SYNTHESIS

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Central European forest–steppe: An ecosystem shaped by climate, topography and disturbances

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Abstract

The occurrence and origin of dry grasslands and their rich biota in the moderately humid Central-European climate have fascinated scientists for over a century. Modern palaeoecological and phylogeographical data support earlier hypotheses that these grasslands are late Pleistocene relicts and can therefore be considered part of the Eurasian forest–steppe biome. However, it is still unclear which factors fostered the maintenance of steppe patches in Central Europe throughout the Holocene. Here, we provide an overview of the main hypotheses, which stress, respectively, the effects of climate, edaphic conditions and disturbances. We then develop a general conceptual framework on how these three factors interact to form forest–steppe mosaics. We thereby emphasize the role of topography as a crucial control on forest–steppe patterns at the landscape scale. Topography is related to several mechanistic drivers that influence vegetation processes, such as near-surface microclimate and soil formation. Consequently, topographic variation allows both forest and steppe patches to occur beyond their macroclimatic niche, favouring the development of forest–steppe mosaics. To illustrate our framework, we demonstrate the interactive effect of macroclimate and topography on the occurrence of steppe patches at 108 selected Central European forest–steppe sites. Although we developed our framework focusing on the current distribution of Central European forest–steppe, we suggest that it contributes to the understanding of similar transitions between temperate forest and steppe biomes in the past as well as elsewhere in the world.

KEYWORDS
biome, Central Europe, feedback, forest–steppe, microclimate, topography

1 | INTRODUCTION

The natural vegetation of Central Europe is dominated by various types of forest differing in structure and species composition (Bohn et al., 2004). However, the driest Central European regions host an exceptional diversity of species that require open landscape, including continental species that reach their westernmost distribution limit in this area (Horsák et al., 2015; Kaplan, 2012; Niklfeld, 1964). Such species are mostly restricted to steppe patches (Figure 1), usually in hilly landscapes (Illyés, 2007), on sandy (Erdős et al., 2014) or saline soils (Eliáš Jr et al., 2020; Sümegi et al., 2012) or on rock outcrops (Niklfeld, 1964). Central European steppe significantly contributes

FIGURE 1 Forest–steppe landscapes of Central Europe. (a) Modrý vrch, Belianské Hills, Slovakia, mosaic of continental oak forests with meadow steppes on loess soils, (b) Čenkovská lesostep, Danube floodplain, Slovakia, grass steppe–forest mosaic on aeolian sand, (c) Stredná dolina, Strážovské Mts, Slovakia, exposure-related forest–steppe on dolomite with scattered individuals of *Quercus pubescens* on a south-facing slope and (d) Martinka, Pavlov Hills, Czech Republic, a small grass steppe patch surrounded by a forest on a south-facing slope. Photos by Kryštof Chytrý
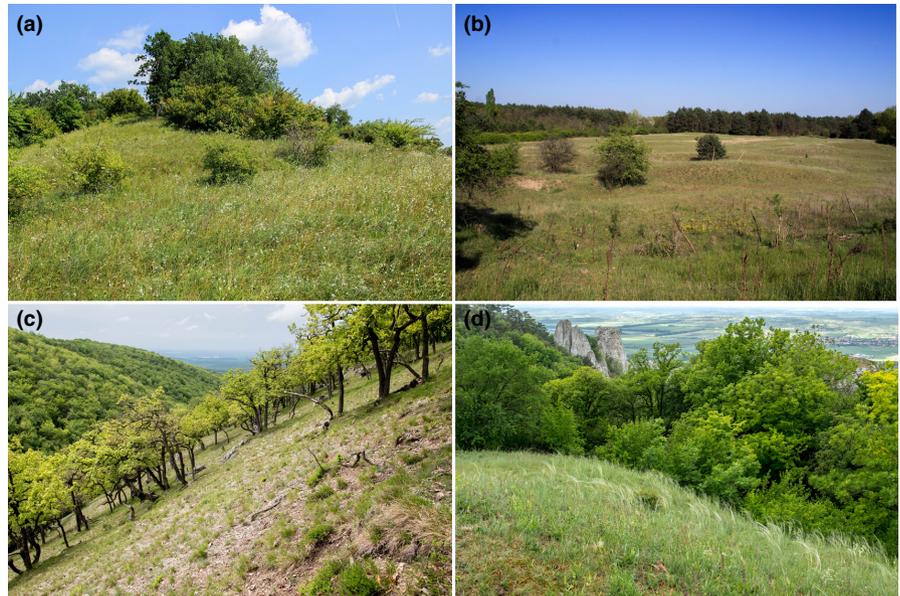
to regional biodiversity (Fekete et al., 2010; Habel et al., 2013; Le Roux et al., 2018; Sádlo et al., 2007). Hence, both the steppe habitats and many of their characteristic species have a high priority in national and European conservation schemes (Natura 2000 and Emerald networks). Understanding the factors responsible for the occurrence of steppe patches and their flora in Central European landscapes is therefore not only of theoretical interest, but also essential for the effective conservation of their species-rich biota.

Transitions between forests and grasslands occur worldwide at the boundary of different climatic zones (Breckle, 2002; Walter, 1974; Woodward, 2008). Tropical forest transitions into various types of savanna while temperate and boreal forest builds patchy mosaics with continental temperate grassland called prairie in North America, pampa in South America and steppe in Eurasia. While forest–grassland transitions in tropical regions are characterized by a gradual change in habitat physiognomy (e.g. Cardoso et al., 2021), the boundary between habitats in the forest–steppe is usually abrupt. Some authors consider such mosaic landscapes as a distinct forest–steppe biome (Erdős et al., 2018; Fekete et al., 2010; Walter, 1974). In addition to zonal biome transitions, azonal forest–grassland ecotones are common in all regions of the world, for example, between mountain forests and alpine grasslands (Körner, 1998). Regardless of spatial scale, understanding the occurrence, structure and dynamics of forest–grassland ecotones has long been of interest to ecologists. The main focus has been on the effects of macroclimate (Barros et al., 2018; Williams et al., 2009), disturbance by livestock and fire (Aleman & Staver, 2018; Behling et al., 2007; Sankey et al., 2006), land use and land abandonment (Gehrig-Fasel et al., 2007; Munteanu et al., 2015; Treml et al., 2016) and plant invasions (Hoffmann et al., 2004).

In the Palaearctic, forest–steppe extends from its westernmost limit in Central Europe through the Balkans, Ukraine, Russia, the Caucasus, the Middle East, northern Kazakhstan and southern Siberia to Mongolia and northern China (Erdős et al., 2018; Wesche

& Treiber, 2012; Woodward, 2008). Outside the Palaearctic, landscapes with similar physiognomy are reported from North America, for example, the Pacific Northwest (Kerns et al., 2018) and the transitional areas between prairie and boreal forest (Frelich & Reich, 2010), as well as from South America, where they frequently occur at the transition between mountain forests and pampas in Argentina and Chile (Anchorena & Cingolani, 2002; Gowda et al., 2012). However, a global synthesis of forest–steppe landscapes from different biogeographical regions is lacking. In contrast to the mosaic structure of forest–steppe, savanna, the zone of the woodland–grassland transition in tropical and subtropical areas, is mostly formed of open woodlands or shrublands. It occurs under a warmer macroclimate than forest–steppe and is characterized by a stronger consumer control (i.e. a joint impact of herbivores and fire; Barbosa, 1999).

The Eurasian forest–steppe reaches its western distributional limit in Central Europe, where it is geographically separated from the zonal steppe biome further east (Fekete et al., 2010). For this reason, the origin and development of Central European forest–steppe has always been a source of controversy (Sümegi et al., 2012). According to current understanding, some steppe patches in this region are relicts of more extensive late-Pleistocene and early-Holocene steppe and forest–steppe environments (Chytrý, Horsák, et al., 2019; Horsák et al., 2015; Niklfeld, 1993; Novák et al., 2019; Zólyomi, 1964). Although the regional macroclimate may have been unsuitable for steppe vegetation in certain periods of the Holocene, particularly during the moist mid-Holocene (Dabkowski et al., 2019; Mauri et al., 2015), the current interpretations of the palaeoecological record support its continuous persistence throughout the Holocene (Feurdean et al., 2015; Kuneš et al., 2015; Magyari et al., 2010; Novák et al., 2019; Pokorný et al., 2015; Šolcová et al., 2018). The human impact may have hindered forest succession, although a relatively humid climate facilitated the spread of forests since the Neolithic settlement of Central Europe approx. 8000–7500 years

BP (Feurdean et al., 2018; Magyari et al., 2010; Novák et al., 2019; Šolcová et al., 2018). In fact, the archaeological record shows a concentration of early-Neolithic settlements in dry and warm lowlands (Pokorný et al., 2015; Šolcová et al., 2018). These lowlands might have been still partially treeless at the time of settlement, which facilitated agricultural use, as already suggested by Gradmann (1933). The further spread of settlements led to the successive expansion of non-forest vegetation through extensive livestock grazing and deforestation (Poschlod et al., 2009; Hejcman et al., 2013).

However, the impact of agricultural societies varied over time and was certainly not the only reason for the persistence of open landscapes in Central Europe (see Kaplan et al., 2009). There are three commonly discussed natural factors that may have contributed to the suppression of forest succession: (1) *Macroclimate*. Its importance, especially in the more continental parts of Central Europe, was already emphasized by Kerner von Marilaun (1863) and later supported by numerous scientists (e.g. Fekete et al., 2010; Podpěra, 1928; Varga, 1989). These authors referred to steppe sites in Central Europe as 'climatic steppes' and claimed that precipitation was low enough to prevent the development of a closed zonal forest. (2) *Consumer control*. Some authors argued that natural herbivory and wildfires are a key factor promoting landscape openness (Vera, 2000; Walter, 1974) because they suppress tree recruitment and thus succession to a forest. (3) *Edaphic control*. Other authors argued that under suboptimal climatic conditions, natural steppe can only develop on specific substrates (Soó, 1929; Wendelberger, 1954; Zólyomi, 1942, 1987). Therefore, they called the Central European steppe sites 'edaphic steppes'.

These three hypotheses for the past and present landscape openness in Central Europe have been developed largely independently (Sümegi et al., 2012), often focusing on specific landscapes or regions. Here, we attempt to unify them into a single framework potentially applicable to forest–steppe ecosystems worldwide. In this framework, we emphasize the critical role of topography in shaping the mosaic of forest and steppe under a particular combination of macroclimate and disturbance regimes. While topography is not a mechanistic driver of plant growth and vegetation processes, it is physically related to many such mechanistic drivers.

2 | MACROCLIMATE – SETTING THE SCENE

Climate is considered the most important factor affecting the coarse-scale distribution of species, communities and whole biomes (Holdridge, 1947; Mucina, 2019; Polis, 1999). Biomes are roughly determined by climatic boundaries that allow for the development of physiognomically uniform, the so-called zonal vegetation (Holdridge, 1947; Hunter et al., 2021; Mucina, 2019). Incorporating forest–steppe sites as 'forest–steppe biome' into such a concept is challenging as this biome is, by definition, a

mosaic of physiognomically contrasting habitats (Erdős et al., 2018; Walter, 1974). Therefore, some authors consider the zonal vegetation of the 'forest–steppe biome' to be a macro-mosaic of forest and meadow steppe, that is, semi-dry perennial calcareous grassland (Walter, 1974; habitat type R1A in the EUNIS habitat classification; Chytrý et al., 2020). The species composition of such grasslands is relatively homogeneous throughout the forest–steppe biome in Central and Eastern Europe (Roleček et al., 2014; Willner et al., 2019), possibly due to their continuous distribution during the late Pleistocene and/or early Holocene. However, on slopes or well-drained sandy soils, meadow steppe is replaced by grass (true) steppe, that is, continental dry grassland (EUNIS habitat type R1B). In hilly landscapes, the forest–steppe mosaic thus mostly consists of grass steppe and forest (Figure 1). In contrast to meadow steppe, grass steppe has sparser vegetation cover and lower productivity. With dominant narrow-leaved grasses such as *Festuca* spp. and *Stipa* spp., it is more closely related to the steppe biome than meadow steppe, which is characterized by broad-leaved grasses such as *Brachypodium pinnatum* and a high proportion of herbs (Willner et al., 2017).

