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The importance of heterogeneity in Eurasian forest-steppes from the continental to the local scale

Dissertation for the title

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Near the inn a dwarfish poplar-wood's found,
Yellows in sand by weeds decorated;
Here lives in its nest the screaming falcon,
By the swarm of kids but undisturbed.

Here is growing woebegone feather-grass
And globe-thistle's proliferous blue bloom;
At its refreshing stem at midday heat
Small lizards find site to have a rest soon.

Sándor Petőfi: The Great Plain
(excerpt; translated by Ottó Tomschey)

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A csárdánál törpe nyárfaerdő
Sárgul a királydinnyés homokban;
Odafészkel a visító vércse,
Gyermekektől nem háborgatottan.

Ott tenyészik a bús árvalyányhaj
S kék virága a szamárkenyérnek;
Hűs tövéhez déli nap hevében
Megpihenni tarka gyíkok térnek.

Petőfi Sándor: Az Alföld
(részlet)

Contents

1 General introduction

According to the forest-grassland continuum concept, several terrestrial ecosystems fall somewhere in the middle range between closed-canopy forests and treeless grasslands (Breshears 2006). Such semi-open ecosystems cover a considerable proportion of the Earth's terrestrial surface (up to 35%, although the figure depends on the exact definition used) (House et al. 2003, see also Bond 2021).

Spatial heterogeneity is of crucial importance in ecosystems featuring a mosaic of woody and non-woody vegetation, given the co-occurrence of habitats that differ strongly regarding structure, species composition, and environmental factors. Consequently, heterogeneity has received ample scientific attention, among others, in tropical and subtropical savannas (e.g., Sankaran et al. 2004, Riginos et al. 2009, Treydte et al. 2009, Mogashoa et al. 2021) and in the North American prairie-forest ecotone (e.g., Breshears et al. 1997, Pogue and Schnell 2001, Meisel et al. 2002, Chhin and Wang 2008, Brudvig and Asbjornsen 2009). In contrast, spatial heterogeneity has been understudied in Eurasian forest-steppes. Several reasons can be mentioned why this topic has been neglected. First, the descriptive analysis of plant communities dominated, and, in some regions, continues to dominate vegetation science. Second, the forest-steppe was sometimes treated as a marginal topic, only as a sub-type of the steppe biome. Third, and most importantly, the steppe and the forest components were studied separately (and edges were almost completeley ignored), which resulted in an incomplete understanding of forest-steppes and prevented a correct appreciation of habitat heterogeneity. Last but not least, a comprehensive continental overview of the Eurasian forest-steppe was lacking.

Eurasian forest-steppes cover vast areas: they extend from the eastern parts of Central Europe (16°E) to the Asian Far East (139°E), the northernmost occurrences reaching the Kuznetski Alatau Mts (56°N) and the southernmost extensions occurring in the Zagros Mts (29°N) (Erdős et al. 2018a). They appear in a wide variety from sub-Mediterranean to ultracontinental climates, from plains to high mountains. Their ecological and conservation importance is enormous. For example, both the grassland (e.g., Walter 1968, Chibilyov 2002, Zlotin 2002) and the forest component (Chytrý et al. 2012) host very high taxonomic diversity at the local scale, not to speak about the whole mosaic with both components. Moreover, forest-steppes are home to several taxa of special conservation importance, including endemics (Erdős et al. 2022). Forest-steppes are also important from an economic perspective: they provide livelihoods for millions of people, although forms of land-use show strong regional variations, with grazing being the most prominent form (Erdős et al. 2018a).

The general aims of this work are (1) to provide a broad-scale characterisation of Eurasian forest-steppes, (2) understand how the permanent coexistence of forest and grassland vegetation is possible, (3) describe habitat heterogeneity at the local scale and examine its conservation implications, with particular emphasis on diversity patterns, and (4) offer a very basic insight into the temporal dynamics of forest-steppe ecosystems.

The first unit of the present work is formed by two reviews. In **Chapter 2** I provide a continental synthesis of Eurasian forest-steppes, with a broad yet accurate definition of the term 'forest-steppe,' and a delineation and basic characterisation of the main forest-steppe regions based on climate, topography, physiognomy, and species composition (Erdős et al. 2018a). **Chapter 3** presents a series of conceptual models, which explain how the permanent forest-grassland coexistence is possible in the Eurasian forest-steppe (Erdős et al. 2022).

The second unit of the dissertation consists of case studies about forest-steppe heterogeneity at the local scale. **Chapter 4** examines patterns of taxonomic, functional and phylogenetic diversity among the various habitats of sandy forest-steppes (Erdős et al. 2023). **Chapter 5** investigates the dominant strategies in various habitats of the forest-steppe ecosystem, and examines what these tell us about community assembly (Erdős et al. 2024a). **Chapter 6** describes a study that combined vegetation sampling and environmental measurements to reveal how different habitats of forest-steppes contribute to the overall conservation value of the whole mosaic ecosystem (Erdős et al. 2018b). **Chapter 7** offers an outlook to a semi-natural forest-grassland mosaic near the periphery of the forest-steppe zone (Erdős et al. 2019a). **Chapter 8** focuses on the forest component of the forest-steppe mosaic, comparing the ecological value of near-natural forests to that of various tree plantations, both native and non-native, which have replaced the original forest-steppe vegetation in large areas in the study region (Ho et al. 2023a). **Chapter 9** summarises the main findings of a seeding and watering experiment that examined the germination and early seedling performance of pedunculate oak (*Quercus robur*) in various habitats of a forest-steppe mosaic (Erdős et al. 2021).

The third unit looks at forest-steppes from a broader perspective. **Chapter 10** presents a comparison of forest-steppes in the Kiskunság Sand Ridge (Hungary) and the Deliblato Sands (Serbia), sampled with unified methodology, providing further insights into patterns of taxonomic, functional, and phylogenetic diversity (Ho et al. 2023b). Finally, **Chapter 11** examines how spatial heterogeneity is changing along the temporal dimension at a decadal time-scale (Erdős et al. 2024b).

2 The edge of two worlds: A new review and synthesis on Eurasian forest-steppes (Erdős et al. 2018a)

Forest-steppes represent a transition between closed-canopy forests and treeless steppes. While forest-steppes or equivalent ecosystems are also present in North America and South America, the largest forest-steppes are found in Eurasia. Despite their enormous importance, knowledge on Eurasian forest-steppes is scattered. The number of case studies has increased recently, but syntheses are scarce, and most of them have been conducted at national or regional scales, while the few continental-scale overviews ignored the forest-steppes of the Middle East and the Tian Shan-Pamir ranges. The aim of this work was to prepare a synthetic overview of Eurasian forest-steppes, to provide a definition of forest-steppes, to delineate the biome, and to delineate and characterise its main regions.

We define forest-steppes as follows: forest-steppes are natural or near-natural vegetation complexes of arboreal and herbaceous components, typically distributed in a mosaic pattern, in the temperate zone (excluding the Mediterranean), where the coexistence of forest and grassland is enabled primarily by the semi-humid to semi-arid climate, complemented by biotic (e.g., grazing) and abiotic (e.g., topography) factors operating at multiple scales. The arboreal cover (with a minimum height of 2 m) is 10–70% across the whole mosaic. The vascular vegetation cover within the grassland component is at least 10%. This definition includes a latitudinal forest-steppe zone extending from eastern Central Europe to the Far East near the Pacific coast, and a southern belt, which, in most cases, is an altitudinal zone in mountain regions from the Middle East to China.

Relying on a combination of previously published material, expert knowledge, and climate data of selected meteorological stations, we delineated the main forest-steppe regions based on four criteria: floristic composition, physiognomy, relief, and climate (Figure 1 on page 349 and Table 1 on page 351).

Region A (Southeast Europe) includes the Carpathian Basin, the Lower Danube Plain, and Inner Thrace. Forest-steppes of this region are sub-continental with Mediterranean climatic influences (mean annual temperature: 9.0–12.5 °C, mean annual precipitation: 420–600 mm). Forest-steppes occur on plains (from sea level to 250 m a.s.l.), and the south-facing slopes of hills and mountains. Forest patches are typically small and have an open canopy, with several oak species (e.g., *Quercus cerris*, *Q. frainetto*, *Q. petraea*, *Q. pubescens*, and *Q. robur*), but other trees become important in some parts of the region (e.g., *Populus alba* and *Tilia tomentosa*). Some of the dominant grasses of the steppe component are *Chrysopogon gryllus*, *Festuca rupicola*, *F. valesiaca*, *F. vaginata*, *Stipa capillata*, *S. pennata*, and *S. pulcherrima*.

Region B (East Europe) includes the southern part of the East European Plain, stretching from the eastern foothills of the Carpathians to the Ural Mts. The climate is temperate continental (mean annual temperature: 3–9 °C, mean annual precipitation: 400–600 mm). Forest-steppes of this region occupy lowlands and hills from ca. 90 to 500 m a.s.l. Large and mesic forest patches dominated by broadleaved deciduous trees (e.g., *Acer platanoides*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, and *Ulmus glabra*) alternate with mesic grassland patches, where the most important grass species include *Festuca valesiaca*, *Stipa capillata*, *S. pennata*, *S. pulcherrima*, and *S. zalesskii*.

Region C (North Caucasus and Crimea) is under considerable Mediterranean climatic influences (mean annual temperature: 9.5–12.0°C, mean annual precipitation: 300–600 mm). Forest-steppes are found from sea level up to ca. 600 m a.s.l. In the North Caucasus, forest patches are dominated by *Carpinus betulus*, *Quercus petraea*, *Q. robur*, and *Tilia dasystyla*. In the northwestern part of the Crimean Mts, characteristic tree species include *Pyrus communis*, *P. elaeagrifolia*, *Q. petraea*, *Q. pubescens*, *Q. robur*, and *Ulmus procera*. In the southern parts of the Crimean Mts, *Arbutus andrachne*, *Juniperus excelsa*, *Pistacia atlantica* and *Q. pubescens* are typical. Some of the most common and characteristic grass species are *Festuca rupicola*, *Stipa capillata*, *S. pennata*, *S. pontica*, and *S. pulcherrima*.

Region D (West Siberia and North Kazakhstan) has continental climate (mean annual temperature: 1-4.5 °C, mean annual precipitation: 270–610 mm). Forest-steppes grow in lowlands (100-200 m a.s.l.), and on hills (up to ca. 400 m a.s.l.). The forest patches are formed by small-leaved deciduous trees (*Betula pendula*, *B. pubescens*, and *Populus tremula*) and *Pinus sylvestris*. The main grass species include *Festuca rupicola*, *F. valesiaca*, *Helictotrichon hookeri*, *Poa angustifolia*, *Phleum phleoides*, *Stipa capillata*, *S. pennata*, *S. tirsa*, and *S. zalesskii*.

Region E (Inner Asia) includes mountain ranges from the Altai Mts to Inner Mongolia. The climate is ultracontinental (mean annual temperature: from -6°C to +2°C, mean annual precipitation: 210–550 mm). Forest-steppes occur from valleys (ca. 200 m a.s.l.) to high mountains (up to 2400 m a.s.l.). The most typical tree species of the forests are *Larix sibirica*, *L. gmelinii*, and *Pinus sylvestris*, while the most common grasses of the steppe component are *Achnatherum sibiricum*, *Agropyron cristatum*, *Cleistogenes squarrosa*, *Festuca valesiaca*, *F. lenensis*, *Koeleria macrantha*, *Leymus chinensis*, *Poa attenuata*, *Stipa baicalensis*, and *S. krylovii*.

Region F (Far East) includes West Manchuria, the southern parts of the Greater Khingan Range, the eastern parts of the Chinese Loess Plateau, the Amur and the Khanka Lowlands, and southwest Sihote Alin. The climate is continental, influenced by the monsoonal circulation (mean annual temperature: from -1°C to +14°C, mean annual precipitation: 360–650 mm). Forest-steppes occur from ca. 50 m up to 2500 m a.s.l. The most typical tree species are *Quercus mongolica* and *Tilia amurensis*. Grasslands are highly variable, with dominant grasses such as *Arundinella hirta*, *Calamagrostis epigejos*, *Leymus chinensis*, *Miscanthus sinensis*, *Poa pratensis*, *Stipa bungeana*, *S. grandis*, and *S. pennata*.

Region G (Middle East) includes mountain regions from Anatolia to the Hindu Kush. The climate is under Mediterranean influences (mean annual temperature: 10.5–17.0°C, mean annual precipitation: 270–860 mm). Forest-steppes occur from ca. 200 m to 3,000 m a.s.l. The most common tree species are *Juniperus excelsa*, *Pinus nigra*, *Pistacia atlantica*, *P. vera*, *Prunus dulcis*, *Pyrus elaeagrifolia*, *Quercus brantii*, *Q. infectoria*, *Q. ithaburensis*, *Q. macranthera*, *Q. pubescens*, and *Q. robur*. Some of the common grasses are *Agropyron cristatum*, *Bothriochloa ischaemum*, *Chrysopogon gryllus*, *Festuca valesiaca*, *Poa bulbosa*, *Stipa arabica*, *S. barbata*, *S. capillata*, *S. lessingiana*, and S. *pulcherrima*.

Region H (Central Asia and southwestern Inner Asia) includes mountains from the Pamir to the Helan ranges. The climate is mostly continental, with Mediterranean influences in the western parts of the region (mean annual temperature: 0–12°C, mean annual precipitation: 380–600 mm). Forest-steppes occur from ca. 800 to 3500 m a.s.l. In the western areas of the region, scattered fruit trees (*Juglans regia*, *Malus sieversii*, *Pistacia* spp., and *Punica granatum*) and *Juniperus* species are typical, embedded in a dry grassland matrix (e.g., *Bothriochloa ischaemum*, *Hordeum bulbosum*, *Poa bulbosa*, and *Thinopyrum intermedium*). In the eastern parts, forest patches of *Picea schrenkiana* and *P. crassifolia* occupy north-facing slopes. Montane steppes grow on south-facing slopes, and the common grasses include *Agropyron cristatum*, *Cleistogenes squarrosa*, *Festuca rupicola*, *Oryzopsis chinensis*, *Ptilagrostis pelliotii*, *Stipa capillata*, *S. breviflora*, and *S. przewalskyi*.

Region I (Eastern Tibetan Plateau) may tentatively be classified among forest-steppes. The elevation is 3200–4000 m a.s.l. Mean annual temperature varies between −3°C and +7°C, mean annual precipitation is 300–700 mm. Forest patches are composed of several species of *Abies* and *Picea*, while several *Kobresia* species are among the dominant graminoids of the steppe component.

3 How climate, topography, soils, herbivores, and fire control forest–grassland coexistence in the Eurasian forest-steppe (Erdős et al. 2022)

A considerable proportion of the Earth's terrestrial surface is covered by semi-open ecosystems, co-dominated by woody and herbaceous species. Ecologists have long sought to explain why these ecosystems exist, i.e., why there is neither a treeless grassland nor a closed-canopy forest, but a mixture of the two types. Significant progress has been made to achieve explanations for tropical and subtropical savannas and the American prairie-forest ecotone, but the Eurasian forest-steppe has received relatively little attention.

Eurasian forest-steppes occupy a 9000 km long and, on average, 430 km wide latitudinal zone extending from Eastern Central Europe to the Asian Far East. There is another forest-steppe zone stretching from the Middle East to Central Asia, which is usually a rather narrow altitudinal belt in mountain regions. As scientific works are hardly available for these southern forest-steppes, in the followings we limit our attention to the northern, latitudinal forest-steppe zone.

To understand how the permanent coexistence of woody and herbaceous vegetation is possible in the Eurasian forest-steppe zone, we developed a series of conceptual models. The first model includes only mean macroclimate, while the next models add climate variability, topography, soils, herbivory, fire, and feedback mechanisms as drivers of forest-grassland coexistence.

According to the **Mean Climate Model**, climatic harshness (defined as the combination of aridity and annual temperature range) generally increases from north to south, and also from peripheral western and eastern areas to the more central parts of Eurasia (Fig 2a on page 2200). Several studies have confirmed that low soil moisture, high summer temperature, and extremely cold winters can control forest distribution by limiting tree germination and survival. Similar to forests, grasslands prefer less harsh conditions, that is, good water supply and smaller temperature extremes. As evidence of this, grasses are able to flourish and form productive hay meadows or pastures where temperate or boreal forests are cleared. There is ample evidence that, with increasing climatic harshness, the height, density and productivity of grasses decrease. Thus, both forest and grassland vitality decrease along the climatic harshness gradient, but forest vitality declines more steeply (Fig. 2a on page 2200). Where the forest and grassland vitality curves intersect, forest gives way to grassland. This Mean Climate Model predicts a sharp transition between forest and steppe, with no mosaic of forest and grassland.

The **Zonal Model** includes interannual variations of precipitation and temperature. Wet periods may open windows for tree recruitment, while drier periods may prevent canopy closure and favour grasslands. Thus, both forest and grassland vitality have a certain range of variability along the mean climate gradient, i.e., vitalities may be lower or higher according to the actual conditions of the given period. This is visualised in the form of wider bands for the vitality curves (Fig. 2b on page 2200). As a result, the climatically determined intersection point expands into a zone where neither the forest nor the grassland component is more vital than the other on a permanent basis. In other words, neither the forest nor the grassland is able to dominate over sufficiently long periods and over large areas, which leads to a mosaic-like forest–grassland coexistence.

The **Climatic–Topographic–Edaphic Model** includes topographic and edaphic factors in addition to macroclimate. Variations in topography and soil can considerably decrease or increase local temperature and/or moisture availability, thereby affecting the vitality of forests and grasslands. For example, in the Inner Asian forest-steppe region (Mongolia, north and northeast China, and south Russia), north-facing mountain slopes are usually occupied by forests, while steppes grow on south-facing slopes. Also, there is evidence from several forest-steppe regions that ravines, erosion gullies, and depressions can support forest survival amid grasslands. Gravelly soils have been shown to maintain forests, probably because coarse-texture soils permit rapid water infiltration to deeper soil layers, where it is accessible to deep-rooted woody plants, but not to grassland species.

Topography and soil play a role in forest–grassland distributions *within* the climatically determined forest-steppe zone, where they influence the quantity and exact distribution of forest or grassland patches, although the mosaic itself would be present even on a completely flat surface with homogeneous soil. *Beyond* this climatically determined forest-steppe zone, special topographical and edaphic circumstances may also result in forest–grassland coexistence by locally reversing the forest and grassland vitality curves (Fig. 2c on page 2200). Here, specific topography and soil circumstances are essential in the formation of forest-steppe (i.e., there would be no mosaic without these specific circumstances). Thus, topography and soil broaden the forest-steppe zone in both directions along the harshness gradient.

The **Climatic–Topographic–Edaphic–Herbivore–Fire Model** takes into account the effects of herbivores and fire in forest-grassland coexistence. In contrast to African savannas and the American prairie-forest ecotone, where grazing may result in woody plant dominance, this is not the case in the Eurasian forest-steppe zone. Here, in addition to browsers, animals that are usually considered grazers also consume woody plants. Such browsing by ‘grazers,’ combined with their trampling, wallowing, and uprooting of trees is a serious limit to forest expansion into grasslands. In addition, domestic ungulates have been shown to act as limiting factors for tree establishment and survival in the Eurasian forest-steppe through browsing and trampling. Also, studies have revealed that some insects heavily damage woody plants, especially at and near forest edges, thereby limiting forest spread. To sum it up, where herbivory disproportionately damages woody plants compared to non-woody species, forest vitality is diminished, and grasslands can occupy areas that climatically would be appropriate to support forests (Fig. 3 on page 2201).

Several non-woody plants are able to regenerate after a fire event relatively quickly (from underground organs and/or from the seedbank), whereas woody species, except for some fire-tolerant or resprouting ones, need considerably longer time, decades or even centuries, to reestablish. Although studies examining the effects of fire on the forest–grassland balance are very scarce for Eurasian forest-steppes, fire is regarded as being capable of limiting woody vegetation (Fig. 3 on page 2201).

Herbivory and fire are able to modify forest–grassland proportions anywhere in the forest-steppe, reducing tree cover below the potential that would be allowed by climate, soil, and topography. However, near the less harsh end of the climatic harshness gradient, herbivory and fire are not just modifiers but are essential to prevent canopy closure, thereby enabling long-term forest–grassland coexistence.

Vegetation feedbacks reinforce herbaceous dominance in grassland patches and tree dominance in forest patches, and contribute to permanent forest-grassland coexistence. Forest patches can modify microclimate and in some cases fire frequency and intensity, in a way that helps tree regeneration while excludes most steppe species. On the other hand, the microclimate of the grassland patches, along with the strong competition of grasses, forms a hostile environment for trees, preventing or, under less harsh climate, slowing the spread of forest patches.

Our conceptual models can explain the permanent coexistence of forest and grassland in Eurasian forest-steppes as a net result of multiple drivers. The framework may help to identify the relative importance of each driver in a given region, which can enable a correct understanding of forest-steppe patterns and processes, and support appropriate conservation and restoration strategies.

4 Taxonomic, functional, and phylogenetic diversity peaks do not coincide along a compositional gradient in forest-grassland mosaics (Erdős et al. 2023)

Forest-steppes are spatially heterogeneous ecosystems with a mosaic arrangement of structurally very different habitat patches. How various aspects of biodiversity are distributed among the different woody and non-woody habitats has outstanding theoretical and practical importance, yet it has received little attention in forest-steppes. The aim of this work was to study how species composition as well as taxonomic, functional and phylogenetic diversity vary in multiple habitat types of forest-steppe ecosystems. Our hypothesis was that the different forest-steppe habitats would form a compositional gradient. In addition, we hypothesised that taxonomic diversity would peak at forest edges (that is, at the middle of the gradient), and that it would gradually decrease both towards forest patches and grasslands. We expected that edges would have their own species that are rare in habitat interiors (edge-species). Furthermore, our hypothesis was that functional diversity and phylogenetic diversity would be parallel to taxonomic diversity along the gradient.

For this study, 13 sites were selected in the Kiskunság Sand Ridge (Hungary). The mean annual temperature is 10.0–10.7°C, while the mean annual rainfall is 520–580 mm. The study sites are covered by calcareous sand dunes and humus-poor sandy soils, which support near-natural forest-steppe mosaics. The following eight habitat types were differentiated: large patches (>0.5 ha) of poplar-juniper forest, medium patches (0.2–0.4 ha) of the same forest type, small patches (<0.1 ha) of this forest type, north-facing forest edges (peripheral zones of forest patches reaching out of the outermost tree trunks but still below the canopy), south-facing forest edges (using the same edge definition), closed perennial grasslands, open perennial grasslands, and open annual grasslands.

All habitat types were sampled with 25 m^2 plots (5 m × 5 m plots for forest interiors and grasslands and 2 m × 12.5 m plots for forest edges in order to prevent their extension into the interiors of forests or grasslands). The total number of plots was 494 (60 plots in large forest patches, 64 plots in medium forest patches, 60 plots in open annual grasslands, 50 plots in closed perennial grasslands and 65 plots in each of the other habitat types). The slightly unbalanced sampling is due to the fact that some habitat types were rare at some sites. The percentage cover of each vascular plant species in each plot was visually estimated in spring (April–May) and summer (July–August), and for each species in each plot, the larger recorded cover value was used for data analyses.

The following nine plant functional traits were used in this work: start of flowering, flowering duration, specific leaf area (SLA), mean plant height, thousand seed mass, life form, seed dispersal, pollination type, and reproduction type. A phylogenetic tree was constructed for the 289 species found in the study plots, and an additional tree by excluding non-angiosperm species. The compositional relations among the eight habitat types were studied with non-metric multidimensional scaling, using Bray-Curtis dissimilarity on the square-root transformed percentage cover values. For each plot, species richness and Shannon diversity were calculated. The diagnostic species of the habitats were identified using the phi-coefficient as an indicator of fidelity. For each plot, Rao's quadratic entropy (RaoQ) was calculated as a measure of functional diversity (FD) based on all nine traits (overall FD), and also for the individual traits. Similarly, RaoQ was used to calculate phylogenetic diversity for all species and then for angiosperms only. For both functional and phylogenetic diversity, the standardised effect size of RaoQ (SES.RaoQ) was computed in order to eliminate the effect of species richness.

A clear compositional gradient was revealed by the NMDS ordination along the first axis, ranging from large forest patches through smaller-sized forest patches and edges to closed and open grasslands (Fig. 3 on page 187).

North-facing edges had the highest species richness, followed by south-facing edges (Fig. 4a on page 188). Species richness showed gradual decrease towards both ends of the vegetation gradient. Shannon diversity was high at edges, but also high in open annual and open perennial grasslands (Figure 4b on page 188).

North-facing forest edges and closed perennial grasslands had the highest number of significant diagnostic species, while medium forest patches, small forest patches, and south-facing forest edges had the lowest number of diagnostic species.

Overall functional diversity (based on all nine traits) was significantly higher in woody habitats (i.e., forests and edges) than in grasslands (Fig. 4c on page 188). Regarding the functional diversity of individual traits, the functional diversities of flowering time, seed dispersal, reproduction type, and plant height were significantly higher in woody habitats than in grasslands (Fig. 5 a-d on page 190), and there was a similar tendency for the functional diversity of seed mass (Fig. 5g on page 190). Regarding life form, south-facing edges, north-facing edges, and small forest patches had the highest functional diversities (Figure 5e on page 190). The highest functional diversity for SLA was found in closed perennial grasslands, open annual grasslands, and medium forest patches (Fig. 5f on page 190). The functional diversity of pollination type showed maxima towards the endpoints of the gradient: in large forest patches and open annual grasslands (Fig. 5h on page 190).

Phylogenetic diversity was significantly higher in woody habitats than in grasslands (Fig. 4d on page 188), and it showed a peak near the middle of the gradient. This peak, however, disappeared when non-angiosperms were excluded from the analysis (Fig 4e on page 188).

The compositional gradient revealed in this study may partly be explained by the ability of vegetation to modify its environment. Forest patches are known to reduce environmental harshness, but this ability may decrease with decreasing forest patch size. Differences in topography and disturbance regime may be responsible for the compositional gradient among the grassland habitats.

The expectation that species richness would show a hump-backed curve along the gradient was supported by our results. We confirmed the existence of edge-species, which may be one explanation for this hump-backed curve. Shannon diversity, similar to species richness, was high at the middle of the gradient, but it was also high in the open grassland habitats, probably because environmental harshness and disturbances reduce the dominance of strong competitors, resulting in high evenness.

One of the most important findings of this study is that patterns of taxonomic diversity did not coincide with those of functional and phylogenetic diversities. The functional diversity of woody habitats (forests and edges) was significantly higher than that of the grassland habitats. The analyses of functional diversity for single traits showed that this pattern was mostly due to the functional diversity of flowering time, seed dispersal, reproduction type, plant height, and, to a smaller degree, seed mass. It is particularly interesting that large forest patches proved to be functionally diverse habitats despite their very low species richness values, emphasising that species richness is not necessarily informative of functional diversity. In the woody habitats, strong competition for light results in a multilayered structure, which naturally leads to high functional diversity of mean plant height, and this in turn may have cascading effects on other traits.

The fact that phylogenetic diversity was higher in woody habitats than in grasslands may be explained by the long evolutionary history of forests, whereas grasslands represent much younger habitats. The peak of phylogenetic diversity near the middle of the gradient was probably due to *Juniperus communis*, which is very typical in smaller-sized forests and at edges. This is why the peak disappeared when non-angiosperms (by far the most frequent of which is *J. communis* in the sites) were excluded.

Emphasising that taxonomic diversity is not necessarily informative of functional and phylogenetic diversity, our study calls for increased attention to functional and phylogenetic aspects alongside more traditional taxonomic diversity indices.

5 Environmental filtering is the primary driver of community assembly in forest–grassland mosaics: A case study based on CSR strategies (Erdős et al. 2024a)

Forest-steppes are inherently heterogeneous ecosystems where strongly different habitats occur in close proximity in a mosaic pattern. While macroclimate may be assumed to be the same for the co-occurring habitats in a single landscape, environmental differences do exist among the different habitats, partly evoked by the vegetation itself. For example, detailed field measurements have revealed that the upper soil layer of forest patches has higher humus and moisture content than that of the grasslands. Also, forest patches have been shown to possess the ability to increase daytime air humidity and to mitigate daily temperature extremes.

According to a widely accepted scheme, three basic ecological phenomena have prominent roles in shaping vegetation: competition, stress, and disturbance. In this framework, each plant species faces an evolutionary trade-off among (1) developing high competitive strength (competitors, C), (2) withstanding environmental stress (stress tolerators, S), and (3) tolerating repeated biomass destruction (ruderals, R). This view proposes that plants have to pass a filter that favours competitors, stress tolerators, or ruderals in productive, harsh, or disturbed environments, respectively.

The aim of the present work was to reveal the dominant strategies of the vegetation types of sandy forest–steppes, and to infer their assembly processes. Our hypothesis was that in the more productive environment of forest patches, competitive exclusion would be the dominant force driving community composition, while under the harsher conditions of grasslands, stress would be the most important driver.

The study was carried out at 13 sites in the Kiskunság Sand Ridge (Hungary), where the mean annual temperature is 10.0–10.7°C, the mean annual rainfall is 520–580 mm, and the vegetation is represented by near-natural forest-steppe mosaics growing on calcareous sand dunes with humus-poor sandy soils. At each site, eight habitat types were sampled: large poplar-juniper forest patches (>0.5 ha), medium poplar-juniper forest patches (0.2–0.4 ha), small poplar-juniper forest patches (<0.1 ha), north-facing forest edges (peripheral zones of forest patches reaching out of the outermost tree trunks but still below the canopy), south-facing forest edges (using the same edge definition), closed perennial grasslands, open perennial grasslands, and open annual grasslands. Forest interiors and grasslands were sampled with 5 m × 5 m plots, while 2 m × 12.5 m plots were used to sample forest edges. A total of 494 plots was established: 60 plots in large forest patches, 64 plots in medium forest patches, 60 plots in open annual grasslands, 50 plots in closed perennial grasslands, and 65 plots in each of the other vegetation types. The cover of all vascular plant species was visually estimated in each plot in spring (April–May) and summer (July–August). In each plot, the higher cover value for each species was then applied for data analyses.

Three leaf traits were used to determine the strategy of each species: leaf area (LA, mm^2), leaf dry matter content (LDMC, mg/g), and specific leaf area (SLA, mm^2/mg). For each species, separate C, S, and R values, representing the strategy of the given species, were calculated.

To analyse the compositional relations among the habitats, we applied detrended correspondence analysis (DCA), using the square-root-transformed cover scores. The mean strategies (defined by the mean C, S and R values) per plot were calculated based on both unweighted (i.e., presence-absence) and square-root-transformed cover-weighted data, and visualised using ternary graphs. To study how ecological strategies correlate with the gradient, linear regression was used between the first DCA scores and each strategy. Linear mixed-effect models were used to evaluate the differences among the strategies of the studied vegetation types.

The DCA ordination showed that the first DCA scores can be interpreted as a compositional gradient (Fig. 2 on page 5). The ternary plot based on unweighted data revealed that the habitats were dominated by the S strategy (Fig. 3 on page 6). The ternary plot based on weighted data showed very similar results (Appendix S2 in the Supporting information).

Using unweighted data, the scores of the sample plots on the first DCA axis were negatively associated with the C strategy (Fig. 4a on page 6), positively associated with the S strategy (Fig. 4b on page 6), while a weak but positive relation was observed with the R strategy (Fig. 4c on page 6). Large and medium forest patches had the highest component C, which gradually decreased towards the other end of the vegetation gradient (Fig. 4d on page 6). Component S was high along the whole gradient but showed a gradually increasing trend from large forest patches to open annual grasslands (Fig. 4e on page 6). Open perennial grasslands and open annual grasslands had the highest component R, while north-facing edges had the lowest component R (Fig. 4f on page 6). Results were generally similar with weighted values (Appendix S4 in the Supporting information), although component S had a more equal distribution along the gradient for weighted than for unweighted values, and the relationship proved to be hump-backed. Also, component R changed more strongly along the gradient for weighted than for unweighted values.

Each habitat type studied in the present work was dominated by the stress-tolerator strategy, which likely reflects the harsh environmental conditions prevailing in the sandy forest-steppes of the study region (unproductive and variable environment characterised by low precipitation with high interannual variations and frequent summer droughts, exacerbated by the low water retention capacity of the sandy soils).

However, although each habitat examined in the present work was dominated by the stress-tolerator strategy, marked differences among the habitats were revealed by our study. Most notably, competition was important in large and medium forest patches, and its importance progressively decreased towards the other end of the gradient. In contrast, the stress-tolerator strategy exhibited an opposite trend. This suggests that the forests of the study region are less harsh and more productive than grasslands, while forest edges have intermediate environments. Thus, in line with ecological theory and some earlier studies, our results suggets that a shift in the importance of abiotic versus biotic factors can be expected along productivity gradients: abiotic constraints become more important toward the harsh end, while the importance of competition increases toward the more productive end of the gradient.

When using weighted instead of unweighted values, the hump-backed shape of the curve of component S suggests that stress loses some importance toward the endpoints of the gradient, likely because competition is important in large and medium forest patches, while disturbance playes an important role in open annual grasslands.

In sum, our hypothesis that community assembly would be dominated by competitive exclusion in the forest patches and by stress (i.e., environmental filtering) in grasslands was supported only partly. While the importance of competition proved to be larger in woody habitats (i.e., forests and edges) than in grasslands, stress (and consequently, environmental filtering) played the dominant role in each of the studied vegetation types (Fig. 5 on page 8). Disturbance had a considerable importance in the open perennial and the open annual grasslands.

Based on the drying tendency projected for the Kiskunság Sand Ridge, we expect that environmental filtering, which already dominates the assembly of the plant communities in the study region, will increase in importance during the 21st century.

6 Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics (Erdős et al. 2018b)

Homogenisation is a world-wide phenomenon that presents an increasing challenge to conservation. Forest-steppes are threatened by different forms of homogenisation. On the one hand, afforestation, the spread of invasive trees or the encroachment of native woody species threatens grassland patches, while in other places the woody component is at risk due to aridification, overgrazing, or mechanised mowing. The conservation importance of habitat heterogeneity has been relatively well studied in agricultural and agroforestry landscapes, whereas it has received less scientific attention in natural or near-natural forest-grassland mosaics, including forest-steppes.

The aim of the present work was to explore how individual habitats, both woody and herbaceous, contribute to the overall conservation value of the entire mosaic. Our specific questions were the following: (1) If we intend to protect the entire species pool of the mosaic, is it enough to conserve one or a few keystone habitats, or is it necessary to conserve all of them? (2) What is the importance of individual habitats regarding conservation-related characteristics (species richness, diversity, the number of species with special conservation relevance, naturalness, tree size-classes and recruitment, non-native trees)? (3) What environmental heterogeneity underlies the observed vegetation pattern?

The study was conducted in the Kiskunság Sand Ridge (Hungary). Three study sites were selected, where the mean annual temperature is 10.3–10.5 °C, and the mean annual precipitation is 520–550 mm, the soils are sandy soils that developed on calcareous sand dunes. The vegetation consists of a mosaic of woody and herbaceous components. At each site, six habitat types were sampled: large poplar-juniper forest patches (>0.5 ha), medium poplar-juniper forest patches (0.2–0.4 ha), small poplar-juniper forest patches (<0.1 ha), north-facing forest edges (peripheral zones of forest patches reaching out of the outermost tree trunks but still below the canopy), south-facing forest edges (using the same edge definition), and open perennial grasslands. A total of 90 plots was sampled (3 sites × 6 habitats × 5 replicates). Plot size was 25 m^2 (2 m × 12.5 m at edges and 5 m × 5 m in the other habitat types). Within each plot, the percentage cover of all vascular plant species was visually estimated in April and July, and for each species in each plot, the highest cover value was used for data analyses. All tree individuals were inventoried in the plots, and the diameter at breast height (DBH) was measured for trees exceeding the height of 1.3 m.

Microclimate variables and soil moisture content were measured in 30 plots (6 habitats × 5 replicates) at the Fülöpháza site. Air temperature (°C) and relative air humidity (%) were measured synchronously for 24 h at 25 cm above the ground surface in the centre of each plot, from August the 3rd to August the 4th, under clear weather conditions. Soil moisture measurement was carried out for the upper 20 cm layer on July the 26th (five measurements for each plot).

To examine the compositional relations of the six habitat types, non-metric multidimensional scaling (NMDS) was performed, using Bray-Curtis dissimilarity on the square-root transformed cover scores. To identify the diagnostic species of the habitats, we calculated the phi coefficient as indicator of fidelity. For each plot, the following variables were calculated: species richness, Shannon diversity, the number of species with special conservation relevance (protected, endemic, red-listed, and specialist species), and mean naturalness. This latter was calculated as the unweighted (i.e., not cover-weighted) mean of the relative naturalness indicator values of all species occurring in a given plot. Relative naturalness indicators reflect species' tolerances to habitat degradation. The six habitat types were compared based on the above variables using linear mixed-effects models. Tree size-class distribution was studied using 5 cm diameter classes. Stand characteristics (e.g., mean and maximum DBH and number of trees per ha) were calculated for both native and non-native species separately.

