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 (Illérys, 2007), on sandy (Erdős et al., 2014) or saline soils (Elíáš Jr et al., 2020; Sümegi et al., 2012) or on rock outcrops (Niklfeld, 1964). Central European steppe significantly contributes
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 relics of more extensive late-Pleistocene and early-Holocene steppe and forest-steppe environments (Chytrý, Horsák, et al., 2019; Horsák et al., 2019; 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.
Zólyomi, anistic drivers. While topography is not a mechanistic driver of plant growth and particular combination of macroclimate and disturbance regimes. Topography in shaping the mosaic of forest and steppe under a worldwide. In this framework, we emphasize the critical role of framework potentially applicable to forest–steppe ecosystems independently (Sümegi et al., 2012), often focusing on specific land-sites ‘edaphic steppes’. Some 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 ‘for- est 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
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 (Hirston 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 (Kunés 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. serpentinite 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 (Elíáš 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. Ougreeva, 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 (Hegedűšová & 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 (Avenkonhonov 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 (Chytry & Tichý, 1998; Endrezs 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 (Lišá & 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 dolomite 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 (Hejman 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. Miklin & 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 & Boublik, 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 (Anenkhnov 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).
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

**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

**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)
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

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**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').

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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 metacommunities (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; Pokorny 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. Divišek 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 micromalclimatic 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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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used are freely available. The locations of the sampling sites and their characteristics can be found in Appendices S1 and S2 and in the Zenodo Repository: https://doi.org/10.5281/zenodo.6351634.

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**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-steppe 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**

Additional supporting information may be found in the online version of the article at the publisher’s website.

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