The macroclimate supporting the formation of forest–steppe is transitional between the steppe and temperate forest climates, especially in terms of precipitation totals and degree of aridity. In Central Europe, forest–steppe is reported to occur under annual precipitation sums between 420 and 600 mm and mean annual temperatures between 8.25 and 13.5°C (Chytrý, 2012; Erdős et al., 2018). The precipitation peaks in late spring, followed by the temperature peak in mid-summer. Winters tend to have low precipitation, with monthly mean temperatures around 0°C and the mean of the coldest month(s) below 0°C (Figure 2). There are no arid periods in the long-term average, but the distribution of precipitation within the year fluctuates considerably. Hence, arid phases of varying length frequently occur in different parts of the year. Long-term observations in permanent plots on shallow calcareous soils in the Czech Republic have shown that such weather fluctuations can suppress succession in Central European grass steppe dominated by *Festuca valesiaca* (Fischer et al., 2020; Hroudová & Prach, 1986). Similar observations have been reported from well-drained sandy soils in central Hungary (Rédei et al., 2008).

Forest–steppe covers extensive areas in Eurasia, where it develops under diverse macroclimates. Compared to Central European forest–steppe, those farther east grow under drier and colder conditions with more pronounced temperature seasonality (Walter, 1974). In contrast, the climate in the southern parts of Central Europe is transitional between continental and sub-Mediterranean, characterized by higher winter temperatures, less pronounced temperature seasonality and drier summers with a weaker or absent summer precipitation peak. Under such a macroclimate, forest–steppe exhibit sub-Mediterranean features, such as a well-developed 'forest mantle' of shrub species with southern European ranges, such as *Amelanchier ovalis* and *Cotinus coggygria* (Erdős et al., 2018; Jakucs, 1961, 1972). Such mantles are physiognomically very different from low-growing forest mantles with *Prunus fruticosa* and
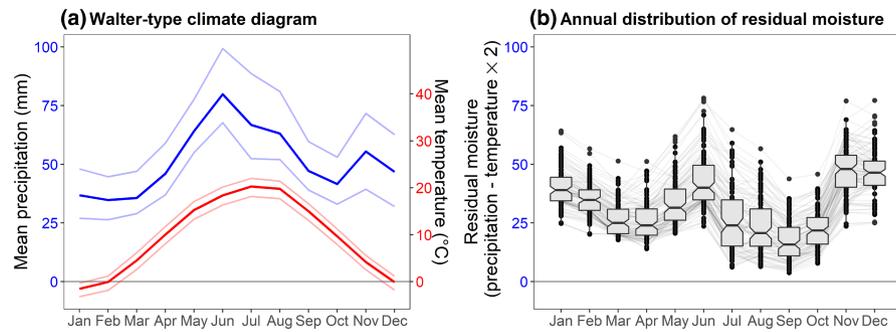
FIGURE 2 (a) Walter-type climate diagram (Walter & Lieth, 1967) for the Central European forest-steppe showing the annual distribution of monthly mean temperature and monthly precipitation totals, scaled in a ratio of 1:2. The three lines for both precipitation and temperature correspond to the 5% quantile, the mean and the 95% quantile. (b) The Walter-type climate diagram assumes that the monthly difference between the precipitation total and the temperature mean, scaled 1:2, is an indicator of the residual moisture in the ecosystem. To facilitate interpretation of the climate diagram, we have plotted these monthly differences for individual sites (connected by lines) using boxplots. Both plots are based on the climate data from the CHELSA model retrieved for 108 Central European forest–steppe sites (see Figure 3)

P. tenella in continental areas. In addition, sub-Mediterranean trees such as *Quercus pubescens* and *Fraxinus ornus* have broader crowns, unlike those prevalent in sub-continental areas, and therefore they cause more shading on dry, south-facing slopes and reduce the area occupied by steppe.

3 | CONSUMER CONTROL – SUPPRESSING VEGETATION SUCCESSION

Zonal vegetation, as determined by the macroclimate, is modified by natural disturbances such as herbivory and wildfires, which are sometimes collectively understood as 'consumer-control' factors (Bond & Keeley, 2005). It is generally accepted that the impact of consumer control can be strong enough to prevent, for centuries and millennia, the successional development of vegetation towards climax stages (Bond & Keeley, 2005; Novák et al., 2019; Vera, 2000). Therefore, consumer-controlled ecosystems may exhibit multiple stable stages (Mucina, 2019; Pausas & Bond, 2020; Zimov et al., 1995), depending on the spatial distribution, frequency and severity of disturbances.

The coevolution of herbivores and grassland plant species has taken place for millions of years, and both large and small mammalian herbivores are natural components of the steppe biome (Chytrý, Horsák, et al., 2019; Guthrie, 2001; Pavelková Řičánková et al., 2018; Zimov et al., 2012). Large mammals that grazed the Pleistocene steppe of Central Europe (also called 'mammoth steppe'), including auroch (*Bos primigenius*), steppe bison (*Bison priscus*), wild horse (*Equus ferus*), woolly mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*; Guthrie, 1982; Kahlke, 2014), were later largely replaced by (mostly non-native) livestock. Currently, the most common species of wild mammal herbivores are deer (larger red deer; *Cervus elaphus*; and medium-sized roe deer; *Capreolus capreolus*), wild boar (*Sus scrofa*) and non-native mouflon (*Ovis gmelini musimon*). Herbivores remove a considerable portion of aboveground biomass through grazing. Apart from the direct effects on plant growth and reproduction through

tissue removal, grazing modifies site conditions, for example, by altering nutrient cycling (Archer & Detling, 1986; McNaughton, 1983; Hobbs, 1996; Hejcman et al., 2013) or the microclimate, which tends to become drier, warmer and less buffered against climatic extremes on grazed sites (De Frenne et al., 2019). In addition, biomass removal can weaken competition among plant species, particularly for light (Hairston et al., 1960; Hulme, 1996). The effects of grazing are often dynamic in time and space due to the seasonal migrations of herbivores and their preferences. In heterogeneous, semi-open landscape, such as forest–steppe, wild herbivores prefer to graze in open areas (Guthrie, 2001) and seek shelter in the shade of solitary trees, forest-patches or in depressions. This behaviour leads to systematic redeposition of nutrients (Hilder & Mottershead, 1963; McNaughton, 1983; Oesterheld et al., 1992), stronger pressure on tree recruits in open parts of the landscape, and thus stabilization of the forest–steppe habitat mosaic. Moreover, browsing of tree recruits can hinder the regeneration of trees within forest patches. The consequent reduction in canopy cover (Vera, 2000) allows grassland species to invade forest areas and eventually convert them to forest–steppe.

Wildfires occur frequently in natural ecosystems worldwide, from arid to humid regions (Bond et al., 2005; Bond & Keeley, 2005). Generally, the most flammable ecosystems are dry grasslands such as savanna with the accumulation of dry litter of fast-growing C4 grasses (Barbosa, 1999), and Mediterranean ecosystems with low rates of mineral decomposition (Morreno & Oechel, 1994; Keeley et al., 2011; Moreira et al., 2011). However, wildfires also occur frequently in steppe (Polchaninova et al., 2019) and forest–steppe (Shumilovskikh et al., 2018). In Central Europe, wildfires are generally considered an important ecological factor in the times before human settlement, and in the Mesolithic, they were largely replaced by human-induced fires (Kuneš et al., 2008). Nowadays, fire dynamics are completely suppressed in the Central European landscape, and the intentional use of fire in nature conservation is prohibited by law in most European countries. Nevertheless, if fire dynamics were still active in the contemporary Central European landscapes,

it is estimated that they could reduce forest area by about a quarter (Bond et al., 2005).

The aboveground biomass consumed by fire is converted into nutrient-rich ash. As a result, fire promotes nutrient-demanding communities in open forests or forest–steppe (Chytrý, Novák, et al., 2019). However, at drier sites, the fertilizing effect of fire-induced nutrient deposition on steppe ecosystems may be small (Polchaninova et al., 2019). Fire regimes (i.e. intensity, severity, frequency and seasonality of fires) depend on ecosystem properties (Bond & Keeley, 2005; Gill, 1975). A particularly important property is fuel load, such as dry litter biomass in open habitats and old tree trunks in forests (D'Odorico et al., 2012). Fuel accumulation is relatively slow in steppe, hence most fires are of low intensity and do not destroy all aboveground renewal buds of steppe species. As a result, fires in steppe have only moderate effects on steppe species composition. Polchaninova et al. (2019) reported that steppe communities fully recover within 1 year after fire, with no successional changes. However, even low-intensity fires can suppress tree regeneration and shrub encroachment (Joubert et al., 2012), while they rarely kill mature trees or shrubs (Görzen et al., 2019). In addition, tree recruitment is hindered by the drier microclimate at burned sites. Thus, similar to grazing, wildfires tend to stabilize the mosaic of forest and steppe habitats.

4 | EDAPHIC CONTROL – EXTRAORDINARY VEGETATION ON UNUSUAL SOILS

Soil substrate is generally considered a strong filter for plant community assembly at a fine scale (Chytrý et al., 2022; Siefert et al., 2012). Soils depend on bedrock, which affects their chemistry and structure. Some soil types developed on specific bedrocks (e.g. serpentine and dolomite) hinder the establishment of trees and thus contribute to landscape openness. The affinity of steppe to certain types of substrate and related soil types under macroclimatic conditions unsuitable for zonal steppe has long been recognized by plant ecologists (e.g. Rédei et al., 2003; Wendelberger, 1954; Zólyomi, 1942, 1953). There are three main ways by which substrate properties suppress forest development and succession: (1) reduction in water availability to plants, (2) toxicity and (3) alteration of competitive networks in plant communities resulting from a non-synchronized response of different plant species to soil chemistry.

Soil properties such as texture directly influence the amount of water available to plants (Fajmonová et al., 2020; Rusanov et al., 2012). In arid regions, fine-grained (silty or clayey) soils tend to be dry because water mostly runs off and evaporates before soaking into the soil (Walter, 1974). The macroclimate of Central Europe is, however, sufficiently humid to ensure rain-fed saturation even of fine-grained soils. Because of their high water-holding capacity (van den Berg et al., 1997; Brady & Weil, 1999), fine-grained soils offer a more stable water supply to plants under such a humid macroclimate. Deeper parts of these soils can retain water even during occasional dry periods, which supports colonization by shrubs and trees.

By contrast, coarse-grained and well-drained soils such as those on sand or dolomite are periodically very dry in the Central European climate (Zólyomi, 1953). Consequently, steppe patches predominantly occur on coarse-grained soils in Central Europe. Steppe is also supported by shallow soils, which tend to develop especially on steep slopes of poorly weathering solid rocks.