Using the measured environmental data, the following variables were calculated: daily air temperature, mean daytime air temperature, mean nighttime air temperature, mean daily relative air humidity, mean daytime relative air humidity, mean nighttime relative air humidity, and mean soil moisture. To assess the relationships between these variables and vegetation, a distance-based redundancy analysis (db-RDA) was conducted, using Bray-Curtis dissimilarity on the square-root transformed cover scores.

The NMDS showed that grassland plots formed a distinct group in the ordination space, while the other habitas overlapped considerably (Fig. 2 on page 75).

Large forest patches harboured seven diagnostic species, most of which were native shrubs (e.g., *Cornus sanguinea*, *Prunus spinosa*). Medium forest patches had two diagnostic species, both of them native shrubs (*Crataegus monogyna* and *Berberis vulgaris*). Small forest patches had seven diagnostic species, mostly herbs (e.g., *Solanum dulcamara*, *Poa angustifolia*). North-facing edges hosted ten diagnostic species (e.g., *Carlina vulgaris*, *Polygala comosa*). South-facing edges had ten diagnostic species (e.g., *Koeleria glauca*, *Poa bulbosa*), of which they shared four species with the grassland. Grasslands contained twenty diagnostic species (e.g., *Alkanna tinctoria*, *Fumana procumbens*).

The highest species richness was observed at north-facing edges, followed by south-facing edges (Fig. 3a on page 76). Large and medium forest patches had the lowest species richness, while grasslands and small forest patches had intermediate species richness. No significant differences were found among the Shannon diversities of the studied habitats (Fig. 3b on page 76). The number of species with special conservation importance increased from the large forest patches towards the grasslands (Fig. 3c on page 76), and a similar pattern was revealed for the mean naturalness values (Fig. 3d on page 76).

The distribution of differently sized trees in the six habitats showed that the recruitment of native trees occurred mostly in south-facing edges, while the recruitment of non-native trees was concentrated in forest interiors (all forest patch sizes) and at north-facing edges (Fig. 4 and Table 1 on page 77). Large native trees (DBH > 50 cm) were found primarily in large and medium forest patches.

The db-RDA indicated that forests had higher soil moisture and daily mean air humidy values and lower daily mean temperature values than grasslands, while edges were mostly intermediate (with north-facing edges being more similar to forest interiors) (Fig 5 on page 78).

Our results clearly show that all studied habitats deserve special consideration in conservation, as all of them contribute considerably to the overall value of the whole mosaic. All six habitats have their typical species composition and all habitats possess some species that are significantly concentrated within them but rare in the other habitats. Forest edges, especially north-facing ones have the highest per plot species richness, while grasslands have the highest per plot number of species with special conservation importance. South-facing edges proved to be important for tree regeneration. Medium and large forest patches contain the most large trees and several native shrub species, and are able to lessen environmental harshness and reduce the daily fluctuations in microclimate.

This study shows that, instead of focusing on either the grassland or the forest component separately, an integrated view of the forest-steppe is needed. The presence of grasslands, variously-sized forest patches, and forest edges with different orientations is a key to the high conservation value of forest-steppes.

7 Plant composition and diversity at edges in a semi-natural forest-grassland mosaic (Erdős et al. 2019a)

Forest edges are key components of many landscapes, consequently, they have received considerable attention in the ecological literature. However, the overwhelming majority of earlier studies has focused on highly anthropogenic forest edges, including those adjacent to clear-cuts and arable fields. Forest edges located in semi-natural ecosystems (i.e., ecosystems that have been modified by human activity but are still dominated by native species that establish and reproduce spontaneously) received less attention. Such semi-natural ecosystems include extensively used or recently abandoned pastures in East and Southeast Europe, which usually consist of a fine-scale mosaic of alternating forest and grassland patches.

Forest edges are often thought to have their own characteristic species composition, harbouring species from both habitat interiors alongside so-called edge-related species (i.e., species that are concentrated at edges). However, field studies supporting this view are surprisingly scarce. The biodiversity of forest edges forms a hotly debated topic: while some authors expect increased edge diversity compared to habitat interiors, other experts claim that this should be the case only for certain edge types (e.g., old and blurred edges with stable environmental factors). Generalisations are hampered by the fact that earlier case studies typically compared forest edges to forest interiors, but failed to include the adjacent treeless habitat in the analysis. Differently exposed edges are thought to differ regarding species composition, diversity, and environmental factors, with the most pronounced differences expected between south-facing and north-facing edges.

This study investigated north- and south-facing forest edges in relation to the neighbouring forest and grassland habitats in a semi-natural mosaic ecosystem. Our study questions were as follows: (1) Do edges have a characteristic species composition that differs from that of the forest and grassland interiors? (2) Do edges have their own edge-related species that are absent or rare in habitat interiors? (3) Do edges have larger species richness and Shannon diversity compared to forest and grassland interiors? (4) Does the proportion of phytosociological preference groups differ between habitat interiors and edges? (5) Do the mean ecological indicator values of edges and habitat interiors indicate different environmental conditions? (6) Are there significant differences between north-facing and south-facing edges considering the above characteristics?

The study was performed in the Samobor Mountains (Croatia), on a south-facing slope, at an elevation of 370–410 m asl. The mean annual temperature is 11 °C, and the mean annual precipitation is 1015 mm. The bedrock is dolomite and the soil is rendzina. The vegetation is a mosaic of thermophilous pubescent oak-hophornbeam forest patches ca. 0.02–0.2 ha in size, and meso-xerophytic basiphilous grassland dominated by *Bromus erectus*.

For the study, twenty forest patches were selected. For each patch, four 2 m × 1 m plots were set up in the following arrangement, corresponding to four different habitats: one plot in the forest patch interior, one plot at the north-facing forest edge, one plot at the south-facing forest edge, and one plot in the adjacent grassland. Edge was defined as the zone outside of the outermost tree trunks but still under the canopy. The percentage cover of all vascular plant species was visually estimated in May.

Detrended correspondence analysis was performed to study the compositional relations among the four habitats, using the square-root transformed cover scores. Diagnostic species of the four habitats were identified by calculating the phi coefficient as an indicator of fidelity. For each plot, we calculated species number, Shannon diversity, and the mean ecological indicator values for soil moisture, light availability, and nutrient supply. All species were categorised into phytosociological groups according to their phytosociological preferences based on literature data. The four habitats were compared based on the above characteristics.

The DCA ordination showed that forest plots and grassland plots formed two clearly separated groups, while edge plots were situated in an intermediate position (Fig. 2 on page 284). North- and south-facing edges showed considerable overlap in the scattergram.

The number of significant diagnostic species was 16 for forests, 11 for grasslands, 10 for north-facing edges, and 5 for south-facing edges (Table 1 on page 285). Interestingly, among the species that proved diagnostic for forest edges, only two species (*Peucedanum cervaria* and *P. oreoselinum*) are regarded as edge-related by the regional phytosociological literature used for our categorisation.

In the total (pooled) dataset, north-facing edges had 93 species, south-facing edges contained 88 species, while 88 species were found in the forests, and 61 species were registered in the grasslands. At the plot scale, north-facing edges proved to be the most species rich, while forests and grasslands had significantly fewer species per plot (Fig. 4a on page 286). South-facing edges did not differ significantly from the other habitats, although their per plot richness seemed to be higher than that of the habitat interiors.

Regarding plot level Shannon diversity, north-facing edges and grasslands were significantly more diverse than forests, while south-facing edges were intermediate (Fig. 4b on page 186).

The frequency distribution of the phytosociological preference groups differed significantly among edges and habitat interiors, but did not differ between north- and south-facing edges (Fig. 5 on page 286).

Forests had significantly higher moisture indicator values than the other habitats under study; grasslands seemed to have somewhat lower indicator values than edges, but no significant difference was revealed in these comparisons (Fig. 6a on page 287). Regarding the indicator values for light availability, forests had the lowest and grasslands the highest values, while edges proved to be intermediate (Fig. 6b on page 287). Finally, indicator values for nutrient supply were the highest in forests and the lowest in grasslands, with edges being intermediate (Fig. 6c on page 287). No significant differences in mean indicator values could be detected between north- and south-facing edges.

Our study confirmed that forest edges have a specific plant species composition that differs from that of the forest and grassland habitats. Thus, it is justified to treat edges as unique communities in their own right. We managed to show that edges had their own species, i.e., species that significantly preferred edges while being rare in, or completely absent from, habitat interiors. Interestingly, species that are regarded as edge-related in the regional phytosociological literature were under-represented among the significant edge diagnostic species revealed in our study. This indicates that regionally identified edge species do not necessarily correspond to the edge species found at a specific site; species that are common in habitat interiors at some sites may be restricted to edges at other sites, and vice versa.

Increased diversity of edges could be confirmed only partly. Both the total (pooled) and the per-plot species richness were the highest at north-facing edges, while this was not the case for south-facing edges. Regarding Shannon diversity, north-facing edges were not more diverse than grasslands, while south-facing edges did not significantly differ from any other habitat under study. This clearly indicates that increased diversity at edges is not a general phenomenon and may depend, among others, on edge orientation, the scale of the study, as well as the diversity metric applied.

8 Non-native tree plantations are weak substitutes for near-natural forests regarding plant diversity and ecological value (Ho et al. 2023a)

Globally, tree plantations make up ca. 3% of all tree-covered areas, but their area is increasing rapidly. The last two centuries have witnessed a marked decline in natural and near-natural forests and a rapid increase of tree plantations in eastern Central Europe. However, it is not sufficiently known to what extent plantations of native and non-native tree species are able to substitute near-natural forests in terms of different aspects of diversity (taxonomic, functional, and phylogenetic) and ecological value.

The aim of this study was to compare the species composition, diversity, and ecological value of near-natural forests with those of various types of tree plantations (native deciduous, non-native evergreen, and non-native deciduous) in the Kiskunság Sand Ridge (Hungary), a region that has lost most of its natural forests to tree plantations. Our specific questions were as follows: (1) How similar or dissimilar is the species composition of the habitats under study? (2) How do taxonomic, functional, and phylogenetic diversity vary among the studied habitat types? (3) What is the ecological value of the near-natural forests and different plantations considering protected, endemic, and red-listed species, as well as naturalness status?

The study was conducted at nine sites of the Kiskunság, where remnants of the natural forest-grassland mosaic vegetation are embedded in a matrix of tree plantations and agricultural areas (Fig 1 on page 3). At each site, the following four habitat types were sampled: near-natural *Populus alba* forests, plantations of the native *P. alba*, plantations of the non-native *Pinus nigra*, and plantations of the non-native *Robinia pseudoacacia*. The vegetation was sampled in 5 m × 5 m plots, in which the percentage cover of all vascular plant species was visually estimated in spring (April–May) and summer (July–August); for each species in each plot, the larger cover value was used for data analyses. In this study, only the herb and the shrub layers were taken into account.

Non-metric multidimensional scaling (NMDS) was performed to compare the species composition of the four habitat types, using Bray-Curtis dissimilarity on the square-root transformed cover values. Diagnostic species of the four habitats were identified by calculating the phi coefficient as an indicator of fidelity. For each plot, the following variables were calculated: number of native species; number of non-native species; Shannon diversity; functional diversity; phylogenetic diversity; and mean naturalness. Rao's quadratic entropy (RaoQ) was calculated as a measure of functional diversity and phylogenetic diversity. The following nine traits were used for functional diversity: start of flowering, flowering duration, specific leaf area, mean plant height, thousand seed mass, life form, seed dispersal, pollination type, and reproduction type (Table 1 on page 4). Plot-level mean naturalness was calculated as the unweighted (i.e., not cover-weighted) mean of the relative naturalness indicator values (values that reflect species' tolerances to habitat degradation) of all species occurring in a given plot. The four habitat types were compared according to the above variables using linear mixed-effects models. Finally, a Venn-diagram was prepared to visualise how many species with special conservation importance (protected, endemic, and red-listed species) are restricted to a single habitat type, and how many occur in two or more habitats.

The highest total (i.e., pooled) species number (126 species) was found in near-natural forests, followed by plantations of *Populus alba* (117 species). *Pinus nigra* and *Robinia pseudoacacia* plantations had 83 species each.

The NMDS showed considerable compositional differences among the four habitat types, although overlaps did exist, particularly between *Populus alba* and *Pinus nigra* plantations (Fig. 2 on page 5).

Near-natural forests had 20 diagnostic species, all of them native, and many of them shrubs (Table 2 on page 5). *Populus alba* plantations possessed 12 diagnostic species, most of which were non-native species. *Pinus nigra* plantations had only one diagnostic species, while *Robinia pseudoacacia* plantations had 13 diagnostic species, among which there were several native weeds and some species that are typical in open grasslands.

The per-plot number of native species was the highest in near-natural forests, followed by *Populus alba* plantations, while non-native tree plantations contained the fewest native species per plot (Fig. 3a on page 6). The per-plot number of non-native species was the highest in *Populus alba* plantations and the lowest in near-natural forests, although this latter did not differ significantly from *Pinus nigra* plantations (Fig. 3b on page 6). *Robinia pseudoacacia* plantations had the lowest plot-level Shannon diversity, while there were no significant differences in this variable among the other three habitat types (Fig. 3c on page 6). Functional diversity was also the lowest in *Robinia pseudoacacia* plantations, while no significant differences were revelaed among the other habitat types (Fig. 3d on page 6). Near-natural forests had the highest phylogenetic diversity, although there was no significant difference compared to *Pinus nigra* plantations (Fig. 3e on page 6). Phylogenetic diversity was the lowest in *Robinia pseudoacacia* plantations. Near-natural forests had the highest and *Robinia pseudoacacia* plantations the lowest naturalness, while the other habitats were intermediate (Fig. 3f on page 6).

Of the 14 species with high conservation importance found in this study, near-natural poplar forests contained 12 species, and six of them were restricted to this habitat type. Seven species with high conservation importance were found in *Populus alba* plantations (one of them was restricted to this habitat), five in *Pinus nigra* plantations (one of them restricted to this habitat), and only one species in *Robinia pseudoacacia* plantations (none restricted to this habitat) (Fig. 4 on page 6).

The compositional differences revealed among the studied habitats can be explained by two sets of factors. First, forestry activities may directly be responsible for the differences between the near-natural forests (with no forestry) on the one hand, and all other types (plantations with forestry) on the other hand. This also offers an explanation for the presence of many native shrubs among the diagnostic species of the near-natural forests. Second, the dominant tree species are able to alter their environment (e.g., soil, microclimate) in a way that affects the species composition of the habitat. The compositional differences among the near-natural forests and the tree plantations may have serious influence on ecological functions. For instance, native shrubs significantly related to near-natural forests can provide habitat, food source, and hiding or nesting place for several animals, while these functions are compromised in tree plantations.

Near-natural forests proved to be ecologically more valuable than any of the studied plantations due to a combination of the high number of native and low number of non-native species, as well as high Shannon diversity, functional and phylogenetic diversity and naturalness, and the high number of protected, red-listed, and endemic species (Table 3 on page 8).

Among the three plantations included in this study, *Populus alba* plantations proved to be the most valuable option in most respects, but they harboured the highest number of non-native species. Therefore, *Populus alba* should be preferred to non-native tree species if the creation of new plantations is unavoidable due to legal or economic reasons. These native plantations could also serve as buffers around, and as green corridors between, near-natural forests and nature reserves.

In this study, plantations of non-native trees, especially *Robinia* plantations, performed poorly in most respects. *Robinia* and *Pinus* plantations cover huge areas in the region (ca. 31 and 20% of all tree-covered surface, respectively), which is undesirable and should be gradually decreased in the long run to reach a more sustainable and ecologically sound state for the Kiskunság Sand Ridge.

9 Oak regeneration at the arid boundary of the temperate deciduous forest biome: insights from a seeding and watering experiment (Erdős et al. 2021)

Pedunculate oak (*Quercus robur*) belongs to the most important trees in European temperate deciduous forests, where the regeneration of the species typically depends on open or semi-open sites such as hedges, forest edges, shelterwoods, openings, and grasslands. While the regeneration of pedunculate oak has received considerable scientific attention in the deciduous forest biome, regeneration patterns in forest-steppes are largely unstudied.

The objective of this study was to understand the effects of different habitats (forest interior, forest edge, and grassland) and watering on oak seedling emergence and early seedling performance in a forest-steppe ecosystem, where growing season precipitation strongly constrains woody vegetation. We hypothesised that oak seedling emergence and performance would be positively affected by water addition, particularly in grasslands. In addition, our hypothesis was that seedling emergence and performance would be high in grasslands (only when watered) and at forest edges, but lower in forest interiors, due to light limitation.

The study was carried out in a forest-steppe mosaic near Fülöpháza (Kiskunság Sand Ridge, Hungary) (Fig. 1a on page 591). We collected *Quercus robur* acorns in October 2015 from a nearby stand of mature oaks. To exclude acorns with reduced viability, visual inspection and a float test was carried out. Sixteen sites were selected within a ca. 400 m × 1100 m area. At each site, three habitats were distinguished: forest interior (within the forest patch, 10 m from the forest edge), forest edge (the zone outside of the outermost tree trunks but still under the canopy, on the north-facing side of forest patches), and grassland (an adjacent treeless area, 10 m from the edge). At each habitat, two 0.5 m × 0.5 m plots were established in a row parallel to the forest edge. Within both plots, three acorns were planted at a depth of 2 cm in November 2015 (Fig. 1b on page 591). In total, 288 acorns were used in the experiment (16 sites × 3 habitats × 2 plots × 3 acorns). At each site and habitat, two precipitation treatments were applied: one plot received ambient precipitation (control), while the other plot received additional watering ten times between April and September in 2016 (15 mm precipitation each time).

Seedlings were censused every two or three weeks during the first year. Seedling performance was assessed towards the end of the growing season of the first and the fourth years (in September 2016 and September 2019, respectively), by recording the following information for each plot: (1) the number of living seedlings, (2) the number of leaves per living seedling, and (3) the height of the living seedlings.

During the growing season of 2016, the soil moisture content of the upper 20 cm was measured every two or three weeks, once before watering at each site, and once five hours after the watering at three a priori chosen sites. The Leaf Area Index (LAI) of the woody canopy was estimated above the herbaceous layer (25 cm) in each plot in July 2016. The total percentage cover of the herb layer in the 0.5 m × 0.5 m plots was visually estimated in September 2016.

The abiotic conditions of the treated and untreated plots in the three habitat types were compared by applying linear mixed-effects models. A generalised mixed-effects model with binomial distribution was used to assess seedling numbers. The effect of habitat type and watering on the leaf number and height of the seedlings in 2016 and 2019 were assessed by using linear mixed-effects models.

The cover of the herb layer did not differ significantly between the grassland and the forest edge habitats, but it was significantly lower in the forest interior habitat (Fig. 2a on page 594). The LAI of the woody canopy was the lowest in grasslands, the highest in the forest interiors, and intermediate at the forest edges (Fig. 2b on page 594). Soil moisture content was the lowest in grasslands, while it was higher at the forest edges and in the forest interior habitats, which latter two habitats did not differ significantly (Figs. 2c and 2d on page 594; control plots).

Watering significantly increased soil moisture content in all three habitats shortly after watering (Fig. 2c on page 594). By ca. 2 weeks after watering, this increased soil moisture had disappeared in the grassland and at the forest edge, but remained detectable in the forest interior habitat (Fig. 2d on page 594).

Seedling emergence rate was low in grassland habitats (on average 0.3 seedlings emerged out of the 3 acorns), and was significantly higher (on average 2.5 out of 3) at forest edges and in forest interiors (Fig. 3a on page 596), and these latter two habitats did not differ significantly from each other in this respect. Water addition had no effect on emergence rate (Fig. 3a on page 596). Seedling survival was very low in grasslands (none of the seedlings survived by 2019), and it was significantly higher at forest edges and in forest interiors (which two habitats did not differ from each other in this respect) (Figs. 3b and 3c on page 596). Water addition did not affect seedling survival (Figs. 3b and 3c on page 596).

No difference was detected between the forest edge and the forest interior habitats regarding the leaf number of the seedlings in September 2016 (Fig. 4a on page 597), while seedlings at forest edges had more leaves than seedlings in forest interiors in September 2019 (Fig. 4b on page 597). Seedlings were taller in the forest interior than at the edge in 2016 (Fig. 4c on page 597), but there was no difference in plant height between forest edges and forest interiors in 2019 (Fig. 4d on page 597). Watering had no significant effect on leaf number and plant height either in 2016 or in 2019. Seedlings grew very little from 2016 to 2019, and they were still short and had only few leaves at the age of four years.

In contrast to our first hypothesis, watering did not improve oak seedling emergence and performance at any of the studied habitat types. Our second hypothesis was not supported by the results either. In contrast to the deciduous forest biome, where pedunculate oak most often regenerates in open or semi-open habitats, seedling emergence and survival were extremely low in the grassland habitat in our study. No negative effect of the forest interiors compared to forest edges could be detected on seedling numbers and performance, despite previous studies emphasising the very low shade tolerance of oak seedlings. We conclude that patterns of early oak regeneration differ between forest-steppes and the deciduous forest biome, probably because there is a shift from light limitation in the deciduous forest biome to other limiting factors in forest-steppes.

In Western Europe, pedunculate oak is able to colonise treeless habitats such as ploughlands, heathlands, grasslands, and bramble thickets. On the other hand, many studies from the Mediterranean region indicate that various oak species have poor regeneration in open habitats, probably because of water limitation. These findings are in good agreement with our results. In addition to water limitation, the lack of a humus layer, high solar radiation, and microclimatic extremes might also have contributed to poor seedling emergence and survival in the grassland habitat.

The similarity of forest interiors and forest edges regarding oak seedling emergence and performance may be surprising, given the high light requirements of pedunculate oak seedlings. The explanation for this finding may be that oak seedlings tolerate shade during the first few years of their lives. A second cause is offered by the fact that forests in our study region have open canopies, thus enough light may be able to reach the forest floor to support oak seedlings. Third, we think that, compared to the deciduous forest biome, water limitation plays a much more important role in forest-steppes, which may also explain the extremely small size of the 4-year old oak seedlings.

10 Forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity (Ho et al. 2023b)

Vegetation edges have a disproportionately high importance in ecosystems that consist of a mosaic of forest and grassland patches. However, while anthropogenically created edges have been intensively studied in the last couple of decades, natural and near-natural edges have received less attention. Appropriate field studies are still scarce and usually inconsistent, making generalisations hard.

The aim of this study was to scrutinise how the species composition and diversity of edge habitats are related to those of the forest and grassland interiors in two forest-steppe ecosystems. Our questions were as follows: (1) Do edges differ from habitat interiors regarding species composition? (2) Do edge-related species (i.e., species that prefer edges and are rare or absent in habitat interiors) exist? (3) Are there detectable differences between the edges and habitat interiors regarding taxonomic, functional, and phylogenetic diversity?

The study was carried out at two sandy forest-grassland mosaics of the Carpathian Basin: the Kiskunság Sand Ridge (Hungary), which is located in the central part of the Basin, and the Deliblato Sands (Serbia), which is situated at the southern edge of the Basin (Fig. 1 on page 3). Mean annual temperature is 10.0–10.7 °C and mean annual precipitation is 520–580 mm in the Kiskunság. The site selected for our study is located north of the town of Kiskunhalas. In the Deliblato, mean annual temperature is 12.5 °C, mean annual precipitation is 664 mm. The site selected for our study was southeast of Šušara village.

Four habitat types were differentiated at both sites: forest patches (>0.5 ha), north-facing forest edges, south-facing forest edges, and grasslands. Forest edge was defined as the peripheral zone of a forest patch, out of the outermost tree trunks but still below the tree and/or shrub canopy. A total of 80 plots was established (4 habitats × 10 replicates × 2 study sites). We used 5 m × 5 m plots in the forests and grasslands, while 2 m × 12.5 m plots were used at forest edges to avoid their extension into the forest or grassland interiors. The percentage cover of each vascular plant species within each plot was visually estimated in spring (April) and summer (July), and the larger value for each species in each plot was used for data analyses.

To compare the species composition of the four habitat types, non-metric multidimensional scaling (NMDS) was performed on the square-root transformed cover values using Bray-Curtis dissimilarity. Diagnostic species of the four habitat types were identified in the Kiskunság and the Deliblato, relying on the phi-coefficient as an indicator of fidelity. For each plot, we calculated species richness, Shannon diversity, functional diversity, and phylogenetic diversity (this latter was computed for all species and then also for angiosperms only). Rao’s quadratic entropy (RaoQ) was used for both functional and phylogenetic diversity. The overall (i.e., multi-trait) functional diversity per plot was calculated based on nine traits: flowering start, flowering duration, specific leaf area, mean plant height, thousand seed mass, life form, seed dispersal, pollination type, and reproduction type. Functional diversity was also calculated for each single trait separately. To remove the impact of species richness on RaoQ, the standardised effect size of RaoQ (SES.RaoQ) was calculated. The four habitat types in the two study sites were compared based on species richness, Shannon diversity, functional and phylogenetic diversity, using the Kruskal-Wallis test.

The NMDS ordinations revealed that edges were distinct from both forest and grassland interiors at both sites (Fig. 2 on page 5). North-facing and south-facing edges overlapped considerably but were still significantly different.

Grasslands had the highest number of diagnostic species, whereas forests and south-facing edges had the fewest diagnostic species both in the Kiskunság (13, 4, and 4 species, respectively) and in the Deliblato (20, 7, and 7 species, respectively). The number of diagnostic species was intermediate at north-facing edges, with 8 and 11 species in the Kiskunság and the Deliblato, respectively (Tables S4 and S5 in the Supporting information).

Forest patches had the lowest species richness at both sites (Fig. 3a on page 6). In the Kiskunság, north-facing edges had the highest per-plot species-richness, while the species richness of south-facing edges and grasslands was intermediate. Surprisingly, there was no significant difference between the species richness of edges and that of grasslands in the Deliblato. Edges and grasslands contained significantly more species per plot in the Deliblato than in the Kiskunság. Shannon diversity showed generally similar patterns (Fig. 3b on page 6).

The overall functional diversity was significantly higher in woody habitats (i.e., in forest patches and at edges) than in grasslands in the Kiskunság, while it did not differ among the four habitat types in the Deliblato (Fig. 3c on page 6). Woody habitats of the Kiskunság had higher functional diversity than those of the Deliblato, but the grasslands of the two sites did not differ in this respect.

As for the functional diversity of single traits, there were some common patterns at the two sites. The functional diversity of seed dispersal, reproduction type, and mean plant height were mostly higher in woody habitats than in grasslands (Fig. 4b–d on page 7). The functional diversity of life form seemed to peak at the edges (although differences were not always significant) (Fig. 4e on page 7). The functional diversity of both SLA and pollination type showed a reverse pattern, peaking in forest interiors and grasslands and showing minima at the edges (although, again, between-habitat differences were not always significant) (Fig. 4f, h on page 7).

Patterns of functional diversity for flowering time and thousand seed mass differed between the Kiskunság and the Deliblato. In the Kiskunság, the functional diversity of flowering time was higher in woody habitats than in grasslands, while the opposite trend was revealed in the Deliblato (Fig. 4a on page 7). The functional diversity of thousand seed mass decreased from forests to grasslands in the Kiskunság, while the four habitat types in the Deliblato did not differ significantly in this respect (Fig. 4g on page 7).

Phylogenetic diversity was higher in forests and at edges than in grasslands at both sites when all species were considered, and also when only angiosperms were included (Fig. 3d, e on page 6).

Our results showed that forest edges have rather distinct species composition and their own set of diagnostic species that avoid habitat interiors. This reinforces the view that the forest edge deserves scientific attention in its own right.

Our findings concerning the patterns of species richness and Shannon diversity emphasise that increased taxonomic diversity at edges compared to habitat interiors (usually referred to as ‘edge effect’) is not a general phenomenon and depends on the characteristics of the two adjoining communities (e.g., soil, edge structure, characteristics of the adjacent vegetation units, etc.).

The low overall functional diversity of woody habitats in the Deliblato contradicts the stress-dominance hypothesis, which predicts high functional diversity in forests due to less harsh environmental factors. Rather, our study suggests that canopy openness and traits of the dominant trees have a profound influence on the functional diversity of woody habitats.

The high phylogenetic diversity of woody habitats probably reflects their longer evolutionary history compared to grasslands, which are considerably younger.

Our work emphasises that more studies are needed on diversity patterns of natural and near-natural forest-grassland mosaics. These studies should consider forest, edge, and grassland habitats simulatneously, and focus on multiple aspects of diversity (taxonomic, functional, and phylogenetic).

11 Forest encroachment in Eastern European forest-steppes at a decadal time scale (Erdős et al. 2024b)

In forest-grassland mosaic ecosystems, the balance between the woody and herbaceous components substantially influences key ecosystem properties. However, studies on how the forest versus grassland proportion is changing at the decadal time scale in the Eurasian forest-steppe are extremely scarce. In this study, we compared old and recent aerial photographs of near-natural forest-steppe mosaics in the Kiskunság Sand Ridge. Our goal was to find out whether and how the forest proportion and the number of forest patches have changed in forest-steppe ecosystems at a decadal time-scale.

We selected study sites according to the following criteria: (1) the land-use history was known in detail and (2) a period of at least 20 years free of major human interventions could be reliably identified. Sites were not excluded if a low level of grazing was present, because grazing is understood as a natural part of forest-steppe dynamics. Based on the above criteria, four study sites were selected: Bugac, Fülöpháza, Orgovány, and Tázlár. The climate of the sites is sub-continental, with sub-Mediterranean influences; the mean annual temperature is 10.2–10.5°C across the sites, while the mean annual precipitation is 520–550 mm. There was a significant increase in mean annual temperature at all sites between 1971 and 2019, while no significant change was detected for annual precipitation (Fig. 2 on page 5). The drying of the climate is exacerbated by processes such as irrigation from subsurface sources, drainage canals, and large-scale afforestation. The vegetation of the sites is a mosaic of poplar-juniper forests and mainly fescue-feathergrass grasslands.

The Bugac site has been protected since 1975 as part of the Kiskunság National Park. Grazing ceased here around 1930. Wildfires occurred in 1976 and 1983 as a result of nearby military activity, but the areas affected by these fires were excluded from the study. A large fire event in 2012 affected almost the whole area; therefore, the study period ended in 2009, when the last aerial photograph was taken before this wildfire. The Fülöpháza site also became protected in 1975 as part of the Kiskunság National Park. Grazing ceased in the 1970s and no wildfires have happened during the last few decades. The Orgovány site has also been part of the Kiskunság National Park since 1975. A very low grazing pressure was present and there was a large wildfire in 2000. Therefore, the study period ended in 2000, when an aerial photograph was taken prior to the fire. The Tázlár site belongs to the Natura 2000 protected area network of the European Union. It was occasionally grazed and no fires happened here. Restricted forestry activity, such as the removal of invasive trees, was present at the sites, but the areas affected were excluded from the study. Our aim was to find old photos that were taken around the beginning of the intervention-free interval, and recent photos taken around the end of the intervention-free period (Table 1 on page 4).

For sampling, the study sites were covered with a 1 ha square grid (Fig. 3 on page 6). From these grids, 10 or 15 cells per site were randomly selected. The extent of the forest vegetation in the old and the recent photos was then digitised in the 1 ha cells. Two variables were calculated for each cell: the proportion of the forest vegetation and the number of forest patches, and these variables were statistically compared between the old and the recent dates.

The area covered by forest significantly increased in all study sites (Fig. 4 on page 7). Considerable differences were found among the four sites regarding both the initial forest cover and the change in forest cover during the study periods. The initial forest cover was the lowest at the Fülöpháza site (mean: 1.22%), and it increased more than tenfold during the 44 years covered by the study. The Bugac site had the highest initial forest cover, and the mean forest cover increased here from 65.68% to 83.23% during 33 years. The Orgovány and the Tázlár sites were between the above two extremes considedring the mean initial forest cover (22.15% and 18.82%, respectively). The final forest cover values were 46.74% and 32.62%, in Orgovány and Tázlár, respectively.

The number of forest patches significantly decreased at two sites. In Bugac, the mean number of forest patches per 1 ha fell from 46 to 5.9. At the Orgovány site there was a drop from 41.1 to 20.1 patches per 1 ha (Fig. 5 on page 7). In contrast, there was a significant increase in forest patch number at the Fülöpháza site, where the mean forest patch number per 1 ha increased from 6.73 to 20.13. No significant change happened in the number of forest patches at the Tázlár site.

Our finding about increasing forest cover fits worldwide observations on current woody encroachment in several forest-grassland mosaics. Two possible explanations should be considered for the process observed in the forest-steppes of the Kiskunság Sand Ridge.

First, increasing temperature (particularly in winter) and rising atmospheric CO_2 level may have a positive influence on forests, as long as water is not limiting. Mean annual temperature shows an increasing trend in the Kiskunság Sand Ridge, but this is not accompanied by decreasing annual precipitation (Fig. 2 on page 5). It seems that the observable drop in the water-table is not able to reduce forest cover either. The dominant tree of the study sites, *Populus alba*, can tolerate very hot and dry conditions. Also, *P. alba* spreads primarily vegetatively, through horizontal roots, which may have a length of 40 m or more. The individual trees are able to allocate resources through these roots: trees growing in a very dry micro-environment may receive support from trees situated in a better micro-environment such as a dune-slack. Similarly, older trees reaching deeper and moister soil layers are able to provide water for younger saplings. These may explain why forest patches are able to withstand a certain level of aridification. Thus, the forest encroachment revealed by this study may indicate that increasing temperature and CO_2 concentration are pushing the forest-grassland balance towards a more forested landscape (Fig. 6 on page 8). To put it differently, forest area is increasing until the new (increased) potential forest cover is reached. However, increasing temperature promotes forests only until either the thermal optimum of the dominant tree species is passed, or water availability is compromised. Thus, with continuing increases in temperature, forest encroachment is expected to stop and may eventually turn into forest loss.

The second potential explanation for the current forest encroachment may be provided by the land-use history of the region. Two of our study sites were not grazed during the study period (Bugac and Fülöpháza), but they had been grazed in earlier times. The other two sites (Orgovány and Tázlár) experienced light grazing pressure during the study period, but grazing pressure must have been higher in earlier times. In the Eurasian forest-steppe, most large herbivores are either browsers (e.g., goats), or mixed grazers/browsers (e.g., cattle and sheep), thus they are able to limit forest expansion. Once grazing pressure decreases or ceases, forests are released and can invade grasslands until the potential forest cover defined by climate and soil is reached (Fig. 6 on page 8).

The fact that there was a substantial increase in the number of forest patches at the Fülöpháza site, while the reverse process happened at the Bugac and the Orgovány sites shows that forest encroachment can happen in two different ways. First, new forest patches can emerge in the grassland, which may be typical at sites where the initial forest cover is low. Second, existing forest patches extend and coalesce, which may be more typical at sites with higher initial forest cover.

Similar studies may be carried out in other sandy forest-steppes in the Eastern European region and beyond, as well as in forest-steppes growing on other types of bedrock (e.g., rocky surfaces). Analyses including a larger number of study sites, and using a fine-scale temporal and spatial resolution can provide further information on forest-steppe dynamics and its drivers.

12 Summary, conclusions, and outlook

Forest-steppes are natural or near-natural complexes of arboreal and herbaceous components in the temperate zone, where the coexistence of forest and grassland is enabled by climate, topography, soil, herbivory, fire, and feedback loops (Erdős et al. 2018a).

We delineated the forest-steppes of Eurasia, and then we divided the biome into nine regions, based on floristic composition, physiognomy, relief, and climate (Erdős et al. 2018a). Our more recent analysis based only on climate suggests that some refinement may be necessary, especially in the Far East region, which might further be sub-divided (Bede-Fazekas et al. 2023).

The results presented in this work suggest that a holistic view is necessary for a correct understanding of Eurasian forest-steppes, with simultaneous consideration of the various forest, grassland, and edge components (Erdős et al. 2018b, 2019, 2021, 2023, Ho et al. 2023b). It can be concluded that each component deserves specific attention in its own right, and each contributes differently to the overall mosaic (also see Erdős et al. 2014, 2015, Bátori et al. 2018). At the plot scale, edges (especially north-facing ones), and, in some cases, closed grasslands support high species richness, while phylogenetic diversity is high in all woody habitats (forests and edges). Functional diversity is the greatest in open-canopied forest patches and at edges with a not too dense shrub layer. Several native shrub species are signifcantly concentrated in large and medium forest patches. Open perennial grasslands were shown to have the best naturalness state and to contain the most species with special conservation importance. Edges seem to be especially important habitats for the regeneration of native tree species.

