soils beneath them, potentially suppressing their own growth (Tölgyesi *et al.*, 2020). Misguided afforestation is thus a looming threat to tropical savannas and grasslands globally (Veldman *et al.*, 2015; Tölgyesi *et al.*, 2022) and may be a similarly important, albeit less recognised concern for the Eurasian forest-steppe.

III. MODELS OF FOREST–GRASSLAND COEXISTENCE

(1) Climate

Most authors attribute the existence of the forest-steppe to intermediate climate, given that it occurs between the temperate forest and the continental steppe, two biomes over which climate exerts considerable control (e.g. Chibilyov, 2002; Pfadenhauer & Klötzli, 2014; Wesche *et al.*, 2016; Erdős *et al.*, 2018*a*; Wagner *et al.*, 2020). Indeed, around the globe there are many examples of how climate constrains tree growth: arctic and alpine timberlines develop due to low temperature and arid timberlines are the result of low moisture availability (Stevens & Fox, 1991; Breshears, 2006; Bond, 2019). Consistent with these patterns, at the southern edge of the temperate forests of Eurasia, increasing climatic harshness deriving from decreasing precipitation and increasing annual temperature range (increasingly hot summers but still cold winters) plays a major role in constraining forest growth (Walter & Breckle, 1989; Schultz, 2005). This climatic harshness – defined as the combination of hot summers, cold winters, and aridity – is thus hypothesised to control forest distribution by limiting tree germination and survival. In Eurasian forest-steppes, climatic control has been confirmed for some species. For example, Dulamsuren *et al.* (2008*b*) found that the seedlings of *Larix sibirica*, one of the most important tree species in Mongolian forest-steppes, die in the steppe patches due to physiological damage caused by drought and high temperature, even if competition from grassland vegetation is eliminated. Similarly, *Pinus sylvestris* is limited primarily by low soil moisture (Dulamsuren *et al.*, 2013). *Quercus robur* acorns in the sandy forest-steppes of the Carpathian Basin are often unable to germinate in grassland patches, and those that do germinate eventually suffer drought-induced mortality (Erdős *et al.*, 2021). In addition to low moisture availability, extreme cold winters, which are typical of the interior of Eurasia due to the large distance from oceans and the dry, seldom overcast sky, can also decrease tree recruitment and growth (d'Odorico *et al.*, 2013). Likewise, heat waves of the continental summers are also detrimental to trees, especially for isolated individuals that lack the protection of cooler microclimates of large forest patches (Shi *et al.*, 2021).

Similar to forests, grasslands have their physiological optima under less harsh conditions, i.e. good water supply and lower temperature extremes. As evidence of this, where temperate or boreal forests are cleared to create hay meadows or pastures, highly productive grasses flourish (e.g. Rychnovská, 1993; Hejcman *et al.*, 2013; Erdős *et al.*, 2019*b*). With increasing climatic harshness towards the south, the height, density and productivity of grasses decrease; this trend continues throughout the steppe biome until grasslands are no longer viable, and deserts occur (Walter & Breckle, 1989; Schultz, 2005; Smelansky & Tishkov, 2012; Pfadenhauer & Klötzli, 2014; Li *et al.*, 2020; Tishkov *et al.*, 2020). In sum, both forest and grassland vitality decrease along the climatic harshness gradient, but forest vitality declines more sharply (Fig. 2A). At the intersection of the forest and grassland vitality curves, forest gives way to grassland. This Mean Climate Model suggests a sharp transition between forest and steppe, but not mosaics of forest and grasslands across broad geographic and climatic ranges (Fig. 2A).

The idea of mean climate parameters is, of course, a gross simplification of the many components of climate. The climate of forest-steppes is characterised by large interannual variation in precipitation and temperature (e.g. Walter & Breckle, 1989; Chibilyov, 2002), which results in variable levels of climatic harshness for trees. For example, the forest-steppes of the Carpathian Basin (mean annual precipitation = 500–600 mm) regularly experience years with less than 350 mm and years with more than 800 mm precipitation (Tölgyesi *et al.*, 2016), while the long-term limit of tolerance of forests in the region is assumed to be around 500–550 mm. Wet periods may open windows for tree recruitment, whereas drier periods may prevent canopy closure and favour grassland species (Dulamsuren, Hauck & Mühlenberg, 2005*b*). This means that both forest and grassland vitality can have a certain range of variability along the mean climate gradient, expanding the climatically determined intersection point into a zone where neither forest nor grassland is more vital than the other on a permanent basis (Fig. 2B). As vegetation response to climate variability is often delayed (Yin *et al.*, 2013; Hao *et al.*, 2014), neither the forest nor the grassland can be expected to gain dominance over sufficiently long periods and over large areas, leading to forest–grassland coexistence in a mosaic pattern (House *et al.*, 2003). This climatically determined conceptual model of forest-steppe is often referred to as the zonal forest-steppe in the literature (e.g. Molnár *et al.*, 2012; Pfadenhauer & Klötzli, 2014; Bátori *et al.*, 2018). This Zonal Model can explain forest–grassland coexistence only in a relatively narrow range. Thus, other factors in addition to climate have to be taken into consideration if we are to understand forest–grassland coexistence across the entire distribution of forest-steppe mosaics in Eurasia.

(2) Topography

Variations in topography can considerably modify the effect of climate by either decreasing or increasing local temperature and moisture availability in ways that affect the vitality of forests and grasslands (Walter & Breckle, 1989; Chibilyov, 2002; Schultz, 2005; Pfadenhauer & Klötzli, 2014). Topography plays a role in forest–grassland distributions within and beyond the climatically determined forest-steppe zone (Fig. 2B, C). Within the climatically determined (zonal) forest-steppes, topography influences where forest or grassland ecosystem states form and persist. Beyond this climatically determined zone, special topographical circumstances may also result in forest–grassland coexistence (Fig. 2C). This latter situation is frequently called extrazonal (e.g. Zolotoreva, 2020), although we know of no substantial difference between the physiognomy of zonal and extrazonal forest-steppes, and their species compositions are similar (e.g. Borhidi, 2004).