Soils derived from the weathering of ultramafic bedrock such as serpentinite and picrite have a high content of magnesium and heavy metals, which are directly toxic to some plant species (Kruckeberg, 2002; Roberts & Proctor, 1991). Plant growth is also limited by nutrient imbalance in such soils, especially high magnesium–calcium ratios, and low water-holding capacity. In Central Europe, serpentinite is relatively rare but hosts unique forest–steppe ecosystems with a considerable number of relict species (Kaplan, 2012). In the driest parts of Central Europe, high summer evapotranspiration causes the capillary rise of alkaline ions into the upper soil layers, leading to the formation of saline soils. Some types of such soils ('solonetz') favour the development of salt steppe, which is particularly well developed in the eastern part of the Great Hungarian Plain and partly on its western edge (Eliáš Jr et al., 2020). The high salinity contributes to suppressing succession and is considered an important driver of the landscape openness in the Carpathian Basin (Sümegi et al., 2012).

5 | TOPOGRAPHY – FINE-SCALE CONTROLS OF THE FOREST–STEPPE MOSAIC

Forest–steppe in topographically heterogeneous landscapes, such as in Central Asia, often show a distinct spatial pattern with forest on north-facing and steppe on south-facing slopes (Dulamsuren et al., 2005; Liu et al., 2015; Makunina, 2016). Hais et al. (2016) coined the term 'exposure-related forest–steppe' for such aspect-dependent mosaics, based on the terminology used in the Russian geobotanical literature (e.g. Ogureeva, 1980). In the hilly landscapes of Central Europe, steppe also predominantly occupy south-facing slopes (Chytrý et al., 2022; Futák, 1947; Illyés, 2007; Niklfeld, 1964; Sillinger, 1930; Slavíková, 1983; Figure 1), while slopes of other aspects are covered either by forest or by secondary, managed semi-dry grassland (Hegedüšová & Senko, 2011; Teleki et al., 2020). Despite these similarities between Central European and Central Asian forest–steppe, neither the term nor the concept of exposure-related forest–steppe has ever been used in Central Europe (compare Erdős et al., 2018). Here, we refine this concept by explicitly addressing the causal factors linking steppe occurrence to topography.

5.1 | Microclimate

Climate data are usually recorded at standard heights above the ground surface and on sites not affected by local microclimatic effects. Conditions recorded in this way can deviate considerably from those at the ground level, which are most important for herbaceous

plants and the recruits of shrubs and trees (Bütikofer et al., 2020; Stoutjesdijk & Barkman, 2014). For example, mean summer ground temperatures can differ from the mean summer air temperatures by up to 5°C (Bramer et al., 2018; measured in the Alps and Scandinavia, 46°N and 78°N), and temperature extremes may be either buffered or amplified (Maclean, 2020). Deviations in temperature maxima are even more pronounced: Jakucs (1972; measured in Hungary, 46°N) found that the daily maximum summer air temperature in a dry grassland patch on a gentle south-facing dolomite slope was about 29°C, while the maximum ground temperature was 15°C higher. The actual difference between ground and air temperature depends mainly on insolation, which, in turn, is modulated by the slope and aspect of the receiving ground surface, especially under clear skies (McCune & Keon, 2002). The effects of radiation income on ground temperature are then amplified by lower wind speeds and hence reduced thermal mixing near the ground (Bütikofer et al., 2020). The influence of incident solar radiation on ground temperatures leads to a pronounced microclimatic difference between south-facing and north-facing slopes in temperate areas of the northern hemisphere, such as in Central Europe (Tichý, 1999). Mean annual temperatures can differ by up to 2–3°C on a single hill, corresponding to approximately 500 m of elevation or 5° of latitude (Rorison et al., 1986; Bennie et al., 2008; measured in England, 50°N and 53°N). Similar differences have been found in exposure-related forest–steppe in Transbaikalia (Anenkhonov et al., 2020, measured in Buryatia, Russia, between 50°N and 53°N). However, the differences between south-facing and north-facing slopes can depend on the season: while the south-facing slopes exhibit higher temperatures than the north-facing slopes in summer, this pattern can be reversed in winter (Slavíková, 1983). The likely cause is a feedback between vegetation and microclimate: the more productive grasslands on north-facing slopes produce more litter, which buffers temperature extremes (Facelli & Pickett, 1991). In addition, snow persists longer on north-facing slopes in winter, further mitigating temperature variability.

Topography, in combination with prevailing wind direction, may also account for differences in precipitation totals. For an isolated volcanic hill in Bohemia, precipitation totals were approximately 30% lower on west-facing, wind-exposed slopes than on east-facing slopes, probably because the raindrops were blown away from the windward side of the hill (Slavíková, 1983). This finding is particularly interesting because a reverse pattern of wetter windward slopes is usually observed on a coarser scale in large mountain ranges (Colle, 2004). More importantly, topography co-determines water retention in soils. First, steep slopes tend to be drier than gentle slopes because surface run-off is faster (Bramer et al., 2018; with modifications in concave vs. convex relief locations, Wilcox et al., 2003). Second, higher ground temperatures on south-facing slopes increase evaporation rates. As a consequence, south-facing slopes were measured to be 15% drier in summer than north-facing slopes, and the difference was even greater in winter (Slavíková, 1983).

Within the forest–steppe biome, topographic modification of temperature and water balance can create a micro-mosaic of climates typical of either forest or steppe biomes. Consequently, plant species and vegetation types are sorted by topography (Moeslund et al., 2013; Tichý, 1999). South-facing slopes favour plant growth earlier in the growing season (Chytrý & Tichý, 1998; Endresz et al., 2005) but they become a very stressful micro-environment in summer when most of the aboveground biomass dies. Moreover, differences in soil moisture affect nutrient turnover and balance, with drier, south-facing slopes generally being less productive (Bennie et al., 2008; Boyko, 1947; Olivero & Hix, 1998). Harsh conditions on south-facing slopes disfavour tree recruitment. In contrast, the more productive vegetation on the wetter, north-facing slopes additionally buffers temperature extremes under the canopy (De Frenne et al., 2019; Jakucs, 1972), resulting in a positive feedback loop by reducing evaporation, enhancing water retention and further increasing vegetation productivity.

5.2 | Soil processes

Soil formation (pedogenesis) is a complex process that depends, both directly and indirectly, on topography. The main indirect effects result from feedback loops between microclimate, soil and vegetation. Apart from the consequences for soil moisture and nutrient supply discussed above, the more stable microclimate on north-facing slopes buffers the effects of weathering and erosion, and in turn, supports the development of more productive vegetation with more decomposing biomass (Jakucs, 1972), which further promotes pedogenesis (Sabau & Morar, 2011).

In addition, the slope aspect co-determined accumulation rates of aeolian sediments, and hence the build-up of loess, during cold phases of the Pleistocene. In Central Europe, west–east wind directions predominated during the Quaternary, resulting in the highest accumulation rates on east-facing slopes (Lisá & Uher, 2006). Furthermore, slope inclination and aspect influence the extent of rock weathering and soil erosion (Slavíková, 1983; Burnett et al., 2008). In this context, topographic control interacts with the type of bedrock. Soils containing gravelly to sandy particles of weathered bedrock, such as those on dolomite, are generally more prone to microscale erosion than heavier soils, such as those on limestone. As noted above, the combination of low water-holding capacity (e.g. on dolomitic soils) and high erosion rates on steep slopes may result in suppression of forest succession even under a moderately humid macroclimate (Feng et al., 2020; Zólyomi, 1953).

Topography and bedrock may also hinder forest succession through landslides, which are well documented in the Carpathian Flysch Belt (Pánek & Hradecký, 2016). Flysch consists of layered sediments that differ in their chemistry, physical structure and water permeability. Therefore, landslides easily occur in sloping terrain after heavy rainfall. The importance of landslides for the preservation of steppe flora in the Carpathian Flysch Belt is under debate. However, landslides might have a strong impact on the forest–steppe mosaic in the river valleys around the Miocene stratovolcanoes in southern Slovakia and northern Hungary, where erosion exposed layered pyroclastic and epiclastic sediments of volcanic conglomerates (compare Chernyshev et al., 2013).

5.3 | Human impact

Human impact has pronouncedly altered the landscapes of Central Europe since the Neolithic. Land use and its intensity have varied over time (Kaplan et al., 2009), but they have always reflected the local topography. In forest–steppe regions, south-facing slopes, covered with either steppe patches or open woodlands, were frequently grazed. The low productivity of these dry habitats only allowed low livestock densities, which had little effect on the species composition of grassland plant communities. Livestock grazing replaced the natural consumer-control of forest succession and thus contributed to the maintenance of landscape openness (Dúbravková & Hajnalová, 2012). In open woodlands, grazing helped prevent canopy closure and favoured light-demanding forest–steppe plants in the understory. In contrast to south-facing slopes, more productive vegetation was managed more intensively on other slope aspects or in flat terrain. Large areas of forest, especially in plains, were cleared and converted into mesic hay meadows or grazed semi-dry grasslands and later, especially in the 18th century, into crop fields (Hejcman et al., 2013; Molnár et al., 2012). The coverage of forest continuously decreased until the 18th century and the remaining forest areas, mostly in colline landscapes, were frequently coppiced and grazed (Szabó et al., 2018; Szabó & Hédl, 2013).

The shift away from traditional management and the intensification of agriculture in the 20th century (Dúbravková & Hajnalová, 2012; Molnár et al., 2012) led to profound landscape changes (e.g. Miklín & Hradecký, 2016) and local to regional species extinctions (e.g. Reich et al., 2020). Again, topography co-determined these changes. Intensification focused on terrain that was easily accessible to agricultural machinery. In contrast, poorly accessible sites such as steeper slopes, including those covered by steppe patches, have often been completely abandoned since the 1950s. Nowadays, such sites are partly managed for conservation purposes (e.g. Elias & Tischew, 2016). The associated changes in traditional forest management, such as the abandonment of coppicing and forest grazing, led to the successional changes of forests into darker and more homogeneous stands unsuitable for forest–steppe and meadow-steppe species (Roleček et al., 2017; Vojík & Boublík, 2018). These processes magnified the structural and compositional differences between open and forested patches in the forest–steppe mosaic.

5.4 | Empirical evidence for the interplay of macroclimate, topography and bedrock

To explore the interactive effect of macroclimate and topography on the formation of forest–steppe, we plotted 108 Central European forest–steppe sites (see Appendices S1 and S2 for a list and details of site selection) in a macroclimate-topography scatterplot (Figure 3). We represented macroclimate by growing season precipitation totals (May–September; also used by Hais et al., 2016 for modelling forest–steppe patterns in southern Siberia). Climate data were downloaded

from the CHELSA database (Karger et al., 2017) and downscaled to 100-m resolution using methods described by Dullinger et al. (2012). Topography was characterized by the terrain ruggedness index (Riley et al., 1999) calculated from a digital elevation model at 25-m resolution (European Environment Agency, 2019). Individual sites occupy a triangle approximately below the diagonal (in the lower left sector of the plot), suggesting that topographical variation is responsible for the occurrence of steppe patches in relatively mesic and predominantly forested regions. In other words, hilly terrain extends the suitable area for forest–steppe habitats towards wetter macroclimates.

To elucidate the importance of substrate, we further plotted the substrate types (dolomite, limestone, deep soil, sandy, serpentine and volcanic) of all 108 sites (Figure 3). However, we were unable to explore the full interaction between substrate, macroclimate and topography because some substrate types were spatially clustered in areas with specific climates. Loess deposits and especially sandy deposits are well developed only in the driest areas, and volcanic bedrock is restricted within the study area to warm and dry regions of southern Slovakia and northern Hungary, where otherwise flat landscapes are punctuated by isolated volcanic hills and mountains. Nevertheless, we found that in the wettest subset of our sites (i.e. those with a mean precipitation of more than 400 mm in the growing season), forest–steppe develops only on very steep slopes on calcareous bedrocks. This is especially true for dolomite and less so for limestone karst areas (Slovak Karst and Aggtelek Karst). The restriction of forest–steppe to dolomite slopes in wetter macroclimates is consistent with the earlier assumptions of Zólyomi (1953), who considered steppe on dolomite as naturally open habitat due to the low water-holding capacity and erosion susceptibility of dolomitic soils. However, although dolomites, along with the rare serpentines, are arguably the most extreme substrate in our dataset, they show a similar pattern to the overall dataset: while under dry macroclimates forest–steppe on dolomites occurs in landscapes with both low and high topographic heterogeneity, under a wetter macroclimate, it is restricted to sites with high topographic heterogeneity and steep south-facing slopes.