Both the analysis of ecological indicator values and instrumental measurements show that forest patches can lessen environmental harshness (Erdős et al. 2018b, 2019a, 2021, also see Erdős et al. 2014, 2020, Ho et al. 2024). This may be one reason why a recent study found that the species richness of large and medium forest patches seems to be generally less sensitive to increasing macroclimatic aridity than the richness of other habitats (Erdős et al. 2019b).

In sum, all the above works suggest that, instead of focusing on one or a few components, conservation management actions and ecological restoration projects should encourage the heterogeneity of natural and near-natural habitat types in forest-steppe ecosystems.

Not only is the restricted focus on only one component (either the grassland or the forest separately) unsatisfactory, but our results show that even the dichotomic view is an oversimplification. Instead, forest-steppes should be viewed as consisting of a variety of habitats (forest patches of different sizes, differently exposed forest edges, and various types of grasslands) that form a compositional gradient, which corresponds to gradients of multiple environmental factors (Erdős et al. 2020). Our studies have focused on forest-steppes where forest patches are dominated by *Populus alba* (or *Tilia tomentosa* in the Deliblato). **Although similar ecosystems with *Quercus robur* are extremely rare in the region (Ónodi et al. 2022), we plan to include these oak forest-steppes in our studies, using the same methodology, which will effectively complement our earlier studies outlined in this dissertation.**

We showed that tree plantations are weak substitutes for near-natural forests in the sandy forest-steppe ecosystems under study (Ho et al. 2023a). However, significant differences among different types of plantations do exist: plantations of the native *Populus alba* perform better in most respects and thus are of higher ecological and nature conservation value than plantations of the non-native *Pinus nigra* and *Robinia pseudoacacia*. We conclude that the establishment of new plantations of non-native tree species in the study region is undesirable from an ecological point of view. We reached the same conclusion based on our recent study in the Deliblato Sands, Serbia (Ho et al. 2025), and we think the same applies to other forest-steppe and steppe regions as well (e.g., Török et al. 2025).

In addition to their relevance to the ecology and conservation of Eurasian forest-steppes, the studies outlined above also provide information on some more general ecological phenomena. According to a wide-spread view, which is usually referred to as the edge effect hypothesis, forest edges are expected to have high species richness because they contain species from both adjacent habitats as well as their own species. Our work has shown that edges do in fact have their own species, although these do not necessarily coincide with species that are treated as typically edge-related in regional phytocoenological works (Erdős et al. 2018b, 2019a, Ho et al. 2023b, also see Erdős et al. 2013). However, while plot-level species richness was usually higher at forest edges than in habitat interiors, this was not always the case (and even less so for Shannon diversity) (Erdős et al. 2018b, 2019a, 2023, Ho et al. 2023b). This suggests that patterns of taxonomic diversity may also depend on edge orientation, study scale, the diversity metric applied, and the characterstics of the neighbouring habitats (e.g., whether the forest is in contact with an open or a closed grassland).

Our results point out that patterns of taxonomic, functional, and phylogenetic diversities do not necessarily coincide (Erdős et al. 2023, Ho et al. 2023a, b). Thus, instead of using one aspect of diversity as a proxy for other aspects, taxonomic, functional, and phylogenetic diversities merit careful scientific attention for a better understanding of how ecosystems work.

Moreover, functional diversity itself has three components: *functional richness* is the volume of trait space filled by the species of a given community, *functional evenness* describes how evenly this space is filled, and *functional divergence* captures how the extremities of the trait space are filled (Mason et al. 2005, Pavoine and Bonsall 2011, Mammola et al. 2021). In our earlier research, we have focused on functional divergence (measured by the RaoQ index). According to our preliminary analyses, functional richness and functional richness provide important complementary information and do not show the same pattern as functional divergence. Therefore, **we plan to include these additional aspects of functional diversity into our future forest-steppe studies.**

The stress-dominance hypothesis (Weiher and Keddy 1995) expects low functional diversity in harsh environments, where only a restricted range of traits is thought to be appropriate. According to this hypothesis, in less harsh environments, strong competition would exclude species with similar traits, resulting in higher functional diversity. While our results from the Kiskunság seemed to support the stress-dominance hypothesis (high functional diversity in forests compared to grasslands), patterns found in the Deliblato clearly contradict the hypothesis (low functional diversity both in grasslands and forests) (Erdős et al. 2023, Ho et al. 2023b), suggesting that canopy openness and the traits of the dominant trees have a profound influence on the functional diversity of woody habitats.

Despite its crucial importance for key ecosystem properties, the temporal dynamics of woody versus grassland vegetation has received very little attention in the Eurasian forest-steppe. Our results showed that there was a significant increase in forest cover at our four study sites in the Kiskunság Sand Ridge (Erdős et al. 2024b). This is in good agreement with a recent study where we analysed sand grasslands across 16 sites in the same region, and found that *Populus alba* has become significantly more frequent during the 17-year study period (Erdős et al. 2024c). We suggest that the primary reason of the process is that grazing pressure diminished or ceased completely during the 20th century, and the current woody encrachment is in fact woody regeneration until the potential forest cover allowed by climate and soil is reached. Interestingly, an earlier analysis of aerial photographs (Erdős et al. 2015) found almost no net change in forest cover during a 60-year interval. This may be connected to the fact that the small nature reserve analysed in that study has been protected from grazing since 1885, thus, forest vegetation had ample time to recover, and had already reached the climatic-edaphic potential by the starting date of the study period. **Our currently running analyses on forest-steppe dynamics rely on a whole series of aerial photographs with a 5-10 year temporal resolution (rather than only on two photos at the starting and the end of the study period). Also, this work includes a large number of replicates and also takes into account the effects of fire.** This new study will hopefully shed more light on the forest versus grassland dynamics of the study region.

13 List of publications that form the basis of the dissertation

Erdős L., Ambarlı D., Anenkhonov O. A., Bátori Z., Cserhalmi D., Kiss M., Kröel-Dulay Gy., Liu H., Magnes M., Molnár Zs., Naqinezhad A., Semenishchenkov Y. A., Tölgyesi Cs., Török P. (2018a): The edge of two worlds: A new review and synthesis on Eurasian forest-steppes. *Applied Vegetation Science* 21: 345-362. **Q1**, **IF**: 3.568

Erdős L., Ho K. V., Bátori Z., Kröel-Dulay Gy., Ónodi G., Tölgyesi Cs., Török P., Lengyel A. (2023): Taxonomic, functional, and phylogenetic diversity peaks do not coincide along a compositional gradient in forest-grassland mosaics. *Journal of Ecology* 111: 182–197. **D1**, **IF**: 5.3

Erdős L., Ho K. V., Bede-Fazekas Á., Kröel-Dulay G., Tölgyesi C., Bátori Z., Török P. (2024a): Environmental filtering is the primary driver of community assembly in forest–grassland mosaics: A case study based on CSR strategies. *Journal of Vegetation Science* 35: e13228. **Q1**, **IF**$_{2023}$: 2.2

Erdős L., Kröel-Dulay Gy., Bátori Z., Kovács B., Németh Cs., Kiss P. J., Tölgyesi Cs. (2018b): Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics. *Biological Conservation* 226: 72-80. **D1**, **IF**: 4.451

Erdős L., Krstonošić D., Kiss P. J., Bátori Z., Tölgyesi Cs., Škvorc Ž. (2019a): Plant composition and diversity at edges in a semi-natural forest-grassland mosaic. *Plant Ecology* 220: 279-292. **Q1**, **IF**: 1.509

Erdős L., Ónodi G., Tölgyesi Cs., Kröel-Dulay Gy., Bátori Z., Aradi E., Török P., Ho K. V. Puspitasari I., Körmöczi L. (2024b): Forest encroachment in Eastern European forest-steppes at a decadal time scale. *Journal of Plant Ecology* 17: rtae086. **Q1**, **IF**$_{2023}$: 3.0

Erdős L., Szitár K., Öllerer K., Ónodi G., Kertész M., Török P., Baráth K., Tölgyesi Cs., Bátori Z., Somay L., Orbán I., Kröel-Dulay Gy. (2021): Oak regeneration at the arid boundary of the temperate deciduous forest biome: insights from a seeding and watering experiment. *European Journal of Forest Research* 140: 589-601. **Q1**, **IF**: 3.140

Erdős L., Török P., Veldman J. W., Bátori Z., Bede-Fazekas Á., Magnes M., Kröel-Dulay Gy., Tölgyesi Cs. (2022): How climate, topography, soils, herbivores, and fire control forest–grassland coexistence in the Eurasian forest-steppe. *Biological Reviews* 97: 2195-2208. **D1**, **IF**: 10.0

Ho K. V., Ćuk M., Šikuljak T., Kröel-Dulay Gy., Bátori Z., Tölgyesi Cs., Fűrész A., Török P., Hábenczyus A. A., Hegyesi A., Coşgun L. Z., Erdős L. (2023b): Forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity. *Global Ecology and Conservation* 46: e02625. **Q1**, **IF**: 3.5

Ho K. V., Kröel-Dulay Gy., Tölgyesi Cs., Bátori Z., Tanács E., Kertész M., Török P., Erdős L. (2023a): Non-native tree plantations are weak substitutes for near-natural forests regarding plant diversity and ecological value. *Forest Ecology and Management* 531: 120789. **D1**, **IF**: 3.7

14 Further publications of the candidate directly related to the topic of the dissertation

Bátori Z., Erdős L., Kelemen A., Deák B., Valkó O., Gallé R., Bragina T. M., Kiss P. J., Kröel-Dulay Gy., Tölgyesi Cs. (2018): Diversity patterns in sandy forest-steppes: a comparative study from the western and central Palaearctic. *Biodiversity and Conservation* 27: 1011–1030. **Q1**, **IF**: 3.142

Bede-Fazekas Á., Török P., Erdős L. (2023): Empirical delineation of the forest-steppe zone is supported by macroclimate. *Scientific Reports* 13: 17379. **D1**, **IF**: 3.8

Erdős L., Bátori Z., Bede-Fazekas Á., Biró M., Darányi N., Magnes M., Pásztor L., Sengl P., Szitár K., Tölgyesi Cs., Kröel-Dulay Gy. (2019b): Trends in species composition and richness along a centre-to-periphery gradient in forest-steppes of the southern Carpathian Basin. *Tuexenia* 39: 357–375. **Q3**, **IF**: 1.0

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Erdős L., Ónodi G., Ho K. V., Tanács E., Akinyi R. Q., Török P., Tölgyesi Cs., Bátori Z., Kröel-Dulay Gy. (2024c): Between-year weather difference and long-term environmental trends both contribute to observed vegetation changes in a plot resurvey study. *Ecology and Evolution* 14: e70244. **Q1**, **IF**$_{2023}$: 2.3

Erdős L., Tölgyesi Cs., Cseh V., Tolnay D., Cserhalmi D., Körmöczi L., Gellény K., Bátori Z. (2015): Vegetation history, recent dynamics and future prospects of a Hungarian sandy forest-steppe reserve: forest-grassland relations, tree species composition and size-class distribution. *Community Ecology* 16: 95–105. **Q2**, **IF**: 1.019

Erdős L., Tölgyesi Cs., Horzse M., Tolnay D., Hurton Á., Schulcz N., Körmöczi L., Lengyel A., Bátori Z. (2014): Habitat complexity of the Pannonian forest-steppe zone and its nature conservation implications. *Ecological Complexity* 17: 107–118. **Q2**, **IF**: 1.931

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SYNTHESIS

The edge of two worlds: A new review and synthesis on Eurasian forest-steppes

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Abstract

Aims: Eurasian forest-steppes are among the most complex non-tropical terrestrial ecosystems. Despite their considerable scientific, ecological and economic importance, knowledge of forest-steppes is limited, particularly at the continental scale. Here we provide an overview of Eurasian forest-steppes across the entire zone: (a) we propose an up-to-date definition of forest-steppes, (b) give a short physiogeographic outline, (c) delineate and briefly characterize the main forest-steppe regions, (d) explore forest-steppe biodiversity and conservation status, and (e) outline forest-steppe prospects under predicted climate change.

Location: Eurasia (29°–56°N, 16°–139°E).

Results and Conclusions: Forest-steppes are natural or near-natural vegetation complexes of arboreal and herbaceous components (typically distributed in a mosaic pattern) in the temperate zone, where the co-existence of forest and grassland is enabled primarily by the semi-humid to semi-arid climate, complemented by complex interactions of biotic and abiotic factors operating at multiple scales. This new definition includes lowland forest–grassland macromosaics (e.g. in Eastern Europe), exposure-related mountain forest-steppes (e.g. in Inner Asia), fine-scale forest–grassland

Nomenclature: Catalogue of Life (www.catalogueoflife.org; accessed 15 Apr 2017)

mosaics (e.g. in the Carpathian Basin) and open woodlands (e.g. in the Middle East). Using criteria of flora, physiognomy, relief and climate, nine main forest-steppe regions are identified and characterized. Forest-steppes are not simple two-phase systems, as they show a high level of habitat diversity, with forest and grassland patches of varying types and sizes, connected by a network of differently oriented edges. Species diversity and functional diversity may also be exceptionally high in forest-steppes. Regarding conservation, we conclude that major knowledge gaps exist in determining priorities at the continental, regional, national and local levels, and in identifying clear target states and optimal management strategies. When combined with other threats, climate change may be particularly dangerous to forest-steppe survival, possibly resulting in compositional changes, rearrangement of the landscape mosaic or even the latitudinal or altitudinal shift of forest-steppes.

KEYWORDS
habitat complexity, landscape heterogeneity, meadow steppe, prairie, semi-arid vegetation, steppe, vegetation mosaic, wooded-steppe, woodland

1 | INTRODUCTION

Mosaic vegetation complexes consisting of woody and herbaceous patches are in the spotlight of current ecological research (e.g. Breshears, 2006; Innes, Anand, & Bauch, 2013; Prevedello, Almeida-Gomes & Lindenmayer, 2018). Forest-steppes belong to the most complex ecosystems outside the tropics in terms of composition, structure and function (Erdős et al., 2014; Walter & Breckle, 1989). While also present in North America (e.g. Leach & Givnish, 1999) and South America (e.g. Kitzberger, 2012), the largest forest-steppes are found in Eurasia.

Eurasian forest-steppes have outstanding ecological and conservation importance. They occupy large areas and appear in a wide variety of types and sub-types on various terrains (plains, hills, mountain ranges, plateaus) from the sea level up to 3,500 m a.s.l. and from sub-Mediterranean to ultracontinental to monsoon climates (Berg, 1958; Walter & Breckle, 1989; Wesche et al., 2016). Forest-steppes have a very high net primary production compared to other non-tropical systems (Pfadenhauer & Klötzli, 2014; Schultz, 2005; Zlotin, 2002), as well as a considerable biomass and C sequestration capacity (Müller, 1981; Schultz, 2005). Species diversity is also high, with many taxa of special conservation interest such as endemics, endangered species and wild relatives of cultivated plants (Bannikova, 1998; Chibilyov, 2002; Olson & Dinerstein, 1998; Zlotin, 2002). Furthermore, forest-steppes are important from an economic perspective, as they are often used as pastures and provide livelihoods for many people (e.g. Ambarlı et al., 2016; Chibilyov, 2002; Pfadenhauer & Klötzli, 2014; Smelansky & Tishkov, 2012). Unfortunately, forest-steppes are among the most threatened ecosystems due to habitat loss, fragmentation and an inadequate network of protected areas (Hoekstra, Boucher, Ricketts, & Roberts, 2005).

The scientific knowledge on Eurasian forest-steppes is relatively scattered (Bone, Johnson, Kelaidis, Kintgen, & Vickerman, 2015). Although the number of studies has increased recently, syntheses are scarce, with several limitations we outline here. First, most reviews have been conducted at national (e.g. Korotchenko & Peregrym, 2012; Molnár, Biró, Bartha & Fekete, 2012) or regional scales (e.g. Berg, 1958; Chibilyov, 2002; Dokhman, 1968; Golubev, 1965; Krasheninnikov, 1954; Lavrenko, 1980; Makunina, 2016a; Milkov, 1950, 1951, 1977), while continental-scale studies are almost entirely lacking (but see Walter & Breckle, 1989). Second, most syntheses have focused on the steppe biome, discussing forest-steppes only as a marginal topic (e.g. Lavrenko, 1980; Lavrenko, Karamysheva, & Nikulina, 1991; Nosova, 1973; Rachkovskaya & Bragina, 2012; Wesche et al., 2016). Third, the few regional and continental overviews usually neglect the forest-steppes of the Middle East and the Tian Shan-Pamir ranges (e.g. Lavrenko, 1969; Wendelberger, 1989), resulting in an incomplete view of the ecosystem.

Our aim in this paper was to provide a synthetic overview of Eurasian forest-steppes, by collecting diffuse knowledge of the entire area covered by forest-steppes. First, we provide a formal definition of forest-steppes, identifying inherent difficulties in producing an exact definition and delineation. We briefly discuss spatial extents and gradients. A substantial part of our review focuses on the delineation and brief description of the main forest-steppe regions. Then we review forest-steppe diversity in terms of habitats, species and functional traits, and outline the conservation status of forest-steppes. Finally, we explore the future prospects of forest-steppes under predicted climate change.

2 | DEFINING FOREST-STEPPES

Forest-steppes are known by different names in the literature and across different regions. In most of Eastern Europe and northern

Asia, the terms “forest-steppe” or “wooded-steppe” are used, compared to “steppe forest”, “open woodland” and “sparse arid woodland” in southwestern Asia. In this paper, we treat these terms as synonyms.

The majority of researchers mention one or more of the following points as decisive characteristics in defining forest-steppes: (a) the transitional spatial position (between closed forests and treeless steppes), (b) semi-humid to semi-arid climatic features, and (c) a mosaic-like vegetation pattern. (d) Special soil characteristics as key drivers for vegetation may be considered a fourth criterion (soil is a basic part of nearly all steppe definitions; see for example: Allan, 1946; Berg, 1958; Chibilyov, 2002; Dokuchaev, 1899; Walter & Breckle, 1989). We henceforth discuss the suitability of each of the above four points for defining forest-steppes.

- Standard forest-steppe definitions usually begin with an emphasis on the transitional spatial position of forest-steppes between closed forests (nemoral forests, taiga or Mediterranean forests) and mostly treeless true steppes (e.g. Berg, 1958; Bredenkamp, Spada, & Kazmierczak, 2002; Chibilyov, 2002; Illyés, Bölöni, Kovács, & Kállay-Szerényi, 2007; Kleopov, 1990; Lavrenko, 1980; Magyari et al., 2010; Müller, 1981; Pócs, 2000; Walter & Breckle, 1989), a description which does not apply to all regions. For example, the definition is problematic in both the Carpathian Basin and the Russian Far East, due to the lack of a southern steppe border (Fekete, Molnár, Magyari, Somodi, & Varga, 2014; Ivanov, 2002). Furthermore, forest-steppes occur not only near the northern edge of the steppe zone, but also in the steppe region of the Middle East, without necessarily forming a transition towards the closed forests (Wesche et al., 2016). For instance, in some Iranian and Afghan mountain ranges, open woodlands can be found between low-elevation semi-desert-like steppes and high-mountain thorn cushion communities (Breckle, 2007; Sagheb-Talebi, Sajedi, & Pourhashemi, 2014; Zohary, 1973). In the Qilian Mts, forest-steppes have developed above the lower (arid) timber line, but the closed forest zone is lacking due to the proximity of the upper (cold) timber line (Walter & Breckle, 1989). A simplistic definition of forest-steppe as a transitional zone between treeless steppe and closed forest may therefore be inadequate, and other factors such as topography or soil grain size should be considered.
- Climate is a key defining element for forest-steppes in many scientific publications (e.g. Chibilyov, 2002; Kleopov, 1990; Schultz, 2005; Walter & Breckle, 1989). In the temperate zone, aside from edaphic variations, humid environments are able to support forests, while primary grasslands are typical under more arid conditions (Dengler, Janišová, Török, & Wellstein, 2014). Where climate is transitional (i.e. semi-humid to semi-arid, close to neutral moisture balance), a mosaic of forests and grasslands can develop, as neither of them has a decisive advantage over the other (Berg, 1958; Borhidi, 2002; Bredenkamp et al., 2002; Budyko, 1984; Chibilyov, 2002; Djamali et al., 2011; Kleopov, 1990; Lavrenko & Karamysheva, 1993; Walter & Breckle, 1989).
- An obvious feature of forest-steppes is their mosaic-like pattern. Definitions usually refer to the macromosaic feature, i.e. the spatial alternation of large forest patches and extensive grasslands (e.g. Bredenkamp et al., 2002; Chibilyov, 2002; Müller, 1981; Walter & Breckle, 1989). However, fine-scale mosaics become typical as Mediterranean climatic influences increase (Donită, 1970; Varga et al., 2000; Wendelberger, 1989; Wesche et al., 2016; Zólyomi & Fekete, 1994). Here, individual patches may be very small. In some cases, the grassland matrix is scattered with solitary trees, which may be regarded as small forest patches (cf. Erdős, Tölgyesi, Cseh, et al., 2015). In sum, forest-steppes may appear as macro- or micromosaics, thus restricting the definition to macromosaics is not justifiable. Another recurring element of forest-steppe definitions is that the grassland component is represented by meadow steppes (e.g. Chibilyov, 2002; Kleopov, 1990; Lavrenko, 1980; Lavrenko & Karamysheva, 1993; Müller, 1981; Zlotin, 2002), i.e. rather mesic tall grasslands with numerous forbs. Several cases, most notably in regions with considerable mediterranean influences, demonstrate that the grassland component is in fact a dry grassland with short grasses, and limited number and cover of forbs. Tragacanthic species are typical, especially in the mountains of the Middle East (Akhani, 1998; Zohary, 1973).
- Generally, the steppe component of forest-steppes frequently grows on chernozem soils, and the forest component on grey forest soil (Knapp, 1979; Rychnovská, 1993; Zamotaev, 2002; Zech, Schad & Hintermaier-Erhard, 2014). Different chernozem varieties may also occur under forest patches (Berg, 1958; Wallis de Vries, Manibazar & Dügerlham, 1996). Solonetz and solonchak soils are quite usual under the steppe component (Lavrenko & Karamysheva, 1993; Müller, 1981; Sochava, 1979; Walter & Breckle, 1989), and solonetz occasionally occurs under forests (Horvat, Glavač, & Ellenberg, 1974; Molnár & Borhidi, 2003). Planosols may support *Betula* stands, while podzols can be found under *Pinus* stands (Berg, 1958; Rachkovskaya & Bragina, 2012). On chestnut soils, both forest patches and steppes can develop (Berg, 1958; Shahgedanova, Mikhailov, Larin & Bredikhin, 2002; Tamura, Asano & Jamsran, 2013; Zhu, 1993). Gley soils are typical of *Larix* forests of Inner Asian mountains with permafrost (Shahgedanova et al., 2002; Walter & Breckle, 1989). Under a strong mediterranean climatic influence, in the Middle East (e.g. Turkey, Iraq, Iran), sierozems are widespread (Kürschner & Parolly, 2012; Singh & Gupta, 1993). For more detail on soil types in the forest-steppes, see also Schultz (2005) and Zech et al. (2014).

Based on the reviewed criteria we argue that a broad yet accurate definition of forest-steppes requires both climatic (semi-humid to semi-arid) and physiognomic (a mosaic of arboreal and herbaceous components) features. In the climatic range where neither closed forest nor treeless grassland is favoured, both have a roughly equal chance to develop. Competition outcomes usually depend on local factors such as aspect, microclimate or soil (e.g. Anenkhonov et al., 2015; Borhidi, 2002; Hais, Chytrý, & Horsák, 2016; Liu et al., 2012; Mayer, 1984; Walter & Breckle, 1989). When the distribution of forest-steppe is determined primarily by macroclimate, the forest-steppe is zonal. However, forest-steppes may also develop outside this transitional climatic range, provided that local factors modify water availability so that neither component has a competitive advantage. For example, in a region of sufficient humidity to support forests, soils with an extremely low water retention capacity or steep south-facing slopes with a warm microclimate may result in a forest–grassland mosaic. In this case, the forest-steppe is considered extrazonal.

Many additional drivers contribute to the dynamics of the forest-grassland co-existence. The interplay of climate, competition, facilitation, fire, grazing and browsing in maintaining the vegetation mosaic is as yet not fully understood for complex forest-grassland ecosystems (e.g. House, Archer, Breshears, Scholes, & Tree-Grass Interactions Participants, 2003; Sankaran, Ratnam & Hanan, 2004; Scholes & Archer, 1997; Stevens & Fox, 1991).

An exact definition and the accurate delineation of forest-steppes is complicated by inherent ambiguity. The grassland–forest continuum ranges from totally treeless grasslands to closed forests (Breshears, 2006). Based on the physiognomy, forest-steppes lie somewhere between the two extremes, but the proportion of grasslands and forest patches varies widely (Illyés et al., 2007). The middle of the continuum (i.e. 50% arboreal and 50% grassland vegetation) is clearly a forest-steppe, but the designation of lower and upper thresholds is necessarily arbitrary and often difficult (e.g. Berg, 1958; Chibilyov, 2002).

An additional question is whether a mosaic of grasslands and shrubby vegetation should be regarded as forest-steppe. If low shrubs occur only, such as *Prunus tenella*, the complex may be termed shrub-steppe and classified among steppes (Berg, 1958; Lavrenko & Sochava, 1956; Lavrenko, Karamysheva & Nikulina, 1991). In contrast, 2–6-m tall *Pistacia* spp., *Juniperus excelsa* or *Quercus pubescens* individuals or small stands in a grassland matrix are usually classified among forest-steppes.

Considering the arguments outlined above, our definition of forest-steppes is as follows: forest-steppes are natural or near-natural vegetation complexes of arboreal and herbaceous components (typically distributed in a mosaic pattern) in the temperate zone (excluding the Mediterranean), where the co-existence of forest and grassland is enabled primarily by the semi-humid to semi-arid climate, complemented by complex interactions of biotic (e.g. grazing, land use) and abiotic (e.g. soil, topography) factors operating at multiple scales. The arboreal cover (with a minimum height of 2 m) is 10%–70% across the entire landscape mosaic. The vascular vegetation cover within the grassland is at least 10% (corresponding to the grassland definition of Dixon, Faber-Langendoen, Josse, Morrison, & Loucks, 2014; and the steppe definition of Wesche et al., 2016).

Our forest-steppe definition therefore rests on physiognomic features and the underlying environmental factors, the most important of which is climate. This broad understanding of forest-steppes includes lowland forest-grassland macromosaics (e.g. in Eastern Europe and the southern parts of West Siberia), exposure-related mountain forest-steppes (e.g. in Inner Asia), fine-scale forest-grassland mosaics (e.g. in the Carpathian Basin) and open woodlands (e.g. in the Middle East).

3 | ARE FOREST-STEPPES A BIOME?

Whether forest-steppe is a biome in its own right or only a transition between two neighbouring biomes may be considered a merely semantic question. However, it should be pointed out that forest-steppes differ considerably from both closed forests and treeless steppes in terms of numerous features, including physiognomy, habitat complexity, ecological functions and abiotic parameters, as has been shown for a number of forest-grassland mosaic ecosystems (e.g. Bannikova, 2003; Breshears, 2006; Erdős et al., 2014; Scholes & Archer, 1997; Wendelberger, 1989).

Based on the biogeographic view of Lomolino et al. (2010) and Cox, Moore, and Ladle (2016), who define biomes based on their climate and physiognomy (i.e. vegetation structure), we may conclude that forest-steppes satisfy the criteria to be considered a biome as they have a specific climate and a characteristic physiognomy. Here we have to emphasize that this concept includes latitudinal as well as altitudinal vegetation zones, which fits well with our understanding of forest-steppes. However, the recognition of forest-steppes as a biome is a subject of scientific controversy. Some of the well-known global classification systems treat forest-steppes as a mere contact area between two adjacent biomes or zones (rather than a separate biome or zone in its own right). For example, in the classification of Walter (1979), our forest-steppe definition is equivalent to those of zonoecotone VI/VII (transition between nemoral forest and steppe), zonoecotone VII/VIII (transition between taiga and steppe) and zonoecotone IV/VII (transition between the Mediterranean and steppe), complemented by some parts of the Tibetan subzonobiome (within zonobiome VII) and areas from mountain orobiomes (e.g. Crimean Mts, Caucasus, Kopet Dag, Pamir-Alai, Tian Shan). Regarding the scheme of Schultz (2005), our forest-steppe definition is included in the ecozone “dry midlatitudes” and the contact zone between the ecozones “subtropics with winter rain” and “dry tropics and subtropics”. In the system of Pfadenhauer and Klötzli (2014), our forest-steppes are included mainly in the dry nemoral subzone, but considerable parts belong to the subtropical subzone with winter rain.

4 | PHYSIOGEOGRAPHIC SETTING

Forest-steppes cover vast areas in Eurasia (2.9 million km^2 according to Wesche et al., 2016; although the figure may be higher, depending on the defining criteria). The altitudinal range of forest-steppes extends from sea level (e.g. Turkey-in-Europe and Crimea) up to some 3,500 m a.s.l. (Qilian Mts), including lowlands, hilly

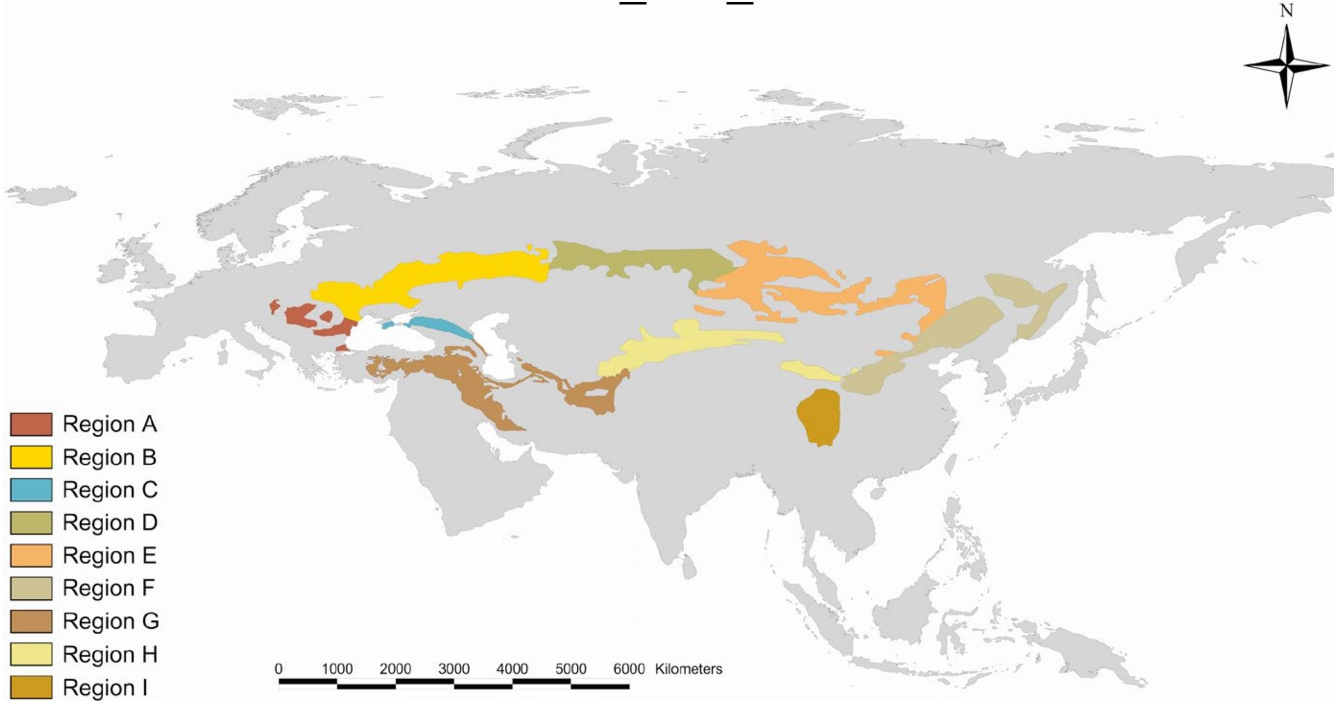

FIGURE 1 The distribution of Eurasian forest-steppes and the main forest-steppe regions. Region A: Southeast Europe, Region B: East Europe, Region C: North Caucasus and Crimea, Region D: west Siberia and north Kazakhstan, Region E: Inner Asia, Region F: Far East, Region G: Middle East, Region H: Central Asia and southwestern Inner Asia, Region I: eastern Tibetan Plateau. The GIS map (shp file) may be found in Appendix S1. Methods and sources used for delineating forest-steppe areas are given in Appendix S2

areas and mountain ranges. Forest-steppes form two distinct latitudinal belts (Figure 1): northern (ranging from the Carpathian Basin to the Russian Far East), and southern (ranging from Central Anatolia to the Tian Shan). The northernmost reaches of the forest-steppe zone are found in Russia, north of the city of Yekaterinburg in the Ural Mts (56°N) and north of the Kuznetski Alatau Mts (56°N). The southernmost extensions are in Iran, in the Zagros Mts near Shiraz (29°N). The longitudinal extension of the forest-steppe zone is 9,000 km, stretching from the westernmost parts of the Carpathian Basin (near Vienna, Austria, 16°E) to the Amur Lowlands in Russia (139°E).

The most important latitudinal climatic gradient is along the increase in aridity to the south (Zlotin, 2002). Plant species richness usually decreases toward the steppe zone (Liu & Cui, 2009; Zlotin, 2002), although the most obvious change is the reduction of tree abundance (Schultz, 2005). In forest-steppe areas within the proximity of the closed forest zone, steppes are limited to small patches (Walter & Breckle, 1989). As aridity increases towards the south, grasslands become more extensive, while forest patches become smaller. Within the southern forest-steppe belt, forest patches are almost always very small.

Concerning longitudinal gradients, continentality generally increases towards Inner Asia (Chibilyov, 2002; Wesche et al., 2016; Zhu, 1993; Zlotin, 2002). This means that mean annual precipitation decreases (summer precipitation increases, while winter precipitation decreases), mean annual temperature simultaneously decreases, while yearly temperature range increases (summers remain hot, but winters are long and extremely cold). These changes are accompanied by pronounced changes in cardinal vegetation characteristics (Bannikova, 1998; Berg, 1958; Chibilyov, 2002; Lavrenko, 1942, 1970a,b; Lavrenko et al., 1991; Liu, Cui, Pott, & Speier, 2000; Liu et al., 2012; Zlotin, 2002): with increasing continentality, species richness usually decreases, especially for shrubs and trees, while the root/shoot ratio increases. There are deviations from the described general patterns, depending on the scale of the study and whether it concerns forest or grassland (Lashchinskiy, Korolyuk, Makunina, Anenkhonov, & Liu, 2017; Palpurina et al., 2015) (Box 1) .

5 | FOREST-STEPPES ON A COARSE SCALE: MAJOR DIVISIONS

A north–south divide bisects forest-steppes into a western and an eastern part. The transition zone is considered to be either near Lake Baikal (Berg, 1958) or near the Altai Mts and the Yenisei River (Lavrenko, 1969; Lavrenko et al., 1991). Phytogeographic ranges of forest-steppe species lend support to both of these propositions, suggesting a blurred boundary (Hilbig, Jäger, & Knapp, 2004; Nimis et al., 1994; Popov, 1963). However, given that the main floristic and vegetation changes begin in the western part of the Altai Mts, classifying the Altai-Sayan-Baikal area to the eastern forest-steppe section appears well founded. In terms of climate, plant species composition and syntaxa, a major boundary exists at the

Box 1 Eurasian forest-steppes: A fact sheet

Definition: natural or near-natural vegetation complexes of arboreal and herbaceous components (typically distributed in a mosaic pattern) in the temperate zone, where the co-existence of forest and grassland is enabled primarily by the semi-humid to semi-arid climate, complemented by complex interactions of biotic and abiotic factors operating at multiple scales. The arboreal cover (height >2 m) is 10–70% across the entire landscape mosaic, while the vascular vegetation cover within the grassland is at least 10%.

Forest-steppes as a transitional zone or a separate biome: as biome definitions usually rest on climate and physiognomy, it may be concluded that forest-steppes satisfy the criteria to be considered a biome. However, this is a subject of scientific controversy, and some well-known global vegetation classification schemes treat forest-steppes as a mere contact area between two adacent biomes, rather than a separate biome in its own right.

Geographic extent: 29°–56°N, 16°–139°E.