The importance of topography is especially evident in the Inner Asian forest-steppe region (Mongolia, north and northeast China, and south Russia), where steep north-facing mountain slopes are usually covered by forests, steep south-facing slopes are occupied by steppes, and less extreme exposures can support either ecosystem state (e.g. Liu *et al.*, 2000;

Dulamsuren *et al.*, 2005*b*; Anenkhonov *et al.*, 2015; Hais, Chytrý & Horsák, 2016; Makunina, 2017). Liu *et al.* (2012) showed that topography controls forest and steppe distribution mainly through soil moisture. North-facing slopes receive a reduced amount of direct solar radiation, resulting in lower evaporation and, consequently, better soil moisture supply. This local decrease in aridity increases the vitality of forests relative to the steppe (Fig. 2C). By contrast, higher direct solar radiation on south-facing slopes increases temperature and reduces soil moisture. The associated local increase in aridity and heat stress decreases forest vitality relative to steppe vitality.

Ravines, erosion gullies, and depressions have cool and moist microclimates and increased soil water supply. Consequently, they support forests embedded among steppes in West Siberia (Lashchinsky, Korolyuk & Wesche, 2020) and eastern Europe (Walter & Breckle, 1989; Goncharenko & Kovalenko, 2019). Even very small topographical features may permit the formation of forest–grassland mosaics. For example, in the forest-steppes of western Siberia and northern Kazakhstan, shallow saucer-like depressions harbour circular forest patches in a steppe matrix, due to increased moisture input (Lavrenko & Karamysheva, 1993; Rachkovskaya & Bragina, 2012; Lashchinsky *et al.*, 2020). Similarly, small and shallow depressions support forest patches in the Carpathian Basin (Borhidi, Kevey & Lendvai, 2012) (Fig. 2C).

(3) Soil

Soil properties also profoundly influence water and nutrient availability for plants and thus are able significantly to influence forest and grassland distribution (Schultz, 2005; Pfadenhauer & Klötzli, 2014; Zech, Schad & Hintermaier-Erhard, 2014). Similar to topography, soils can modify both forest and grassland vitality within the climatically determined forest-steppe zone, and also broaden the forest-steppe zone in both directions along the harshness gradient (Fig. 3). In mosaics of the forest-steppe, soils beneath forests usually differ from those below grasslands, but it is often difficult to determine if these differences are primarily due to substrate or caused secondarily by the vegetation itself (Walter & Breckle, 1989). There are some cases in which primary soil characteristics apparently play a decisive role in forest *versus* grassland occurrence. For instance, gravelly soils within the Mongolian forest-steppe usually support the forest ecosystem state (Wallis de Vries, Manibazar & Dügerlham, 1996; Dulamsuren *et al.*, 2009), apparently because coarse-texture soils permit rapid infiltration of precipitation to deeper soil layers where it is accessible by deep rooted woody plants, but not grassland species (Fig. 2C). Coarse soil texture can also contribute to the emergence of forest-steppe beyond its climatically determined interval (Fig. 2C). In the Naurzum Nature Reserve of Kazakhstan, a vast sandy forest-steppe occurs surrounded on all sides by pure steppic grassland matrix associated with loamy and clayey soils (Rachkovskaya & Bragina, 2012; Bátori *et al.*, 2018). In a reversal of this pattern, in high-precipitation regions with a preponderance of temperate forest, shallow rocky soils often support patches of steppe-specialist plant species (Erdős *et al.*, 2014*b*; Boch *et al.*, 2019).

(4) Herbivory

Herbivory by large mammals is regarded as one of the main factors controlling the relative abundances of woody and herbaceous plants in savannas and forest–grassland mosaics. In tropical savannas grazers tend to increase, while browsers tend to decrease, woody cover (Roques, O’Connor & Watkinson, 2001; Augustine & McNaughton, 2004; Sankaran *et al.*, 2005; Bond, 2008; Archer *et al.*, 2017). Such effects may be dependent on herbivore pressure: Sankaran, Ratnam & Hanan (2008) found that grazers of African savannas increase woody abundance only at high grazing pressure, while low and medium grazing pressure have an opposite effect. Similarly, for semi-arid African savannas, Asner *et al.* (2004) and Archer (2010) concluded that heavy grazing increases woody plant abundance. In contrast to African ecosystems, the distinction between grazers and browsers is less clear in temperate regions (Owen-Smith, 2008). In the Eurasian forest-steppe, there is no evidence of grazer-induced woody encroachement. Here, in addition to browsers such as various species of deer (Cervidae) and goats (*Capra* spp.), animals that are typically considered grazers such as horses (*Equus* spp.), cattle (*Bos taurus* Linnaeus), European bison (*Bison bonasus* Linnaeus), and sheep (*Ovis* spp.) also feed on woody plants. Such browsing by ‘grazers’ combined with their trampling, wallowing, and uprooting of trees limits forest expansion into grasslands (Walter & Breckle, 1989; Wallis de Vries *et al.* 1996; Sankey, 2012). Grazers may also alter soil moisture availability indirectly by preventing the accumulation of dead plant material, which increases evaporation from the topsoil, rendering grasslands less suitable for tree seedlings (Walter & Breckle, 1989).