6 | A SYNTHETIC MODEL

6.1 | The concept

Based on the empirical evidence presented in Figure 3, we propose a conceptual model (Figure 4) that describes how the interaction of various factors controls the distribution and structure of forest–steppe landscapes. The model is based on the idea that the key factor limiting the development of shrub and tree vegetation in dry landscapes is a stable water supply (Anenkhonov et al., 2015; Liu et al., 2012; Slavíková, 1983; Tercero-Bucardo et al., 2007; Walter, 1974). Water supply is jointly controlled by (a) macroclimate, which determines large-scale patterns of precipitation and evaporation, (b) consumers, which reduce biomass, thus increasing evaporation and moisture loss from the upper soil layers (Bond & Keeley, 2005; Vera, 2000)
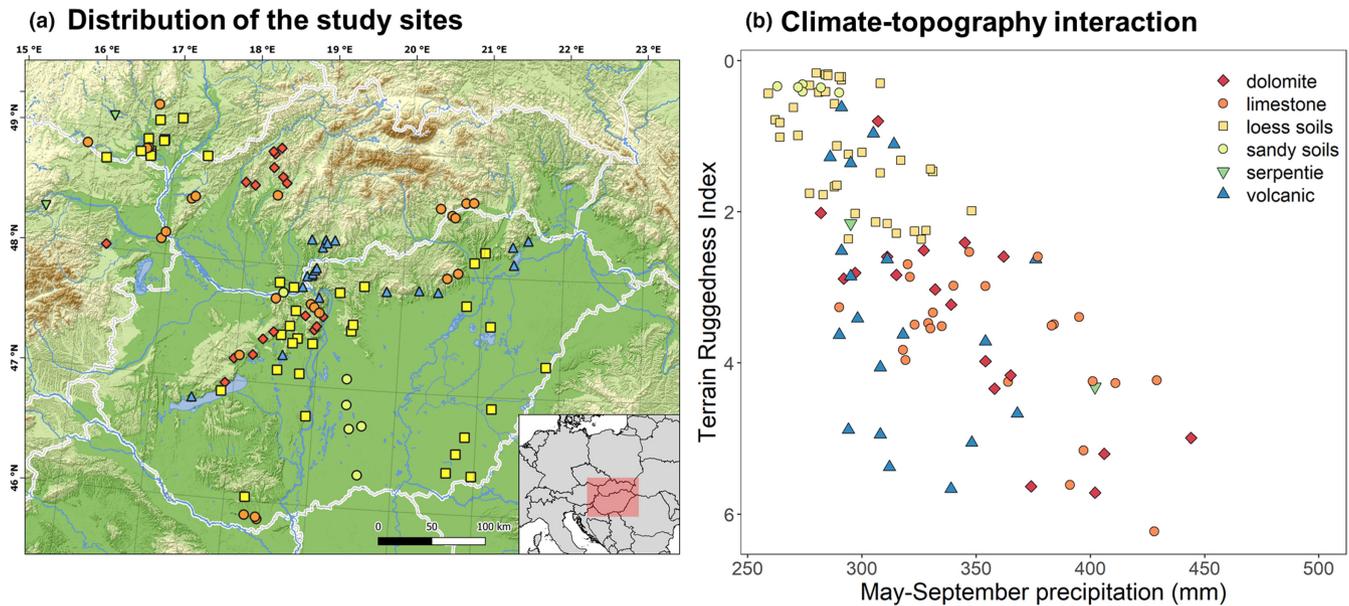
(a) Distribution of the study sites

(b) Climate-topography interaction

FIGURE 3 (a) The distribution of 108 forest–steppe sites in the Carpathian Basin and its northern margins in Austria (*n* = 3), the Czech Republic (*n* = 16), Hungary (*n* = 65) and Slovakia (*n* = 24). Details of individual sites are shown in Appendix S1. Note that in the current cultural landscape of this area, the lowlands (green) are largely open landscapes, whereas the uplands are covered by an anthropogenic mosaic of forest and open land. (b) Scatterplot of the 108 forest–steppe sites along a climatic and topographic gradient. The area macro-climatically suitable for forest–steppe is extended by increasing topographic heterogeneity. The subgroup of loess soils also includes other fine-grained, deep soils
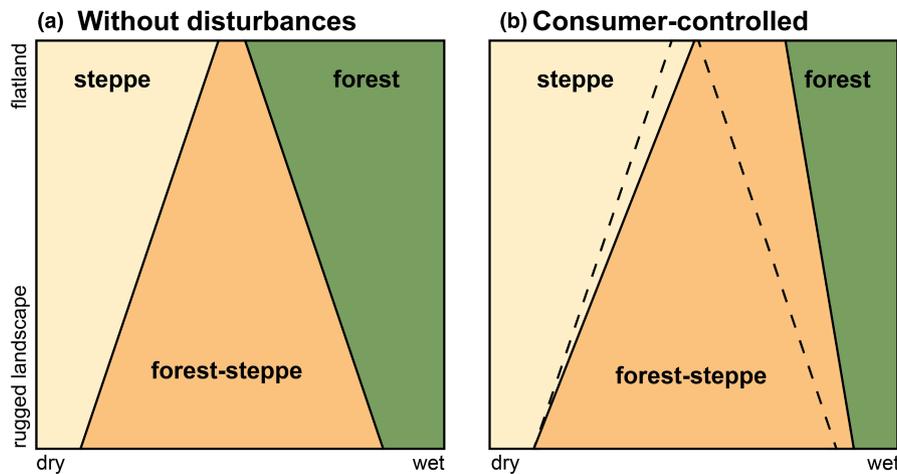
(a) Without disturbances

(b) Consumer-controlled

FIGURE 4 A synthetic model showing how macroclimate and topography co-determine the distribution of forest–steppe in relation to neighbouring biomes without (a) and with (b) consumer control. The macroclimatic niche of forest–steppes broadens with terrain ruggedness as topographic variation creates a mosaic of patches micro-climatically suitable for either forest or steppe. Consumer control, that is, grazers and fires, broadens the macroclimatic niche of forest–steppe towards wetter conditions on flat terrain, but has less influence on the width of the macroclimatic niche in rugged landscapes where it tends to stabilize the topographically determined forest–steppe mosaic. For more information, see text. The dashed line in panel (b) corresponds to the boundaries in panel (a)

and (c) local water balance, which is regulated by microclimate and soils, and thus indirectly by topography. We believe that this conceptual model is applicable to both Central European forest–steppe and similar biomes in other parts of the world, especially at higher latitudes where topographically driven differences between slopes with different aspects are more pronounced than near the equator. Although the precise macroclimatic (and topographic) boundaries of forest–steppe may vary from region to region depending on regional

species pools and their specific adaptations, the overall pattern is probably universal.

Forest–steppe landscapes combine two ecosystems that prevail in different biomes under different macroclimatic conditions. The main reason for their co-occurrence is the topographically determined, fine-scale modification of microclimatic conditions near the macroclimatic boundary between the two biomes. As a corollary, the magnitude of topographic variation in a region, that is, the degree of

terrain ruggedness, determines the width of the realized macroclimatic niche of the forest–steppe in that region, and thus probably also its geographical extent (Figure 5). In plain terrain, forest–steppe develops within a narrow macroclimatic window where soil conditions, minute differences in relative ground elevation, consumer control or stochastic events determine the mosaic of the two vegetation types. In hilly landscapes, the macroclimatic niche of forest–steppe becomes wider because topographic variation guarantees the representation of both forest and steppe, promoting microclimates in the same landscape even if the macroclimate is not suitable for either steppe or forest. In other words, in humid regions, where forest is the zonal vegetation, high topographic heterogeneity supports the occurrence of steppe patches, especially on south-facing slopes. Conversely, in dry regions, where steppe represents the zonal vegetation, forest patches occur mainly in less dry parts of the terrain, for example on north-facing slopes or in terrain depressions (Figure 5). The co-occurrence of these two ecosystems in a topographically diverse landscape is further stabilized by positive habitat-microclimate feedback loops (Wilson & Agnew, 1992). The relatively stable microclimate of tree undergrowth (De Frenne et al., 2019) supports shrub and tree recruitment. In contrast, treeless grasslands on south-facing slopes experience a dry microclimate that is unfavourable for tree recruitment and forest succession. In preserved natural forest–steppe landscapes, these two extremes are often linked by gradual transitions. Landscape structure along such a gradient was studied in southern Siberia (Hais et al., 2016), but such landscapes also occur, for example, in the Pacific Northwest of North America (Kerns et al., 2018) and in Patagonia (Anchorena & Cingolani, 2002).

In topographically uniform landscapes, consumers make an important contribution to the maintenance of forest–steppe mosaics. However, we hypothesize that their importance decreases with increasing topographic heterogeneity. This is because the habitat-microclimate feedback loops are more pronounced in topographically diverse landscapes, affecting population size and behaviour of consumers. In topographically heterogeneous landscapes dominated by steppe, wild herbivores and livestock feed mainly on grasslands and tend to avoid forested areas. In addition, intensive grazing reduces the frequency of grassland fires due to the lack of flammable

biomass (D'Odorico et al., 2012). Neither wild herbivores nor fire activity therefore significantly alters the microclimatically determined forest–steppe mosaic, although they tend to stabilize existing patterns. Conversely, in predominantly forested landscapes, a lower productivity of forest undergrowth keeps herbivore numbers low. Although the wild herbivores tend to concentrate on small steppe patches, they usually do not enlarge grassland at the expense of forests but, again, stabilize the boundaries of the forest–steppe mosaic. As the macroclimate is relatively humid in those areas, wildfires are also rare and contribute less to landscape openness. To illustrate the interaction between macroclimate, topography, and consumer control, we present two versions of our conceptual model, one without (Figure 4a) and one with (Figure 4b) assumed consumer control. These two models represent extreme situations, while reality is usually somewhere in between. Some of the Central European forest–steppe sites, especially those in the lowlands, indeed require some degree of consumer control, provided either by wild herbivores or by conservation management.