Main regions: Southeast Europe, East Europe, north Caucasus and Crimea, west Siberia and north Kazakhstan, Inner Asia, Far East, Middle East, Central Asia and southwestern Inner Asia, Eastern Tibetan Plateau.

Dominant life forms: mainly phanerophytes and hemicryptophytes, but also chamaephytes and therophytes, in places many geophytes.

Dominant taxa: Anacardiaceae, Apiaceae, Asteraceae, Betulaceae, Cupressaceae, Cyperaceae, Fabaceae, Fagaceae, Lamiaceae, Pinaceae, Poaceae, Ranunculaceae, Rosaceae, Salicaceae.

northwestern foothills of the Altai Mts (Lashchinskiy et al., 2017), which also appears for edaphic grasslands in the forest-steppe biome (Ermakov, Chytrý, & Valachovič, 2006). Hilbig and Knapp (1983) and Lavrenko and Karamysheva (1993) subsequently place the border to the western foothills of the Altai Mts. Similarly, Pott (2005), in agreement with Wesche et al. (2016), regards the Altai Mts as forming the boundary between western and eastern steppes and forest-steppes.

Another major division must be made between northern and southern forest-steppes, the border running from the Sea of Marmara along the main ridge of the Caucasus and through the arid lands east of the Caspian Sea to the Tian Shan. Generally, northern forest-steppes are relatively mesic, steppes are typically closed and forest patches are often large, although exceptions do exist, especially in extrazonal situations. Southern forest-steppes are more arid, with open grasslands and usually solitary and widely spaced trees (Memariani, Zarrinpour & Akhani, 2016; Zohary, 1973). The position of forest-steppes between the neighbouring vegetation belts differs strongly between northern and southern forest-steppes. While northern forest-steppes occupy space between mesic steppes and forests, southern forest-steppes usually appear in a transitional zone (a) between forests and semi-desert-like steppes, (b) between forests and alpine communities, or (c) between steppes and alpine/sub-alpine communities.

6 | MAIN FOREST-STEPPE REGIONS

We here provide a basic description of the main regions (Figure 1). Our delineation rests on a combination of floristic and physiognomic characteristics, as well as relief and climate features. We relied on previously published material and expert knowledge, complemented by climatic data of selected stations located within forest-steppe areas. Climate data, as well as information about the remaining forest-steppe areas and current land-use practices are given in Table 1.

6.1 | Region A – Southeast Europe

Carpathian Basin, Lower Danube Plain and Inner Thrace (northeast Austria, southeast Czech Republic, Hungary, south Slovakia, northeast Croatia, Romania, north and northeast Serbia, south Moldova, southwest Ukraine, north and southeast Bulgaria, northeast Greece, Turkey-in-Europe; Bodrogközy, 1957; Zólyomi, 1957; Niklfeld, 1964; Szodfridt, 1969; Donită, 1970; Horvat et al., 1974; Mayer, 1984; Wallnöfer, 2003; Tzonev, Dimitrov & Roussakova, 2006; Bölöni, Molnár, Biró, & Horváth, 2008; Chytrý, 2012; Molnár et al., 2012) (Figure 2a).

Forest-steppes in this region are under considerable mediterranean climatic influences, with increasing continental effects towards the northeast. Thrace is transitional towards the Anatolian forest-steppes (Region G). Forest-steppes typically occupy plains (from sea level to 250 m a.s.l.), but some hills and mountains (often on south-facing slopes) also host similar forest-grassland mosaics. Mean annual temperature is 9.0–12.5°C (up to 13.5°C in Thrace). Summers are hot, winters are mild. Mean annual precipitation is 420–600 mm, with a maximum in early summer, a secondary maximum in autumn and a semi-arid period in between.

Both forest and grassland patches are mostly xeric. Forest patches are usually small and have an open canopy, with a high number of oak species (among others: *Quercus cerris*, *Quercus frainetto*, *Quercus petraea*, *Q. pubescens*, *Quercus robur*). Other tree species such as *Acer tataricum*, *Carpinus orientalis*, *Fraxinus ornus*, *Populus alba* and *Tilia tomentosa* are also typical. Grasslands are usually characterized by *Chrysopogon gryllus*, *Festuca rupicola*, *Festuca valesiaca*, *Festuca vaginata*, *Stipa capillata*, *S. pennata* and *S. pulcherrima*. Important herbs include *Astragalus austriacus*, *Astragalus dasyanthus*, *Astragalus onobrychis*, *Fragaria viridis*, *Salvia austriaca*, *Salvia nemorosa* and *Salvia nutans*.

6.2 | Region B – East Europe

Southern part of the East European Plain (northeast Romania, Moldova, southeast Poland, Ukraine, southwest Russia; Milkov,

TABLE 1 Basic climatic parameters (to the nearest 0.5°C and 10 mm), remaining areas (+: small, ++: medium, +++: large) and current land-use practices (–: absent or very rare, +: rare, ++ moderately widespread, +++: widespread) of forest-steppes

Region	A	B	C	D	E	F	G	H	I
Mean annual temperature (°C)	9–13.5	3–9	9.5–12	1–4.5	−6 to 5	−1 to 14	10.5–17	0–12	−3 to 7
Mean January temperature (°C)	−3 to 3	−15 to −3	−4 to 1	−20 to −14	−28 to −12	−26 to 0	−5 to 4.5	−24 to −3	−12 to −2
Mean July temperature (°C)	19–25	18–22	21–24	19–22	14–20	20–27	22–31	18–26	8–16
Mean annual precipitation (mm)	420–600	400–660	300–770	270–610	210–550	360–650	270–860	380–600	300–700
Mean summer precipitation (mm)	100–210	160–260	160– 230	100–240	150–290	220–400	1–170	40–400	230–490
Proportion of summer precipitation (%)	17–36	28–43	25–40	37–44	36–72	40–70	0.5–34	10–70	47–76
Remaining forest-steppe area	+	+	+	++	+++	++	+	++	+++
Land use of near-natural forest-steppes									
Grazing	++	+++	++	++	++	+++	+++	+++	+++
Mowing	+	+	+	++	+	++	+	+	–
Burning	+	+	–	+	++	++	–	–	–
Traditional crop cultivation	–	–	–	–	–	–	++	–	–
Abandoned	+++	+	++	++	+	+	+	–	+

1950; Krasheninnikov, 1954; Berg, 1958; Soó, 1957; Jakucs, Fekete, & Gergely, 1959; Borhidi, 1966; Dokhman, 1968; Lavrenko, 1980; Walter & Breckle, 1989; Kleopov, 1990; Chibilyov, 2002; Molnár, Türke & Csathó, 2007; Safronova, 2010; Korotchenko & Peregrym, 2012; Kuzemko et al., 2014; Semenishchenkov, 2015) (Figure 2b).

Stretching from Podolia and the eastern foothills of the Carpathians to the southern foothills of the Ural Mts, forest-steppes of this region occupy lowlands and hilly areas between ca. 90 and 500 m a.s.l. Climate is temperate continental, with some mediterranean influence in the westernmost parts. Mean annual temperature is approximately 9°C in the west, and ca. 3°C in the east. Summers are warm, winters are moderately cold. Mean annual precipitation varies between 400–600 mm (up to 660 mm in Podolia), with a peak in June (–July) and a semi-arid period in late summer.

Large and mesic forest patches are formed mainly by broadleaved deciduous trees (*Acer platanoides*, *Fraxinus excelsior*, *Q. robur*, *Tilia cordata*, *Ulmus glabra*), although *Populus tremula* and *Betula pendula* are also common. The grassland patches are mesic, hence the names "meadow steppe" and "steppified meadow" (the two differ regarding the role of xeric species, although the distinction is used mainly by Russian and Ukrainian authors; e.g. Kuzemko, 2009; Semenishchenkov, 2009; Averinova, 2010). Important species of the grassland patches include *F. valesiaca*, *Filipendula vulgaris*, *Fragaria viridis*, *Koeleria macrantha*, *Phlomoides tuberosa*, *Poa angustifolia*, *Ranunculus polyanthemos*, *Salvia pratensis*, *S. nutans*, *Stipa capillata*, *S. pennata*, *S. pulcherrima*, *S. zalesskii*, *Teucrium chamaedrys* and *Trifolium montanum*, as well as different *Tulipa* and *Iris* species.

6.3 | Region C – North Caucasus and Crimea

North Caucasus, Crimea (Southwest Russia, Crimea; Berg, 1958; Walter & Breckle, 1989; Serebryanny, 2002; Volodicheva, 2002) (Figure 2c).

Forest-steppes occupy substantial areas from sea level up to ca. 600 m a.s.l. The whole region is under marked mediterranean climatic influence. Mean annual temperature is 9.5–12.0°C. Mean annual precipitation varies from 300 to 600 (–770) mm, with the maximum in summer.

In the North Caucasus, mesic forest patches are composed of *Acer campestre*, *Carpinus betulus*, *Q. petraea*, *Q. robur* and *Tilia dasystyla*. In the Crimea, forest-steppes are more xeric and show remarkable similarities with those of the Middle East (Region G) and the Lower Danube Plain (in Region A) (Doniță, 1970). In the northwestern part of the Crimean Mts, the most characteristic tree species are *Pyrus communis*, *P. elaeagrifolia*, *Q. petraea*, *Q. pubescens*, *Q. robur* and *Ulmus procera*, while *Arbutus andrachne*, *J. excelsa*, *Pistacia atlantica* and *Q. pubescens* are typical in the southern parts of the Crimean Mts. Some of the most common and characteristic species of the grassland patches in the region are *Adonis vernalis*, *F. rupicola*, *Paeonia tenuifolia*, *Phleum phleoides*, *Stipa capillata*, *S. pennata*, *S. pontica* and *S. pulcherrima*.

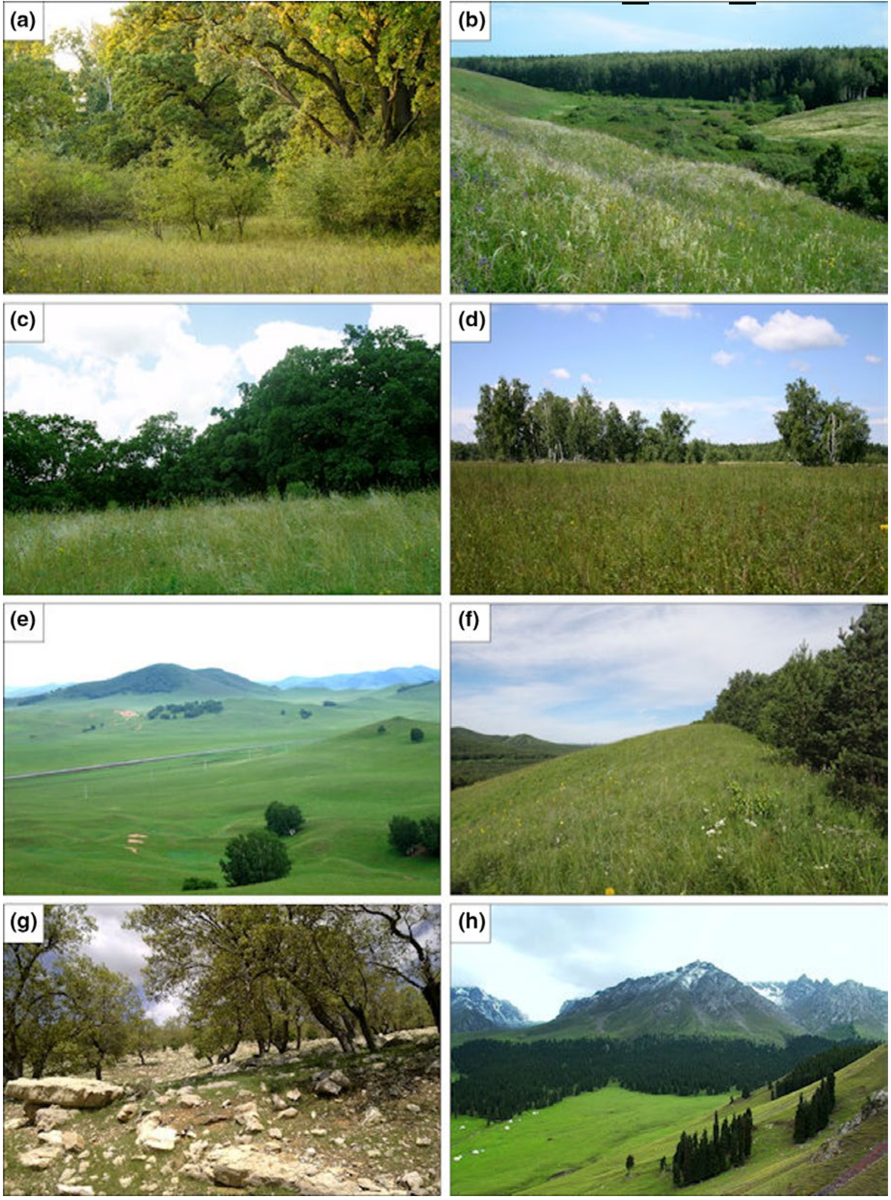

FIGURE 2 Eurasian forest-steppe landscapes. (a) *Quercus robur* forest with grasslands of *Festuca rupicola*, *F. wagneri* and *Stipa capillata* in the Kiskunság sand region of the Carpathian Basin, HU (photo Á. Molnár). (b) *Betula pendula*–*Quercus robur* forest and *Stipa pennata* steppe patch with *Salvia pratensis* in the Kulikovo Polye reserve, Tula region, RU (photo Yu. A. Semenishchenkov). (c) *Quercus pubescens* forest and *Stipa pontica* steppe in the Crimean Peninsula (photo Y. P. Didukh). (d) *Betula pendula* patches and *Festuca*–*Stipa* grasslands in the Kostanay Region, north Kazakhstan (photo Z. Bátori). (e) *Betula platyphylla* individuals and groves embedded in a *Leymus chinensis*–*Filifolium sibiricum* grassland in the Ulan Buton area of Inner Mongolia, CN (photo H. Liu). (f) Forest-steppe landscape dominated by *Betula platyphylla* and *Stipa baicalensis* in the southern part of the Greater Khingan Range, China (photo H. Liu). (g) *Quercus brantii* woodland with *Bromus* spp. on calcareous and gypsiferous alluvium deposits in the Zagros Mts, Iran (photo A. Daneshi). (h) Mosaic of *Picea schrenkiana* forests and *Stipa capillata* steppes in the Tian Shan, Xinjiang Uygur Autonomous Region, CN (photo H. Liu)

6.4 | Region D – West Siberia and north Kazakhstan

West Siberia, north Kazakhstan (South Russia, North Kazakhstan; Berg, 1958; Lavrenko & Karamysheva, 1993; Rachkovskaya & Bragina, 2012; Makunina, 2016a; Korolyuk & Yamalov, 2015; Mathar et al., 2016; Bátori et al., 2017; Lashchinskiy et al., 2017; Lebedeva et al., 2017; Tölgyesi et al., 2017) (Figure 2d).

The majority of the forest-steppes of this region occur in lowlands (100-200 m asl), but some, mainly in Kazakhstan, occupy hills (ca. 300-400 m asl). The climate is continental, with mean annual temperatures of 1-4.5 °C. Summers are warm, winters are very cold. Mean annual precipitation is 270-610 mm. Most precipitation falls during the summer months.

Large mesic to semi-dry forest patches alternate with extensive, mostly mesic grasslands. The forest patches are composed of small-leaved deciduous trees (*Betula pendula*, *B. pubescens*, *Populus tremula*) and *Pinus sylvestris*. Principal steppe species include *Artemisia glauca*, *A. pontica*, *Filipendula vulgaris*, *Festuca rupicola*, *F. valesiaca*, *Fragaria viridis*, *Gypsophila paniculata*, *Helictotrichon hookeri*, *Lathyrus pisiformis*, *L. pratensis*, *P. angustifolia*, *Phleum phleoides*, *Phlomoides tuberosa*, *Pimpinella saxifraga*, *Potentilla incana*, *R. polyanthemos*, *Scorzonera ensifolia*, *Stipa capillata*, *S. pennata*, *S. tirsa*, *S. zalesskii*, *Vicia cracca*. The large amount of various halophytic communities is characteristic within the forest-steppes of this region.

6.5 | Region E – Inner Asia

Altai Mts and their northern foothills, Sayan Mts and their northern foothills, Baikal area, Transbaikal Mts, Tarbagatai Mts, Saur Mts, Khangai Mts, Khentei Mts, Inner Mongolia (south Russia, east Kazakhstan, Mongolia, north and northeast China; Hilbig & Knapp, 1983; Hou, 1983; Karamysheva & Khramtsov, 1995; Wallis de Vries et al., 1996; Korotkov & Krasnoshchekov, 1998; Korolyuk & Makunina, 2000; Liu et al., 2000; Shahgedanova et al., 2002; Bannikova, 2003;

Dulamsuren, Hauck, & Mühlenberg, 2005b; Namzalov & Baskhaeva, 2006; Rachkovskaya & Bragina, 2012; Makunina, 2010, 2013, 2014, 2016b, 2017; Hais et al., 2016) (Figure 2e).

The region includes Inner Asian mountain ranges. (The Tarbagatai-Saur range as well as the westernmost extensions of the Altai Mts are transitional towards Region H and Region D, respectively. They are consequently sometimes treated as belonging either to the northern Tian Shan, or to the west Siberian–north Kazakhstan forest-steppes.) Mountain forest-steppes, extending as high as 2,400 m a.s.l., are typically situated between the steppe and forest elevational belts. Forests are usually found on north-facing slopes (often with permafrost), whereas the steppe component occupies mainly south-facing slopes and intermountain depressions. In more arid parts, only small forest patches occur amid dry grasslands. In valleys, forest-steppes can be found as low as 200 m a.s.l. The climate here is ultracontinental. Mean annual temperature is between −6°C and +2°C (up to +5°C in southern Inner Mongolia). Summers are warm, winters are extremely cold. Mean annual temperature amplitude may exceed 50°C. Mean annual precipitation is 210–550 mm; winters are dry, most precipitation falls during summer (July–August).

Forest patches are composed of *Betula pendula*, *B. platyphylla*, *Larix sibirica*, *L. gmelinii*, *Pinus sylvestris* and *Ulmus pumila*. The most common plant species of the grasslands include *Achnatherum sibiricum*, *Agropyron cristatum*, *Artemisia frigida*, *Carex pediformis*, *Cleistogenes squarrosa*, *Cymbaria daurica*, *Filifolium sibiricum*, *Festuca valesiaca*, *F. lenensis*, *K. macrantha*, *Leymus chinensis*, *Nepeta multifida*, *Poa attenuata*, *Pulsatilla patens*, *Stellera chamaejasme*, *Stipa baicalensis* and *S. krylovii*.

6.6 | Region F – Far East

West Manchuria (=northeast China Plain), southern parts of the Greater Khingan Range, eastern parts of the Chinese Loess Plateau, Amur Lowland, southwest Sihote Alin, Khanka Lowland (northeast China, southeast Russia; Berg, 1958; Hou, 1983; Rychnovská, 1993; Zhu, 1993; Ivanov, 2002; Qian et al., 2003; Liu et al., 2015) (Figure 2f).

Forest-steppes of this region occur across a wide range of terrains and altitudinal gradients. Examples of occurrence at low altitudes include the Amur Lowland (ca. 50 m a.s.l.), and west Manchuria of China (120–150 m a.s.l.). Some forest-steppes have developed on low hills, while forest-steppes of the Chinese Loess Plateau and the Greater Khingan Range are found between 800 and 2,500 m a.s.l. Regional climate is influenced by the monsoonal circulation, particularly in the east, while continental influence positively correlates to increasing distance from the ocean. The northeast–southwest direction of the forest-steppe zone in Manchuria, the greater Khingan Range and the Chinese Loess Plateau can be explained by the diminishing effects of the monsoon; the main vegetation zones run more or less parallel with the coast. Mean annual temperature ranges between −1°C and +14°C. Mean annual precipitation is 360–650 mm. Winters are cold and dry, summers are warm (western Manchuria of China, Greater Khingan Range, Chinese Loess Plateau) to cool (Amur and Khanka Lowlands, Sihote Alin). Most precipitation falls during the summer months. Forest-steppes of the Amur Lowland are also known as “Amur prairies”, while those of the Amur and the Khanka Lowlands are sometimes referred to as “East Asian savannas”.

The most typical tree species of the forest patches is *Quercus mongolica*, although *Betula dahurica*, *B. platyphylla* and *Tilia amurensis* are also frequent. Grasslands are steppe and meadow steppe ecosystems with different subtypes occurring in dry and more mesic environments. Typical species include *Arundinella hirta*, *Bothriochloa ischaemum*, *Calamagrostis epigejos*, *Cymbaria daurica*, *Filifolium sibiricum*, *Leymus chinensis*, *Miscanthus sinensis*, *Poa pratensis*, *Stipa baicalensis*, *S. bungeana*, *S. grandis* and *S. pennata*.

6.7 | Region G – Middle East

The peripheral areas of central Anatolia, east and southeast Anatolia, south and east Caucasus, Abdulaziz Mts, Zagros Mts, Persian Plateau, Alborz Mts, Kopet Dag, Badkhyz Mts, central Afghan Mts (Turkey, South Georgia, Armenia, Azerbaijan, southwest Russia, northeast Syria, northeast Iraq, Iran, south Turkmenistan, Afghanistan; Assadi, 1988; Akhani, 1998; Ambarlı et al., 2016; Breckle, 2007; Çolak & Rotherham, 2006; Kürschner & Parolly, 2012; Memariani et al., 2016; Merzlyakova, 2002; Nakhutsrishvili, 2013; Naqinezhad, Zare-Maivan & Gholizadeh, 2015; Popov, 1994; Ravanbakhsh, HamzeH'Ee, Etemad, Marvie Mohadjer & Assadi, 2016; Ravanbakhsh & Moshki, 2016; Uğurlu, Roleček & Bergmeier, 2012;Volodicheva, 2002; Zohary, 1973) (Figure 2g).

The forest-steppes of the Middle East occur on hills and mountains from ca. 200 m (foothills of south and east Caucasus, southwest Iran) to 3,000 m a.s.l. (central Afghan Mts). Other names include “southern forest-steppes”, “arid open woodlands”, “savannoid vegetation”, “semisavanna”, “pseudosavanna”, “steppe-forests” and “light forests”. “Wild orchards”, i.e. grasslands with scattered wild fruit trees, are structurally similar to forest-steppe landscapes, but have probably developed from oak woodlands through selective cutting (Kramer, 1984; Mayer, 1984; Woldring & Cappers, 2001). Mean annual temperature ranges between 10.5 and 17.0°C. Mean annual precipitation varies between 270 and 860 mm. Summers are hot and arid, winters are cold. Forest-steppes are under considerable mediterranean climatic influences. The central Afghan Mts form a transitional zone towards the Pamir and the Tian Shan (Region H), with scattered trees in a semi-desert-like steppe matrix.

The region has been under human influence for so long that it is very difficult to infer its pre-human vegetation (Asouti & Kabukçu, 2014; Frey & Probst, 1986; Wesche et al., 2016). Trees in the forest-steppes of this region either form small groves or occur as scattered individuals. The most common tree species are *Juniperus excelsa*, *J. foetidissima*, *Pinus nigra*, *P. sylvestris*, *Pistacia atlantica*, *P. vera*, *Prunus dulcis*, *Pyrus elaeagrifolia*, *Quercus brantii*, *Q. infectoria*, *Q. ithaburensis*, *Q. macranthera*, *Q. petraea*, *Q. pubescens*, *Q. robur*. Some of the most common taxa of the grasslands are *Agropyron cristatum*, *Astragalus angustifolius*, *A. lycius*, *B. ischaemum*, *C. gryllus*, *F. valesiaca*, *K. macrantha*, *Poa bulbosa*, *Seriphidium fragrans*, *S. sieberi*, *Stipa arabica*, *S. barbata*, *S. capillata*, *S. Lessingiana* and *S. pulcherrima*.

6.8 | Region H – Central Asia and southwestern Inner Asia

Pamir Mts, Alai Mts, Tian Shan, Qilian Mts, Helan Mts (southeast Kazakhstan, Kyrgyzstan, Tajikistan, east and southeast Uzbekistan, northwest China; Berg, 1958; Bone et al., 2015; Jiang, Kang, Liu, Tian, & Lei, 2000; Merzlyakova, 2002; Pang et al., 2013; Rychnovská, 1993; Sang, 2009; Tian, 1996; Wang et al., 2001; Walter & Breckle, 1989; Wu, 1980) (Figure 2h).

Forest-steppes are present in altitudes between ca. 800–3,500 m a.s.l. Climatic influences in the region vary, resulting in significantly different precipitation and temperature records among both individual mountain chains and among slopes of differing aspects. The climate is mostly continental, with mediterranean influences in the western areas. Mean annual temperature is 0–12°C. Mean yearly precipitation varies between 380 and 600 mm, with a maximum occurring during spring (in the west) or summer (in the east).

In the western part of the region (Pamir and Alai Ranges, western and northwestern Tian Shan) forest-steppes are characterized by scattered fruit trees (*Juglans regia*, *Malus sieversii*, *Pistacia* spp. and *Punica granatum*) and *Juniperus* species, embedded in a dry steppe or even a semi-desert-like matrix (*B. ischaemum*, *Ferula tenuisecta*, *Hordeum bulbosum*, *Poa bulbosa* and *Thinopyrum intermedium*). The complex is also known as “open woodland”, “desert with scattered wooded patches”, “orchard” and “wooded field”. While this type shows clear similarities towards the open woodlands of the Middle East (Region G), in the eastern parts of the region (northern and eastern Tian Shan, Qilian Mts, Helan Mts), forest-steppes are similar to those on the mountains of Region E. Such cases are usually located at higher elevations than the fruit tree woodlands. Here, forest patches are found on north-facing slopes, and are formed primarily by *Picea schrenkiana* and *P. crassifolia*, with additional species such as *Betula pendula*, *Larix sibirica*, *Picea asperata*, *Populus tremula* and *Ulmus glaucescens*. Montane steppes occupy south-facing slopes, with the most common species being *Agropyron cristatum*, *Ajania fruticulosa*, *Artemisia frigida*, *A. lagopus*, *Cleistogenes squarrosa*, *F. rupicola*, *K. macrantha*, *Medicago falcata*, *Oryzopsis chinensis*, *Ptilagrostis pelliotii*, *P. purpurea*, *Stipa capillata*, *S. breviflora* and *S. przewalskyi*.

6.9 | Region I – Eastern Tibetan Plateau

Eastern parts of the Tibetan Plateau (southwest China; Wu, 1980; Chang, 1981; Zhao, Wu, Yin & Yin, 2011). Forest-grassland mosaics of the eastern areas of the Tibetan Plateau may only tentatively be classified among forest-steppes owing to the ambiguity of the primary cause underlying the mosaic pattern. From the southeastern periphery to the central parts of the Plateau, forests gradually give way to meadows and steppes, with a broad transitional zone. The opening up of the forest is a result of a combination of decreasing temperature and decreasing precipitation, although temperature appears as the primary driver in most cases. The elevation is 3,200–4,000 m a.s.l. Mean annual temperature is between −3°C and +7°C. Mean annual precipitation is 300–700 mm.

Forest patches are composed of *Abies fabri*, *A. fargesii*, *A. recurvata*, *A. squamata*, *Picea asperata*, *P. brachytyla*, *P. likiangensis*, *P. purpurea* and *P. wilsonii*. The most typical grassland species are *Kobresia* species (*Kobresia capillifolia*, *K. humilis*, *K. littledalei*, *K. royleana*, *K. tibetica* and *K. vidua*). Other important species are *Argentina stenophylla*, *Carex atrofusca*, *Gentiana algida* and *Thalictrum alpinum*.

7 | BIODIVERSITY FEATURES

Forest-steppes are characterized by a high level of habitat diversity. Forests, scrubs, and grasslands have strongly different physical environmental conditions, resulting in plant communities that differ in terms of vegetation structure and floristic composition (e.g. Anenkhonov et al., 2015; Bannikova, 1985; Berg, 1958; Erdős et al., 2014; Hais et al., 2016; Hilbig & Knapp, 1983; Hilbig et al., 2004; Walter & Breckle, 1989). Moreover, forest, scrub and grassland patches have a number of different types (usually aligned along micro-topographic gradients), further increasing the habitat diversity of forest-steppes (Bátori et al., 2014; Dulamsuren, Hauck, & Mühlenberg, 2005a; Makunina, 2014, 2017; Namzalov & Baskhaeva, 2006; Namzalov et al., 2012; Tölgyesi, Erdős, Körmöczi & Bátori, 2016; Tölgyesi, Zalatnai, et al., 2016; Wallis de Vries et al., 1996). In addition, differently sized patches of the same type may also possess dissimilar environmental and vegetation characteristics. For example, small, medium and large forest patches differed considerably in tree size class distribution and seedling composition (Erdős, Tölgyesi, Cseh, et al., 2015), while the species composition of grasslands also appears to relate to size (Molnár, 1998). Forest-steppes harbour an extensive network of boundaries between different patches, which may be regarded as distinct plant communities, deviating from the communities of habitat interiors (Erdős, Gallé, Körmöczi, & Bátori, 2013; Erdős, Tölgyesi, Körmöczi, & Bátori, 2015; Molnár, 1998). Edges with different orientations may also represent slightly different habitats, showing dissimilar environmental conditions and vegetation features (Erdős et al., 2013). Consequently, forest-steppes should by no means be conceived as simple two-phase systems. Instead, they are characterized by multi-level spatial heterogeneity, where forest, scrub and grassland patches of many types and different sizes, connected by a network of differently oriented edges, form an intricate and highly complex system. An integrated view of these complex ecosystems, including all components, is a prerequisite for the efficient conservation and sustainable use of forest-steppes (cf. Luza, Carlucci, Hartz & Duarte, 2014).

Forest-steppes have been recognized as important biodiversity hotspots (Bannikova, 1998; Habel et al., 2013; Kamp et al., 2016; Makunina, 2016a; Oprea, Goia, Tănase & Sîrbu, 2010; Zlotin, 2002). Habitat diversity, together with vegetation history, is a key determinant of species diversity in forest-steppes (cf. Dengler et al., 2012; Feurdean et al., 2015; Novenko et al., 2016). The grassland component of the forest-steppe may have very high fine-scale plant species richness (Chytrý et al., 2015; Dengler et al., 2016;

Lashchinskiy et al., 2017). For example, meadow steppes that typically form the grassland component of the forest-steppes in Russia may contain on average 64 plant species per 100 m^2 (Korolyuk, Egorova, Smelansky, & Filippova, 2008). In the forest component, up to 114 species per 100 m^2 have been registered within the forest-steppe landscape of the northern Altai Mountains, suggesting that those forests are probably the most species-rich forests in non-tropical Eurasia (Chytrý et al., 2012). Diversity and composition of the shrub and herb layers are influenced by variations in canopy cover. If the canopy is relatively open, many xeric steppe species may survive under the trees (Erdős, Tölgyesi, Körmöczi, et al., 2015). Under a closed canopy, mesic conditions develop, providing suitable habitats for plants adapted to more humid conditions (Walter & Breckle, 1989). Forest edges are typically of higher biodiversity than habitat interiors, and provide habitat for several species that are rare or absent in the patch interiors of the studied forest-steppe system (e.g. *Achillea seidlii*, *Cervaria rivini*, *Geranium sanguineum*, *Hieracium umbellatum*, *Polygonatum odoratum*, *R. polyanthemos*, *Tragopogon pratensis*; Erdős et al., 2013; Erdős, Tölgyesi, Cseh, et al., 2015; Varga, 1989; Wendelberger, 1986; Molnár, 1998).

Forest-steppes provide habitats for many rare, endemic and threatened plants, including IUCN red-listed species (e.g. *Artemisia pancicii*, *Astragalus wolgensis*, *Colchicum arenarium*, *Malus sieversii*, *Pistacia vera* and *P. tenella*; Zlotin, 2002; Oprea et al., 2010; Habel et al., 2013; Kamp et al., 2016).

Because of their high structural heterogeneity, forest-steppes also host a high diversity of life-forms. Forests are dominated by phanerophytes (trees and shrubs). In their herb layer, geophytes, hemicryptophytes and/or therophytes are typical, depending on local site conditions. Shrubs are the most characteristic life form in forest edges and steppe thickets. The steppe component is characterized by hemicryptophytes (both graminoids and forbs) and usually chamaephytes. In the steppes of Europe, west Siberia and the Middle East, geophytes play an important role, while therophytes are frequent in dry areas and around disturbed sites (Berg, 1958; Breckle, 2007; Erdős et al., 2014; Kürschner & Parolly, 2012; Rachkovskaya & Bragina, 2012; Rychnovská, 1993; Schultz, 2005; Tzonev et al., 2006; Walter & Breckle, 1989; Wesche et al., 2016).

The functional diversity of forest-steppes is exceptionally high. Although usually not very tall, forests are multi-layered, with evergreen or deciduous woody species (usually both of them in the same place). The steppe component also has multiple layers, with both tall and short herbs, mosses and sometimes even lichens. Both tussock and rhizomatous graminoids are typical. The amount of N-fixing species is considerable (e.g. *Astragalus*, *Medicago* and *Vicia* species). The flowering time of forbs is variable, starting in early spring and lasting till autumn. Steppe plants have evolved numerous strategies to withstand drought, cold, grazing, fire or other natural disturbances, further enhancing the diversity of functional types (Berg, 1958; Korotchenko & Peregrym, 2012; Kürschner & Parolly, 2012; Schultz, 2005; Walter & Breckle, 1989).

8 | CONSERVATION STATUS

Forest-steppes and steppes have been transformed by human activity more than any other part of Northern Eurasia (Chibilyov, 2002), although there are regional differences concerning the level of anthropogenic impacts (Table 1). The proportion of destroyed or severly degraded forest-steppes generally decreases towards the east, where agriculture began later (Zlotin, 2002). Forest-steppes have largely persisted in many Asian landscapes east of the Ural Mts (Lavrenko & Karamysheva, 1993; Smelansky & Tishkov, 2012). However, the situation is much worse in the western parts of the forest-steppe zone.

A large proportion of the steppe patches has been converted into croplands or plantations of non-native species such as *Robinia pseudoacacia*, while many forest patches have been logged or replaced with plantations (e.g. Ambarlı et al., 2016; Berg, 1958; Molnár et al., 2012; Parnikoza & Vasiluk, 2011; Walter & Breckle, 1989). The remaining forest-steppe areas are usually edaphic ones (e.g. on rocky surfaces) and/or small fragments with varying levels of degradation (Smelansky & Tishkov, 2012). As an extreme case of fragmentation, small areas of anthropogenic habitats, such as field margins (Cizek, Hauck, & Pokluda, 2012), railway embankments (Dudáš, Eliáš, & Mártonfi, 2016), river dykes (Bátori et al., 2016), kurgans (Deák et al., 2016) and road verges (Heneberg, Bogusch, & Řezáč, 2017), may serve as the last refuges for steppe and forest-steppe species.

Forest-steppes are highly sensitive to even small changes in factors determining forest/grassland proportion and distribution (Bartha et al., 2008; Kovács-Láng et al., 2000). In many European forest-steppes, the main threats are the invasion of non-native species (e.g. *Asclepias syriaca*, *Elaeagnus angustifolia*, *Robinia pseudoacacia*) and the effects of current agricultural and forestry practices (Molnár et al., 2008; Protopopova, Shevera & Mosyakin, 2006; Smelansky & Tishkov, 2012). In Turkey, forest-steppe ecosystems are negatively affected by agricultural intensification and conversion to croplands, deep ploughing, choosing non-native trees for afforestation, over-exploitation of wild plants and animals (e.g. collecting plants for firewood, poaching and the illegal collection of bulbous plants), overgrazing and road construction (Ambarlı et al., 2016). Iranian pistachio-almond forest-steppe remnants are severely degraded due to firewood cutting (Djamali et al., 2009), while oak forest-steppes suffer from heavy overgrazing (Sagheb-Talebi et al., 2014). The *Pistacia vera* and *J. excelsa* woodlands of Afghanistan are exploited for charcoal production (Breckle, 2007). The biodiversity of the Kazakh forest-steppe is highly threatened by farming and collection of plants (Rachkovskaya & Bragina, 2012). The rapid increase in the number of grazing livestock (especially goats) and logging negatively affect the flora and fauna of the Mongolian forest-steppes (Liu, Evans, et al., 2013; Wallis de Vries et al., 1996). However, since the regime change in the eastern bloc around 1990, abandonment of former croplands has increased (Alcantara et al., 2013; Schierhorn et al., 2013; Smelansky & Tishkov, 2012), providing a unique opportunity for the spontaneous recovery or planned restoration of the steppe component (Hölzel, Haub, Ingelfinger, Otte, & Pilipenko, 2002; Sojneková & Chytrý, 2015; Török, Vida, Deák, Lengyel & Tóthmérész, 2011).