In addition to wild native herbivores, domestic ungulates are important to the ecology of the forest-steppe. Sheep, cattle, goats and horses are all regarded as limiting factors for tree establishment and survival in livestock-producing areas of Eurasia (e.g. Wallis de Vries *et al.*, 1996; Smelansky & Tishkov, 2012; Hais *et al.*, 2016; Török *et al.*, 2018). In Mongolia, Khishigjargal *et al.*, (2013) found that livestock grazing can effectively limit forest encroachment at grassland edges by reducing sapling number through trampling. In temperate pastures of Mongolia, goats consume tree saplings even when fresh herbs are available (Lkhagvadorj *et al.*, 2013). In both Hungary and Mongolia, livestock prevent shrub establishment in grazed grasslands, whereas in areas with herbivore exclusion, shrubs can establish and survive (Varga *et al.*, 2015; Takatsuki *et al.*, 2018).

The capacity of large native herbivores to push forest–grassland balance towards grasslands is generally accepted in the temperate zone of Eurasia (e.g. Lavrenko &

Karamysheva, 1993; Vera, 2000; Wagner *et al.*, 2020) and other temperate regions (Bredenkamp, Spada & Kazmierczak, 2002). Great populations of now-threatened or extinct Holocene herbivores such as tarpan (wild horse, *Equus ferus* Boddaert), takh (Przewalski's horse, *E. przewalskii* Poliakov), onager (Asian wild ass, *E. hemionus* Pallas), wild ox (*Bos taurus primigenius*), Eurasian elk (*Alces alces* Linnaeus), and saiga antelope (*Saiga tatarica* Linnaeus) once inhabited the Eurasian forest-steppe and certainly influenced forest–grassland dynamics (Walter & Breckle, 1989; Chibilyov, 2002; Pfeiffer, Dulamsuren & Wesche, 2020; Török *et al.*, 2020; Wagner *et al.*, 2020). Although the historical population sizes of these large native herbivores are unknown, some authors assume that low densities of domestic livestock may serve a similar ecological function to maintain grasslands (Wallis de Vries *et al.*, 1996; Wesche & Treiber, 2012; Pfeiffer *et al.*, 2020).

In addition to large ungulates, other important groups of animals in the forest-steppe are rodents and insects. Hamster (*Cricetus cricetus* Linnaeus), marmots (*Marmota* spp.), and voles (e.g. *Microtus* spp. and *Myodes* spp.) (Walter & Breckle, 1989; Lavrenko & Karamysheva, 1993; Chibilyov, 2002) consume seeds and seedlings of trees, and thus may limit tree establishment in the grassland ecosystem state and at the forest edge (Dulamsuren *et al.*, 2008*b*; Hauck *et al.*, 2008). Insects such as orthopterans and gypsy moth (*Lymantria dispar* Linnaeus) contribute to tree mortality by defoliating seedlings in the grassland ecosystem state (Dulamsuren *et al.*, 2008*b*) and damaging both seedlings and mature trees at the forest edges (Hauck *et al.*, 2008).

In sum, where herbivory disproportionately damages woody plants relative to grasses and forbs, forest vitality is reduced and grasslands may occupy areas where the climate is humid enough and soil moist enough theoretically to support forests. In light of the extensive evidence that the forest-steppe developed under the influence of a rich assemblage of Holocene large herbivores, and is now maintained by both native animals and domestic livestock, we suggest that our understanding of the coexistence of forests and grasslands should incorporate herbivory (Fig. 3), not just climate, soils, and topography (Fig. 2C).

(5) Fire

Most grasses and forbs are able to resprout after a fire event relatively quickly from underground organs and regenerate from the seedbank, whereas woody species, except some fire-tolerant or resprouting ones, need decades if not centuries to reestablish (Bond, 2008). Although few Eurasian studies examine the effects of fire on vegetation in general, and on the forest–grassland balance in particular (Valkó *et al.*, 2014), fire is regarded as being capable of limiting woody vegetation, even in moist sites that would otherwise permit development of forests (e.g. Walter & Breckle, 1989; Korotchenko & Peregrym, 2012). According to Kertész *et al.* (2017) and Ónodi *et al.* (2021), severe wildfires are able to eliminate the forest ecosystem state from the forest-steppes, shifting the forest–grassland balance in favour of grasslands. Forest patches containing *Juniperus communis* L. are particularly vulnerable to fires, as juniper is highly flammable and cannot resprout (Kertész *et al.*, 2017; Ónodi *et al.*, 2021). Erdős (2014) found that wildfires in forest-steppes can open up the canopy layer, and the regeneration of the forest may take several decades. *Pinus sylvestris* of large diameter are able to withstand surface fires of low to medium intensity (Wirth, 2005), but not high-intensity crown fires; *Pinus sylvestris* stands killed by fire can be very slow to recover, requiring decades to regrow (Ivanova *et al.*, 2010; Barrett *et al.*, 2020).