6.2 | Applying the model to understand past vegetation processes

Although topographical variation may expand the macroclimatic niche of forest–steppe, such habitat mosaics cannot develop beyond certain macroclimatic boundaries (Figure 5). Consequently, past climatic changes led to fluctuating geographical ranges of forest, steppe and their mosaics across Central Europe. While the cold and dry periods of the Pleistocene favoured the occurrence of steppe, the warm and humid climate of the Holocene supported the spread of forest. Unlike macroclimate, however, topography is much more stable through time, and our model allows predictions of how topography modulated climate-induced fluctuations of forest and steppe. In topographically uniform landscapes, past transitions between biomes may have been complete, for example, the vast treeless steppe of the Pleniglacial (between ~73 and 13 thousand years ago) was replaced by closed forest of the Mid-Holocene. Conversely, in rugged landscapes, the presence of sites with different microclimatic conditions probably promoted the
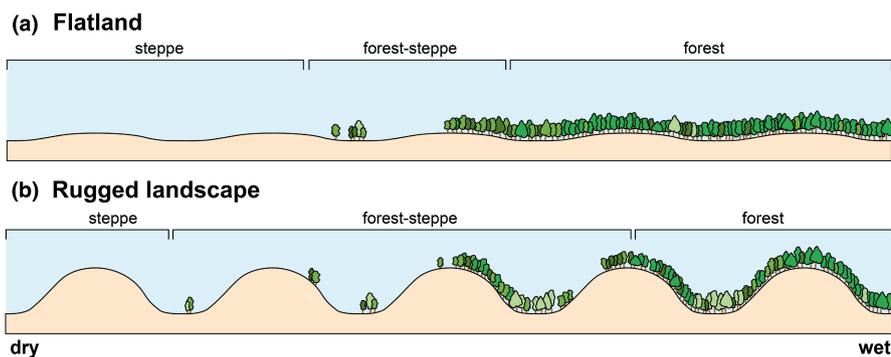

FIGURE 5 Topographic effect on landscape openness. (a) On flatlands, the coexistence of forest and steppe is confined to a relatively narrow zone. (b) Rugged landscapes support an extended zone of topographically controlled mosaic of forests on north-facing slopes and steppes on south-facing slopes ('exposure-related forest–steppe')

coexistence of forest and steppe patches. The co-occurrence of such contrasting habitats likely buffered the effects of climate change on biodiversity and stabilized the species composition of regional meta-communities (i.e. a set of communities in a landscape, linked by dispersal of individuals or propagules). Indeed, the scattered reports of the presence of trees in Central Europe during the Pleniglacial mostly relate to rugged landscapes (Willis & van Andel, 2004). Conversely, the survival of steppe patches in the humid Mid-Holocene (Feurdean et al., 2015; Pokorný et al., 2015) is probably also due to such rugged landscapes. In particular, steppe species might have survived this wet period in the lower mountain ranges around the Pannonian Basin (Willner et al., 2021). In some cases, human influence might have been of predominant importance (Novák et al., 2019). In recent years, modern palaeoecological methods have steadily advanced the knowledge of landscape history and enabled the compilation of synthetic studies dealing with past landscape structures of Central Europe (e.g. Divíšek et al., 2020; Jamrichová et al., 2017; Magyari et al., 2010; Willis & van Andel, 2004). The same questions are also addressed by phylogeographical analyses (Kajtoch et al., 2016; Kirschner et al., 2020; Willner et al., 2021). These studies support the hypothesis that forest–steppe mosaics have survived in several regions of Central Europe during periods of both arid and humid climatic conditions since the last ice age. We propose our synthetic model as a framework to understand why and where such survival was possible.

7 | CONCLUSIONS

Forest–steppe is a transitional ecosystem, which enhances the species richness of regional metacommunities through the coexistence of contrasting habitats. As such, it is particularly important for biodiversity conservation. Its development and maintenance depend on an intricate combination of factors acting and interacting at different spatial scales. These factors can be thrown out of balance by human land use, for example, overgrazing or pasture abandonment. However, the generic link between forest–steppe extent and topographic heterogeneity that we propose in our conceptual model depends largely on the interaction of macro- and microclimate and is less sensitive to moderate changes in land management. With respect to future climate change, we learn from the environmental history of Central Europe that forest–steppe has been quite resistant to changes in macroclimate, at least in topographically heterogeneous landscapes. Greater topographic heterogeneity results in greater microclimatic variability, which can support both steppe and forest in a single forest–steppe landscape. However, the current fragmentation of natural and semi-natural habitats due to more intensive human land use, such as conversion to arable land or urbanization, may make this habitat type and its biota more sensitive to macroclimatic changes. Regarding the direct effects of a warmer climate, it seems intuitive that higher temperatures, resulting in higher evaporation, will shift the balance between forest and steppe towards more open areas and make flat terrain more suitable for steppe species now restricted to the driest microclimates on steep slopes. However, a

drier macroclimate might also lead to the decline of some species currently occurring in steppe patches and their retreat to forest ecotones or micro-climatically less extreme sites. A better understanding of forest–steppe landscapes will therefore be crucial for the conservation of their biodiversity in the future. Our conceptual model provides a basis for such understanding, but further research is certainly needed to improve our knowledge of community-level processes as well as biodiversity and landscape changes in forest–steppes and similar topography-dependent mosaic landscapes.

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REFERENCES

Aleman, J. C., & Staver, A. C. (2018). Spatial patterns in the global distribution of savanna and forest. Global Ecology and Biogeography, 27, 792–803. https://doi.org/10.1111/geb.12739

Anchorena, J., & Cingolani, A. (2002). Identifying habitat types in a disturbed area of the forest-steppe ecotone of Patagonia. Plant Ecology, 158, 97–112. https://doi.org/10.1023/A:1014768822737

Anenkhonov, O. A., Korolyuk, A. Y., Sandanov, D. V., Liu, H., Zverev, A. A., & Guo, D. (2015). Soil-moisture conditions indicated by field-layer plants help identify vulnerable forests in the forest-steppe of semi-arid southern Siberia. Ecological Indicators, 57, 196–207. https://doi.org/10.1016/j.ecolind.2015.04.012

Anenkhonov, O. A., Sandanov, D. V., Liu, H., Korolyuk, A. Y., Xu, C., Guo, W., Zverev, A. A., Naidanov, B. B., & Chimitov, D. G. (2020). Using data on the thermal conditions of soils for the differentiation of vegetation in the exposure-related forest-steppe of Transbaikalia. Contemporary Problems of Ecology, 13, 522–532. https://doi.org/10.1134/S1995425520050029

Archer, S., & Detling, J. K. (1986). Evaluation of potential herbivore mediation of plant water status in a North American mixed-grass prairie. Oikos, 473, 287–291. https://doi.org/10.2307/3565439

Barbosa, P. M. (1999). An assessment of fire in Africa (1981–1991): Burnt areas, burnt biomass and atmospheric emissions. *Global Biochemical Cycles*, 13, 933–950. https://doi.org/10.1029/1999GB900042

Barros, C., Thuiller, W., & Münkemüller, T. (2018). Drought effects on the stability of forest-grassland ecotones under gradual climate change. *PLoS ONE*, 13, e0206138. https://doi.org/10.1371/journal.pone.0206138

Behling, H., Pillar, V. D., Müller, S. C., & Overbeck, G. E. (2007). Late-Holocene fire history in a forest-grassland mosaic in southern Brasil: Implications for conservation. *Applied Vegetation Science*, 10, 81–90. https://doi.org/10.1658/1402-2001(2007)10[81:LFHIAF]2.0.CO;2

Bennie, J., Huntley, B., Wiltshire, A., Hill, M. O., & Baxter, R. (2008). Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling*, 216, 47–59. https://doi.org/10.1016/j.ecolmodel.2008.04.010

Bohn, U., Neuhäusl, R., Gollub, G., Hettwer, C., Neuhäuslová, Z., Raus, T., Schlüter, H., & Weber, H. (2004). *Map of the natural vegetation of Europe*. Landwirtschaftsverlag.

Bond, W. J., & Keeley, J. E. (2005). Fire as a global "herbivore": The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, 20, 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bond, W. J., Woodward, F. I., & Midgley, G. F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, 165, 525–538. https://doi.org/10.1111/j.1469-8137.2004.01252.x

Boyko, H. (1947). On the role of plants as quantitative climate indicators and the geo-ecological law of distribution. *Journal of Ecology*, 35, 138–157. https://doi.org/10.2307/2256504

Brady, N. C., & Weil, R. R. (1999). *The nature and properties of soils* (12th ed.). Prentice-Hall, Inc.

Bramer, I., Anderson, B. J., Bennie, J., Bladon, A. J., De Frenne, P., Hemming, D., … Gillingham, P. K. (2018). Advances in monitoring and modelling climate at ecologically relevant scales. *Advances in Ecological Research*, 58, 101–161. https://doi.org/10.1016/bs.aecr.2017.12.005

Breckle, S. W. (2002). *Walter's vegetation of the earth*. Springer.

Burnett, B. N., Meyer, G. A., & McFadden, L. D. (2008). Aspect-related microclimatic influences on slope forms and processes northeastern Arizona. *Journal of Geophysical Research: Earth Surface*, 113, 1–18. https://doi.org/10.1029/2007JF000789

Bütikofer, L., Anderson, K., Bebber, D. P., Bennie, J. J., Early, R. I., & Maclean, I. M. D. (2020). The problem of scale in predicting biological responses to climate. *Global Change Biology*, 26, 6657–6666. https://doi.org/10.1111/gcb.15358

Cardoso, A. W., Oliveras, I., Abernethy, K. A., Jeffery, K. J., Glover, S., Lehmann, D., Edzang Ndong, J., White, L. J., Bond, W. J., & Malhi, Y. (2021). A distinct ecotonal tree community exists at central African forest-savanna transitions. *Journal of Ecology*, 109, 1170–1183. https://doi.org/10.1111/1365-2745.13549

Chernyshev, I. V., Konečný, V., Lexa, J., Kovalenker, V. A., Jeleň, S., Lebedev, V. A., & Goltsman, Y. V. (2013). K-Ar and Rb-Sr geochronology and evolution of the Štiavnica stratovolcano (Central Slovakia). *Geologica Carpathica*, 64, 327–351. https://doi.org/10.2478/geoca-2013-0023

Chytrý, M. (2012). Vegetation of The Czech Republic: Diversity, ecology, history and dynamics. *Preslia*, 84, 427–504 http://www.preslia.cz/P123Chytry.pdf

Chytrý, K., Novák, P., Kalníková, V., Večeřa, M., Prokešová, H., Dřevojan, P., & Chytrý, M. (2019). Dry grassland vegetation in the Transcarpathian Lowland (western Ukraine). *Tuexenia*, 39, 335–355. https://doi.org/10.14471/2019.39.009

Chytrý, M., Horsák, M., Danihelka, J., Ermakov, N. B., German, D. A., Hájek, M., Hájková, P., Koci, M., Kubešová, S., Lustyk, P., Nekola, J. C., Pavelková Řičánková, V., Preislerová, Z., Resl, P., & Valachovič, M. (2019). A modern analogue of the Pleistocene steppe-tundra ecosystem in southern Siberia. *Boreas*, 48, 36–56. https://doi.org/10.1111/bor.12338

Chytrý, K., Prokešová, H., Duchoň, M., Grulich, V., Chytrý, M., & Divíšek, J. (2022). Substrate associated biogeographical patterns in the north-western Pannonian forest-steppe. *Preslia* [accepted], 94(2).