Forest-steppes have a long history of human presence, and have historically provided humans with countless ecosystem services such as food sources (including crop progenitors), medicinal plants, grazing areas, as well as material for cooking, heating, construction or leaf fodder (Asouti & Kabukçu, 2014; Mosaddegh, Naghibi, Moazzeni, Pirani & Esmaeili, 2012). Some forest-steppes in present-day Turkey, Iraq and Iran are located in the region known as "the cradle of civilization" (Asouti & Kabukçu, 2014; Poschlod, 2015; Zohary, 1973). Nomadic, semi-nomadic and sedentary herders of the forest-steppe belt continue to possess rich traditional ecological knowledge of the steppes, their forage species and the spatial and temporal patterns of forage availability (Fernández-Giménez, 2000; Molnár, 2012, 2014). They have developed complex herding systems that utilize diverse pasture types and adapt to the unpredictability of grazing conditions and extremely harsh winters. At the same time, social rules and cultural taboos sometimes protect steppes and forest patches from destruction and over-exploitation. Herders living in forest-steppes, together with ecologists and conservationists, can effectively co-produce knowledge and develop tradition-based but conservation-oriented management systems (Molnár, 2013; Molnár et al., 2016; Zhang et al., 2007).

Forest-steppe conservation requires addressing certain knowledge gaps. First of all, conservation targets at continental, regional, national and local levels must be identified. Second, more research is needed to decide where the conservation of the status quo is a realistic goal, and where inevitable changes must be accepted or even facilitated. Third, practitioners must be equipped with adequate knowledge to choose between non-intervention and active management strategies. It is not yet fully known where the re-establishment of traditional practices in forest-steppe landscapes is a useful strategy, and where land-use pressure should be reduced. While identifying optimal management is challenging, we believe that a thorough knowledge of local circumstances combined with trial-and-error may be the way to success.

9 | CLIMATE CHANGE

Although climate change is not yet considered the greatest threat to forest-steppes (Ambarlı et al., 2016; Kamp et al., 2016), these ecosystems, where both forests and grasslands are near the margin of their tolerances, may be particularly vulnerable. Although drought-adapted forest types such as those in forest-steppes may be able to withstand short (seasonal) droughts, they are threatened by long (multi-year) droughts (Allen et al., 2010).

In line with global trends, increasing temperatures have been detected in many Eurasian forest-steppe areas, including Eastern Europe (Matveev et al., 2017), Turkey (Ambarlı et al., 2016), Kazakhstan (Kamp et al., 2016), Siberia (Tchebakova, Parfenova & Soja, 2011), the Altai Mts (Lkhagvadorj, Hauck , Dulamsuren & Tsogtbaatar, 2013) and Inner Mongolia (Zhang et al., 2011). Precipitation changes, both observed and predicted, are much more variable (Ambarlı et al., 2016; Angerer, Han, Fujisaki, & Havstad, 2008; Matveev et al., 2017; Tchebakova et al., 2011).

Vegetation responses to changing climate may include (a) changing species composition within patches but sustained patchwork of grassland and forest stands, (b) altered pattern of grassland and forest patches, such as shrinkage or expansion of one patch type at the expense of the other, and (c) complete disappearance of one patch type and thus a shift of biome boundaries.

In Trans-Baikalian and northern Mongolian forest-steppes, *Pinus sylvestris* may replace *Larix sibirica* in a drier climate due to its capacity to cope with drought stress (Anenkhonov et al., 2015; Dulamsuren et al., 2009). In the Carpathian Basin, species diversity in forest-steppe grasslands may decrease with increasing aridity, while interannual variability and the number of annual species may increase (Bartha et al., 2008; Kovács-Láng et al., 2000).

The response of forest patches to future climatic changes may mimic behaviour along climatic gradients, where forest patch size and cover decrease with increasing aridity (Kovács-Láng et al., 2000; Xu et al., 2017). Xu et al. (2017) found that small forest patches had increased mortality and decreased regeneration after disturbances than larger patches. A recent field study in Inner Asia has already revealed widespread tree mortality and decreased tree growth at the most xeric sites in response to increased water deficit (Liu, Williams, et al., 2013). Permafrost melting is likely to affect vegetation, including reducing forest cover (Sharkhuu & Sharkhuu, 2012). Continued warming and drying may lead to broad-scale biome shifts. Northward movement of vegetation belts is predicted for several parts of Eurasia (e.g. Angerer et al., 2008; Ishii & Fujita, 2013; Kamp et al., 2016; Zhang et al., 2011). This would lead to an overall decline of forest-steppes in Mongolia (Angerer et al., 2008). Central parts of the Carpathian Basin may be replaced by treeless steppes in the long term (Hickler et al., 2012), with an increase in the proportion of Mediterranean species (Thuiller, Lavorel , Araújo, Sykes & Prentice, 2005).

The non-linear nature of climate change impacts renders detection difficult; systems may resist certain levels of environmental change, which may then be followed by a sudden and large-scale vegetation shift (Liu & Piao, 2013). Extreme climatic events or disturbances may be catalysts of such changes (Kröel-Dulay et al., 2015).

Changing climate may affect ecosystems not only directly, but also in combination with other factors, such as land use or biological invasion. For example, in the forest steppe of the Mongolian Altai Mts, earlier snow melt resulting from warming climate caused reduced migration of pastoral nomads, which, in turn, led to an intensified use of local forest patches (Lkhagvadorj et al., 2013). Drought and associated insect damage resulted in severe forest mortality in Anatolian forest-steppes (Allen et al., 2010).

All these examples demonstrate that forest-steppe ecosystems are already responding to changing climate. With predicted further warming and changing precipitation regimes in the 21st century (IPCC 2014), climate change may become one of the most important threats to the biodiversity and integrity of numerous ecosystems (Sala et al., 2000), including forest- steppes. Moreover, it has been suggested that the interaction of climate change and habitat fragmentation may have disastrous consequences for biodiversity (Travis, 2003), worsening forest-steppe prospects, given the high level of habitat loss in the biome (Hoekstra et al., 2005).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1.

APPENDIX S2. Methods and sources used for the delineation of the forest-steppe biome and the main forest-steppe regions as shown in Fig. 1.

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Appendix S2. Methods and sources used for the delineation of the forest-steppe biome and the main forest-steppe regions as shown in Fig. 1.

In delineating the biome, we relied on previously published maps about either the whole biome or some parts of it. All maps were digitized manually in ArcView GIS 3.2 (ESRI). When two or more maps were inconsistent, we generally opted for the wider concept (i.e. ambiguous cases near the biome peripheries were included). However, borders were modified according to expert knowledge where necessary. The delineation of the forest-steppe biome and the main regions was based on Keller (1927), Wilhelmy (1943), Leimbach (1948), Berg (1958), Zohary (1973), Horvat et al. (1974), Kramer (1984), Mayer (1984), Noirfalise (1987), Frey and Kürschner (1989), Walter and Breckle (1989), Lavrenko and Karamysheva (1993), Zhu (1993), Wallis de Vries et al. (1996), Pócs (2000), Varga et al. (2000), Chibilyov (2002), Merzlyakova (2002), Zlotin (2002), Bohn et al. (2004), Breckle (2007), Dulamsuren et al. (2005a), Zólyomi (2007), Chytrý et al. (2008), Karácsonyi (2009), Baas et al. (2012), Chytrý (2012), Rachkovskaya and Bragina (2012), Smelansky and Tishkov (2012), Sanjmyatav (2012), Nakhutsrishvili (2013),Liu et al. (2015), Memariani et al. (2016), Raingruber (2016), Wesche et al. (2016), Makunina (2017). The digital map of Olson et al. (2001) was also consulted, but the shp file itself was used for parts of Region G only. It has to be noted that polygons are not necessarily covered by forest-steppes in their total area, especially in mountainous regions, where forest-steppes are restricted to certain elevational belts.

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

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ABSTRACT

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

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goals are being undermined by tree-planting campaigns that view the open grasslands as opportunities for afforestation. Improved understanding of the interactive roles of climate variability, soils, topography, fire, and herbivores will help scientists and policymakers recognise the antiquity of the grasslands of the Eurasian forest-steppe.

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

CONTENTS

I. INTRODUCTION

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

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

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

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

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

Forest-steppes form mosaic landscapes of two ecosystem states: forest and grassland (Fig. 1B, C) (Erdős *et al*., 2018*a*). The forest state is dominated by deciduous and/or evergreen trees, including *Betula pendula* Roth (species nomenclature according to the Catalogue of Life, catalogueoflife.org), *B. pubescens* Ehrh. (Betulaceae), *Larix gmelinii* (Rupr.) Kuzen., *L. sibirica* Ledeb., *Pinus sylvestris* L. (Pinaceae), *Populus neimongolica* Doweld, *P. tremula* L. (Salicaceae), and *Quercus robur* L. (Fagaceae), whereas the grassland state is typically composed of perennial C$_3$ grasses, primarily species in the genera *Festuca* and *Stipa* (Poaceae). Boundaries between forests and grassland are typically stark and support a rich community of forbs and deciduous shrubs. In addition to many plant species that are common in the neighbouring temperate forest or steppe biomes, forest-steppes also have their own characteristic taxa that primarily occur in mosaics. These include the trees *Acer tataricum* L. (Sapindaceae) and *Quercus robur* (subspecies *pedunculiflora*; Fagaceae), the shrubs *Prunus fruticosa* Pall. (Rosaceae) (Fig. 1D), *Ribes diacanthum* Pall. (Grossulariaceae) and *Spiraea aquilegifolia* Pall. (Rosaceae), the perennial C$_3$ grasses (Poaceae) *Brachypodium pinnatum* (L.) P. Beauv., *Helictochloa hookeri* (Scribn.) Romero Zarco, and *Melica altissima* L., the sedges (Cyperaceae) *Carex humilis* Leyss. and *C. michelii* Host, and numerous forbs, including *Artemisia latifolia* Ledeb. (Asteraceae), *Anemone sylvestris* L. (Ranunculaceae), *Cervaria rivini* Gaertn. (Apiaceae), *Iris ruthenica* Ker Gawl. and *Iris variegata* L. (Fig. 1E) (Iridaceae), *Pulsatilla patens* (L.) Mill. (Ranunculaceae), *Ranunculus polyanthemos* L. (Ranunculaceae), and *Trifolium montanum* L. (Fabaceae). The forest-steppe is home to several endemics, including *Colchicum arenarium* Waldst. & Kit. (Colchicaceae) (Fig. 1F) and *Dianthus diutinus* Schult. (Caryophyllaceae) for the Carpathian Basin and *Leymus tuvinicus* Peschkova (Poaceae) and *Pilosella tjumentzevii* (Serg. & Üksip) Tupitz. (Asteraceae) for the South Siberian mountains (Jakucs, 1961; Walter & Breckle, 1989; Simon, 2000; Peshkova, 2001; Korotchenko & Peregrym, 2012; Rachkovskaya & Bragina, 2012; Smelansky & Tishkov, 2012; Makunina, 2017; H. Liu, personal communication).

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

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

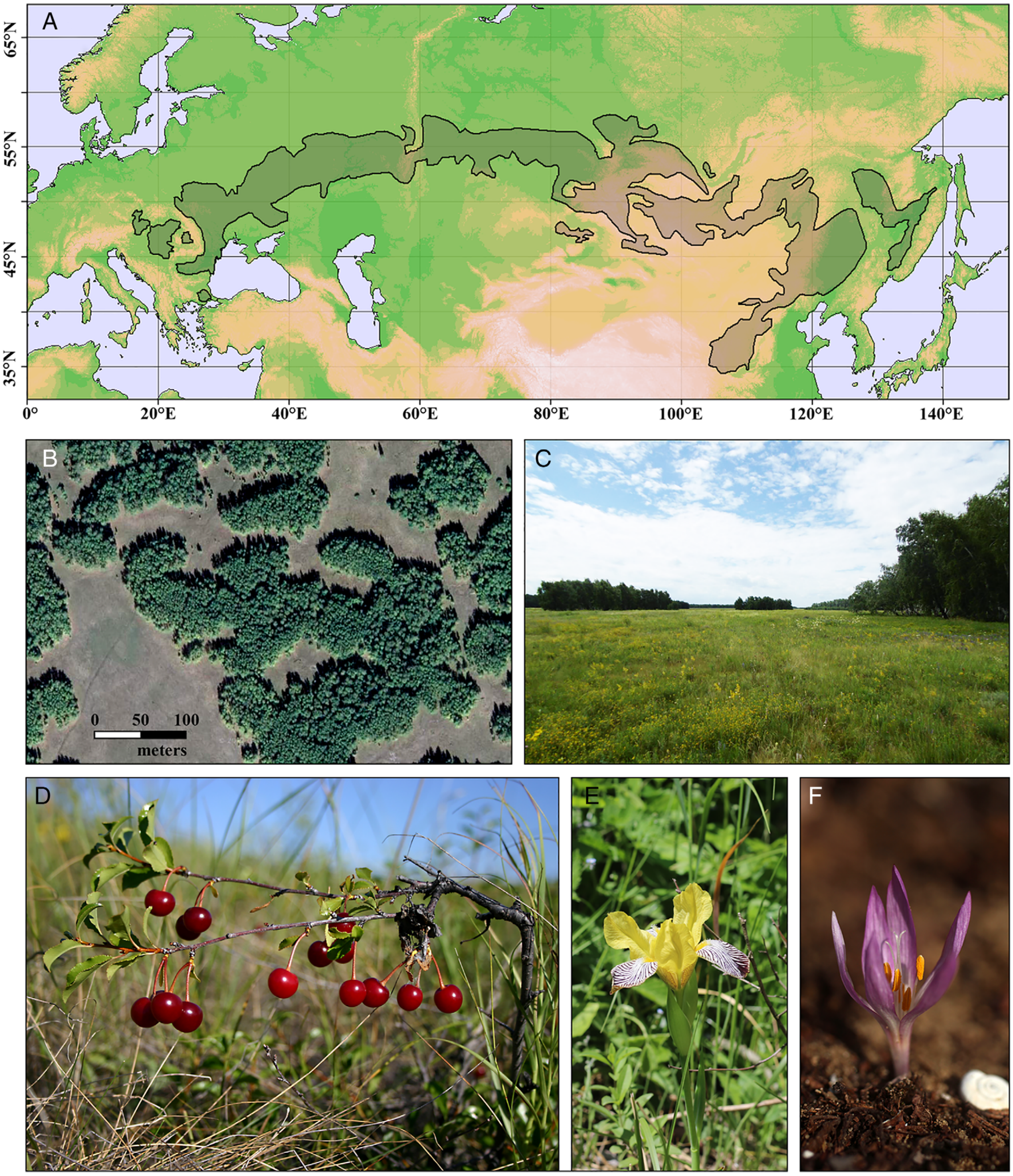

Fig. 1. The distribution of forest-steppes in Eurasia (A), mosaic of forest and grassland ecosystem states in northern Kazakhstan (B, C), *Prunus fruticosa*, a typical shrub of forest-steppe ecosystems (D), *Iris variegata*, a forest-steppe herb (E), *Colchicum arenarium*, a grassland species endemic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

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

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

III. MODELS OF FOREST–GRASSLAND COEXISTENCE

(1) Climate

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

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

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

(2) Topography

Variations in topography can considerably modify the effect of climate by either decreasing or increasing local

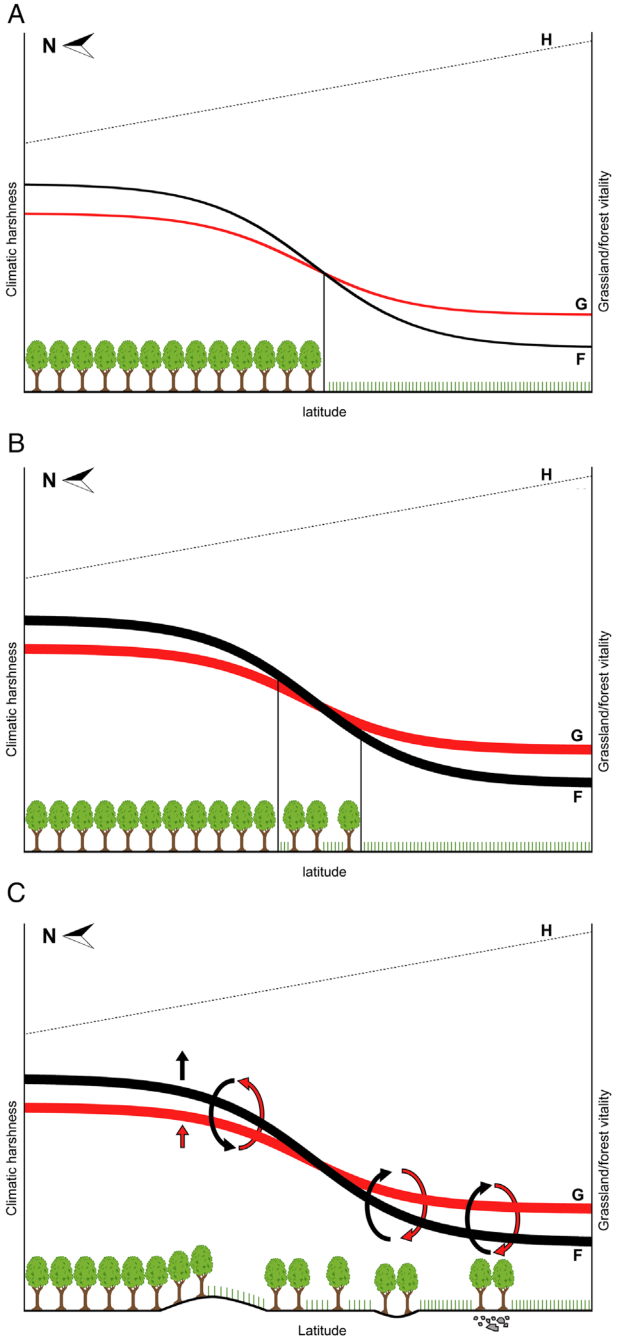

Fig. 2. Conceptual models of the distribution of forest and grassland along a continuous climatic harshness gradient (H) in Eurasia. Climatic harshness reflects (generally north to south) gradients in temperature extremes (hot summers and cold winters) and aridity (precipitation and potential evapotranspiration).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

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

The importance of topography is especially evident in the Inner Asian forest-steppe region (Mongolia, north and northeast China, and south Russia), where steep north-facing mountain slopes are usually covered by forests, steep south-facing slopes are occupied by steppes, and less extreme exposures can support either ecosystem state (e.g. Liu *et al*., 2000; Dulamsuren *et al*., 2005*b*; Anenkhonov *et al*., 2015; Hais, Chytrý & Horsák, 2016; Makunina, 2017). Liu *et al*. (2012) showed that topography controls forest and steppe distribution mainly through soil moisture. North-facing slopes receive a reduced amount of direct solar radiation, resulting in lower evaporation and, consequently, better soil moisture supply. This local decrease in aridity increases the vitality of forests relative to the steppe (Fig. 2C). By contrast, higher direct solar radiation on south-facing slopes increases temperature and reduces soil moisture. The associated local increase in aridity and heat stress decreases forest vitality relative to steppe vitality.

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

(3) Soil

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

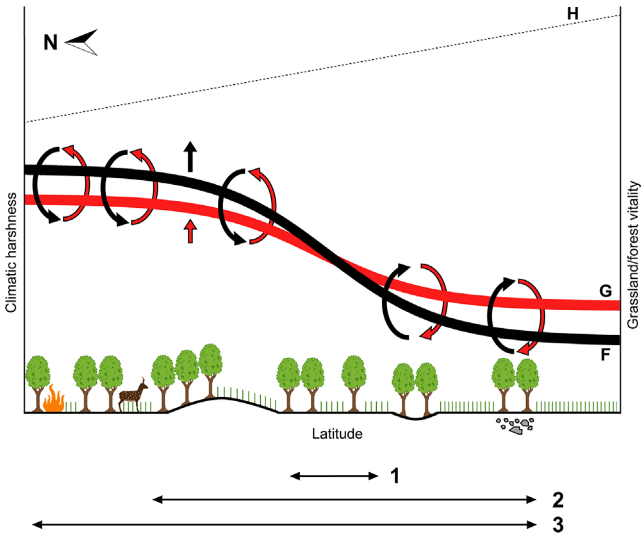

Fig. 3. Climatic–Topographic–Edaphic–Herbivore–Fire Model of forest–grassland coexistence, as determined by (1) climate (mean and variability), (2) topographic and edaphic factors (slope, aspect, soil texture, moisture availability), and (3) herbivory and fire. Circular arrows show how forest and grassland vitality (F and G, respectively) change as a result of local conditions evoked by special topographical or soil conditions (in zone 2) or as a result of fire and herbivores (in zone 3).

(4) Herbivory

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

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

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

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

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

(5) Fire

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

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

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

(6) Vegetation feedbacks and alternative ecosystem states

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

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

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

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

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

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

IV. IMPLICATIONS AND FUTURE CHALLENGES

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

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

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

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

V. CONCLUSIONS

(1) The emerging fire–herbivore paradigm, as well as the recent increase in the number of case studies makes it timely to revisit the determinants of forest–grassland coexistence at the interface of closed-canopy forests and open steppes. Through conceptual modelling and a literature review, we provide a comprehensive overview of the interacting drivers of forest–grassland coexistence in the Eurasian forest-steppe.
(2) Although mean climate is the most widely acknowledged determinant, we show that the Mean Climate Model should result in a sharp transition between the temperate or boreal forest and steppe biomes, but not a mosaic of forests and grasslands (Fig. 2A).
(3) Accounting for temporal variation in climate, the Zonal Model can only explain the coexistence of forest and grassland within a relatively narrow geographic range (Fig. 2B).
(4) Topography and edaphic conditions can modify forest and grassland patterns within the climatically determined forest-steppe zone, and are essential to explain the presence of forest-steppe across broad gradients in climatic harshness (Climatic–Topographic–Edaphic Model, Fig. 2C).
(5) Herbivory and fire are able to limit forest vitality and to decrease forest cover throughout the forest-steppe. However, their role is most important towards the humid end of the climatic harshness gradient, where herbivory and fire prevent canopy closure and thus favour the forest-steppe against closed-canopy forests (Climatic–Topographic–Edaphic–Herbivore–Fire Model, Fig. 3).
(6) Once the scene is set by these determinants of forest–grassland coexistence, vegetation feedbacks stabilise grassland and forest ecosystem states, lending considerable stability to the forest-steppe landscape configuration.
(7) Our hierarchical conceptual model highlights that many forest-steppes that have traditionally been considered secondary, represent, in fact, the historical landscape structure. Targets to restore native biodiversity or sequester atmospheric carbon should be revisited accordingly, and restorationists should think twice regarding the global call for tree planting in the Eurasian forest-steppe.

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RESEARCH ARTICLE

Taxonomic, functional and phylogenetic diversity peaks do not coincide along a compositional gradient in forest-grassland mosaics

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Abstract

1. Ecosystems with forest and grassland patches as alternative stable states usually contain various closed, semi-open and open habitats, which may be aligned along a vegetation cover gradient. Taxonomic diversity usually peaks near the middle of the gradient, but our knowledge on functional and phylogenetic diversity trends along gradients is more limited.
2. We investigated the eight main habitats of Hungarian forest-grassland mosaics, representing various vegetation cover values, and compared their species composition as well as their taxonomic, functional and phylogenetic diversity.
3. We found a compositional gradient ranging from large forest patches through smaller-sized forest patches and edges to closed and open grasslands. Species richness peaked at the middle of the gradient (at edges). Shannon diversity was high near the middle and at the open end of the gradient. Functional diversity was high throughout woody habitats (in forests and at edges) and was significantly lower in grasslands. When considering all species, phylogenetic diversity tended to peak at north-facing forest edges. When excluding non-angiosperms, this peak disappeared.
4. The high taxonomic diversity at the middle of the gradient is in line with the edge-effect theory. Our results suggest that community assembly in grasslands may be dominated by environmental filtering, while competition may be decisive in woody habitats. The low phylogenetic diversity of grassland habitats can be explained by their young evolutionary age compared to forests.
5. *Synthesis*. Functional and phylogenetic diversity do not necessarily coincide with taxonomic diversity along vegetation cover gradients. In ecosystems where

forest and grassland patches represent alternative stable states, the trends of taxonomic diversity may be similar to those revealed here, but functional diversity patterns may be more system-specific for some traits. Trends in phylogenetic diversity may vary according to the evolutionary age of the habitats.

KEYWORDS
alternative stable state, forest edge, forest-steppe, functional traits, habitat heterogeneity, semi-arid ecosystems, semi-open habitats

1 | INTRODUCTION

The alternative stable state hypothesis suggests that in certain ecosystems, two or more states (e.g. forest and grassland) can co-exist in the long run under the very same macroclimatic conditions (Bond, 2019; Petraitis, 2013). This coexistence results in a spatially heterogeneous landscape with a mosaic arrangement of structurally different habitat patches (Breshears, 2006; Innes et al., 2013). Such ecosystems include tropical and subtropical forest-savanna systems (e.g. Lehmann et al., 2011; Staal et al., 2016), the prairie-forest ecotone in North America (e.g. Brudvig & Asbjornsen, 2007; Nowacki & Abrams, 2008), and much of the Eurasian forest-steppe zone (Erdős, Ambarlı, et al., 2018). They cover a considerable proportion of the Earth's terrestrial surface and have enormous conservation and scientific importance, while also providing livelihoods for tens of millions of people (Bond, 2019; Erdős et al., 2020).

According to the forest-grassland continuum concept (Breshears, 2006), closed-canopy forests and treeless grasslands represent the two extremes of a continuum of woody plant coverage. Most terrestrial ecosystems fall somewhere along this continuum. The concept can be extended so as to differentiate among grassland types based on their vegetation cover (Figure 1a). Through the lens of this framework, the peculiarity of forest-steppes and similar forest-grassland ecosystems lies in the fact that they contain a whole range of closed, semi-open and open habitats in immediate spatial proximity; that is, several states of the continuum can be found in a single landscape. While macroclimate is the same for all these habitats, considerable secondary differences (caused by the vegetation itself) may arise among the habitats regarding some environmental factors such as light at soil surface, air humidity or topsoil moisture content. Thus, the gradient of varying vegetation cover may correspond to multiple environmental gradients (Figure 1b).

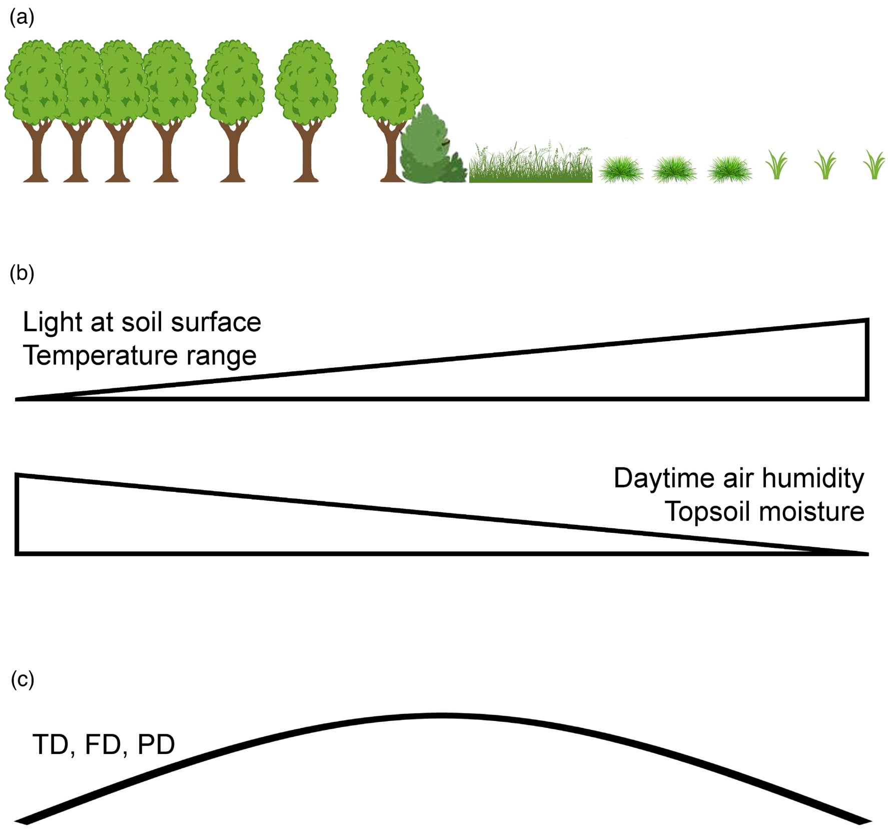

FIGURE 1 (a) Gradient of vegetation cover, ranging from closed-canopy forests to sparse grasslands, (b) environmental gradients caused by the vegetation gradient, (c) assumed pattern of taxonomic, functional and phylogenetic diversity (TD, FD and PD, respectively) along the vegetation cover gradient.

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Taxonomic diversity has been shown to vary along environmental gradients (e.g. Janssens et al., 1998; Wilson & Keddy, 1988). The most typical, though not universal, response is hump-backed (Figure 1c), that is, diversity tends to peak at intermediate levels, but this also depends on the environmental factors under study and the range of the gradient covered by the research (Pausas & Austin, 2001). In addition, the edge-effect theory also predicts taxonomic diversity to be the highest towards the middle of the gradient: the theory expects edges to be the most diverse, as they contain species from both adjoining habitats as well as their own species (so-called edge-species, Odum, 1971; Risser, 1995). The edge effect theory has considerable support from field studies conducted in natural (e.g. Bátori et al., 2018; Pinder & Rosso, 1998), semi-natural (e.g. Erdős et al., 2019) and anthropogenic (e.g. Harper et al., 2005) ecosystems, though contradictory results also exist (Kark & van Rensburg, 2006; Murcia, 1995). Taxonomic diversity may show a decreasing trend towards the endpoints of the gradient (Figure 1c): shading by tall and large plants is able to exclude most other species under dense canopies, while environmental harshness (low topsoil moisture, low air humidity, high temperature range, etc.) may limit the number of species at the opposite end (Ashton, 1993; Tilman & Pacala, 1993).

Ecologists have increasingly recognised that besides taxonomic diversity, functional and phylogenetic diversity may provide valuable insight into the origin and functioning of ecosystems (Díaz et al., 2006; Díaz & Cabido, 2001; Tilman et al., 1997). Functional diversity greatly influences ecosystem processes, dynamics and stability and has an effect on ecosystem goods and services (Cadotte et al., 2011; Hallett et al., 2017; Scherer-Lorenzen, 2008). Some studies conducted at broad spatial scales have shown that plant communities that are more species rich are also more functionally diverse (Echeverría-Londoño et al., 2018; Li et al., 2018; Swenson et al., 2012), pointing towards the possibility that taxonomic and functional diversity peak at the same position along environmental gradients. In addition, natural edges are usually structurally diverse communities, formed by a mix of trees, shrubs, forbs and graminoids, while forest interiors and open grasslands are structurally less complex (Esseen et al., 2016; Franklin et al., 2021; Harper & Macdonald, 2001). This also suggests that functional diversity, similar to taxonomic diversity, should peak near the middle of the gradient. Likewise, high species diversity and high functional diversity are frequently associated with high phylogenetic diversity as well (Cadotte et al., 2009; Flynn et al., 2011; Nagalingum et al., 2015). Accordingly, we might expect all these aspects of diversity to peak near the middle of the gradient. However, several authors caution that taxonomic, functional and phylogenetic diversity do not necessarily coincide (Bernard-Verdier et al., 2013; Díaz & Cabido, 2001; Losos, 2008; Silvertown et al., 2006), suggesting that further studies are needed to investigate their relationship.

In the present study, our aim was to examine how species composition as well as taxonomic, functional and phylogenetic diversity vary in multiple habitat types, both woody and non-woody, in a forest-steppe ecosystem. The forest-steppe is a broad transitional belt between the closed-canopy forest and the treeless steppe biomes stretching from Eastern Europe to the Asian Far East (Erdős, Ambarlı, et al., 2018; Wesche et al., 2016), where forests and grasslands represent two broad categories of alternative stable states, coexisting under the same macroclimatic conditions. Forest-steppe ecosystems consist of differently sized forest and grassland patches of various structure and composition and an intricate network of their contact zones (i.e. habitat edges). We hypothesised that these habitats can be aligned along a gradient of vegetation openness from shady forests to semi-arid grasslands, co-varying with multiple environmental factors and community composition. Our hypothesis was that taxonomic diversity would peak at forest edges (i.e. at the middle of the gradient), gradually decreasing both towards forest patches and grasslands and that edges have their own species that are rare in habitat interiors (edge-species). Furthermore, we hypothesised that functional diversity and phylogenetic diversity would also show a hump-backed curve along the gradient (Figure 1c).

2 | MATERIALS AND METHODS

2.1 | Study area

For this study, we selected 13 sites in the Kiskunság Sand Ridge, a lowland area situated between the rivers Danube and Tisza in Hungary (Figure S1; Table S1). The selected sites represent all remaining near-natural forest-steppe mosaics larger than 10 ha in the region. The climate of the study area is sub-continental with sub-Mediterranean influences. The mean annual temperature is 10.0–10.7°C, and the mean annual rainfall is 520–580 mm, 56%–59% of which falls during the vegetation period from April to September (Borhidi, 1993; Dövényi, 2010). The study sites are composed of calcareous sand dunes covered by humus-poor sandy soils with low water retention capacity (Várallyay, 1993).

All study sites are under legal protection and are covered with near-natural forest-steppe vegetation (Figure 2a). The poplar-juniper forest patches (*Junipero-Populetum albae*) have a total canopy cover of *c.* 50%–80% and are dominated by 10–15 m tall *Populus alba* trees. The shrubs, with the height of 1–5 m, cover between 5% and 80% of the area, and include species such as *Berberis vulgaris*, *Crataegus monogyna*, *Juniperus communis* and *Ligustrum vulgare*. The common herbaceous species of the forest patches are *Anthriscus cerefolium*, *Asparagus officinalis*, *Lithospermum officinale* and *Viola rupestris*. Other forest types are also present in the region, but they are extremely rare and degraded (Molnár et al., 2012), therefore, they were not included in the study. The size of the poplar-juniper forest patches varies from a few dozen square metres to *c.* 1 ha. As large forest patches are able to buffer environmental extremes, while smaller forest patches are considerably influenced by the surrounding grassland habitats (Erdős, Kröel-Dulay, et al., 2018; Ylisirniö et al., 2016), which may have a strong influence on species composition, we differentiated three forest patch size classes: large forest

FIGURE 2 (a) The natural vegetation of the Kiskunság Sand Ridge (Hungary) is forest-steppe, that is, a mosaic of forests and grasslands. The following eight habitat types were included in this study: (b) large forest patch, (c) medium forest patch, (d) small forest patch, (e) north-facing forest edge, (f) south-facing forest edge, (g) closed perennial grassland, (h) open perennial grassland and (i) open annual grassland.

patches (>0.5 ha), medium forest patches (0.2–0.4 ha) and small forest patches (<0.1 ha; Figure 2b–d).

In the present study, the forest edge was defined as the peripheral zone of each forest patch reaching out of the outermost tree trunks (diameter at breast height > 10 cm), but still below the canopy. The edges in the studied ecosystem are relatively narrow and are usually densely covered by shrubs (primarily *Crataegus monogyna* and *Juniperus communis*) and herbs (e.g. *Calamagrostis epigeios*, *Carex liparicarpos*, *Poa angustifolia* and *Teucrium chamaedrys*). Differently oriented edges tend to have different environmental parameters, and, consequently, may show differences in vegetation characteristics (e.g. Erdős, Kröel-Dulay, et al., 2018; Wicklein et al., 2012). As north- and south-facing edges are expected to show the greatest differences (Harper et al., 2005; Ries et al., 2004), they were included in the study (Figure 2e–f).

Grasslands in the study area are classified into closed perennial grasslands, open perennial grasslands and open annual grasslands. The closed perennial grassland *(Astragalo austriacae-Festucetum rupicolae*; Figure 2g) has a relatively high vegetation cover (usually >80%). The typical dominant species include *Festuca rupicola*, *Stipa* *borysthenica*, *S. capillata* and *Calamagrostis epigeios*. The species *Galium verum*, *Poa angustifolia*, *Potentilla arenaria* and *Teucrium chamaedrys* are also common.

The open perennial grassland (*Festucetum vaginatae*; Figure 2h) is the most common natural grassland at the study sites. The overall cover of vascular plants is approximately 40%–70%. This type of grassland is dominated by *Festuca vaginata*, *Stipa borysthenica* and *S. capillata*. Additional typical species include *Alkanna tinctoria*, *Euphorbia seguieriana*, *Fumana procumbens*, *Potentilla arenaria* and *Poa bulbosa*. Mosses, lichens and bare sand fill the gaps among the vascular species.