Because humans are responsible for many fires today, the current frequency of fires in the forest-steppe is often regarded as ‘unnatural’. While it is true that fire has long been used by humans to prevent woody encroachment into grasslands and to maintain pastures for livestock (Smelansky & Tishkov, 2012; Valkó *et al.*, 2014; Novenko *et al.*, 2016; Unkelbach *et al.*, 2018), burning by humans may be viewed as perpetuating fire as an ancient ecological process in the region. Indeed, paleoecological evidence suggests that natural (lightning-ignited) wildfires regularly occurred in many regions of the forest-steppe, including the Carpathian Basin (Magyari *et al.*, 2010); the Mongolian Altai (Unkelbach *et al.*, 2018), and European Russia (Novenko *et al.*, 2018). This may not be recognised, because fires today are usually suppressed near human settlements. But in remote forest-steppe regions fire continues to play an important ecological role to maintain grasslands in places that could otherwise develop into forests (e.g. Kertész *et al.*, 2017; Erdős *et al.*, 2018a; Kolár *et al.*, 2020; Wagner *et al.*, 2020). In contrast to tropical savannas of C_4 grasses, which can burn annually, wildfires are much less frequent in forest-steppes: recent research indicates that fire-free intervals in Eurasian forest-steppes have ranged from several years to a couple of decades or even centuries during the Holocene, with considerable temporal variations due to climatic modifications and human activity (Ivanova *et al.*, 2010; Hessl *et al.*, 2012, 2016; Feurdean *et al.*, 2013; Novenko *et al.*, 2018; Rudenko *et al.*, 2019; Kolár *et al.*, 2020). Generally, fires in forest-steppes are more frequent than in boreal forests but less frequent than in open grasslands of the steppe biome (Barrett *et al.*, 2020).

In sum, fire is able to limit forest vitality, and thus modify forest–grassland proportions anywhere in the forest-steppe, reducing tree cover below the potential allowed by climate, soil, and topography. For our understanding of the wide climatic and geographic distribution of the forest-steppe, the effects of fire are most important at the humid end of the climatic harshness gradient (Fig. 3). Here, fire is not just a modifier but, alongside herbivory, is essential to prevent canopy closure, and enable long-term forest–grassland coexistence.

(6) Vegetation feedbacks and alternative ecosystem states

Emerging theory on grassland–forest coexistence and the distribution of savanna and forest biomes details how vegetation feedbacks that reinforce either grass or tree dominance contribute to the stability of alternative ecosystem states under the same climate (Staver *et al.*, 2011; Hirota *et al.*, 2011; Murphy *et al.*, 2016; Staal *et al.*, 2018*a*,*b*). In the tropics, these ideas have focused on the distinct and generally opposite influences of grasses and trees on ecosystem flammability (fire), forage quantity and quality (herbivory), resource availability (e.g. light, water, nutrients), microclimate (temperature and humidity), and tree establishment and survival (Hoffmann *et al.*, 2012; Murphy & Bowman, 2012; Pausas & Dantas, 2017). Based on our review of literature from the forest-steppe, we suggest that vegetation feedbacks are also important for understanding the distributions and stability of grassland–forest mosaics in Eurasia. These feedbacks are critical to the interpretation of our hierarchical models, in which grassland and forest plant communities are not merely passive entities whose distributions are determined by combined effects of climate variability, soils, topography, herbivores, and fire. Instead, we view trees and herbaceous plants of the forest-steppe as active ecosystem engineers, who themeselves influence forest and grassland vitality across a wide geographic range in Eurasia.

Trees of the forest-steppe have strong feedbacks on local conditions beneath their canopy. Tree canopies intercept solar radiation, leading to low light availability, cooler diurnal temperature and higher relative air humidity at the forest floor, and the canopy reduces heat loss at night compared to the steppes (Breshears *et al.*, 1997; D'Odorico *et al.*, 2013; Tölgyesi *et al.*, 2018, 2020; Süle *et al.*, 2020). Microclimatic extremes are also tempered within forest patches by the edges acting as wind breaks and thus attenuating evaporation compared to adjacent grasslands (Davies-Colley, Payne & van Elswijk, 2000). The altered conditions impose a strong filter, limiting the growth of light-demanding plant species, while facilitating shade-tolerant and drought-sensitive species, for which the steppe does not offer suitable habitat (Erdős *et al.*, 2014*a*; Lashchinskiy *et al.*, 2017; Tölgyesi *et al.*, 2018).

As for soil moisture availability, the effects of trees are rather mixed in the forest-steppe, and it is difficult to separate *a priori* moisture differences caused by topography and soil structure from true forest–moisture feedbacks. The proportion of precipitation intercepted by tree canopies and the leaf litter can be high (up to 70% of each rainfall event; Yang *et al.*, 2019), especially in coniferous forests, where interception captures not just rain, but also causes considerable amounts of snow to sublime before reaching the ground. At the arid southern edge of the forest-steppe in Kazakhstan, mid-summer topsoil can be drier under forest tree canopies than in adjacent open steppes (Tölgyesi *et al.*, 2018). In climatically less harsh sites, such as the sand regions of the Carpathian Basin, forest topsoil tends to be moister than that of the steppe patches (Erdős *et al.*, 2018*b*, 2021) but deeper soils are desiccated, with the rate of desiccation dependent on whether trees are deciduous or evergreen (Tölgyesi *et al.*, 2020). It is an open question though, whether the moisture surplus in the topsoil is solely a consequence of the reduced evaporation due to the cool shaded microclimate or if trees bring deep water up to the topsoil *via* hydraulic lift, as occurs in many semi-arid regions (Yu & D'Odorico, 2015).

The overall effect of trees on grassland species seems to be negative, with a sparser herbaceous layer in forests compared to grasslands (Erdős *et al.*, 2014*a*; Tölgyesi *et al.*, 2018). The herbaceous layer species compositions in grasslands and forests show little overlap, thus it is unclear whether the trees directly exclude steppe species, or do so indirectly by allowing the growth of species that are competitively superior in shaded conditions. Conditions beneath forests, which are unsuitable for grassland species, can facilitate tree recruitment by attenuating heat and water stress during the summer, and reducing cold stress in winter and early spring (Dulamsuren *et al.*, 2008*a*,*b*; Erdős *et al.*, 2021). In addition, the sparser herb layer in the forests is less flammable, limiting the spread and intensity of wildfires compared to the grasslands. Saplings are thus more likely to survive fires inside the forest, but this has not been tested. Such fire protection may not apply to forests composed of highly flammable conifers (*Pinus* spp. or *Juniperus* spp.), which can burn intensely and regenerate slowly if their crown catches fire (Kolár *et al.*, 2020; Ónodi *et al.*, 2021). Shaded conditions in the forest patches are likely to limit tree saplings too, but less than by the grassland species, since most forest-steppe trees are widespread components of closed-canopy temperate and boreal forests where there has been strong evolutionary selection for shade tolerance (Valladares & Niinemets, 2008).