Chytrý, M., & Tichý, L. (1998). Phenological mapping in a topographically complex landscape by combining field survey with an irradiation model. *Applied Vegetation Science*, 1, 225–232. https://doi.org/10.2307/1478952

Chytrý, M., Tichý, L., Hennekens, S. M., Knollová, I., Janssen, J. A. M., Rodwell, J. S., Peterka, T., Marcenò, C., Landucci, F., Danihelka, J., Hájek, M., Dengler, J., Novák, P., Zukal, D., Jiménez-Alfaro, B., Mucina, L., Abdulhak, S., Aćić, S., Agrillo, E., & Schaminée, J. H. J. (2020). EUNIS habitat classification: Expert system, characteristic species combinations and distribution maps of European habitats. *Applied Vegetation Science*, 23, 648–675. https://doi.org/10.1111/avsc.12519

Colle, B. A. (2004). Sensitivity of orographic precipitation to changing ambient conditions and terrain geometries: An idealized modeling perspective. *Journal of the Atmospheric Sciences*, 61, 588–606. https://doi.org/10.1175/1520-0469(2004)061<0588:SOOPTC>2.0.CO;2

Dabkowski, J., Frodlová, J., Hájek, M., Hájková, P., Petr, L., Fiorillo, D., Dudová, L., & Horsák, M. (2019). A complete Holocene climate and environment record for the Western Carpathians (Slovakia) derived from a tufa deposit. *Holocene*, 29, 493–504. https://doi.org/10.1177/0959683618816443

De Frenne, P., Zellweger, F., Rodríguez-Sanchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology and Evolution*, 3, 744–749. https://doi.org/10.1038/s41559-019-0842-1

Divíšek, J., Hájek, M., Jamrichová, E., Petr, L., Večeřa, M., Tichý, L., Willner, W., & Horsák, M. (2020). Holocene matters: Landscape history accounts for current species richness of vascular plants in forests and grasslands of eastern Central Europe. *Journal of Biogeography*, 47, 721–735. https://doi.org/10.1111/jbi.13787

D'Odorico, P., Okin, G. S., & Bestelmeyer, B. T. (2012). A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecohydrology*, 5, 520–530. https://doi.org/10.1002/eco.259

Dúbravková, D., & Hajnalová, M. (2012). The dry grasslands in Slovakia: History, classification and management. In M. J. A. Werger & M. A. van Staalduinen (Eds.), *Eurasian steppes: Ecological problems and livelihoods in a changing world* (pp. 253–271). Springer. https://doi.org/10.1007/978-94-007-3886-7_8

Dulamsuren, C., Hauck, M., & Mühlenberg, M. (2005). Vegetation at the taiga forest-steppe borderline in the western Khentey Mountains, northern Mongolia. *Annales Botanici Fennici*, 42, 411–426 https://www.jstor.org/stable/4620445

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnböck, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J. C., Psomas, A., Schmatz, D. R., Šilc, U., … Hülber, K. (2012). Extinction debt of high-mountain plants under 21st-century climate warming. *Nature Climate Change*, 2, 619–622. https://doi.org/10.1038/nclimate1514

Elias, D., & Tischew, S. (2016). Goat pasturing – A biological solution to counteract shrub encroachment on abandoned dry grasslands in Central Europe? *Agriculture, Ecosystems & Environment*, 234, 98–106. https://doi.org/10.1016/j.agee.2016.02.023

Eliáš, P., Jr., Dítě, D., & Dítě, Z. (2020). Halophytic vegetation in the Pannonian Basin: Origin, syntaxonomy, threat, and conservation. In M. N. Grigore (Ed.), *Handbook of halophytes* (pp. 1–38). Springer. https://doi.org/10.1007/978-3-030-17854-3_11-1

Endresz, G., Zöld-Balogh, Á., & Kalapos, T. (2005). Local distribution pattern of *Brachypodium pinnatum* (Poaceae) – Field experiments in xeric loess grassland in N. Hungary. *Phyton – Annales Rei Botanicae*, 45, 249–265. https://www.zobodat.at/pdf/PHY_45_2_0249-0265.pdf

Erdős, L., Ambarlı, D., Anenkhonov, O. A., Bátori, Z., Cserhalmi, D., Kiss, M., Kröel-Dulay, G., Liu, H., Magnes, M., Molnár, Z., Naqinezhad, A., Semenishchenkov, Y. A., Tölgyesi, C., & Török, P. (2018). The edge of two worlds: A new review and synthesis on Eurasian forest-steppes. *Applied Vegetation Science*, *21*, 345–362. https://doi.org/10.1111/avsc.12382

Erdős, L., Tölgyesi, C., Horzse, M., Tolnay, D., Hurton, Á., Schulz, 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

European Environment Agency (2019) Copernicus Programme. https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1 .

Facelli, J. M., & Pickett, S. T. A. (1991). Plant litter: Light interception and effects on an old-field plant community. *Ecology*, *72*, 1024–1031. https://doi.org/10.2307/1940602

Fajmonová, Z., Hájková, P., & Hájek, M. (2020). Soil moisture and a legacy of prehistoric human activities have contributed to the extraordinary plant species diversity of grasslands in the white Carpathians. *Preslia*, *92*, 35–56. https://doi.org/10.23855/preslia.2020.035

Fekete, G., Somodi, I., & Molnár, Z. (2010). Is chorological symmetry observable within the forest steppe biome in Hungary? A demonstrative analysis of floristic data. *Community Ecology*, *11*, 140–147. https://doi.org/10.1556/comec.11.2010.2.2

Feng, S., Wu, L., Liang, B., Wang, H., Liu, H., Zhu, C., & Li, S. (2020). Forestation does not necessarily reduce soil erosion in a karst watershed in southwestern China. *Progress in Physical Geography*, *45*, 1–16. https://doi.org/10.1177/0309133320958613

Feurdean, A., Marinova, E., Nielsen, A. B., Liakka, J., Veres, D., Hutchinson, S. M., Braun, M., Timar-Gabor, A., Astalos, C., Mosburgger, V., & Hickler, T. (2015). Origin of the forest steppe and exceptional grassland diversity in Transylvania (Central-Eastern Europe). *Journal of Biogeography*, *42*, 951–963. https://doi.org/10.1111/jbi.12468

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S. M., & Hickler, T. (2018). Biodiversity-rich European grasslands: Ancient, forgotten ecosystems. *Biological Conservation*, *228*, 224–232. https://doi.org/10.1016/j.biocon.2018.09.022

Fischer, F. M., Chytrý, K., Těšitel, J., Danihelka, J., & Chytrý, M. (2020). Weather fluctuations drive short-term dynamics and long-term stability in plant communities: A 25-year study in a central European dry grassland. *Journal of Vegetation Science*, *31*, 711–721. https://doi.org/10.1111/jvs.12895

Frelich, L. E., & Reich, P. B. (2010). Will environmental changes reinforce the impact of global warming on the prairie-forest border of Central North America? *Frontiers in Ecology and the Environment*, *8*, 371–378. https://doi.org/10.1890/080191

Fuťák, J. (1947). *Xerotermná vegetácia skupiny Kňažieho stola*. Spolok svätého Vojtecha.

Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science*, *18*, 571–582. https://doi.org/10.1111/j.1654-1103.2007.tb02571.x

Gill, A. M. (1975). Fire and the Australian flora: A review. *Australian Forestry*, *38*, 4–25. https://doi.org/10.1080/00049158.1975.10675618

Görzen, E., Borisova, K., Fenesi, A., Ruprecht, E., & Donath, T. (2019). Effects of woody species encroachment and fire on vegetation and the soil seed bank in dry grasslands of Transylvania. *Applied Vegetation Science*, *22*, 409–422. https://doi.org/10.1111/avsc.12435

Gowda, J. H., Kitzberger, T., & Premoli, A. C. (2012). Landscape responses to a century of land use along the northern Patagonian forest-steppe transition. *Plant Ecology*, *213*, 259–272. https://doi.org/10.1007/s11258-011-9972-5

Gradmann, R. (1933). Die Steppenheidetheorie. *Geographische Zeitschrift*, *39*, 265–278.

Guthrie, R. D. (1982). Mammals of the mammoth steppe as paleoenvironmental indicators. In D. M. Hopkins, J. V. Matthews, Jr., C. E. Schweger, & S. B. Young (Eds.), *Paleoecology of Beringia* (pp. 307–326). Academic Press. https://doi.org/10.1016/B978-0-12-355860-2.50030-2

Guthrie, R. D. (2001). Origin and causes of the mammoth steppe: A story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews*, *20*, 549–574. https://doi.org/10.1016/S0277-3791(00)00099-8

Habel, J. C., Dengler, J., Janišová, M., Török, P., Wellstein, C., & Wiezik, M. (2013). European grassland ecosystems: Threatened hotspots of biodiversity. *Biodiversity and Conservation*, *22*, 2131–2138. https://doi.org/10.1007/s10531-013-0537-x

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *American Naturalist*, *94*, 421–425 https://www.jstor.org/stable/2458808

Hais, M., Chytrý, M., & Horsák, M. (2016). Exposure-related forest-steppe: A diverse landscape type determined by topography and climate. *Journal of Arid Environments*, *135*, 75–84. https://doi.org/10.1016/j.jaridenv.2016.08.011

Hegedüšová, K., & Senko, D. (2011). Successional changes of dry grasslands in southwestern Slovakia after 46 years of abandonment. *Plant Biosystems*, *145*, 666–687. https://doi.org/10.1080/11263504.2011.601605

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. https://doi.org/10.1111/gfs.12066

Hilder, E. J., & Mottershead, B. E. (1963). The redistribution of nutrients through free grazing sheep. *Australian Journal of Science*, *26*, 88–89.

Hobbs, N. T. (1996). Modification of ecosystems by ungulates. *Journal of Wildlife Management*, *60*, 695–713. https://doi.org/10.2307/3802368

Hoffmann, W. A., Lucatelli, V. M. P. C., Silva, F. J., Azeuedo, I. N. C., Marinho, M. S., Albuquerque, A. M. S., Lopes, A. O., & Moreira, S. P. (2004). Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. *Diversity and Distributions*, *10*, 99–103. https://doi.org/10.1111/j.1366-9516.2004.00063.x

Holdridge, L. (1947). Determination of world plant formations from simple climatic data. *Science*, *105*, 367–368. https://doi.org/10.1126/science.105.2727.367

Horsák, M., Chytrý, M., Hájková, P., Hájek, M., Danihelka, J., Horsáková, V., Ermakov, N., German, D. A., Kočí, M., Lustyk, P., Nekola, J. C., Preislerová, Z., & Valachovič, M. (2015). European glacial relict snails and plants: Environmental context of their modern refugial occurrence in southern Siberia. *Boreas*, *44*, 638–657. https://doi.org/10.1111/bor.12133

Hroudová, Z., & Prach, K. (1986). Vegetational changes on permanent plots in a steppe community. *Preslia*, *58*, 55–62 http://www.preslia.cz/archive/Preslia_58_1986_55-62.pdf

Hulme, P. (1996). Herbivory, plant regeneration, and species coexistence. *Journal of Ecology*, *84*, 609–615. https://doi.org/10.2307/2261482

Hunter, J., Franklin, S., Luxton, S., & Loidi, J. (2021). Terrestrial biomes: A conceptual review. *Vegetation Classification and Survey*, *2*, 73–85. https://doi.org/10.3897/VCS/2021/61463

Illyés, E. (2007). *Slope steppes, loess steppes and forest steppe meadows in Hungary*. MTA ÖBKI.

Jakucs, P. (1961). *Die Phytozönologischen Verhältnisse der Flaumeichen-Buschwälder Südostmitteleuropas*. Akadémiai Kiadó.

Jakucs, P. (1972). *Dynamische Verbindung der Wälder und Rasen*. Akadémiai Kiadó.

Jamrichová, E., Hédl, R., Kolář, J., Téth, P., Bobek, P., Hajnalová, M., Procházka, J., Kadlec, J., & Szabó, P. (2017). Human impact on open temperate woodlands during the middle Holocene in Central Europe. *Review of Palaeobotany and Palynology*, *245*, 55–68. https://doi.org/10.1016/j.revpalbo.2017.06.002

Joubert, D. D., Smit, G. N., & Hoffman, M. T. (2012). The role of fire in preventing transitions from a grass dominated state to a bush thickened state in arid savannas. *Journal of Arid Environments*, 87, 1–7. https://doi.org/10.1016/j.jaridenv.2012.06.012

Kahlke, R. D. (2014). The origin of Eurasian mammoth faunas (Mammuthus–Coelodonta faunal complex). *Quaternary Science Reviews*, 96, 32–49. https://doi.org/10.1016/j.quascirev.2013.01.012

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

Kaplan, J. O., Krumhardt, K. M., & Zimmermann, N. (2009). The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews*, 28, 3016–3034. https://doi.org/10.1016/j.quascirev.2009.09.028

Kaplan, Z. (2012). Flora and phytogeography of the Czech Republic. *Preslia*, 84, 505–573 http://www.preslia.cz/P123Kaplan.pdf

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, P., & Kessler, M. (2017). Climatologies at high resolution for the earth land surface areas. *Scientific Data*, 4, 170122. https://doi.org/10.1038/sdata.2017.122

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16, 406–411. https://doi.org/10.1016/j.tplants.2011.04.002

Kerner von Marilaun, A. (1863). *Das Pflanzenleben der Donauländer*. Wagnersche Universitätsbuchhandlung.