The open annual grassland (*Secali sylvestris-Brometum tectorum*; Figure 2i) usually appears in the form of small islands surrounded by perennial grasslands. Its total vegetation cover varies between 20% and 50%. The stands are co-dominated by *Bromus tectorum* and *Secale sylvestre*. Other typical species include *Bromus squarrosus*, *Kochia laniflora*, *Poa bulbosa* and *Silene conica*. Spaces among vascular plants are typically covered by mosses. Plant species nomenclature follows Király (2009), and plant association names are according to Borhidi et al. (2012). Permission to carry out the fieldworks in protected areas was granted by the Department of Environmental Protection, Nature Conservation and Waste Management of the Government Office of Pest County (permit number: PE/KTFO/1615/2021).

2.2 | Data collection

Each of the eight habitats was sampled using 25-m^2 plots (5 m × 5 m plots for forest interiors and grasslands and 2 m × 12.5 m plots for forest edges in order to rule out their extension into the interiors of forests or grasslands), following the design of earlier studies (Erdős et al., 2019, 2020; Erdős, Kröel-Dulay, et al., 2018). This plot size was large enough to prepare standard phytocoenological relevés and small enough to examine the smallest forest patches and narrow edges. Edge plots were established in more or less straight peripheral zones of forest patches larger than 0.2 ha. The total number of plots was 494 (60 plots in large forest patches, 64 plots in medium forest patches, 60 plots in open annual grasslands, 50 plots in closed perennial grasslands and 65 plots in each of the other habitat types; Table S1). The slightly unbalanced sampling effort was explained by the fact that some habitat types were rare at some sites. The percentage cover of all vascular plant species in each plot was visually estimated in spring (April–May) and summer (July–August), and the largest recorded cover value was used for data analyses. All vegetation layers (canopy, shrub and herb layer) were estimated and included in all analyses.

2.3 | Trait data

Nine plant functional traits were used in this study: start of the flowering, flowering duration, specific leaf area (SLA), mean plant height, thousand seed mass, life form, seed dispersal, pollination type and reproduction type (Table S2). SLA, plant height and seed mass are usually considered the most important and ecologically most informative traits (Díaz et al., 2004; Westoby, 1998). The other traits used in the study reflect key ecosystem functions (see Weiher et al., 1999). Plant height, thousand seed mass, SLA and flowering duration were log-transformed prior to analysis. Seven unidentified taxa (*Acer* sp., *Epipactis* sp., *Fraxinus* sp., *Hieracium* sp., *Lathyrus* sp., *Prunus* sp. and *Silene* sp., none of them present in more than 3 of the 494 plots) were excluded from the analyses involving functional and phylogenetic indices.

2.4 | Phylogenetic tree

To construct a phylogenetic tree of the 289 species found in the study plots, plant species nomenclature was standardised with The Plant List (http://www.theplantlist.org/). A phylogenetic tree with genus resolution was created with the 'phylo.maker' function of the PhyloMaker package in R version 4.1.2 using the 74,533-species mega-tree GBOTB.extended.tre, in which undetermined species were bound to their close relatives (Jin & Qian, 2019). The final tree with 289 tips is shown in Figure S2. As gymnosperms and pteridophytes are known to have a strong influence on phylogenetic structure (Feng et al., 2014; Mastrogianni et al., 2019), an additional genus-resolution phylogenetic tree was generated by excluding all non-angiosperm species (*Botrychium lunaria*, *Ephedra distachyia*, *Equisetum ramosissimum*, *Juniperus communis*, *J. virginiana*, *Pinus nigra* and *P. sylvestris*).

2.5 | Data analyses

To reveal the compositional relation among the eight habitat types, non-metric multidimensional scaling (NMDS) was performed using Bray–Curtis dissimilarity on the square-root transformed percentage cover values. The compositional distinctness of the habitats was then assessed using a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations. The 'metaMDS' and 'adonis2' functions in the vegan package of R version 4.1.2 were applied for NMDS and PERMANOVA, respectively (Oksanen et al., 2022; R Core Team, 2021). We used the 'pairwise.adonis' function in the funfuns package with *p*-value adjusted by the Bonferroni method to test the pairwise differences (Trachsel, 2022).

Species richness and Shannon diversity were calculated for each plot with the 'specnumber' and 'diversity' functions of the R vegan package, respectively (Oksanen et al., 2022).

The diagnostic species of each habitat were identified by calculating phi-coefficients as indicators of fidelity (Chytrý et al., 2002). A species was considered diagnostic if its phi was higher than 0.200 (on a −1 to +1 scale) in a particular habitat. Significant diagnostic species ($p < 0.001$) were identified with Fisher's exact test. The analyses were carried out in JUICE 7.1 (Tichý, 2002).

Rao's quadratic entropy (RaoQ) was used to reveal the functional diversity (FD) of each plot, as it is an appropriate measure of functional diversity (Botta-Dukát, 2005; Ricotta, 2005). We calculated overall functional diversity for each plot by combining nine traits: start of flowering, flowering duration, SLA, plant height, thousand seed mass, life form, seed dispersal, pollination type and reproduction type. Functional diversity was also calculated for each individual trait, with the exception of two individual traits (flowering start and flowering duration), which were combined to form a trait group (called flowering time), upon which its functional diversity was assessed. We chose the 'gawdis' function of the GAWDIS package in R to calculate species dissimilarity because it was designed to handle problems with uneven trait contribution as well as fuzzy coded traits (de Bello, Botta-Dukát, et al., 2021).

RaoQ was also used to analyse phylogenetic diversity (PD), ensuring to handle phylogenetic and functional diversity within the same conceptual and mathematical framework (Jucker et al., 2013; Swenson, 2014). RaoQ was calculated for two scenarios: (i) all species and (ii) only angiosperm species. The phylogenetic distance matrix was created with the 'cophenetic' function of the PICANTE package in R (Kembel et al., 2010). We selected the 'rao.diversity' function of the SYNCSA package in order to calculate RaoQ for both FD and PD (Debastiani & Pillar, 2012).

To eliminate the effect of species richness on RaoQ and to determine whether the habitats are functionally and phylogenetically over- or underdispersed, the standardised effect size of RaoQ (SES.RaoQ) was measured as (observed RaoQ value − mean expected RaoQ values)/standard deviation of expected RaoQ values (de Bello, Carmona, et al., 2021). The null models for functional indices were generated by permuting the species labels of the trait matrix (999 randomisations) using the R code provided by de Bello, Carmona, et al. (2021), whereas the names of the species on the phylogeny were shuffled to create null models for phylogenetic indices using the R code in Swenson (2014). Positive SES.RaoQ values indicate that the species of a given habitat are functionally or phylogenetically more distant than expected by chance (overdispersed or divergent habitats), and negative SES.RaoQ values indicate that species are closer to one another than expected by chance (underdispersed or clustered habitats). To test the statistical significance of observed SES values with null expectation SES values, we used a two-sided Wilcoxon signed rank test (Bernard-Verdier et al., 2012; Nooten et al., 2021).

To explain the relationship between functional trait and phylogenetic diversity, we calculated Blomberg's K-statistic of the phylogenetic signal for each single trait (Blomberg et al., 2003). Close-to-zero K values indicate that there was less phylogenetic signal than expected from Brownian Motion trait evolution, implying that closely related species are functionally distinct. To determine the significance of the phylogenetic signal, a randomisation test (999 times) was computed in the 'phylosig' function of the PHYTOOLS package, which simulated the random trait data across the tips of the phylogenetic tree to create the null distribution (Revell, 2012).

Species richness, Shannon diversity and SES.RaoQ were analysed using linear mixed-effects models. The random factor was the site, and the fixed factor was the habitat. The 'glmmTMB' function of the GLMMTMB package in R was used to build the models with Poisson family for count data (species richness) and Gaussian family for continuous variables (Shannon diversity and SES.RaoQ; Brooks et al., 2017). Analysis of variance was computed to test the linear mixed-effects models, and if the model had a significant proportion of variability, all pairwise comparisons of the fixed factor levels were performed, and the *p*-values were adjusted with the Bonferroni method by the 'emmeans' function in the EMMEANS package in R (Lenth, 2022).

3 | RESULTS

3.1 | Vegetation gradient

The NMDS ordination revealed a compositional gradient along the first NMDS axis, ranging from large forest patches through smaller-sized forest patches and edges to closed and open grasslands (Figure 3). Although many groups overlapped substantially, the PERMANOVA confirmed highly significant differences between the habitat types ($F = 59.0$, $R^2 = 0.46$, $p = 0.001$). Most pairwise comparisons revealed significant ($p < 0.05$) differences between habitats,

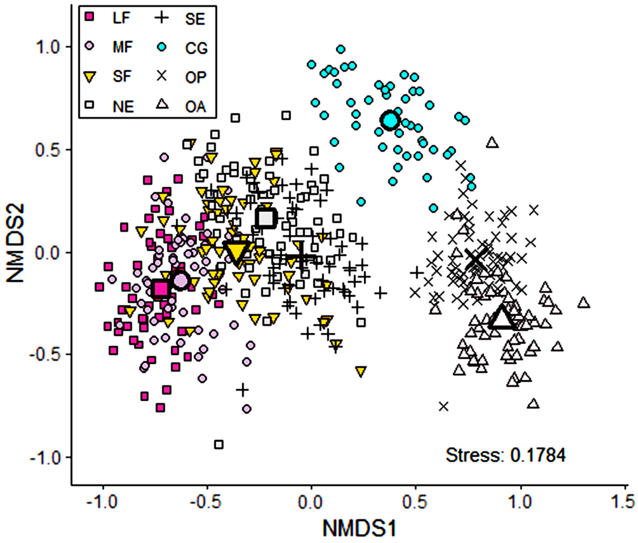

FIGURE 3 Habitat types along the forest-grassland gradient have high turnover in species composition. Forest, edge and grassland types are placed in accordance with their position along the vegetation openness gradient in the ordination diagram. The NMDS ordination was prepared using square-root transformed cover percentages and Bray–Curtis dissimilarity. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; CG: closed perennial grasslands; OP: open perennial grasslands; OA: open annual grasslands. Large symbols indicate the centroids for each habitat.

with the exception of only one pair: large forest patches and medium forest patches ($p > 0.05$; Table S3).

3.2 | Taxonomic diversity and edge species

Habitat type significantly affected species richness ($\chi^2 = 435.9$, $p < 0.001$) and Shannon diversity ($\chi^2 = 60.6$, $p < 0.001$). The highest species richness was found at north-facing edges, followed by south-facing edges (Figure 4a; Table S4). Species richness gradually decreased towards both ends of the vegetation gradient. Shannon diversity was high at edges as well as in open annual and open perennial grasslands (Figure 4b; Table S4).

The list of diagnostic species related to the eight habitats is presented in Table S5. Several species were diagnostic for two or more habitats (the number of shared diagnostic species was especially high among woody habitats and among grassland habitats). Here, we only consider those species that were diagnostic for a single habitat type. Large, medium and small forest patches had 8, 3 and 0 diagnostic species, respectively. The number of diagnostic species was 16 for north-facing edges and 4 for south-facing edges. There were 15, 5 and 11 significant diagnostic species in closed grasslands, open perennial grasslands and open annual grasslands, respectively.

3.3 | Functional diversity

Habitat type significantly affected overall functional diversity ($\chi^2 = 1266$, $p < 0.001$). Functional diversity was significantly higher in woody habitats (i.e. forests and edges) than in grassland habitats (Figure 4c; Table S4). Among the grassland habitats, the lowest functional diversity was found in closed perennial grasslands. Woody habitats were overdispersed, whereas grassland habitats were underdispersed (Figure 4c; Table S6).

The functional diversity of individual traits was significantly influenced by habitat type (Table 1). Taking into consideration the pairwise comparisons (Table S7), the functional diversities of flowering time, seed dispersal, reproduction type and plant height were significantly higher in woody habitats than in grassland habitats

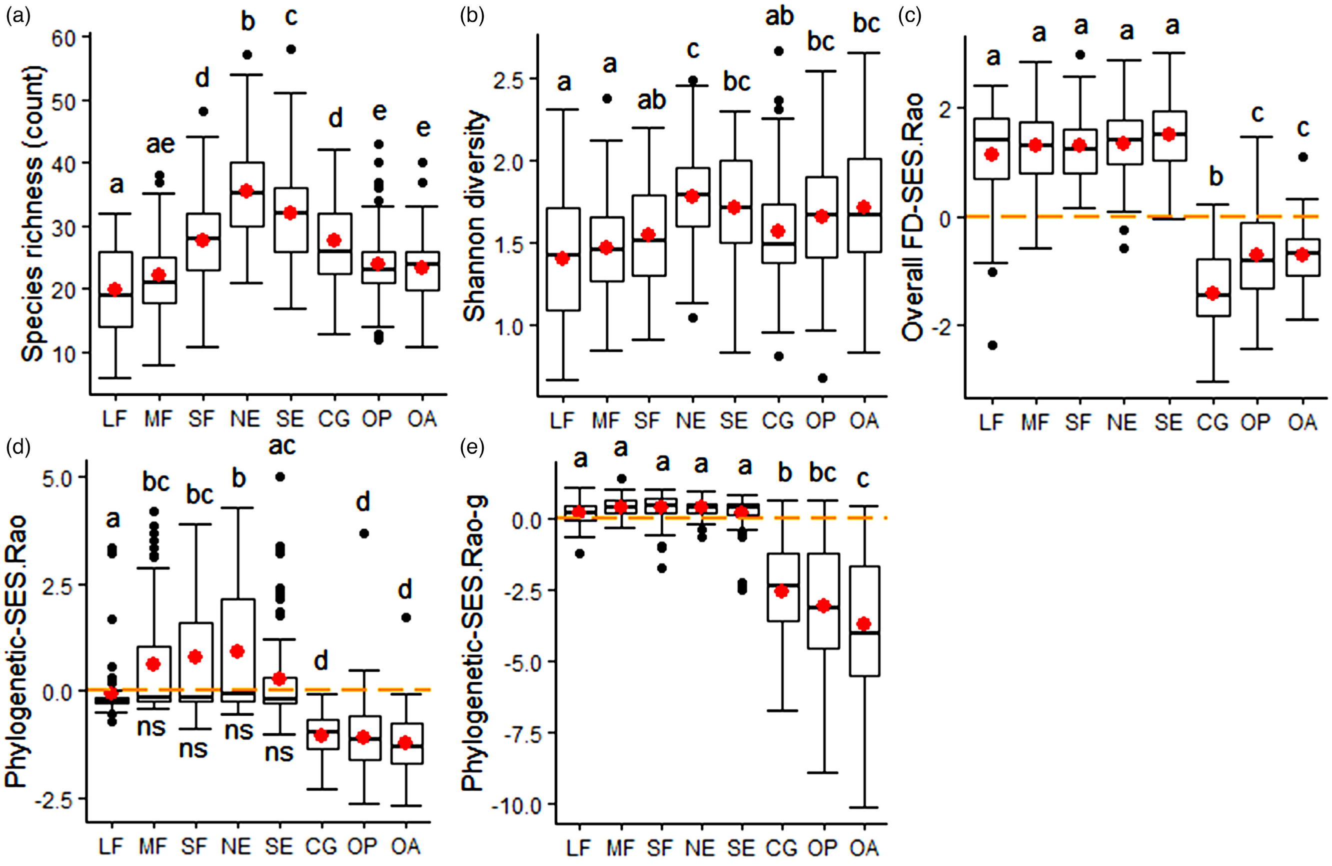

FIGURE 4 Differences in diversity measures between habitat types. Diversity measures include species richness (a), Shannon diversity (b), standardised effect size of Rao's quadratic entropy (SES.RaoQ) for functional diversity based on all traits (c), SES.RaoQ for phylogenetic diversity (d) and SES.RaoQ for phylogenetic diversity with non-angiosperm species excluded (e). Habitat type abbreviations are according to the caption of Figure 3. Different letters indicate significant differences among habitats. The red dots in the box-plots indicate mean values. Null model expectation is shown by dashed horizontal line. Negative SES values indicate trait underdispersion, positive values indicate trait overdispersion; 'ns' indicates non-significant differences between observed SES.RaoQ values and the null model expectation (two-sided Wilcoxon signed rank test).

TABLE 1 Among-type variation is significantly higher than expected under random assembly for all traits. Analysis of variance table for linear mixed-effect models

Trait	Chi square (χ^2)	*p*-value	Trait	Chi square (χ^2)	*p*-value
Flowering time	667.8	<0.001	Life form	142.3	<0.001
Seed dispersal	489.6	<0.001	Specific leaf area (SLA)	97.1	<0.001
Reproduction type	2565	<0.001	Thousand seed mass	268.9	<0.001
Mean plant height	1921	<0.001	Pollination type	95.4	<0.001

(Figure 5a–d), and there was a similar tendency regarding the functional diversity of seed mass (Figure 5g). With a few exceptions, woody habitats were overdispersed, whereas grassland habitats were underdispersed for these traits. Regarding life form and mean plant height, south-facing edges had the highest functional diversity, followed by north-facing edges and small forest patches (Figure 5d–e). Closed perennial grasslands, open annual grasslands and medium forest patches had the highest functional diversity for SLA (Figure 5f). The SES.RaoQ values of life form and SLA indicated underdispersion in most habitats. The functional diversity of thousand seed mass showed a gradual decrease along the vegetation gradient (Figure 5g). The functional diversity of pollination type reached its maxima towards the endpoints of the gradient, that is, in large forest patches and open annual grasslands, while it was low at the middle of the gradient (Figure 5h).

3.4 | Phylogenetic diversity and phylogenetic signal

Habitat type had a significant effect on phylogenetic diversity ($\chi^2 = 319.1$, $p < 0.001$). Phylogenetic diversity was significantly higher in woody than in grassland habitats (Figure 4d; Table S4). Phylogenetic diversity appeared to show a peak near the middle of the gradient: north-facing edges had the highest phylogenetic diversity, although this habitat did not differ significantly from medium and small forest patches. Large forest patches proved to be underdispersed, while the other woody habitats showed no significant differences with the null model expectation (Figure 4d; Table S6). All grassland habitats were underdispersed.

If only angiosperms were included in the calculation, habitat type still had a significant effect on phylogenetic diversity ($\chi^2 = 797.8$, $p < 0.001$). Pairwise comparisons revealed significant differences between the woody and the grassland habitats (Figure 4e; Table S4). However, there were no significant differences in phylogenetic diversity among the woody habitats. All woody habitats were overdispersed, while all grassland habitats were underdispersed (Figure 4e; Table S6).

Blomberg's *K* values for the nine functional traits were less than one (Table 2), ranging from 0.042 (self-pollination of pollination-type trait) to 0.794 (Semi-shrub of life-form trait). Most traits, however, had *K* values that were higher than expected under random trait assembly, indicating a weak but significant phylogenetic signal.

4 | DISCUSSION

4.1 | Vegetation gradient

Many ecosystems with alternative stable states are mosaics of differently sized forest patches and one or more types of grassland. Our hypothesis that these habitats can be aligned along a gradient could be verified in the present study (Figure 3). Forest patches are known to reduce environmental harshness, which has been shown to alter the species composition of the understory, especially under arid and semi-arid conditions (Belsky et al., 1993; Holmgren et al., 1997). This ability of tree canopies to influence their environments decreases with decreasing forest patch size (e.g. Erdős, Kröel-Dulay, et al., 2018; Kovács et al., 2020). Consequently, the smallest forest patches do not have a core area and are in practice very similar to edges (Erdős et al., 2020). Environmental factors at edges are strongly influenced by neighbouring treeless areas (Schmidt et al., 2017). In addition, forest canopy tends to be most open at edges (de Casenave et al., 1995; Williams-Linera, 1990). As a result, the species composition of forest edges is transitional between forest interiors and grasslands. As predicted by Ries et al. (2004), north-facing edges proved to be compositionally more similar to forest interiors, while south-facing edges were more similar to grasslands (Figure 3). Among the grassland habitats, open perennial grasslands and open annual grasslands were situated at the extreme end of the compositional gradient. This likely reflects their harsh conditions (Bodrogközy, 1982), while the environmental factors of closed perennial grasslands are less harsh (Borhidi et al., 2012).

Similar compositional gradients are likely to occur in other ecosystems with alternative stable states, provided that forest patches or groups of trees are able to alter their environment significantly, resulting in different species compositions between the open areas and under the canopies. However, tree's ability to alter their environment depends on their density and canopy characteristics (e.g. Mogashoa et al., 2021; Randle et al., 2018). If trees are widely spaced and solitary, have thin leaves and/or show limited lateral branching, they may not be able to alter their environment sufficiently to support a community that differs from the grassland matrix. For example, grasses may be excluded under the closed canopies of groves, but the grass layer can survive under solitary trees in African savannas (Osborne et al., 2018). In the eastern Alps, *Pinus sylvestris* forms mosaics with xeric grasslands (Erdős et al., 2017). Pine trees have thin leaves and tall and straight trunks, with branches only near the

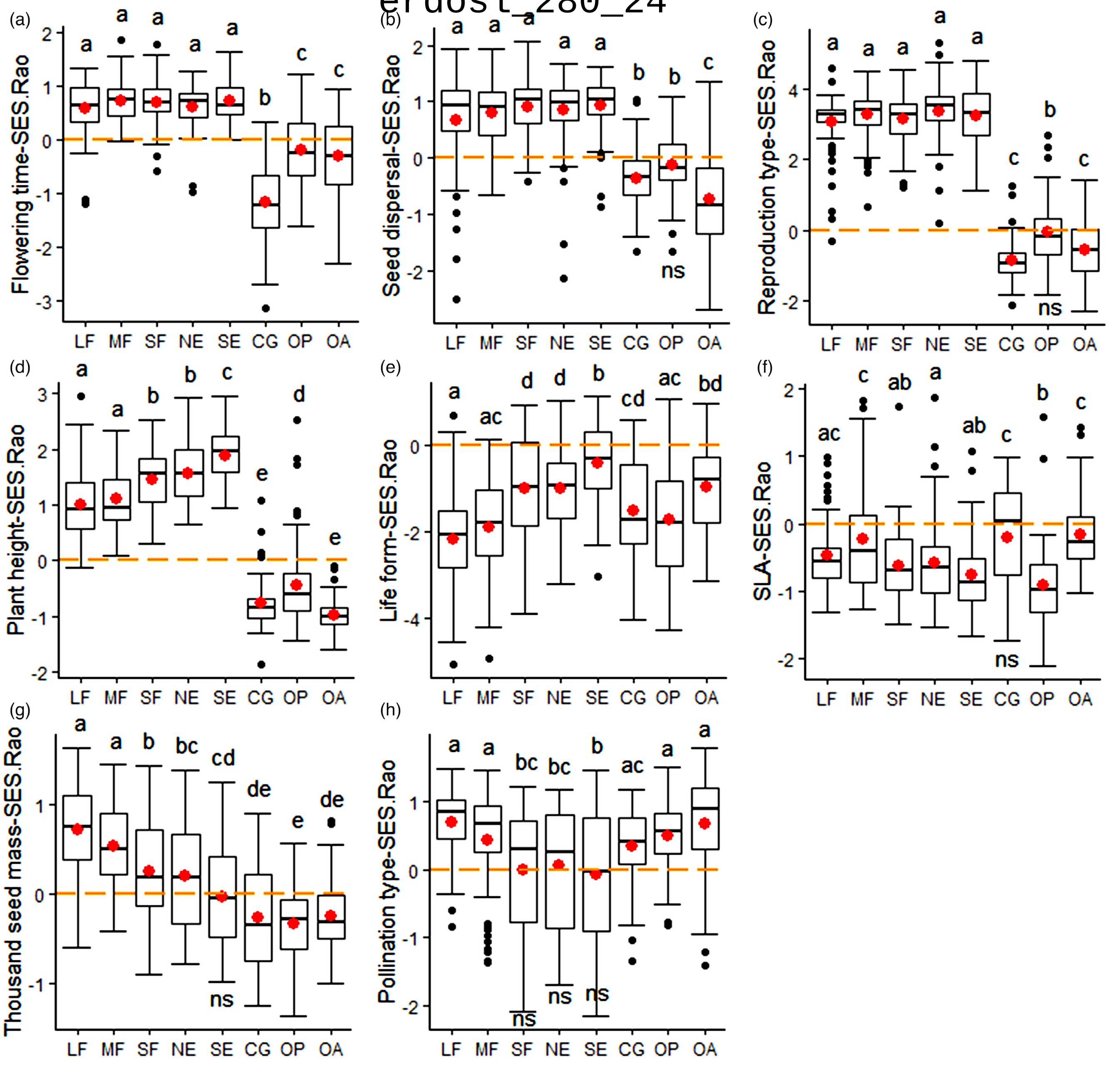

FIGURE 5 Differences in trait-wise functional diversity between habitat types. Traits include flowering time (a), seed dispersal (b), reproduction type (c), plant height (d), life form (e), specific leaf area (f), thousand seed mass (g) and pollination type (h). Habitat type abbreviations are according to the caption of Figure 3. Different letters indicate significant differences among habitats. The red dots in the box-plots indicate mean values. Null model expectation is shown by dashed horizontal line. Negative SES values indicate trait underdispersion, positive values indicate trait overdispersion; 'ns' indicates non-significant differences between observed SES.RaoQ values and the null model expectation (two-sided Wilcoxon signed rank test).

top. As a result, the vegetation is rather similar in open areas and under the trees or groups of trees.

4.2 | Taxonomic diversity and edge-species

The hypothesis that taxonomic diversity would show a hump-backed curve along the gradient was partly supported by our results. Species richness peaked at the middle of the gradient and gradually decreased towards both ends (Figure 4a). This result was in good accordance with earlier observations in natural or semi-natural forest edges (e.g. Bátori et al., 2018; Erdős et al., 2019; Molnár, 1998; Pinder & Rosso, 1998) as well as with the edge effect theory (e.g. Odum, 1971; Risser, 1995). This theory assumes that edges are more species-rich than habitat interiors are, as they contain species from both adjacent habitats as well as their own species (edge-species). Our results confirmed the existence of edge-species: we were able to identify species that preferred either north-facing or south facing

TABLE 2 Nine functional traits and their characteristics. Blomberg's *K* together with respective *p*-values represent the phylogenetic signal (values higher than random are in bold)

Trait	Mean value	Blomberg's *K*	*p*-value
1. Specific leaf area (SLA; $mm^2\ mg^{-1}$)	2.914	**0.081**	**0.001**
2. Height (cm)	3.947	**0.173**	**0.001**
3. Seed mass (g)	0.271	**0.460**	**0.001**
4. Flowering duration (Month)	1.103	**0.043**	**0.017**
5. Start of flowering			
Blooming from early spring (months 1 to 4)	0.252	**0.049**	**0.012**
Blooming from early summer (months 5 to 6)	0.643	**0.047**	**0.005**
Blooming from late summer (months 7 to 9)	0.105	0.049	0.051
6. Life form			
Tree and shrub	0.131	**0.708**	**0.001**
Semi-shrub	0.020	**0.794**	**0.001**
Dwarf shrub	0.046	0.047	0.148
Hemicryptophyte	0.376	**0.089**	**0.001**
Geophyte	0.117	**0.353**	**0.001**
Therophyte	0.244	**0.080**	**0.002**
Hemitherophyte	0.063	0.046	0.104
Epiphyte	0.003	**0.677**	**0.012**
7. Seed dispersal			
Anemochor	0.312	**0.249**	**0.001**
Rainwash	0.009	0.051	0.227
Autochor	0.052	**0.112**	**0.004**
Zoochor	0.627	**0.188**	**0.001**
8. Pollination type			
Insects	0.635	**0.312**	**0.001**
Wind	0.242	**0.360**	**0.001**
Self-pollination	0.123	0.042	0.089
9. Reproduction type			
Generative	0.793	**0.064**	**0.002**
Vegetative	0.207	**0.064**	**0.001**

edges while they were rare in habitat interiors (Table S5). Thus, the high species richness at the middle of the gradient is at least partly due to edge-species. North-facing edges had the highest number of diagnostic species, which is in accordance with the results of a study carried out in a semi-natural forest-grassland mosaic (Erdős et al., 2019).

Risser (1995) suggested that forest edges support especially high species richness if the edge is old and stable for a long time. This view has some support from field studies (e.g. Harper & Macdonald, 2002) and is in good accordance with our results, as all the edges included in the present work were old, undisturbed and stable.

Compared to species richness, Shannon diversity showed a slightly different pattern (Figure 4b). While Shannon diversity, similar to species richness, was high at the edges (at the middle of the gradient), it was also high in the open grassland habitats. It is possible that environmental harshness (low soil moisture, temperature extremes and low soil humus content; Borhidi et al., 2012) prevents vascular plant species from reaching high cover values, resulting in greater species evenness, which leads to higher Shannon diversity. Similarly, Bernard-Verdier et al. (2012) found that species evenness increased with decreasing soil depth, which was due to the fact that the species that reached high cover values on deep soils could not become dominant under harsher conditions. In addition to the harsh environment, disturbance may also support great species evenness by preventing a few competitive species from reaching high cover values (Cardinale et al., 2000; Svensson et al., 2012). Compared to any other habitat in the studied ecosystem, open annual grasslands are more affected by disturbances (trampling of grazers and browsers, extreme droughts and moving sand; Borhidi et al., 2012). This may effectively limit their species richness, but at the same time, it can ensure high Shannon diversity.

Results from other woody-herbaceous ecosystems are in line with our findings only partly. For example, Mogashoa et al. (2021) studied a gradient of woody plant cover in a semi-arid African savanna and found that the Shannon diversity of grasses was the highest at medium woody cover, while tree diversity was the lowest at this point. In an Australian woodland, Price and Morgan (2008) found that species richness was the highest at the shrubless end of the gradient, with a second peak appearing at medium shrub cover.

4.3 | Functional diversity

One of the most important findings of our study is that patterns of taxonomic and functional diversity differed considerably among the habitats of the forest-steppe ecosystem (Figure 4a–c). Contrary to species richness and Shannon diversity, functional diversity was significantly higher in woody habitats (forests and edges) than in grasslands (Figure 4c). The functional diversity of single traits revealed that this pattern was mainly driven by the functional diversity of flowering time, seed dispersal, reproduction type, mean plant height, and, to a lesser degree, thousand seed mass (Figure 5a–d, g). Earlier studies have suggested that lower functional diversity should be expected under harsh environmental conditions (de la Riva et al., 2018; Dovrat et al., 2021; Moradi & Oldeland, 2019), which is in accordance with our results, as grassland habitats are characterised by stronger environmental stress than woody habitats (Bodrogközy, 1982; Erdős et al., 2014). A possible explanation for this is the stress-dominance hypothesis (Weiher & Keddy, 1995), which suggests that under harsh environmental conditions, community assembly is determined by environmental filtering, while under more favourable conditions, interspecific competition and other density-dependent factors become more important. Thus, harsh environments are expected to host species with similar traits adapted to those environments, resulting in lower functional diversity. In contrast, strong competition in less harsh environments tends to exclude species with similar traits, leading to higher functional diversity.

Competition for light in the woody habitats leads to a multilayered structure and results in high functional diversity of mean plant height (Figure 5d). This may have cascading effects on other traits. For example, light seeds may be adaptive both in grasslands and the canopy layer of the woody habitats, whereas heavy seeds are better suited to the canopy and the shrub layers, from where they can disperse farther by air or can easily be caught by birds. Thus, two or more functional strategies can be equally important in woody habitats (leading to high functional diversity for these traits), while one strategy tends to dominate in grassland habitats (resulting in lower functional diversity).

It is worth emphasising that large forest patches proved to be functionally diverse habitats in our study, even though they had the lowest species richness values. This reinforces the view that species richness is not necessarily informative of functional diversity (e.g. De Pauw et al., 2021; Díaz & Cabido, 2001; Purschke et al., 2013). In forests, the average size of individual plants is larger than that in grasslands, which may imply that fewer individuals are sampled in a plot, possibly resulting in lower species richness (Luczaj & Sadowska, 1997). At the same time, it is possible that large plants tend to exclude other plants with similar traits in their proximity, while they can coexist with plants possessing different traits because of their lower niche overlap, indicating the importance of competition towards the less harsh end of the gradient (cf. Weiher & Keddy, 1995). This may have resulted in a higher functional diversity at the sampling scale used in the present study.

North- and south-facing edges and small forest patches were the most functionally diverse habitats regarding the traits mean plant height (Figure 5d) and life form (Figure 5e). This reflects the diverse structural features of the edges and edge-like habitats, which harbour a wide variety of herbs, shrubs and trees. It is important to note here that all the edges included in this study were near-natural, that is, they were not anthropogenically created. While anthropogenic edges are typically abrupt, (near-)natural edges are usually gradual (Esseen et al., 2016), allowing the coexistence of woody and herbaceous species in a few metre wide zone.

Grasslands had low overall functional diversity values (Figure 4c), but some of them had high values for particular traits. The functional diversity of SLA was high in closed perennial grasslands and open annual grasslands (Figure 5f). Closed grasslands host many species adapted to dry and nutrient-poor environments, which typically have low SLA values (Pérez-Harguindeguy et al., 2013). At the same time, closed grasslands also contain some species that have relatively high SLA values and usually occur in environments with slightly better water and nutrient supply (e.g. *Festuca rupicola*). Open annual grasslands also contain several species that can tolerate dry and nutrient-poor conditions and are characterised by small SLAs. On the other hand, many of their species avoid the mid- to late-summer drought by completing their life cycles during spring and early summer, when there is sufficient precipitation. These species (e.g. *Bromus tectorum* and *Setaria viridis*) have high SLAs. This indicates that two distinct functional strategies coexist in closed grasslands and open perennial grasslands (cf. Bernard-Verdier et al., 2012). The functional diversity of pollination type proved to be high in open perennial and open annual grasslands (Figure 5h). This is due to the fact that habitats at the middle of the gradient are dominated by insect-pollinated species, while the proportion of insect-, wind- and self-pollinated species is more even in the open grasslands.

Alternative stable states have been studied primarily in aquatic ecosystems and small artificial communities (Petraitis, 2013). We expect that, in ecosystems where forest and grassland patches represent alternative stable states, the main trends of functional diversity may be similar to those revealed in the present study. Functional diversity for plant height, in particular, is likely to be higher in forest than in grassland habitats, and this may have a cascading effect on other traits such as seed mass or seed dispersal. The high functional diversity of life forms in edges and edge-like habitats may also be a widespread phenomenon in forest-grassland mosaics of natural origin. Functional diversity patterns, however, may be more system-specific for some traits. For example, the diversity of reproduction type may strongly depend on the reproduction strategy of the dominant and most frequent woody and graminoid species.

4.4 | Phylogenetic diversity and phylogenetic signal

We found that phylogenetic diversity showed a peak near the middle of the gradient, but the peak disappeared if non-angiosperms were excluded from the analysis (Figure 4d–e). The difference was probably caused by *Juniperus communis*, by far the most frequent non-angiosperm species in our study. This species cannot survive in the largest and most dense forest patches and is very rare in grasslands (Borhidi et al., 2012), which leads to lower phylogenetic diversity. However, *Juniperus communis* is very typical in smaller-sized forests and at edges, contributing to the increased phylogenetic diversity of these habitats. All the other non-angiosperm species were so rare that we think they did not have a large influence on the patterns of phylogenetic diversity.

Phylogenetic diversity was higher in woody habitats than in grasslands (Figure 4d). This difference did not disappear if non-angiosperm species were excluded from the analysis (Figure 4e), indicating that the difference was not due to the woody gymnosperms that occur primarily in forest interiors and/or edges but are rare in grasslands (*Juniperus communis*, *J. virginiana*, *Pinus nigra* and *P. sylvestris*). Similarly, in a Brazilian savanna ecosystem, Gastauer et al. (2017) found that woodlands had higher phylogenetic diversity than grasslands. Using a global dataset for phylogenetic diversity analysis, Massante et al. (2019) also reported higher phylogenetic diversity for forests than for grasslands. A potential explanation for this pattern could be related to the history of these habitats: phylogenetic diversity was found to be high in evolutionarily old habitats and low in young habitats (Gerhold et al., 2015, 2018). In a study examining the plant community types in the Czech Republic, Lososová et al. (2015) found that forests were phylogenetically more dispersed than grasslands were. They argued that in the eastern Central European region, forests have a long evolutionary history (since the Mesozoic), whereas grasslands of the region only appeared during late Tertiary. Thus, only a few lineages had enough time to adapt to grasslands, resulting in lower phylogenetic diversity in grasslands than in forests. Similarly, Procheş et al. (2006) reported lower phylogenetic diversity in the evolutionarily young fynbos, karoo and grassland vegetation in a South African landscape and higher phylogenetic diversity in the much older thicket vegetation.