Parallel to the favourable recruitment conditions of trees inside forests, conditions in the grassland state promote the recruitment and persistence of steppe species for a number of reasons. Fire, which can suppress saplings in the steppe, causes little harm to the belowground organs or the seedbank of grasses and forbs, for which the conditions after the fire provide excellent opportunities for regeneration *via* resprouts, clonal spread, or seed germination (Ónodi *et al.*, 2021). Contributing to a positive fire feedback, after burning, aboveground plant productivity is enhanced relative to pre-fire levels (Valkó *et al.*, 2016). Herbaceous plants in steppes benefit from a sharper drop in nocturnal temperature relative to temperatures in forests, which often leads to dew formation (Lellei-Kovács *et al.*, 2008; Tölgyesi *et al.*, 2018), which is an important moisture source for herbaceous plants in water-limited ecosystems (Agam & Berliner, 2006). Tree saplings in the steppes are less able to benefit from dew because they have few superficial roots. Furthermore, there is evidence that the belowground competitive effects of grasses can directly constrain tree growth in the Eurasian forest-steppe (Walter & Breckle, 1989; Peltzer & Köchy, 2001). However important direct grass–tree competition may be, competition alone is not necessarily strong enough to exclude trees completely from invading grass-dominated communities (Wilson & Peltzer, 2021). In Eurasian forest-steppes, competitive effects of grasses on trees are probably best viewed a minor vegetation feedback, relative to the strong influence of the steppe microclimate, fires, and herbivores in limiting tree establishment.

The effective recruitment of trees and grasses in association with the forest and the steppe ecosystem states, respectively, stabilises their position and distinctness, contributing to the mosaic vegetation structure. The resulting stability of the forest edges is also reflected by distinct, species-rich edge communities in forest-steppes (Erdős *et al.*, 2014*a*; Bátori *et al.*, 2018). This overall pattern means for our hierarchical conceptual model that in sites where climate as well as topography, soil, herbivory and fire allow the co-existence of forest and steppe, vegetation feedbacks further stabilise spatial patterns by hindering state transitions (i.e. hysteresis; Ratajczak *et al.*, 2018). This stable patch pattern has been confirmed for Hungarian forest-steppes by historical map interpretation (Erdős *et al.*, 2015). The stabilising feedbacks may lend considerable resilience of both forest and grassland ecosystem states to environmental changes, as highlighted by Xu *et al.* (2017) for Siberian forest-steppes.

IV. IMPLICATIONS AND FUTURE CHALLENGES

Our conceptual models illustrate that the vegetation pattern in the Eurasian forest-steppe is a net result of multiple drivers with varying relative importance. Focussing on only one or a subset of the drivers can lead to a misinterpretation of patterns and processes and eventually to misguided conservation and restoration strategies. Ignoring the importance of natural disturbances is a common source of such problems. The northern and western fringes of the forest-steppe have long been assumed to be anthropogenic, given that the potential vegetation, determined by climate, soil and topography, was thought to be closed-canopy forest (Feurdean *et al.*, 2018). This notion was reinforced by the fact that land abandonment leads to shrub encroachment and forest establishment in these areas (e.g. Deák *et al.*, 2016). But how far should we look back to determine historical forest and grassland distributions? Given that prehistoric herds of wild ungulates that contributed to the forest-steppe physiognomy were extirpated millennia ago (Vera, 2000; Pfeiffer *et al.*, 2020; Török *et al.*, 2020), we suggest that the resulting lack of natural disturbance may have yielded forest expansion in otherwise uncultivated areas. If one takes a long-term view, deforestation in some areas may be viewed as a reversal of past forest expansion that was itself due to human-caused disruption of herbivore and fire disturbance regimes. Indeed, palaeoecological records show that steppe-specialist plants and animals were continuously present throughout the Holocene in many of the forest-steppes of debated origin, such as in the Carpathian Basin, i.e. the westernmost part of the present-day forest-steppe (Magyari *et al.*, 2010; Feurdean *et al.*, 2018). The meadow-steppe patches in the northern edge of south Siberian forest-steppes were also mostly considered end-products of forest clearing (e.g. Ermakov & Maltseva, 1999), even though they are often rich in steppe-specialist plants, while ruderal species are scarce (Kämpf *et al.*, 2016), which is inconsistent with a purely anthropogenic orign. Similarly, while Hilbig (2000) argued that the Mongolian forest-steppe has formed as a result of anthropogenic activity, field evidence suggests that this ecosystem is of natural origin (Dulamsuren, Hauck & Mühlenberg, 2005*a*). With this in mind, we suggest that it is necessary to update our concept of primary (i.e. natural) forest-steppe ecosystems, and also consider natural disturbances as determinants of forest–grassland coexistence (Bond & Parr, 2010; Weigl & Knowles, 2014; Veldman *et al.*, 2015). We hope that future research in the forest-steppe will improve our understanding of the relative contributions of these different factors to forest–grassland coexistence (i.e. climate, topography, soil, herbivores, and fire).