Kerns, B. K., Powell, D. C., Mellmann-Brown, S., Carnwath, G., & Kim, J. B. (2018). Effects of projected climate change on vegetation in the Blue Mountains ecoregion, USA. *Climate Services*, 10, 33–43. https://doi.org/10.1016/j.cliser.2017.07.002

Kirschner, P., Záveská, E., Gamisch, A., Hilpold, A., Trucchi, E., Paun, O., Sanmartín, I., Schlick-Steiner, B. C., Frajman, B., Arthofer, W., The STEPPE Consortium, Steiner, F. M., & Schönswetter, P. (2020). Long-term isolation of European steppe outposts boosts the biome's conservation value. *Nature Communications*, 11, 1968. https://doi.org/10.1038/s41467-020-15620-2

Körner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115, 445–459. https://doi.org/10.1007/s004420050540

Kruckeberg, A. R. (2002). *Geology and plant life*. University of Washington Press.

Kuneš, P., Pokorný, P., & Šída, P. (2008). Detection of the impact of early Holocene hunter-gatherers on vegetation in the Czech Republic, using multivariate analysis of pollen data. *Vegetation History and Archaeobotany*, 17, 269–287. https://doi.org/10.1007/s00334-007-0119-5

Kuneš, P., Svobodová-Svitavská, H., Kolář, J., Hajnalová, M., Abraham, V., Macek, M., Tkáč, P., & Szabó, P. (2015). The origin of grasslands in the temperate forest zone of east-central Europe: Long-term legacy of climate and human impact. *Quaternary Science Reviews*, 116, 15–27. https://doi.org/10.1016/j.quascirev.2015.03.014

Le Roux, D. S., Ikin, K., Lindenmayer, D. B., Manning, A. D., & Gibbons, P. (2018). The value of scattered trees for wildlife: Contrasting effects of landscape context and tree size. *Diversity and Distributions*, 24, 69–81. https://doi.org/10.1111/ddi.12658

Lisá, L., & Uher, P. (2006). Provenance of Würmian loess and loess-like sediments of Moravia and Silesia (Czech Republic): A study of zircon typology and cathodoluminiscence. *Geologica Carpathica*, 57, 397–403.

Liu, H., He, S., Anenkhonov, O. A., Hu, G., Sandanov, D. V., & Badmaeva, N. K. (2012). Topography-controlled soil water content and the coexistence of Forest and steppe in northern China. *Physical Geography*, 33, 561–573. https://doi.org/10.2747/0272-3646.33.6.561

Liu, H., Yin, Y., Wang, Q., & He, S. (2015). Climatic effects on plant species distribution within the forest-steppe ecotone in northern China. *Applied Vegetation Science*, 18, 43–49. https://doi.org/10.1111/avsc.12139

Maclean, I. M. D. (2020). Predicting future climate at high spatial and temporal resolution. *Global Change Biology*, 26, 1003–1011. https://doi.org/10.1111/gcb.14876

Magyari, E. K., Chapman, J. C., Passmore, D. G., Allen, J. R. M., Huntley, J. P., & Huntley, B. (2010). Holocene persistence of wooded steppe in the Great Hungarian Plain. *Journal of Biogeography*, 37, 915–935. https://doi.org/10.1111/j.1365-2699.2009.02261.x

Makunina, N. I. (2016). Botanical and geographical characteristics of forest steppe of the Altai-Sayan mountain region. *Contemporary Problems of Ecology*, 9, 342–348. https://doi.org/10.1134/s1995425516030100

Mauri, A., Davis, B. A. S., Collins, P. M., & Kaplan, J. O. (2015). The climate of Europe during the Holocene: A gridded pollen-based reconstruction and its multi-proxy evaluation. *Quaternary Science Reviews*, 112, 109–127. https://doi.org/10.1016/j.quascirev.2015.01.013

McCune, B., & Keon, D. (2002). Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science*, 13, 603–606. https://doi.org/10.1111/j.1654-1103.2002.tb02087.x

McNaughton, S. J. (1983). Serengeti grassland ecology: The role of composite environmental factors and contingency in community organization. *Ecological Monographs*, 53, 291–320 https://www.jstor.org/stable/1942533

Miklín, J., & Hradecký, J. (2016). Confluence of the Morava and Dyje Rivers: A century of landscape changes in maps. *Journal of Maps*, 12, 630–638. https://doi.org/10.1080/17445647.2015.1068714

Moeslund, J. E., Arge, L., Bøcher, P. K., Dalgaard, T., Odgaard, M. V., Nygaard, B., & Svenning, J. C. (2013). Topographically controlled soil moisture is the primary driver of local vegetation patterns across a lowland region. *Ecosphere*, 4, 1–26. https://doi.org/10.1890/ES13-00134.1

Molnár, Z., Biró, M., Bartha, S., & Fekete, G. (2012). Past trends, present state and future prospects of Hungarian forest-steppes. In J. A. M. Werger & M. A. van Staalduinen (Eds.), *Eurasian steppes. Ecological problems and livelihoods in a changing world* (pp. 209–252). Springer. https://doi.org/10.1007/978-94-007-3886-7_7

Moreira, F., Viedma, O., Arianoutsou, M., Curt, T., Koutsias, N., Rigolot, E., Barbati, A., Corona, P., Vaz, P., Xanthopoulos, G., Mouillot, F., & Bilgili, E. (2011). Landscape–wildfire interactions in southern Europe: Implications for landscape management. *Journal of Environmental Management*, 92, 2389–2402. https://doi.org/10.1016/j.jenvman.2011.06.028

Morreno, J. M., & Oechel, W. C. (1994). *The role of fire in Mediterranean-type ecosystems*. Springer Verlag. https://doi.org/10.1007/978-1-4613-8395-6_4

Mucina, L. (2019). Biome: Evolution of a crucial ecological and biogeographical concept. *New Phytologist*, 222, 97–114. https://doi.org/10.1111/nph.15609

Munteanu, C., Kuemmerle, T., Keuler, N. S., Müller, D., Balázs, P., Dobosz, M., Griffiths, P., Halada, L., Kaim, D., Király, G., Konkoly-Gyuró, É., Kozak, J., Lieskovsky, J., Ostafin, K., Ostapowicz, K., Shandra, O., & Radeloff, V. C. (2015). Legacies of 19th century land use shape contemporary forest cover. *Global Environmental Change*, 34, 83–94. https://doi.org/10.1016/j.gloenvcha.2015.06.015

Niklfeld, H. (1964). Zur xerothermen Vegetation im Osten Niederösterreichs. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, 103–104, 152–181 https://www.zobodat.at/pdf/VZBG_103-104_0152-0181.pdf

Niklfeld, H. (1993). Pflanzengeographische Charakteristik Österreichs. In L. Mucina, G. Grabherr, & T. Ellmauer (Eds.), *Die Pflanzengesellschaften Österreichs 1* (pp. 43–75). Gustav Fischer.

Novák, J., Roleček, J., Dresler, P., & Hájek, M. (2019). Soil charcoal elucidates the role of humans in the development of landscape of extreme biodiversity. *Land Degradation and Development*, *30*, 1607–1619. https://doi.org/10.1002/ldr.3350

Oesterheld, M., Sala, O. E., & McNaughton, S. J. (1992). Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature*, *356*, 234–236. https://doi.org/10.1038/356234a0

Ogureeva, G. N. (1980). *Botanicheskaya geografiya Altaya (Botanical geography of the Altai)*. Nauka.

Olivero, A. M., & Hix, D. M. (1998). Influence of aspect and stand age on ground flora of southeastern Ohio forest ecosystems. *Plant Ecology*, *139*, 177–187. https://doi.org/10.1023/A:1009758501201

Pánek, T., & Hradecký, J. (2016). *Landscapes and landforms of the Czech Republic*. Springer. https://doi.org/10.1007/978-3-319-27537-6

Pausas, J. G., & Bond, W. J. (2020). Alternative biome states in terrestrial ecosystems. *Trends in Plant Science*, *25*, 250–263. https://doi.org/10.1016/j.tplants.2019.11.003

Pavelková Řičánková, V., Horsák, M., Hais, M., Robovský, J., & Chytrý, M. (2018). Environmental correlates of the Late Quaternary regional extinctions of large and small Palaearctic mammals. *Ecography*, *41*, 516–527. https://doi.org/10.1111/ecog.02851

Podpěra, J. (1928). Steppe und Waldsteppe des Hutberges oberhalb Pouzdřany (Pausram). *Preslia*, *7*, 153–167 http://www.preslia.cz/archive/Preslia_07_1928_153-167.pdf

Pokorný, P., Chytrý, M., Juřičková, 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? *Holocene*, *25*, 716–726. https://doi.org/10.1177/0959683614566218

Polchaninova, N., Savchenko, G., Ronkin, V., Drogvalenko, A., & Putchkov, A. (2019). Summer fire in steppe habitats: Long-term effects on vegetation and autumnal assemblages of cursorial arthropods. *Hacquetia*, *18*, 213–231. https://doi.org/10.2478/hacq-2019-0006

Polis, G. A. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, *86*, 3–15 https://www.jstor.org/stable/3546565

Poschlod, P., Baumann, A., & Karlik, P. (2009). Origin and development of grasslands in Central Europe. In P. Veen, R. Jefferson, J. de Smidt, & J. van der Straaten (Eds.), *Grasslands in Europe of high nature value* (pp. 15–25). KNNV Publishing. https://doi.org/10.1163/9789004278103_003

Rédei, T., Botta-Dukát, Z., Csiky, J., Kun, A., & Tóth, T. (2003). On the possible role of local effects on the species richness of acidic and calcareous rock grasslands in northern Hungary. *Folia Geobotanica*, *38*, 543–467. https://doi.org/10.1007/BF02803252

Rédei, T., Csecserits, A., Kröel-Dulay, G., & Lhotsky, B. (2008). The effects of extreme droughts on sand grasslands. In E. Kovács-Láng, E. Molnár, G. Kröel-Dulay, & S. Barabás (Eds.), *The KISKUN LTER: Long-term ecological research in the Kiskunság, Hungary* (pp. 55–56). Institute of Ecology and Botany.

Reich, D., Wrbka, T., Plutzar, C., & Greimler, J. (2020). The effect of land-use change on the distribution of *Gentianella austriaca* and *G. praecox* in Austria. *Preslia*, *92*, 213–234. https://doi.org/10.23855/PRESLIA.2020.213

Riley, S. J., DeGloria, S. D., & Eliot, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, *5*, 23–27.