The potential link between phylogenetic diversity and the evolutionary age of habitats may have a decisive effect on the diversity patterns of ecosystems where alternative stable states co-occur. Grasslands may have higher phylogenetic diversity in ecosystems where open habitats have a longer history, while their phylogenetic diversity is expected to be smaller where grasslands appeared more recently.

We found weak but significant phylogenetic signal for the majority of traits (Table 2), suggesting that these traits are phylogenetically conserved. The results of previous studies investigating the relationship between ecological similarity and phylogenetic relatedness vary considerably (Losos, 2008). For example, Prinzing et al. (2001) detected phylogenetic signal for ecophysiological traits among Central European vascular plant species. Chazdon et al. (2003) found phylogenetic signal for reproductive traits and growth form in Neotropical woody taxa. In contrast, examining a North American subalpine plant community, CaraDonna and Inouye (2015) detected significant phylogenetic signal for only a subset of the studied flowering traits. Silvertown et al. (2006) found no phylogenetic signal for plant niches in English meadow communities. Thus, the presence of phylogenetic signal for traits revealed in our study should not be considered a general phenomenon, as the relation between functional traits and phylogeny may vary among habitats, taxa and traits.

5 | CONCLUSIONS

We confirmed the hypothesis that the habitats of the studied forest-grassland mosaics form a compositional gradient according to vegetation cover. Although similar studies are largely lacking, we think that the systematic sampling of multiple habitats in other ecosystems with alternative stable states could reveal similar gradients. In line with our second hypothesis and the edge effect theory, species richness showed a hump-backed curve, peaking in semi-open habitats (at the middle of the gradient) and gradually decreasing towards both ends of the gradient. Shannon diversity was high at edges as well as in open annual and open perennial grasslands. We also confirmed the hypothesis that edges have their own species that are rare in habitat interiors (edge-species). We expect that taxonomic diversity shows similar trends in other ecosystems where forest and grassland patches represent alternative stable states. However, as the overwhelming majority of edge research has focused on anthropogenic edges (e.g. forest-clearcut edges), while natural edges have been understudied (Franklin et al., 2021), more work on the latter type is needed to improve our ability to make generalisations.

Contrary to our hypothesis, functional diversity was significantly higher in woody habitats (forests and edges) than in grasslands, which is in good accordance with the stress-dominance hypothesis (Weiher & Keddy, 1995).

Our hypothesis that phylogenetic diversity would show a hump-backed curve was supported only partly: while phylogenetic diversity tended to show a peak near the middle of the gradient when all species were considered, this pattern disappeared when non-angiosperms were excluded from the analysis. Phylogenetic diversity was significantly higher in woody than in grassland habitats, which may be related to the evolutionary age of the habitats. Importantly, our results underline that taxonomic diversity is not necessarily informative of functional and phylogenetic diversity. Thus, in addition to simple taxonomic indices, studies on diversity patterns should also take into account functional and phylogenetic aspects if we are to gain a better understanding of how ecosystems work.

AUTHOR CONTRIBUTIONS

László Erdős designed the study, László Erdős, Khanh Vu Ho, Zoltán Bátori, György Kröel-Dulay, Gábor Ónodi, Csaba Tölgyesi and Péter Török conducted the field works, Khanh Vu Ho, Csaba Tölgyesi and Attila Lengyel analysed the data, László Erdős, Khanh

Vu Ho, Zoltán Bátori, György Kröel-Dulay, Gábor Ónodi, Csaba Tölgyesi, Péter Török and Attila Lengyel interpreted the results, László Erdős and Khanh Vu Ho wrote the first draft of this manuscript, and László Erdős, Khanh Vu Ho, Zoltán Bátori, György Kröel-Dulay, Gábor Ónodi, Csaba Tölgyesi and Attila Lengyel edited the manuscript.

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data necessary to reproduce the analyses are deposited at Zenodo https://doi.org/10.5281/zenodo.7215118 (Erdős et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Supporting Information

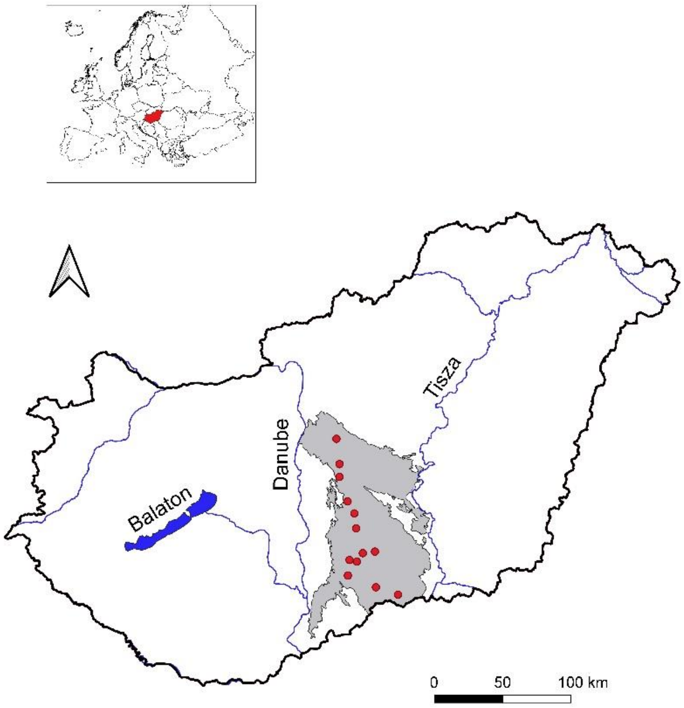

Figure S1. The position of the 13 study sites (red dots) in the Kiskunság Sand Ridge (gray) between the Rivers Danube and Tisza in Hungary. The inset shows the position of Hungary in Europe.

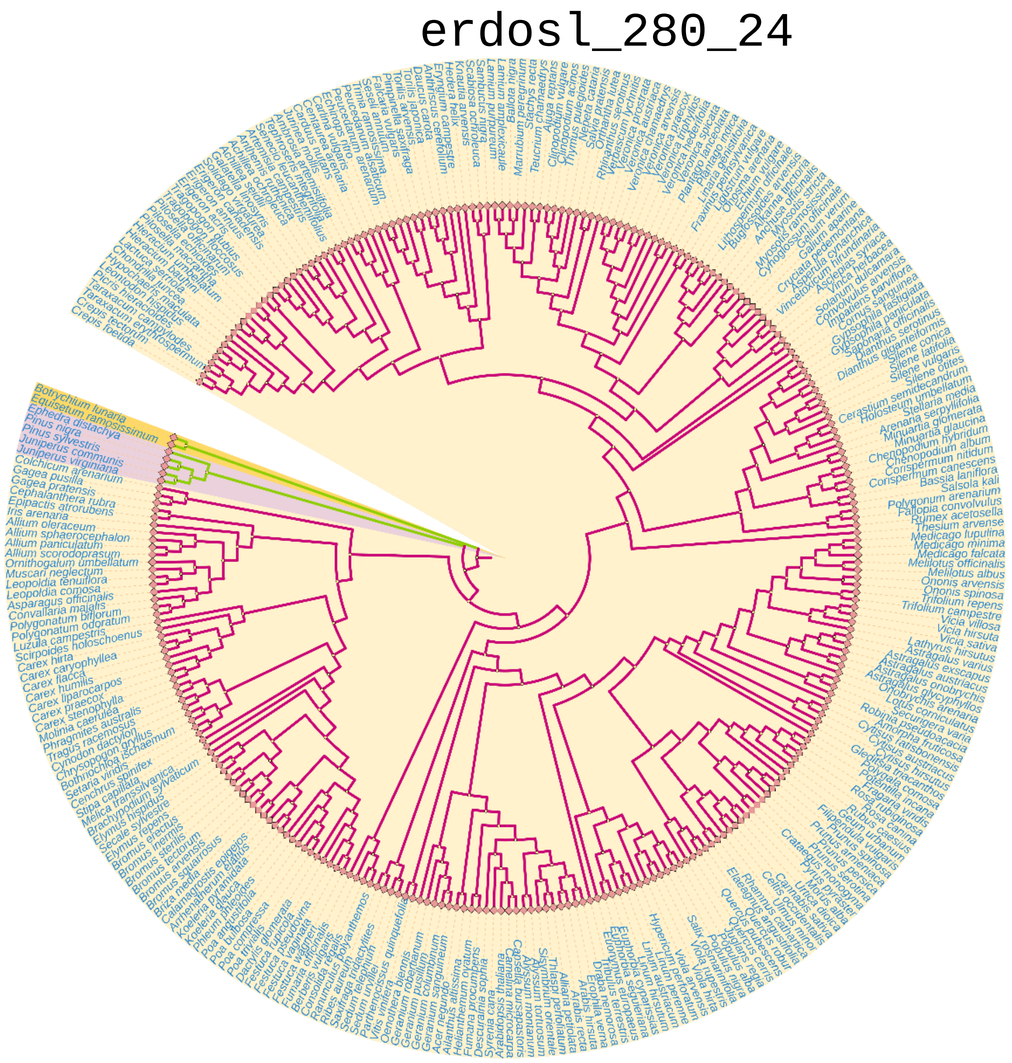

Figure S2. Phylogenetic tree containing 289 species. The orange zone includes two pteridophyte species, the purple zone includes five gymnosperms species, while the remaining species are angiosperms.

Table S1 The 13 study sites used in this study with coordinates and elevation, and the distribution of relevés across habitats and sites. Habitat type abbreviations are according to the caption of Figure 3.

Study sites	Coordinates		Altitude (m a.s.l.)	Number of relevés							
				LF	MF	SF	NE	SE	CG	OP	OA
Ásotthalom	N 46°13'	E 19°47'26"	111–115	5	5	5	5	5	5	5	5
Bócsa	N 46°41'	E 19°28'	110–117	5	5	5	5	5	1	5	5
Bodoglár	N 46°31'	E 19°37'	114–123	5	5	5	5	5	5	5	5
Csévharaszt	N 47°17'26"	E 19°23'30"	125–137	3	4	5	5	5	4	5	–

Fülöpháza	N 46°52'	E 19°25'	105–119	10	5	5	5	5	5	5	11
Imrehegy	N 46°29'	E 19°22'	121–133	5	5	5	5	5	1	5	5
Kéleshalom	N 46°23'	E 19°20'	137–147	1	5	5	5	5	5	5	5
Négyestelep	N 46°17'	E 19°35'40"	131–137	5	5	5	5	5	5	5	5
Orgovány	N 46°47'30"	E 19°28'	105–113	5	5	5	5	5	5	5	5
Pirtó	N 46°28'	E 19°26'	124–132	3	5	5	5	5	5	5	5
Táborfalva	N 47°7'	E 19°23'	116–124	4	5	5	5	5	–	5	–
Tatárszentgyörgy	N 47°2'	E 19°22'	102–111	5	5	5	5	5	4	5	5
Tázlár	N 46°31'	E 19°30'	116–126	4	5	5	5	5	5	5	4

Table S2. Details of the nine traits used for the functional diversity analyses

Trait	Description	Data type	Source
Start of flowering	The season in which the species starts flowering in Hungary	Nominal with three levels: blooming from early spring (Months 1 to 4); blooming from early summer (Months 5 and 6); blooming from late summer (Months 7 to 9)	Király (2009)
Flowering duration	Duration of the flowering period in Hungary	Numeric (number of months)	Király (2009)
Specific leaf area (SLA)	The ratio of leaf area to leaf dry weight	Numeric (mm^2/mg)	Kleyer et al. (2008); Lhotsky et al. (2016); E-Vojtkó et al. (2020); Gyalus et al. (2022); McIntosh-Buday et al. (2022)

Mean height	The mean height of the aboveground shoot (or the length of the shoots in case of vines) for adult plants	Numeric (cm)	Király (2009)
Thousand seed mass	Average weight of one thousand seeds	Numeric (g)	Török et al. (2013, 2016); Royal Botanic Gardens Kew (2017)
Life form	Raunkiær's life form of the species, based on the perennating organs (seeds or buds) and (in case of the latter) the vertical position of buds	Fuzzy coding with eight levels: tree and shrub; semishrub; dwarf shrub; hemicryptophyte; geophyte; therophyte; hemitherophyte; epiphyte	Horváth et al. (1995); Király (2009)
Seed dispersal	The employed dispersal vector(s)	Fuzzy coding with four levels: anemochor; rainwash; autochor; zoochor	Fitter and Peat (1994); Csontos et al. (2002); Royal Botanic Gardens Kew (2017); USDA Forest Service (2017)
Pollination type	The employed pollen vector(s)	Fuzzy coding with three levels: insects; wind; self-pollination	Fitter and Peat (1994); Kühn el al. (2004); USDA Forest Service (2017)
Reproduction type	The mode of reproduction	Fuzzy coding with two levels: generative; vegetative	Kühn et al. (2004)

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Table S3: Statistical results of the pairwise comparisons of species composition. Habitat type abbreviations are according to the caption of Figure 3.

Pair	F. model	R^2	p
LF-MF	1.92	0.016	1.000
LF-SF	10.9	0.082	**0.028**
LF-NE	17.8	0.127	**0.028**
LF-SE	23.2	0.159	**0.028**
LF-CG	94.8	0.467	**0.028**
LF-OP	131.2	0.516	**0.028**
LF-OA	124.7	0.514	**0.028**
MF-SF	6.87	0.051	**0.028**
MF-NE	12.9	0.092	**0.028**
MF-SE	19.4	0.133	**0.028**
MF-CG	92.1	0.451	**0.028**
MF-OP	129.5	0.505	**0.028**
MF-OA	123.7	0.503	**0.028**
SF-NE	3.41	0.026	**0.028**

SF-SE	6.77	0.050	**0.028**
SF-CG	69.6	0.381	**0.028**
SF-OP	101.3	0.442	**0.028**
SF-OA	104.0	0.458	**0.028**
NE-SE	5.96	0.045	**0.028**
NE-CG	54.7	0.326	**0.028**
NE-OP	85.0	0.399	**0.028**
NE-OA	95.1	0.436	**0.028**
SE-CG	53.8	0.323	**0.028**
SE-OP	61.1	0.323	**0.028**
SE-OA	78.2	0.389	**0.028**
CG-OP	61.6	0.353	**0.028**
CG-OA	70.3	0.394	**0.028**
OP-OA	42.5	0.257	**0.028**

Table S4. Statistical results of the pairwise comparisons of species number, Shannon diversity, overall functional diversity, phylogenetic diversity with all species, and phylogenetic diversity with non-angiosperm species excluded. Habitat type abbreviations are according to the caption of Figure 3.

Pair	Species richness		Shannon diversity		Overall FD-SES.RaoQ	
	t	p	t	p	t	p
LF-MF	-2.15	0.884	-0.72	1.000	-1.09	1.000
LF-SF	-8.26	**<0.001**	-1.99	1.000	-1.20	1.000
LF-NE	-15.6	**<0.001**	-5.68	**<0.001**	-1.61	1.000
LF-SE	-12.5	**<0.001**	-4.60	**<0.001**	-2.96	0.091
LF-CG	-7.34	**<0.001**	-2.10	1.000	19.6	**<0.001**
LF-OP	-4.19	**<0.001**	-3.82	**0.004**	15.3	**<0.001**
LF-OA	-3.88	**0.003**	-4.89	**<0.001**	15.2	**<0.001**
MF-SF	-6.33	**<0.001**	-1.29	1.000	-0.10	1.000

MF-NE	-14.1	**<0.001**	-5.06	**<0.001**	-0.52	1.000
MF-SE	-10.8	**<0.001**	-3.96	**0.002**	-1.90	1.000
MF-CG	-5.46	**<0.001**	-1.45	1.000	20.9	**<0.001**
MF-OP	-2.09	1.000	-3.16	**0.047**	16.8	**<0.001**
MF-OA	-1.81	1.000	-4.24	**<0.001**	16.5	**<0.001**
SF-NE	-7.99	**<0.001**	-3.77	**0.005**	-0.42	1.000
SF-SE	-4.56	**<0.001**	-2.67	0.219	-1.80	1.000
SF-CG	0.47	1.000	-0.25	1.000	21.1	**<0.001**
SF-OP	4.27	**<0.001**	-1.87	1.000	16.9	**<0.001**
SF-OA	4.34	**<0.001**	-2.99	0.084	16.6	**<0.001**
NE-SE	3.46	**0.017**	1.10	1.000	-1.39	1.000
NE-CG	7.83	**<0.001**	3.25	**0.034**	21.5	**<0.001**
NE-OP	12.2	**<0.001**	1.90	1.000	17.4	**<0.001**
NE-OA	11.9	**<0.001**	0.68	1.000	17.0	**<0.001**
SE-CG	4.69	**<0.001**	2.23	0.732	22.8	**<0.001**
SE-OP	8.79	**<0.001**	0.80	1.000	18.7	**<0.001**
SE-OA	8.69	**<0.001**	-0.39	1.000	18.4	**<0.001**
CG-OP	3.52	**0.013**	-1.49	1.000	-5.40	**<0.001**
CG-OA	3.64	**0.008**	-2.55	0.308	-5.16	**<0.001**
OP-OA	0.22	1.000	-1.17	1.000	0.15	1.000

Table S4 (continued).

Pair	Phylogenetic-SES.RaoQ		Phylogenetic-SES.RaoQ-g	
	t	p	t	p
LF-MF	-3.61	**0.010**	-0.83	1.000
LF-SF	-4.55	**<0.001**	-0.71	1.000
LF-NE	-5.36	**<0.001**	-0.67	1.000
LF-SE	-1.88	1.000	0.16	1.000

LF-CG	4.73	**<0.001**	10.7	**<0.001**
LF-OP	5.82	**<0.001**	14.0	**<0.001**
LF-OA	5.98	**<0.001**	16.4	**<0.001**
MF-SF	-0.95	1.000	0.12	1.000
MF-NE	-1.77	1.000	0.16	1.000
MF-SE	1.77	1.000	1.02	1.000
MF-CG	8.24	**<0.001**	11.6	**<0.001**
MF-OP	9.64	**<0.001**	15.2	**<0.001**
MF-OA	9.65	**<0.001**	17.4	**<0.001**
SF-NE	-0.83	1.000	0.04	1.000
SF-SE	2.73	0.184	0.90	1.000
SF-CG	9.15	**<0.001**	11.6	**<0.001**
SF-OP	10.6	**<0.001**	15.1	**<0.001**
SF-OA	10.6	**<0.001**	17.4	**<0.001**
NE-SE	3.56	**0.011**	0.86	1.000
NE-CG	9.92	**<0.001**	11.5	**<0.001**
NE-OP	11.5	**<0.001**	15.1	**<0.001**
NE-OA	11.4	**<0.001**	17.3	**<0.001**
SE-CG	6.62	**<0.001**	10.7	**<0.001**
SE-OP	7.90	**<0.001**	14.2	**<0.001**
SE-OA	7.95	**<0.001**	16.5	**<0.001**
CG-OP	0.70	1.000	2.44	0.419
CG-OA	0.95	1.000	4.89	**<0.001**
OP-OA	0.29	1.000	2.67	0.222

Table S5. Significant (P < 0.001) diagnostic species of the eight habitats with phi coefficients > 0.200. Habitat type abbreviations are according to the caption of Figure 3.

Species	LF	MF	SF	NE	SE	CG	OP	OA
Achillea pannonica				0.259				
Ailanthus altissima	0.235							
Alkanna tinctoria							0.561	0.515
Allium sphaerocephalon						0.249		
Alyssum tortuosum							0.330	0.264
Anthriscus cerefolium	0.288	0.242						
Arenaria serpyllifolia							0.436	0.372
Artemisia campestris							0.214	0.287
Asparagus officinalis			0.358	0.281	0.266			
Asperula cynanchica				0.279				
Berberis vulgaris	0.337	0.397	0.324	0.232				
Bothriochloa ischaemum						0.241		
Bromus squarrosus								0.601
Bromus sterilis	0.257	0.208						
Bromus tectorum								0.433
Calamagrostis epigeios				0.284	0.284			
Carex caryophyllea						0.429		
Carlina vulgaris				0.429				
Celtis occidentalis	0.319	0.408	0.410	0.254				
Centaurea arenaria							0.397	0.552
Cerastium semidecandrum						0.527	0.336	
Chenopodium album					0.268			
Chondrilla juncea					0.215			
Conyza canadensis								0.218
Corispermum canescens								0.327
Cornus sanguinea	0.237							
Crataegus monogyna	0.37	0.354	0.321	0.321	0.221			

Crepis rhoeadifolia							0.373	0.388
Cynodon dactylon					0.282			
Cynoglossum officinale	0.20	0.235	0.211					
Dianthus pontederae						0.308		
Equisetum ramosissimum						0.257		
Erophila verna							0.708	
Eryngium campestre				0.30		0.262		
Euonymus europaeus	0.271							
Euphorbia cyparissias				0.205	0.281	0.223		
Euphorbia seguieriana							0.400	0.567
Fallopia convolvulus	0.244	0.308						
Festuca pseudovina						0.214		
Festuca rupicola, F.valesiaca						0.650		
Festuca vaginata					0.244		0.421	0.297
Festuca wagneri							0.223	
Filipendula vulgaris						0.237		
Fumana procumbens							0.563	0.243
Galium aparine	0.278	0.325						
Galium verum				0.219	0.219	0.386		
Geum urbanum	0.263							
Helianthemum ovatum				0.225		0.287		
Hieracium echioides				0.261				
Holosteum umbellatum						0.336	0.497	0.490
Juniperus communis			0.223	0.318				
Kochia laniflora							0.430	0.699
Koeleria cristata						0.684		
Koeleria glauca							0.244	
Leontodon hispidus				0.320				

Ligustrum vulgare	0.259	0.323	0.311	0.311				
Linaria genistifolia								0.221
Lithospermum officinale		0.334						
Medicago falcate				0.307				
Medicago minima							0.378	0.224
Minuartia glaucina							0.343	0.248
Myosotis stricta							0.296	
Ononis spinose						0.246		
Padus serotine		0.212						
Phleum phleoides						0.359		
Pimpinella saxifraga				0.308				
Pinus nigra				0.238				
Poa angustifolia			0.336	0.368		0.224		
Poa bulbosa							0.379	0.401
Polygala comosa				0.329				
Polygonum arenarium							0.569	0.506
Populus alba	0.288	0.288	0.288	0.288	0.288			
Potentilla arenaria				0.241		0.432	0.226	
Prunus spinose	0.258	0.284		0.228				
Rhamnus catharticus	0.306	0.261	0.266	0.327				
Robinia pseudoacacia	0.327							
Rubus caesius	0.209							
Salix rosmarinifolia						0.334		
Salsola kali								0.358
Saxifraga tridactylites						0.342		
Scabiosa ochroleuca				0.408				
Scirpoides holoschoenus						0.617		
Secale sylvestre							0.217	0.759

Senecio vernalis					0.249			
Seseli annuum				0.350				
Setaria viridis								0.506
Silene conica							0.389	0.390
Solidago virgaurea				0.240				
Stellaria media	0.212							
Stipa borysthenica, S. capillata					0.224	0.348	0.392	0.319
Syrenia cana							0.378	0.532
Taraxacum laevigatum agg.		0.262	0.237	0.313				
Taraxacum officinale agg.	0.213							
Tephroseris integrifolia				0.249				
Teucrium chamaedrys				0.344		0.425		
Thesium ramosum				0.307				
Thymus pannonicus				0.321		0.321		
Tragopogon floccosus				0.217				
Tragus racemosus								0.681
Tribulus terrestris								0.253
Trinia ramosissima							0.217	
Verbascum lychnitis					0.221	0.426		
Veronica praecox								0.208
Veronica prostrata						0.223		
Vincetoxicum hirundinaria		0.213						
Viola arvensis								0.271
Viola rupestris				0.428				

Table S6. Statistical results between observed SES.RaoQ values and the null model expectation (two-sided Wilcoxon signed rank test).

Habitat	SES.RaoQ (FD for all traits)		SES.RaoQ (PD for all species)		SES.RaoQ-g (PD with only angiosperm species)	
	V	p	V	p	V	p
LF	1723	**<0.001**	295	**<0.001**	1342	**0.002**
MF	2072	**<0.001**	1092	0.731	1994	**<0.001**
SF	2145	**<0.001**	1292	0.152	1869	**<0.001**
NE	2138	**<0.001**	1319	0.062	1992	**<0.001**
SE	2144	**<0.001**	951	0.429	1645	**<0.001**
CG	3	**<0.001**	0	**<0.001**	13	**<0.001**
OP	245	**<0.001**	71	**<0.001**	16	**<0.001**
OA	71	**<0.001**	45	**<0.001**	18	**<0.001**

Table S6 (continued)

Habitat	SES.RaoQ (FD for flowering time)		SES.RaoQ (FD for seed dispersal)		SES.RaoQ (FD for reproduction type)		SES.RaoQ (FD for plant height)	
	V	p	V	p	V	P	V	p
LF	1700	**<0.001**	1576	**<0.001**	1829	**<0.001**	1826	**<0.001**
MF	2077	**<0.001**	2027	**<0.001**	2080	**<0.001**	2080	**<0.001**
SF	2114	**<0.001**	2117	**<0.001**	2145	**<0.001**	2145	**<0.001**
NE	2043	**<0.001**	2004	**<0.001**	2145	**<0.001**	2145	**<0.001**
SE	2144	**<0.001**	2112	**<0.001**	2145	**<0.001**	2145	**<0.001**
CG	23	**<0.001**	212	**<0.001**	73	**<0.001**	51	**<0.001**
OP	736	**0.028**	798	0.07	831	0.115	363	**<0.001**
OA	515	**0.003**	250	**<0.001**	327	**<0.001**	0	**<0.001**

Table S6 (continued)

Habitat	SES.RaoQ (FD for life form)		SES.RaoQ (FD for SLA)		SES.RaoQ (FD for seed mass)		SES.RaoQ (FD for pollination type)	
	V	p	V	p	V	P	V	p
LF	11	**<0.001**	212	**<0.001**	1780	**<0.001**	1754	**<0.001**
MF	6	**<0.001**	644	**0.008**	1973	**<0.001**	1571	**<0.001**
SF	248	**<0.001**	119	**<0.001**	1586	**<0.001**	1032	0.79
NE	138	**<0.001**	237	**<0.001**	1424	**0.022**	1143	0.647
SE	578	**0.001**	94	**<0.001**	979	0.543	975	0.526
CG	64	**<0.001**	494	0.167	311	**0.002**	1032	**<0.001**
OP	38	**<0.001**	94	**<0.001**	240	**<0.001**	1934	**<0.001**
OA	179	**<0.001**	501	**0.002**	369	**<0.001**	1601	**<0.001**

Table S7. Statistical results of the pairwise comparisons of functional diversity for individual traits. Habitat type abbreviations are according to the caption of Figure 3.

	Flowering time-SES.RaoQ		Seed dispersal-SES.RaoQ		Reproduction type-SES.RaoQ		Mean plant height-SES.RaoQ	
	t	p	t	p	t	p	t	p
LF-MF	-1.33	1.000	-1.37	1.000	-1.55	1.000	-1.04	1.000
LF-SF	-1.20	1.000	-2.34	0.554	-0.63	1.000	-4.61	<**0.001**
LF-NE	-0.41	1.000	-1.85	1.000	-2.33	0.572	-5.77	<**0.001**
LF-SE	-1.48	1.000	-2.73	0.183	-1.28	1.000	-9.24	<**0.001**
LF-CG	17.1	<**0.001**	8.17	<**0.001**	26.2	<**0.001**	17.2	<**0.001**
LF-OP	8.19	<**0.001**	6.90	<**0.001**	22.5	<**0.001**	15.0	<**0.001**
LF-OA	9.33	<**0.001**	12.5	<**0.001**	25.5	<**0.001**	20.4	<**0.001**
MF-SF	0.14	1.000	-0.98	1.000	0.94	1.000	-3.63	**0.009**
MF-NE	0.94	1.000	-0.49	1.000	-0.79	1.000	-4.82	<**0.001**
MF-SE	-0.15	1.000	-1.39	1.000	0.28	1.000	-8.36	<**0.001**
MF-CG	18.7	<**0.001**	9.62	<**0.001**	28.1	<**0.001**	18.5	<**0.001**
MF-OP	9.71	<**0.001**	8.44	<**0.001**	24.5	<**0.001**	16.4	<**0.001**
MF-OA	10.8	<**0.001**	14.1	<**0.001**	27.4	<**0.001**	21.7	<**0.001**
SF-NE	0.81	1.000	0.50	1.000	-1.73	1.000	-1.19	1.000
SF-SE	-0.28	1.000	-0.40	1.000	-0.66	1.000	-4.75	<**0.001**
SF-CG	18.6	<**0.001**	10.6	<**0.001**	27.3	<**0.001**	21.9	<**0.001**
SF-OP	9.61	<**0.001**	9.47	<**0.001**	23.6	<**0.001**	20.1	<**0.001**
SF-OA	10.7	<**0.001**	15.1	<**0.001**	26.6	<**0.001**	25.3	<**0.001**
NE-SE	-1.09	1.000	-0.90	1.000	1.07	1.000	-3.56	**0.012**
NE-CG	17.9	<**0.001**	10.1	<**0.001**	28.9	<**0.001**	23.1	<**0.001**
NE-OP	8.81	<**0.001**	8.97	<**0.001**	25.4	<**0.001**	21.3	<**0.001**
NE-OA	9.90	<**0.001**	14.6	<**0.001**	28.3	<**0.001**	26.5	<**0.001**
SE-CG	18.9	<**0.001**	10.9	<**0.001**	27.9	<**0.001**	26.4	<**0.001**

SE-OP	9.90	**<0.001**	9.87	**<0.001**	24.3	**<0.001**	24.8	**<0.001**
SE-OA	10.9	**<.0001**	15.5	**<0.001**	27.2	**<0.001**	29.9	**<0.001**
CG-OP	9.68	**<0.001**	-1.80	1.000	-5.37	**<0.001**	-3.31	**0.029**
CG-OA	-8.25	**<0.001**	3.72	**0.006**	-1.98	1.000	2.15	0.900
OP-OA	1.33	1.000	5.87	**<0.001**	3.53	**0.013**	5.76	**<0.001**

Table S7 (continued).

	Life form-SES.RaoQ		Specific leaf area (SLA)-SES.RaoQ		Thousand seed mass-SES.RaoQ		Pollination type-SES.RaoQ	
	t	p	t	p	t	p	t	p
LF-MF	-1.62	1.000	-1.98	1.000	1.99	1.000	2.46	0.404
LF-SF	-6.47	**<0.001**	1.85	1.000	5.16	**<0.001**	6.22	**<0.001**
LF-NE	-6.36	**<0.001**	1.51	1.000	5.82	**<0.001**	5.53	**<0.001**
LF-SE	-9.54	**<0.001**	3.08	0.061	8.49	**<0.001**	6.73	**<0.001**
LF-CG	-3.21	**0.040**	-1.91	1.000	10.39	**<0.001**	2.88	0.115
LF-OP	-2.46	0.398	4.67	**<0.001**	11.9	**<0.001**	1.90	1.000
LF-OA	-6.31	**<0.001**	-2.55	0.309	10.8	**<0.001**	0.32	1.000
MF-SF	-4.94	**<0.001**	3.92	**0.003**	3.23	**0.038**	3.84	**0.004**
MF-NE	-4.84	**<0.001**	3.57	**0.011**	3.91	**0.003**	3.13	**0.042**
MF-SE	-8.08	**<0.001**	5.18	**<0.001**	6.63	**<0.001**	4.36	**<0.001**
MF-CG	-1.72	1.000	-0.07	1.000	8.69	**<0.001**	0.60	1.000
MF-OP	-0.86	1.000	6.80	**<0.001**	10.1	**<0.001**	-0.57	1.000
MF-OA	-4.78	**<0.001**	-0.62	1.000	8.95	**<0.001**	-2.12	0.963
SF-NE	0.11	1.000	-0.35	1.000	0.69	1.000	-0.71	1.000
SF-SE	-3.15	**0.049**	1.26	1.000	3.42	**0.019**	0.52	1.000
SF-CG	2.88	0.118	-3.71	**0.006**	5.71	**<0.001**	-2.97	0.088
SF-OP	4.10	**0.001**	2.89	0.112	6.93	**<0.001**	-4.43	**<0.001**
SF-OA	0.04	1.000	-4.44	**<0.001**	5.82	**<0.001**	-5.87	**<0.001**

NE-SE	-3.25	**0.034**	1.61	1.000	2.73	0.183	1.23	1.000
NE-CG	2.78	0.161	-3.39	**0.021**	5.07	**<0.001**	-2.31	0.597
NE-OP	3.99	**0.002**	3.24	**0.036**	6.24	**<0.001**	-3.72	**0.006**
NE-OA	-0.07	1.000	-4.10	**0.001**	5.16	**<0.001**	-5.18	**<0.001**
SE-CG	5.79	**<0.001**	-4.89	**<0.001**	2.54	0.319	-3.45	**0.017**
SE-OP	7.25	**<0.001**	1.63	1.000	3.51	**0.014**	-4.95	**<0.001**
SE-OA	3.10	0.058	-5.66	**<0.001**	2.50	0.357	-6.38	**<0.001**
CG-OP	0.93	1.000	6.39	**<0.001**	0.72	1.000	-1.14	1.000
CG-OA	-2.79	0.153	-0.51	1.000	-0.15	1.000	-2.58	0.283
OP-OA	-3.96	**0.003**	-7.25	**<0.001**	-0.92	1.000	-1.57	1.000

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RESEARCH ARTICLE

Environmental filtering is the primary driver of community assembly in forest–grassland mosaics: A case study based on CSR strategies

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Abstract

Aims: Ecological strategies can provide information about plant community assembly and its main drivers. Our aim was to reveal the dominant strategies of the vegetation types of forest–grassland mosaics and to deduce the assembly processes responsible for their species composition.

Location: Hungary.

Methods: We investigated eight vegetation types of Hungarian forest–steppes. The trade-off between three key traits related to leaf size and economics was used to calculate Grime's competitive–stress tolerance–ruderal (CSR) value for each species, based on which the mean value for each vegetation type was determined. Detrended correspondence analysis (DCA) ordination was used to reveal the compositional differences among the vegetation types under study. To analyze how ecological strategies correlate with the compositional gradient, we used linear regression between plot ordination scores (the first DCA scores) and each strategy (C, S, and R). Linear mixed-effect models were used to evaluate the differences between the vegetation types regarding each strategy (C, S, and R).

Results: Each vegetation type was dominated by the stress-tolerator strategy, indicating the prominent role of environmental filtering in community assembly. However, ecological strategies differed significantly among the communities. The importance of

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the stress-tolerator strategy decreased toward the less harsh end of the gradient (i.e., from grasslands to forests), while the competitor strategy showed a reverse pattern. The ruderal strategy was weakly correlated with the gradient, although its proportion increased toward the harsh end of the gradient.

Conclusions: With ongoing climate change, an increasing importance of environmental filtering is expected in the assembly of the vegetation types in the studied forest–grassland mosaics. We suggest that CSR strategies offer a useful tool for studying plant-community assembly rules along environmental gradients.

KEYWORDS

competitor, CSR, environmental filter, forest–steppe, leaf trait, ruderal, stress-tolerator

1 | INTRODUCTION

Plant community assembly has long been at the focus of ecological research and remains an issue under intensive scientific discussion (Götzenberger et al., 2012; Dias et al., 2020). Assembly rules determine how species of a regional species pool are selected and fit together to form local communities (Menezes et al., 2020). In addition to its theoretical importance, knowledge of assembly processes has outstanding practical implications as well: it can help to predict plant communities' responses to environmental changes and to restore (near-)natural communities (e.g., Temperton et al., 2004; Münkemüller et al., 2020).

The assembly of plant communities is usually represented as a series of various filters that define which traits (and therefore, which species possessing these traits) can enter the realized local plant community (e.g., Keddy, 1992). The most widespread model includes three filters acting in concert: the dispersal filter determines which species arrive at the site, whereas the environmental filter and the biotic filter select species that can tolerate the local abiotic factors and the biotic interactions from the co-existing species respectively (e.g., Götzenberger et al., 2012; Hulvey & Aigner, 2014; Halassy et al., 2016).

Grime and Pierce (2012) proposed a different scheme, based on three basic ecological phenomena that shape vegetation: competition, stress, and disturbance. According to Grime (1974, 1977) and Grime and Pierce (2012), competition means that co-occurring individuals strive to capture the same units of resource, stress is understood as environmental constraints that limit production, while disturbance is the partial or complete destruction of biomass. Grime and Pierce (2012) argue that every plant species faces an evolutionary trade-off among (1) developing strong competitive ability (competitors, C), (2) withstanding environmental stress (stress tolerators, S), and (3) enduring regular biomass destruction (ruderals, R). According to this view, plants have to pass a filter that favors competitors, stress tolerators, or ruderals in productive, harsh, or disturbed environments respectively. Grime and Pierce (2012) also stressed that there is no hierarchy among the different components of the filter; that is why their model includes a single filter instead of a series of filters.