Greater recognition that the forest-steppe is ancient will have consequences for ecosystem management. Some landscapes formerly considered secondary may actually represent the historical ecosystem state and should receive full attention for conservation or restoration. Of particular importance, traditional grassland management in the forest-steppe should be viewed as critical to the maintenance of high-biodiversity natural grasslands. In this sense, abandoning traditional grassland management and promoting afforestation is not restoration (Temperton *et al.*, 2019).

Restoration and management measures in the forest-steppe should become more holistic in their approach. Fortunately, a growing body of information on the ecology of community reassembly and best management practices is leading to growth in grassland restoration (e.g. Kämpf *et al.*, 2016; Török *et al.*, 2018; Tölgyesi *et al.*, 2019). By contrast, restoration of natural forests in the forest-steppe is rare, due to a focus on commercial tree plantations and intensive rotational forestry throughout the entire region (Cao, 2008; Erdős *et al.*, 2018*a*). Future forest-steppe restoration should pay attention to both grassland and forest ecosystem states, with consideration of historical proportions and configuration, while recognising that restoration will require planning for the maintenance of essential, but often overlooked natural levels of disturbance by herbivores and fire.

Forest-steppe restoration is a long-term enterprise; therefore it needs to account for future changes in the driving forces. Located between the temperate forest and grassland biomes, forest-steppes may be particularly susceptible to the effects of climate change. Climatic harshness in the Eurasian forest-steppe is projected to increase in the near future, decreasing forest vitality (Mátyás *et al.*, 2018) and thereby favouring the advance of the steppes against the forests and an overall shift of the forest-steppe against temperate forests (Lu *et al.*, 2009; Tchebakova, Parfenova & Soja, 2009). Thus, forest restoration should be restricted to the most favourable locations (i.e. northern slopes, moist depressions, etc.), and adaptive forestry may stop reforesting (or afforesting) sites where overall forest vitality is expected to fall below that of the grassland ecosystem state in the future. Once the vitality relationships turn in favour of grasslands, forests will no longer be sustainable. Vegetation feedbacks may delay the switch to grassland, but the eventual transition will be unpredictable and abrupt (Scheffer *et al.*, 2001), and is likely to be realised in the form of forest dieback and wildfires. The restoration in the forest-steppe should resist the current global emphasis on forest-based carbon sequestration (Temperton *et al.*, 2019; Tölgyesi *et al.*, 2022), and recognise the belowground carbon and biodiversity benefits of conserving and restoring grasslands alongside forests across Eurasia.

V. CONCLUSIONS

(1) The emerging fire–herbivore paradigm, as well as the recent increase in the number of case studies makes it timely to revisit the determinants of forest–grassland coexistence at the interface of closed-canopy forests and open steppes. Through conceptual modelling and a literature review, we provide a comprehensive overview of the interacting drivers of forest–grassland coexistence in the Eurasian forest-steppe.

(2) Although mean climate is the most widely acknowledged determinant, we show that the Mean Climate Model should result in a sharp transition between the temperate or boreal forest and steppe biomes, but not a mosaic of forests and grasslands (Fig. 2A).

(3) Accounting for temporal variation in climate, the Zonal Model can only explain the coexistence of forest and grassland within a relatively narrow geographic range (Fig. 2B).

(4) Topography and edaphic conditions can modify forest and grassland patterns within the climatically determined forest-steppe zone, and are essential to explain the presence of forest-steppe across broad gradients in climatic harshness (Climatic–Topographic–Edaphic Model, Fig. 2C).

(5) Herbivory and fire are able to limit forest vitality and to decrease forest cover throughout the forest-steppe. However, their role is most important towards the humid end of the climatic harshness gradient, where herbivory and fire prevent canopy closure and thus favour the

forest-steppe against closed-canopy forests (Climatic–Topographic–Edaphic–Herbivore–Fire Model, Fig. 3).

(6) Once the scene is set by these determinants of forest–grassland coexistence, vegetation feedbacks stabilise grassland and forest ecosystem states, lending considerable stability to the forest-steppe landscape configuration.

(7) Our hierarchical conceptual model highlights that many forest-steppes that have traditionally been considered secondary, represent, in fact, the historical landscape structure. Targets to restore native biodiversity or sequester atmospheric carbon should be revisited accordingly, and restorationists should think twice regarding the global call for tree planting in the Eurasian forest-steppe.