Roberts, B. A., & Proctor, J. (1991). *The ecology of areas with serpentinized rocks: A world view*. Kluwer. https://doi.org/10.1007/978-94-011-3722-5

Roleček, J., Čornej, I. I., & Tokarjuk, A. I. (2014). Understanding the extreme species richness of semi-dry grasslands in east-Central Europe: A comparative approach. *Preslia*, *86*, 13–34 http://www.preslia.cz/P141Rolecek.pdf

Roleček, J., Vild, O., Sladký, J., & Řepka, R. (2017). Habitat requirements of endangered species in a former coppice of high conservation value. *Folia Geobotanica*, *52*, 59–69. https://doi.org/10.1007/s12224-016-9276-6

Rorison, I. H., Sutton, F., & Hunt, R. (1986). Local climate, topography and plant growth in Lathkill dale NNR. I. A twelve-year summary of solar radiation and temperature. *Plant, Cell and Environment*, *9*, 49–56. https://doi.org/10.1111/1365-3040.ep11612961

Rusanov, A. M., Milanovskii, E. Y., Verkhoshentseva, Y. P., Voropaev, S. B., & Anilova, L. V. (2012). Physical properties of ordinary chernozems in steppe landscapes adjacent to forests. *Eurasian Soil Science*, *45*, 684–689. https://doi.org/10.1134/S1064229312010140

Sabau, N. C., & Morar, A. (2011). The vegetation's influence over the distribution of the soils in the forest of the hills of Oradea. *Analele Universităţii din Oradea, Fascicula Protecţia Mediului*, *17*, 519–528.

Sádlo, J., Chytrý, M., & Pyšek, P. (2007). Regional species pools of vascular plants in habitats of the Czech Republic. *Preslia*, *79*, 303–321.

Sankey, T. T., Montagne, C., Graumlich, L., Lawrence, R., & Nielsen, J. (2006). Lower forest–grassland ecotones and 20th century livestock herbivory effects in northern Mongolia. *Forest Ecology and Management*, *233*, 36–44. https://doi.org/10.1016/j.foreco.2006.05.070

Shumilovskikh, L. S., Novenko, E., & Giesecke, T. (2018). Long-term dynamics of the East European forest-steppe ecotone. *Journal of Vegetation Science*, *29*, 416–426. https://doi.org/10.1111/jvs.12585

Siefert, A., Ravenscroft, C., Althoff, D., Alvarez-Yépiz, J. C., Carter, B. E., Glennon, K. L., Heberling, J. M., Jo, I. S., Pontes, A., Sauer, A., Willis, A., & Fridley, J. D. (2012). Scale dependence of vegetation–environment relationships: A meta-analysis of multivariate data. *Journal of Vegetation Science*, *23*, 942–951. https://doi.org/10.1111/j.1654-1103.2012.01401.x

Sillinger, P. (1930). Vegetace Tematínských kopců na západním Slovensku. Příspěvek k fytogeografii a fytosociologii vápencových obvodů v jihozápadních výběžcích karpatských. *Rozpravy České akademie věd a umění, Třída II, Matematicko-přírodnická*, *40*, 1–46.

Slavíková, J. (Ed.). (1983). *Ecological and vegetational differentiation of a solitary conic hill*. Academia.

Šolcová, A., Petr, L., Hájková, P., Petřík, J., Tóth, P., Rohovec, J., Bátora, J., & Horsák, M. (2018). Early and middle Holocene ecosystem changes at the Western Carpathian/Pannonian border driven by climate and Neolithic impact. *Boreas*, *47*, 897–909. https://doi.org/10.1111/bor.12309

Soó, R. (1929). Die Vegetation und die Entstehung der Ungarischen Puszta. *Journal of Ecology*, *17*, 329–350. https://doi.org/10.2307/2256046

Stoutjesdijk, P., & Barkman, J. J. (2014). *Microclimate, vegetation and fauna* (2nd ed.). KNNV Publishing. https://doi.org/10.1163/9789004297807

Sümegi, P., Persaits, G., & Gulyás, S. (2012). Woodland-grassland ecotonal shifts in environmental mosaics: Lessons learnt from the environmental history of the Carpathian Basin (Central Europe) during the Holocene and the last ice age based on investigation of paleobotanical and mollusk remains. In R. W. Myster (Ed.), *Ecotones between Forest and grassland* (pp. 17–57). Springer. https://doi.org/10.1007/978-1-4614-3797-0_2

Szabó, P., & Hédl, R. (2013). Socio-economic demands, ecological conditions and the power of tradition: Past woodland management decisions in a Central European landscape. *Landscape Research*, *38*, 243–261. https://doi.org/10.1080/01426397.2012.677022

Szabó, P., Suchánková, S., Křížová, L., Kotačka, M., Kvardová, M., Macek, M., Müllerová, J., & Brázdil, R. (2018). More than trees: The challenges of creating a geodatabase to capture the complexity of forest history. *Historical Methods*, *51*, 175–189. https://doi.org/10.1080/01615440.2018.1444523

Teleki, B., Sonkoly, J., Erdős, L., Tóthmérész, B., Prommer, M., & Török, P. (2020). High resistance of plant biodiversity to moderate native woody encroachment in loess steppe grassland fragments. *Applied Vegetation Science*, *23*, 175–184. https://doi.org/10.1111/avsc.12474

Tercero-Bucardo, N., Kitzberger, T., Veblen, T. T., & Raffaele, E. (2007). A field experiment on climatic and herbivore impacts on post-fire tree regeneration in north-western Patagonia. *Journal of Ecology*, *95*, 771–779. https://doi.org/10.1111/j.1365-2745.2007.01249.x

Tichý, L. (1999). Teplotní poměry a vegetace na lokalitě Sloní hřbet v Národním parku Podyjí (in Czech) (Temperature and vegetation pattern at the Sloní hřbet ridge, Podyjí National Park). *Preslia*, *70*, 349–363 http://www.preslia.cz/archive/Preslia_70_1998_349-363.pdf

Treml, V., Šenfeldr, M., Chuman, T., Ponocná, T., & Demková, K. (2016). Twentieth century treeline ecotone advance in the Sudetes Mountains (Central Europe) was induced by agricultural land abandonment rather than climate change. *Journal of Vegetation Science*, *27*, 1209–1221. https://doi.org/10.1111/jvs.12448

van den Berg, M., Klamt, E., Van Reeuwijk, L. P., & Sombroek, W. G. (1997). Pedotransfer functions for the estimation of moisture retention characteristics of Ferralsols and related soils. *Geoderma*, *78*, 161–180. https://doi.org/10.1016/S0016-7061(97)00045-1

Varga, Z. (1989). Die Waldsteppen des pannonischen Raumes aus biogeographischer Sicht. *Düsseldorfer Geobotanische Kolloquien*, *6*, 35–50.

Vera, F. (2000). *Grazing ecology and forest history*. CABI Publishing.

Vojík, M., & Boublík, K. (2018). Fear of the dark: Decline in plant diversity and invasion of alien species due to increased tree canopy density and eutrophication in lowland woodlands. *Plant Ecology*, *219*, 749–758. https://doi.org/10.1007/s11258-018-0831-5

Walter, H. (1974). *Die Vegetation Osteuropas, Nord- und Zentralasiens*. Gustav Fischer Verlag.

Walter, H., & Lieth, H. (1967). *Klimadiagramm-Weltatlas*. Gustav Fischer Verlag.

Wendelberger, G. (1954). Steppen, Trockenrasen und Wälder des pannonischen Raumes. In E. Janchen (Ed.), *Angewandte Planzensoziologie, Festschrift für Erwin Aichinger zum 60. Geburtstag, Band 1* (pp. 573–634). Springer. http://burgenlandflora.at/wp-content/uploads/Wendelberger1954SW.pdf

Wesche, K., & Treiber, J. (2012). Abiotic and biotic determinants of steppe productivity and performance – A view from Central Asia. In M. J. A. Werger & M. A. van Staalduinen (Eds.), *Eurasian steppes. Ecological problems and livelihoods in a changing world* (pp. 3–43). Springer. https://doi.org/10.1007/978-94-007-3886-7_1

Wilcox, B. P., Breshears, D. D., & Allen, C. D. (2003). Ecohydrology of a resource-conserving semiarid woodland: Effects of scale and disturbance. *Ecological Monographs*, *73*, 223–239. https://doi.org/10.1890/0012-9615(2003)073[0223:EOARSW]2.0.CO;2

Williams, J. W., Shuman, B., & Bartlein, P. J. (2009). Rapid responses of the prairie-forest ecotone to early Holocene aridity in mid-continental North America. *Global and Planetary Change*, *66*, 195–207. https://doi.org/10.1016/j.gloplacha.2008.10.012

Willis, K. J., & van Andel, T. H. (2004). Trees or no trees? The environments of central and eastern Europe during the last glaciation. *Quaternary Science Reviews*, *23*, 2369–2387. https://doi.org/10.1016/j.quascirev.2004.06.002

Willner, W., Kuzemko, A., Dengler, J., Chytrý, M., Bauer, N., Becker, T., Biță-Nicolae, C., Botta-Dukát, Z., Čarni, A., Csiky, J., Igić, R., & Janišová, M. (2017). A higher-level classification of the Pannonian and western Pontic steppe grasslands (central and Eastern Europe). *Applied Vegetation Science*, *20*, 143–158. https://doi.org/10.1111/avsc.12265

Willner, W., Moser, D., Plenk, K., Aćić, S., Demina, O. N., Höhn, M., Kuzemko, A., Roleček, J., Vassilev, K., Vynokurov, D., & Kropf, M. (2021). Long-term continuity of steppe grasslands in eastern Central Europe: Evidence from species distribution patterns and chloroplast haplotypes. *Journal of Biogeography*, *48*, 3104–3117. https://doi.org/10.1111/jbi.14269

Willner, W., Roleček, J., Korolyuk, A., Dengler, J., Chytrý, M., Janišová, M., Lengyel, A., Aćić, S., Becker, T., Ćuk, M., Demina, O., Jandt, U., Kącki, Z., Kuzemko, A., Kropf, M., Lebedeva, M., Semenishchenkov, Y., Šilc, U., Stančić, Z., … Yamalov, S. (2019). Formalized classification of semi-dry grasslands in central and eastern Europe. *Preslia*, *91*, 25–49. https://doi.org/10.23855/preslia.2019.025

Wilson, J. B., & Agnew, D. Q. A. (1992). Positive-feedback switches in plant communities. *Advances in Ecological Research*, *23*, 263–336. https://doi.org/10.1016/S0065-2504(08)60149-X

Woodward, S. L. (Ed.). (2008). *Grassland biomes*. Greenwood Press.

Zimov, S. A., Chuprynin, V. I., Oreshko, A. P., Chapin, F. S., III, Reynolds, J. F., & Chapin, M. C. (1995). Steppe-tundra transition: An herbivore-driven biome shift at the end of the Pleistocene. *American Naturalist*, *146*, 765–794 https://www.jstor.org/stable/2462990

Zimov, S. A., Zimov, N. S., Tikhonov, A. N., & Chapin, F. S., III. (2012). Mammoth steppe: A high-productivity phenomenon. *Quaternary Science Reviews*, *57*, 26–45. https://doi.org/10.1016/j.quascirev.2012.10.005

Zólyomi, B. (1942). A középdunai flóraválasztó és a dolomitjelenség (Die Mitteldonau Florenscheide und das Dolomit-phänomen). *Botanikai Közlemenyek*, *32*, 209–224.

Zólyomi, B. (1953). Die Entwicklungsgeschichte der Vegetation Ungarns seit dem letzten Interglazial. *Acta Biologica Academiae Scientiarum Hungaricae*, *4*, 367–430.

Zólyomi, B. (1964). Pannonische Vegetationsprobleme. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, *103–104*, 144–151.

Zólyomi, B. (1987). Coenotone, ecotone and their role in preserving relic species. *Acta Botanica Hungarica*, *33*, 3–18.

BIOSKETCH

Kryštof Chytrý is broadly interested in Central European flora and vegetation. This paper is a component of his PhD work at the University of Vienna, focusing on the influence of microclimate on vegetation. With this paper, he summarizes his experience with forest–steppes he gained during fieldwork for his Master's degree at Masaryk University, Brno.

Authors' contributions: KC and SD designed the study with the help of MC and WW; KC led the writing with contributions of all co-authors.

SUPPORTING INFORMATION

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