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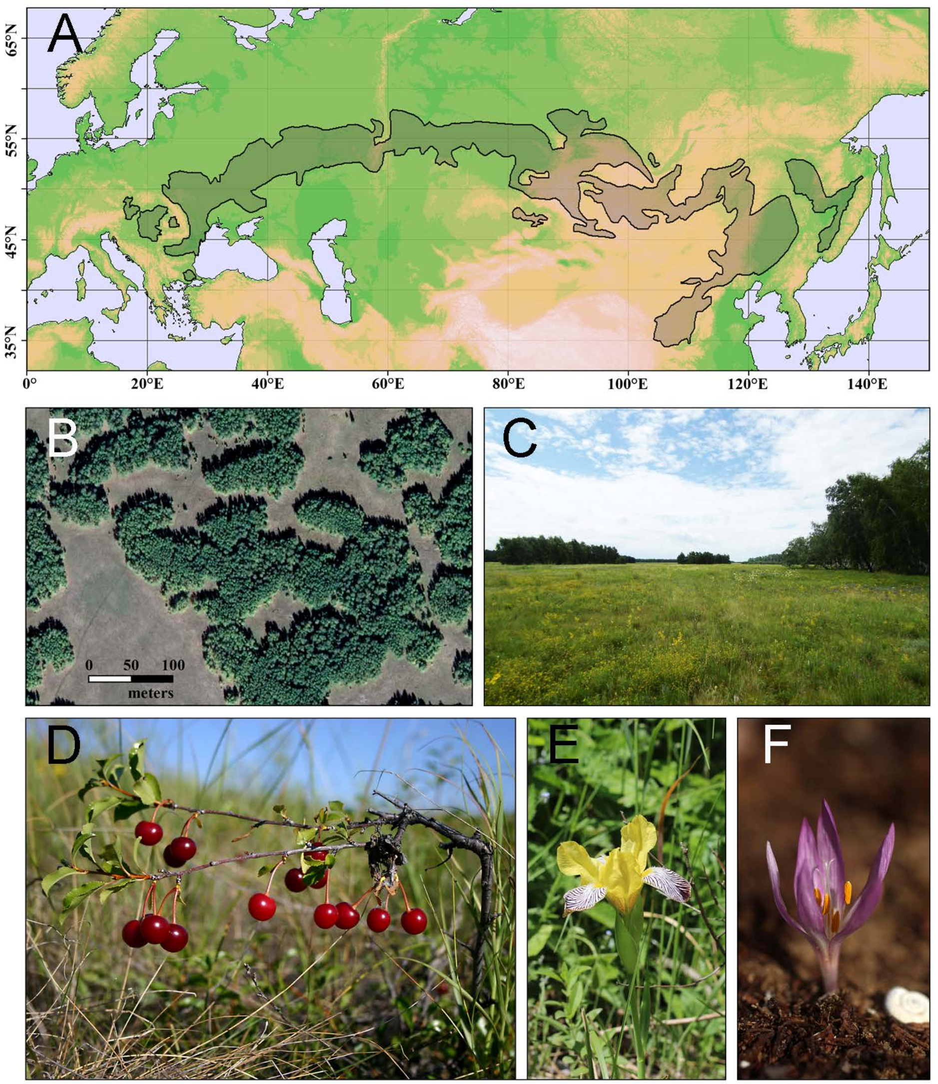
Figure captions

Fig. 1. The distribution of forest-steppes in Eurasia (A), mosaic of forest and grassland ecosystem states in northern Kazakhstan (B, C), *Prunus fruticosa*, a typical shrub of forest-steppe ecosystems (D), *Iris variegata*, a forest-steppe herb (E), *Colchicum arenarium*, a grassland species endemic to the forest-steppes of the Carpathian Basin (F).

Fig. 2. Conceptual models of the distribution of forest and grassland along a continuous climatic harshness gradient (H) in Eurasia. Climatic harshness reflects (generally north to south) gradients in temperature extremes (hot summers and cold winters) and aridity (precipitation and potential evapotranspiration). (A) The Mean Climate Model predicts a sharp forest-grassland boundary (marked by a vertical line) at the latitudinal intersection of forest and grassland vitality curves (F and G, respectively). (B) The Zonal Model accounts for temporal variation in climatic harshness: forest and grassland vitality (F and G, respectively) are represented by bands instead of thin lines, indicating that the vitality of both can vary across a certain range, depending on the actual climatic variations. Forest–grassland coexistence is possible in a narrow zone where grassland and forest bands overlap (enclosed by vertical lines). (C) In the Climatic–Topographic–Edaphic Model, slope, aspect, and soils expand the climatic ranges of forests and grasslands. Circular arrows indicate local reversals of forest and grassland vitality relationships with climate (F and G, respectively), while straight arrows show changes without reversal as a result of modified aridity due to special topographic or soil conditions.

Fig. 3. Climatic–Topographic–Edaphic–Herbivore–Fire Model of forest–grassland coexistence, as determined by (1) climate (mean and variability), (2) topographic and edaphic factors (slope, aspect, soil texture, moisture availability), and (3) herbivory and fire. Circular

arrows show how forest and grassland vitality (F and G, respectively) change as a result of local conditions evoked by special topographical or soil conditions (in zone 2) or as a result of fire and herbivores (in zone 3).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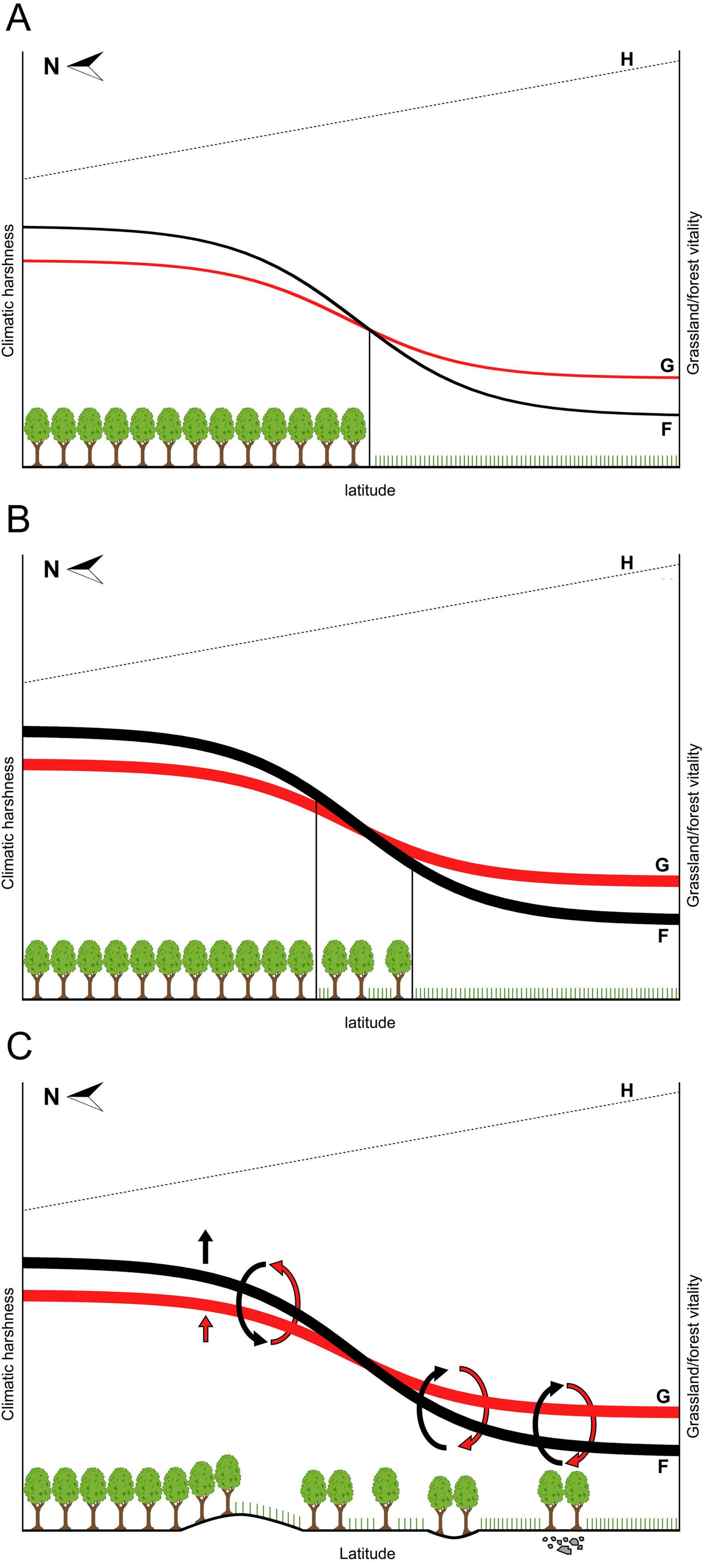
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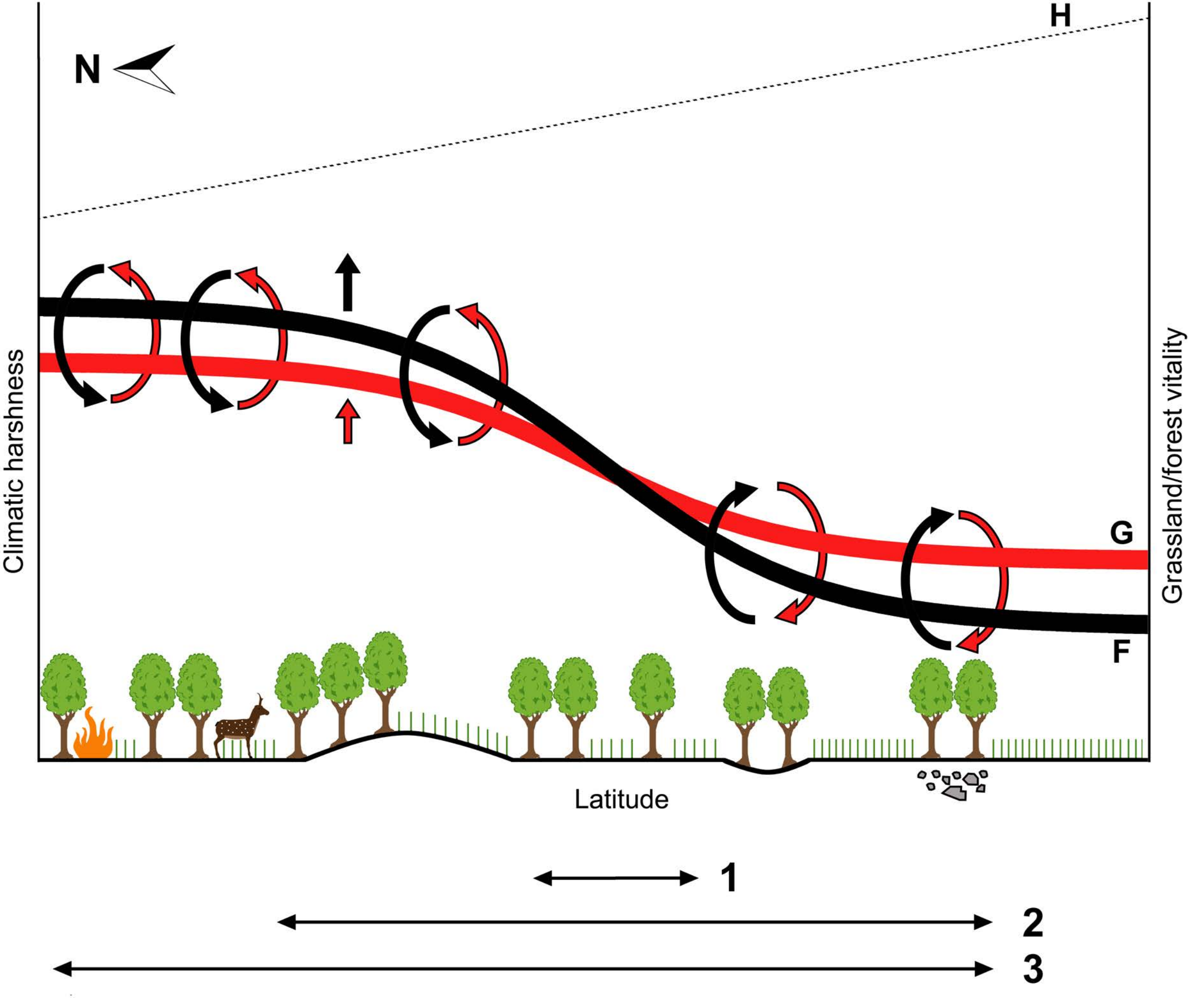
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