As emphasized by Grime and Pierce (2012), there are no living beings that would be exclusively C-, S-, or R-selected. For example, a species that shows a high degree of C-selection also has to cope with some level of S- and R-selection. This means that in reality, individuals have to pass all three components of the CSR-filter, even though each component may represent a greater or smaller obstacle.

The filter proposed by Grime and Pierce (2012) selects individuals possessing traits that are directly beneficial to competitive ability, stress tolerance, and the survival of the population by completing the individual life cycle between two destructive events. These traits (i.e., traits that are directly connected to the CSR strategies) display a plant's general strategy. Consequently, by studying the traits and strategies of the species composing a plant community, we can gather information about the primary drivers that determine community composition.

In the forest–steppe zone, which is a transitional zone between closed-canopy forests and steppes (Erdős et al., 2018a), it is assumed that forest and grassland patches, in most cases, represent alternative stable states, that is, they appear under the very same primary environmental conditions and are stable in time (Petraitis, 2013; Erdős et al., 2023). However, secondary differences emerge among the patches, evoked by the vegetation itself, further stabilizing the pattern of the individual patches. For example, trees and shrubs increase the humus and moisture content of the upper soil and mitigate daily temperature extremes, changes that favor the continuous existence of the forest and hinder the establishment of grassland species (Erdős et al., 2023). As a result, significant environmental differences have been revealed among the various plant communities, which can be arranged along an environmental harshness gradient (Erdős et al., 2018b, 2020; Ho et al., 2024). Generally, daytime temperatures in the growing season are low in large forest patches and increase through smaller-sized forest patches and edges to grasslands, which are the hottest habitats, especially in summer. Nighttime temperatures show a reverse trend, and thus, large forests have the lowest and grasslands the highest daily temperature fluctuations. Both the moisture content of the upper soil layer and daytime air humidity are the highest in large forest patches and become progressively lower toward smaller-sized forest patches and edges, and are the lowest in grasslands.

In this study, our aim was to reveal the dominant strategies of the vegetation types of sandy forest–steppes, and infer the assembly processes responsible for their species composition. We hypothesized that in the more productive environment of forest patches, community composition would be driven by competitive exclusion, while under the harsher conditions of open grasslands, stress (i.e., environmental filtering) would be the most important driver—expressed also in the composition of traits.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in the Kiskunság Sand Ridge in central Hungary, a lowland area in the heart of the Carpathian Basin between the rivers Danube and Tisza. We selected thirteen legally protected sites with near-natural vegetation (Figure 1a; Appendix S1). The subcontinental climate with sub-Mediterranean influences is characteristic of this region with an average annual temperature of 10.3–10.5°C and an average annual precipitation of 520–550 mm (Tölgyesi et al., 2016). Grasslands have humus-poor sandy soil with low water retention capacity (Várallyay, 1993); however, the humus content is slightly higher in forest patches (Erdős et al., 2014).

The area belongs to the westernmost outposts of the forest–steppe zone. Although the overwhelming majority of forest–steppe ecosystems of the region have been converted to agricultural fields or tree plantations (Molnár et al., 2012), a few sandy forest–steppe areas have survived and are currently under legal protection. Within the study sites, the vegetation is characterized by a mosaic-like pattern of forest and grassland patches (Figure 1b). The variously sized forest patches of poplar–juniper stands (*Junipero-Populetum albae*) exhibit a cover of 50%–80% and are dominated by *Populus alba* with heights ranging from 10 m to 15 m. In the shrub layer, typical species include *Berberis vulgaris*, *Crataegus monogyna*, *Juniperus communis*, *Ligustrum vulgare*, and *Prunus spinosa*, and their cover ranges from 5% to 80%. The herb layer hosts species such as *Carex liparocarpos*, *Cynoglossum officinale*, *Euphorbia cyparissias*, and *Teucrium chamaedrys*. Forest patches range in size from a few dozen square meters to as large as 1 ha.

There are three types of grasslands in the study sites. The closed perennial grassland (*Astragalo austriacae-Festucetum rupicolae*), which has a relatively high cover (typically more than 80%),

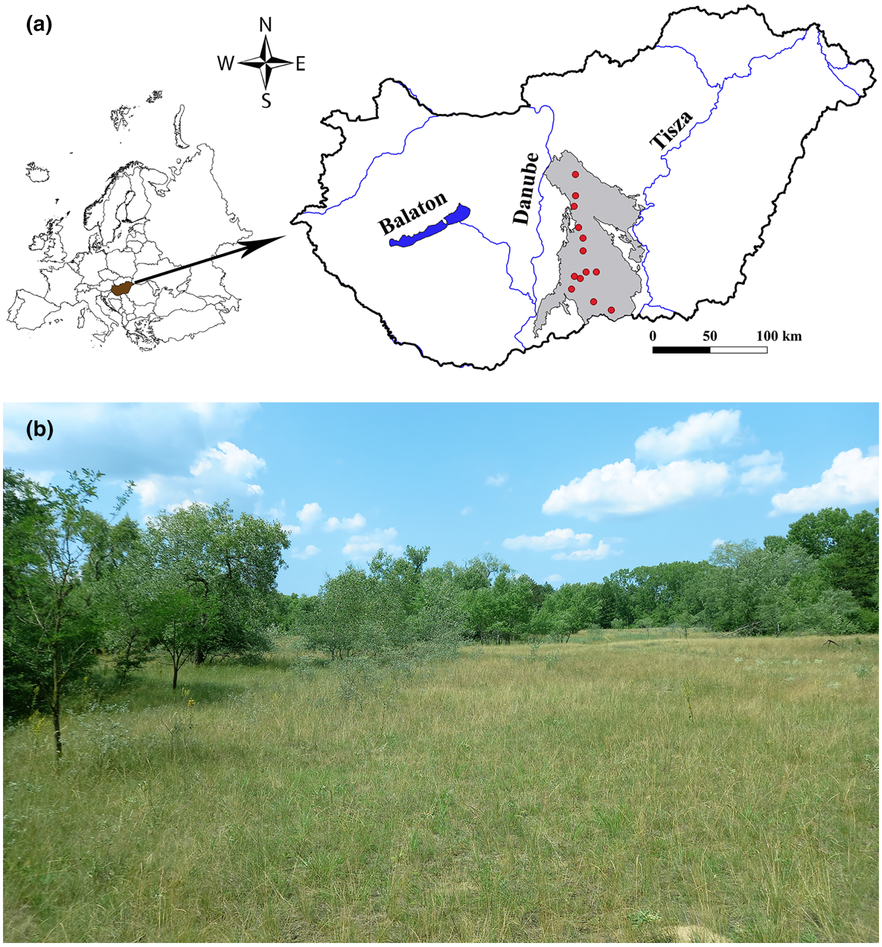

FIGURE 1 (a) The location of Hungary in Europe (brown) and thirteen study sites (red dots) in the Kiskunság Sand Ridge (gray) in central Hungary. (b) A mosaic of forests and grasslands in the study region.

is dominated by *Festuca rupicola*, *Stipa borysthenica*, and *Stipa capillata*. Other typical species are, among others, *Achillea pannonica*, *Calamagrostis epigejos*, *Euphorbia cyparissias*, and *Poa angustifolia*.

The most widespread grassland type is the open perennial grassland (*Festucetum vaginatae*), which is dominated by *Festuca vaginata*, *Stipa borysthenica*, and *Stipa capillata*. The overall total vascular vegetation cover varies between 40% and 70%. Other typical species include *Alkanna tinctoria*, *Centaurea arenaria*, *Koeleria glauca*, and *Syrenia cana*.

The open annual grassland vegetation (*Secali sylvestris-Brometum tectorum*) has a vascular vegetation cover of 20%–50% and is dominated by *Bromus tectorum* and *Secale sylvestre*. Other common species include *Bromus squarrosus*, *Poa bulbosa*, *Silene conica*, and *Viola arvensis*.

Plant species nomenclature is in accordance with Király (2009), while plant association names are based on Borhidi et al. (2012).

2.2 | Field sampling

We distinguished and analyzed eight vegetation types at each site: large forest patches (>0.5 ha), medium forest patches (0.2–0.4 ha), small forest patches (<0.1 ha), north-facing forest edges, south-facing forest edges, closed perennial grasslands, open perennial grasslands, and open annual grasslands. Based on the earlier studies of Erdős et al. (2018b, 2020), we used 5 m × 5 m plots for sampling forest interiors and grasslands, while 2 m × 12.5 m plots were employed to study forest edges, preventing their extension into the interiors of the adjacent vegetation types. In this study, we defined an edge as the area outside of the outermost tree trunks but still under the canopy. Edge plots were established along the relatively straight peripheral zones of forest patches that were larger than 0.2 hectares in size.

A total of 494 plots were used: 60 plots in large forest patches, 64 plots in medium forest patches, 60 plots in open annual grasslands, 50 plots in closed perennial grasslands, and an equal count of 65 plots in each of the other vegetation types (Appendix S1). The number of replicates was determined by the lack or rarity of certain vegetation types at some study sites. We visually estimated the cover of all vascular plant species in all vegetation layers (canopy, shrub, and herb) in each plot in spring (April–May) and summer (July–August). The highest cover value for each species was then applied for subsequent data analyses. Seven taxa unidentified at the species level (*Acer* sp., *Epipactis* sp., *Fraxinus* sp., *Hieracium* sp., *Lathyrus* sp., *Prunus* sp., and *Silene* sp., none of which was found in more than three of the 494 plots), were excluded from the analyses involving strategy.

2.3 | Leaf traits and ecological strategies

To determine the strategy of the species, three leaf traits were used: leaf area (LA, mm^2), leaf dry matter content (LDMC, mg/g), and specific leaf area (SLA, mm^2/mg), based on the observation that species with the C strategy invest resources in increasing LA; species with the S strategy invest in retaining LDMC; and species with the R strategy invest primarily in the ability to increase SLA) (Pierce et al., 2017). It is widely accepted that these traits strongly represent the leaf economics and plant size spectra (sensu the global spectrum of plant form and function; Díaz et al., 2016). Trait data were extracted from Hungarian databases (Lhotsky et al., 2016a, 2016b; E-Vojtkó et al., 2020; Gyalus et al., 2022; McIntosh-Buday et al., 2022). Data were retrieved from PADAPT, the Pannonian Database of Plant Traits (Sonkoly et al., 2023). However, eight of the 289 taxa (2.77%) did not have SLA data in this database. Therefore, we used the LEDA database published by Kleyer et al. (2008) to provide missing values for these species.

We calculated the strategy (separate C, S, and R values) for each species based on the trade-off among the three above leaf traits by the "StrateFy" tool, which regresses trait values against the principal component analysis (PCA) axes extracted from global leaf traits (Pierce et al., 2017). This method enables determining CSR values for a wide range of vascular plant species globally (Pierce et al., 2017). Based on the C, S, and R components of the strategy for each species, we calculated both the unweighted and weighted mean C, S, and R values for each plot, using presence/absence data for the former situation and square-root-transformed cover scores for the latter one.

2.4 | Data analysis

To analyze the differences in species composition among the vegetation types, we applied detrended correspondence analysis (DCA), which was performed on square-root-transformed cover scores. Detrending was performed using the default number of rescaling cycles (4) and segments (26). The first DCA axis was used for the quantification of vegetation types along the compositional gradient, which provides a continuous number interpretable as "compositional similarity to open grassland" or "compositional dissimilarity to a large forest." The analysis was conducted using the *vegan* package in R version 4.1.2 (R Core Team, 2021; Oksanen et al., 2022).

For all vegetation types, the strategy values (C, S and R) per plot were visualized using a ternary graph, which was created using the *ggtern* package in R (Hamilton & Ferry, 2018).

To reveal how ecological strategies (C, S, and R) correlate with the gradient, we used linear regression between plot ordination scores (the first DCA scores) and each strategy (C, S, and R). The models were visually checked using the diagnostic plots.

To evaluate the differences between the vegetation types regarding each strategy (C, S, and R), we used linear mixed-effect models. In our modeling approach, the site was treated as a random factor, while the vegetation type was considered a fixed factor. We applied the *glmmTMB* package in R to construct the models, using the Gaussian family distribution (Brooks et al., 2017). The models were visually checked using the *performance* package in

R (Lüdecke et al., 2021). In order to find a significant proportion of variability, an analysis of variance was performed on the linear mixed-effect models. Afterwards, we used the *emmeans* package to perform pairwise comparisons among the levels of the fixed factor and adjusted the *p*-values using the Bonferroni method (Lenth, 2022).

3 | RESULTS

The DCA ordination revealed a compositional gradient along the first DCA axis with the following order of vegetation types: large forest patches—medium forest patches—small forest patches—north-facing edges—south-facing edges—closed perennial grasslands—open perennial grasslands—open annual grasslands (Figure 2). It demonstrated that the first DCA scores can be used in the subsequent analyses and interpreted as a compositional gradient.

The ternary plot showing unweighted values revealed that the average CSR values were located along the RS-axis with a smaller contribution from component C (Figure 3a). The contributions of mean components S and R were 50%–60% and 20%–30% respectively. The study found a smaller contribution from mean component C (<25%). When taking a closer look (Figure 3b), a separation between values across vegetation types was found, forming different groups: large and medium forest patches belonged to one group, small forest patches, north- and south-facing edges, and closed grasslands formed another group, and open perennial and open annual grasslands formed the third group. Generally, the ternary plot based on weighted values showed a rather similar pattern (Appendix S2).

The scores of the sample plots on the primary ordination axis were negatively associated with the C strategy (Figure 4a) but positively associated with the S strategy (Figure 4b). A weak but positive relation was observed between the R strategy and DCA1 scores (Figure 4c). The vegetation type affected each type of strategy as follows: component C ($\chi^2 = 1637$, $p < 0.001$), component S ($\chi^2 = 242$, $p < 0.001$), and component R ($\chi^2 = 123$, $p < 0.001$). Based on the pairwise comparisons (Appendix S3), the highest component C was found in large and medium forest patches, and it gradually decreased toward the end of the vegetation gradient (Figure 4d). Component S depicted a gradually increasing trend from large forest patches to open annual grasslands (Figure 4e). Open perennial and annual grasslands exhibited the highest component R, whereas north-facing edges displayed the lowest component R (Figure 4f). Again, patterns were similar with weighted values, although some differences did emerge (Appendix S4). For example, component S had a more equal presence along the gradient for weighted than for unweighted values, and the relationship was more hump-backed. In addition, there was a more pronounced change of component R along the gradient for weighted than for unweighted values.

4 | DISCUSSION

In this work, we studied the vegetation types of forest–grassland mosaics in eastern Central Europe. In the framework of the CSR theory (Grime & Pierce, 2012), it is possible to infer community assembly processes from the strategies of plant communities. For example, if a plant community is dominated by the competitor strategy, this suggests that the competition filter is the most notable obstacle for individuals to enter the realized local plant community. However, as already noted in the Introduction, no species can be regarded as exclusively C-, S-, or R-selected, which also applies to communities. Thus, a given plant community that is dominated by the competitor strategy also has a certain level of environmental stress and disturbance. Moreover, there may be additional drivers shaping plant communities, such as dispersal, which is not assessed by the CSR approach used in the present work.

The eight studied vegetation types formed a compositional gradient (Figure 2). Generally, each vegetation type was dominated

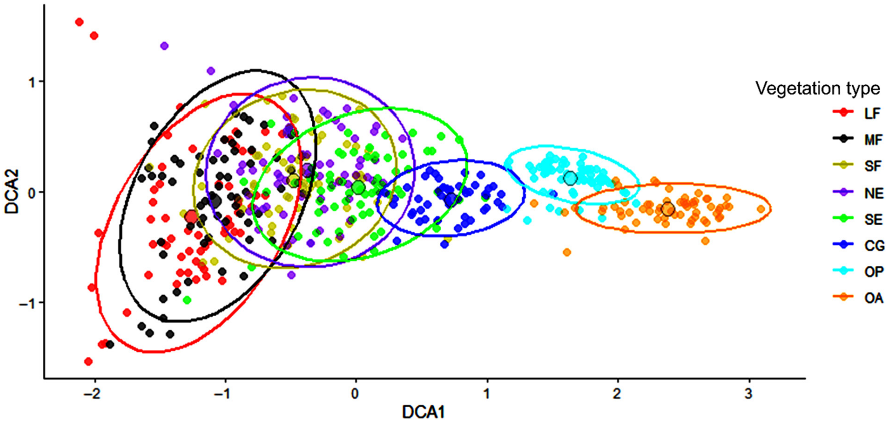

FIGURE 2 DCA ordination scattergram of the 494 plots. Large symbols indicate the centroids for each vegetation type. Ordination ellipses were drawn based on standard deviation of point scores, where the directions of the major axes of the ellipses were defined by the weighted correlation. CG, closed perennial grasslands; LF, large forest patches; MF, medium forest patches; NE, north-facing forest edges; OA, open annual grasslands; OP, open perennial grasslands; SE, south-facing forest edges; SF, small forest patches.

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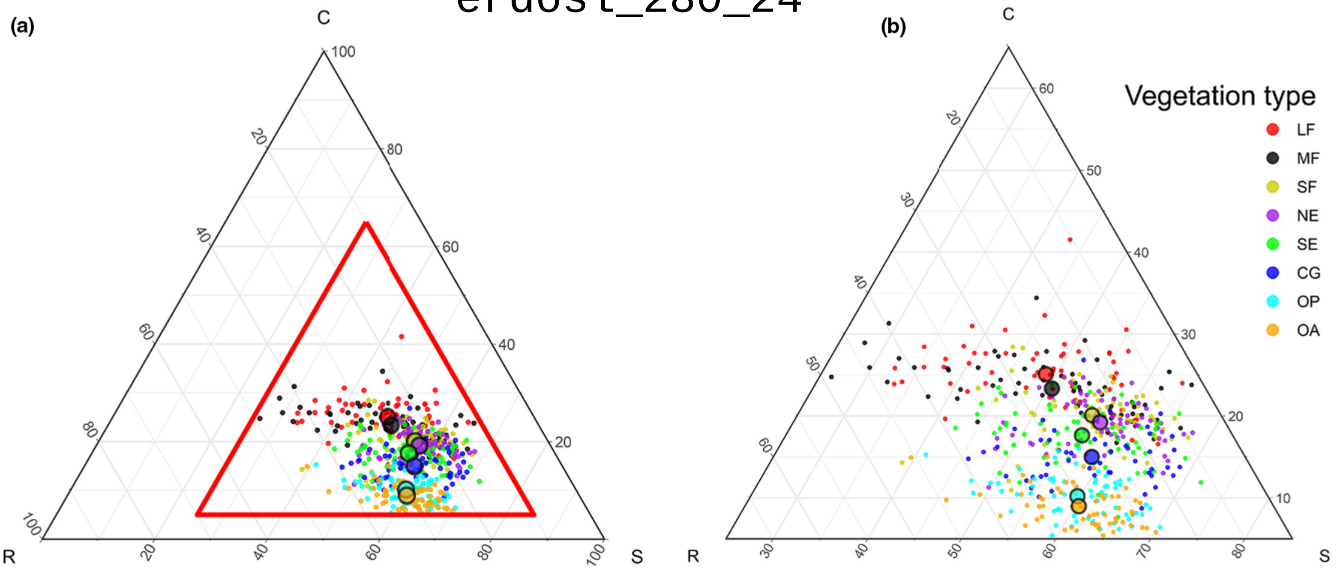

FIGURE 3 Ternary plots showing unweighted mean values of CSR strategies for the eight vegetation types. The red triangle in plot (a) shows the boundaries of plot (b). Larger symbols indicate the mean value for each vegetation type. Vegetation type abbreviations are according to the caption of Figure 2.

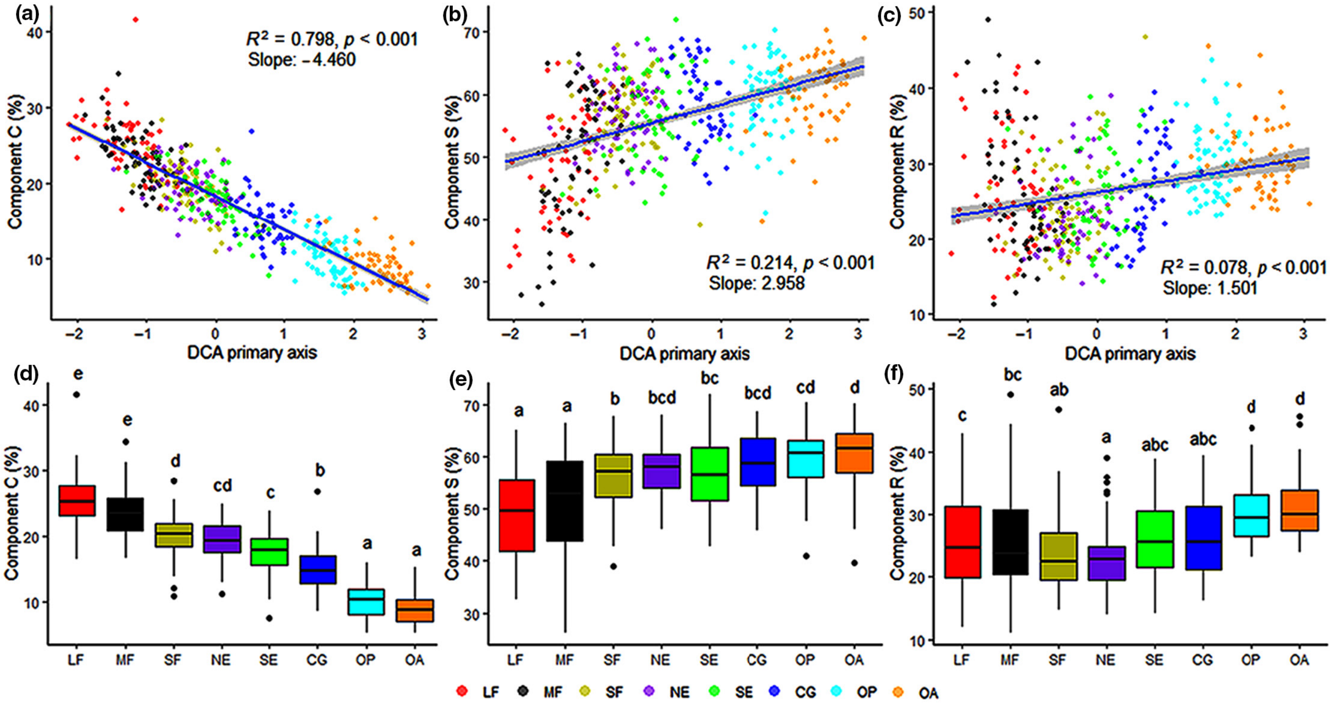

FIGURE 4 Relationships between plot scores on the primary DCA ordination axis and each unweighted strategy component: (a) C; (b) S, and (c) R; *p*-value and adjusted *R*-squared were calculated using linear regression; Slope: the slope value of the regression line; the blue line is the regression line, and the gray area around the line represents the 95% confidence interval. Box plots demonstrate the variability of each strategy component: (d) C, (e) S, and (f) R in the eight communities. Those that do not share a letter are significantly different at the significance level of $\alpha = 0.05$. Vegetation type abbreviations are according to the caption of Figure 2.

by the stress-tolerator strategy (Figure 3a), which reflects the relatively harsh environmental conditions prevailing in the study region. According to Grime and Pierce (2012), stress-tolerator plant species have an advantage over other species in unproductive and variable environments. In the Kiskunság Sand Ridge, most species encounter a harsh environment, as the amount of precipitation is low and shows high interannual variations (from <350 mm in some years to >800 mm in others) (Tölgyesi et al., 2016). The very low water retention capacity of the sandy soils in the region, alongside their low humus content (Várallyay, 1993) further increase the environmental stress.

Although each vegetation type examined in the present work was dominated by the stress-tolerator strategy, ecological strategies differed markedly among the studied vegetation types (Figures 3b and 4). This is similar to the findings of Rosenfield et al. (2019), who revealed distinct plant strategies along a relatively short gradient in South America. In our study region, competition proved to be a relatively important force in community assembly in large and medium forest patches, while its importance progressively diminished along the gradient toward the grasslands. Competition seemed to play the most subordinate role in the open grassland vegetation. The stress-tolerator strategy showed a reverse trend. Our environmental measurements (Erdős et al., 2018b; Ho et al., 2024) suggest that the forests of the study region are more productive and less harsh than grasslands, with forest edges typically providing intermediate environments. Trees and shrubs reduce environmental stress by providing relatively cool and humid circumstances under the canopy during the growing season, including the hot and dry months of late summer. Also, the canopy reduces daily temperature variation and mitigates extremes. In addition, forests have increased soil moisture and improved soil humus content compared to grasslands. Thus, our results are consistent with the predictions of Grime and Pierce (2012) and Adler et al. (2013), who argued that along productivity gradients, a shift in the importance of abiotic vs biotic factors can be expected, with abiotic constraints becoming more important toward the harsh end (in our case, grasslands) and competition becoming more important toward the more productive end of the gradient (in our case, forests). Our results also fit the findings of Dayrell et al. (2018), who reported that in southeast Brazil competition dominates community assembly in forest patches, whereas environmental stress is more important in grasslands. Similarly, Negreiros et al. (2014) claim that grasslands, especially those in highly unproductive environments, tend to be dominated by the stress-tolerator strategy.

When using weighted instead of unweighted values (Appendix S4), the importance of stress was further emphasized, as component S was high throughout the full gradient, and differences among the habitats were only moderate. Since filters have an influence on species' abundances in a given community, this reinforces our findings with unweighted values and makes our results more robust. The somewhat hump-backed shape of the curve suggests that stress loses some importance toward the end points of the gradient, probably because competition becomes more important in large and medium forest patches, while disturbance increases in importance in the open annual grasslands.

We suggest that competition for light is an important force that shapes forest communities in the study region, while competition for water and nutrients may be more limited in this vegetation type. The herb layer is sparse and individuals are usually widely spaced, suggesting low levels of competition, especially because the upper soil layer is relatively moist (Erdős et al., 2018b). Woody species reach much deeper soil layers, resulting in reduced competition between them and herbs.

We found obvious differences in strategies among the differently sized forest patches and the forest edges, suggesting that smaller forest patches and forest edges have a limited ability to buffer environmental stress (Erdős et al., 2023), that is, they are harsher than the larger forest patches.

Focusing on the three grassland types, competition seems to be more important and stress tolerance slightly less important in closed grasslands than in open ones. Similarly, comparing different grasslands of the Tibetan Plateau, Yu et al. (2022) showed that the importance of competition increased and the importance of stress tolerance decreased with increasing productivity. Kelemen et al. (2013) compared various lowland grassland communities and found that competition was more important in stable and productive environments, whereas stress-tolerator species gained advantage in alkaline and highly variable environments. The fact that stress tolerance is more important in open grasslands than in closed ones may reflect the harsher conditions in the former types (Ho et al., 2024). In closed grasslands, there is probably intensive competition both for light (above ground) and water and nutrients (below ground). In contrast, the widely spaced individuals in open grasslands probably experience less competition. Open annual grasslands, in particular, contain individual plants scattered on a relatively open surface, with small roots and limited leaf surfaces, suggesting weak competition.

When using unweighted values, the R strategy was only weakly related to DCA1 scores (Figure 4c) and played the most important role in the open grassland types (Figure 4f). With weighted values, however, the R strategy was much more strongly related to DCA1 scores, and this strategy proved much more important in open annual grasslands than in open perennial grasslands (Appendix S4). The R strategy is typical in early successional stages, on open, recently exposed surfaces (e.g., Caccianiga et al., 2006), which fits our findings. The open perennial grassland (OP) has considerable open sand surfaces between the dominant tussock grasses, where small annual plants are typical, similarly to other vegetation types with an important contribution of component R (Li & Shipley, 2017; Pierce et al., 2017). Open annual grasslands (OA) usually emerge as a result of disturbance, most often wind erosion or trampling by grazers and browsers (Fekete, 1992; Borhidi et al., 2012), although identifying the exact disturbance agents needs further research.

To sum up, our hypothesis that community assembly would be dominated by competitive exclusion in the forest patches and stress (i.e., environmental filtering) would dominate in grasslands was supported only partly. While it is true that the importance of competition was larger in woody habitats (i.e., forests and edges) than in grasslands, environmental filtering was the most important factor in each of the vegetation types (Figure 5). Disturbance played the most important role in the open perennial and the open annual grassland communities.

A significant drying tendency has been observed in Hungary during the last few decades (Jaagus et al., 2022), and the trend is projected to continue during the 21st century (Sábitz et al., 2014). As a result, we expect that vegetation types become even more stressed by aridity. This may result in increasing importance of environmental filtering, which already dominates the assembly of the plant communities in the Kiskunság Sand Ridge.

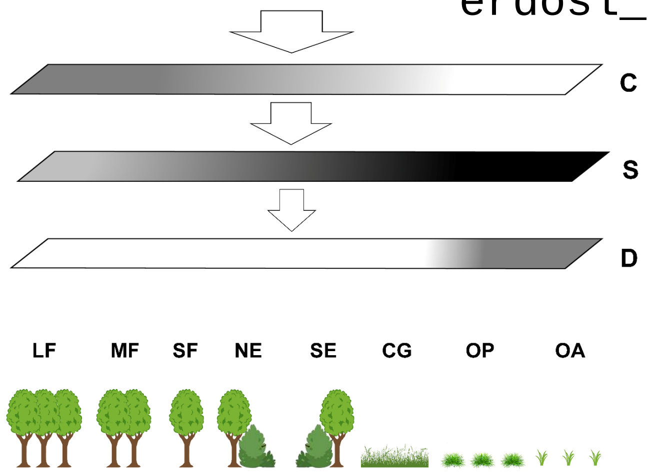

FIGURE 5 Assembly in the eight studied vegetation types of the forest–grassland mosaics in the Kiskunság Sand Ridge. The three components of the filter proposed by Grime and Pierce (2012) are shown as separate filters to increase clarity, but their order should not be interpreted as a hierarchy. Darker colors indicate dominating role of a filter. C, competition; D, disturbance; S, stress. Vegetation type abbreviations are according to the caption of Figure 2.

Similar to Catorci et al. (2011) and Han et al. (2021), we found that the CSR strategy types offer a useful tool for the study of plant-community assembly rules along gradients. However, a considerable limitation of our study was the limited length of the gradient. Studies encompassing more productive (and at the same time, less harsh) vegetation types (such as Lhotsky et al., 2016a, 2016b), or studies that contain a longer section of the disturbance gradient (e.g., Pierce et al., 2007) could provide additional information on assembly rules.

AUTHOR CONTRIBUTIONS

László Erdős designed the study, László Erdős, Khanh Vu Ho, Ákos Bede-Fazekas, György Kröel-Dulay, Csaba Tölgyesi, Zoltán Bátori, and Péter Török conducted the field works, Khanh Vu Ho and Ákos Bede-Fazekas analyzed the data, László Erdős, Khanh Vu Ho, Ákos Bede-Fazekas, György Kröel-Dulay, Csaba Tölgyesi, Zoltán Bátori, and Péter Török interpreted the results, László Erdős and Khanh Vu Ho wrote the first draft of this manuscript, and László Erdős, Khanh Vu Ho, Ákos Bede-Fazekas, György Kröel-Dulay, Csaba Tölgyesi, Zoltán Bátori, and Péter Török edited the manuscript.

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DATA AVAILABILITY STATEMENT

Data necessary to reproduce the analyses are deposited at Zenodo: https://doi.org/10.5281/zenodo.10255319 (Erdős et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. The 13 study sites used in this study with coordinates and elevation, and the distribution of relevés across plant communities and sites.

Appendix S2. Ternary plots of weighted mean values of CSR strategies with square-root-transformed cover scores for the eight vegetation types.

Appendix S3. Statistical results of the pairwise comparisons of unweighted components C, S, and R.

Appendix S4. Relationships between plot scores on the primary DCA ordination axis and each weighted strategy component using square root transformation of cover scores: (a) C; (b) S, and (c) R; *p*-value and adjusted *R*-squared were calculated using linear regression; Slope: the slope value of the regression line; blue line is the regression line, and the gray area around the line represents the 95% confidence interval. Box plots demonstrate the variability of each strategy component: (d) C, (e) S, and (f) R in the eight communities.

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Supporting information to the paper

Erdős, L. et al. Environmental filtering is the primary driver of community assembly in forest-grassland mosaics: a case study based on CSR strategies. *Journal of Vegetation Science.*

Appendix S1. The 13 study sites used in this study with coordinates and elevation, and the distribution of relevés across plant communities and sites. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; CG: closed perennial grasslands; OP: open perennial grasslands; OA: open annual grasslands.

Study sites	Coordinates		Altitude	Number of relevés							
			(m a.s.l.)	LF	MF	SF	NE	SE	CG	OP	OA
Ásotthalom	N 46°13'	E 19°47'	111–115	5	5	5	5	5	5	5	5
Bócsa	N 46°41'	E 19°28'	110–117	5	5	5	5	5	1	5	5
Bodoglár	N 46°31'	E 19°37'	114–123	5	5	5	5	5	5	5	5
Csévharaszt	N 47°17'	E 19°23'	125–137	3	4	5	5	5	4	5	–
Fülöpháza	N 46°52'	E 19°25'	105–119	10	5	5	5	5	5	5	11
Imrehegy	N 46°29'	E 19°22'	121–133	5	5	5	5	5	1	5	5
Kéleshalom	N 46°23'	E 19°20'	137–147	1	5	5	5	5	5	5	5
Négyestelep	N 46°17'	E 19°35'	131–137	5	5	5	5	5	5	5	5
Orgovány	N 46°47'	E 19°28'	105–113	5	5	5	5	5	5	5	5
Pirtó	N 46°28'	E 19°26'	124–132	3	5	5	5	5	5	5	5
Táborfalva	N 47°7'	E 19°23'	116–124	4	5	5	5	5	–	5	–
Tatárszentgyörgy	N 47°2'	E 19°22'	102–111	5	5	5	5	5	4	5	5
Tázlár	N 46°31'	E 19°30'	116–126	4	5	5	5	5	5	5	4

Supporting information to the paper

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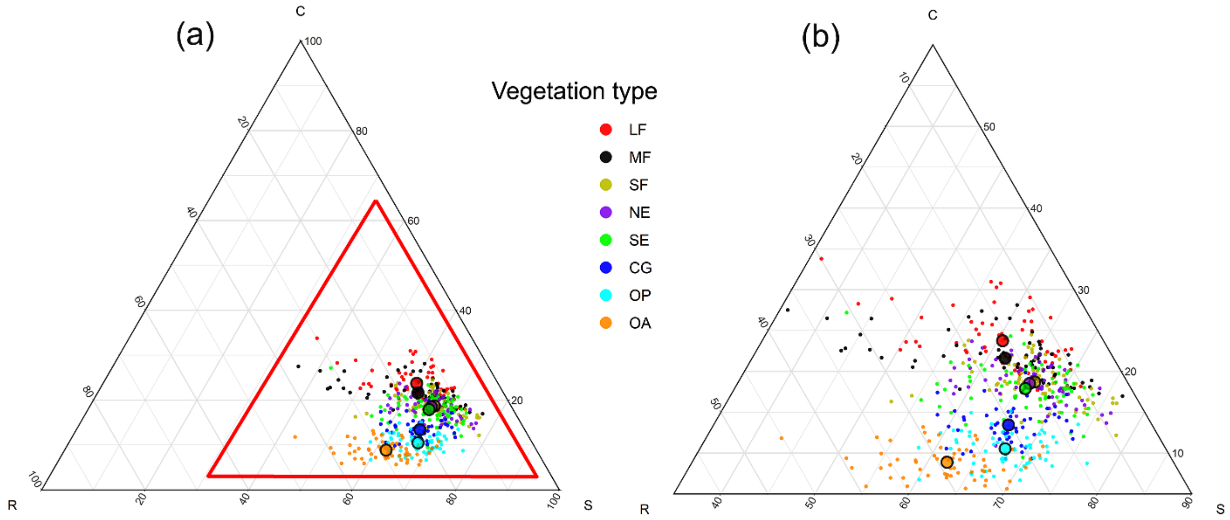

Appendix S2. Ternary plots of weighted mean values of CSR strategies with square-root transformed cover scores for the eight vegetation types. A red triangle in plot (a) shows the boundaries of plot (b). Larger symbols indicate the mean value for each vegetation type. Vegetation type abbreviations are according to the caption of Appendix S1.

Supporting information to the paper

Erdős, L. et al. Environmental filtering is the primary driver of community assembly in forest-grassland mosaics: a case study based on CSR strategies. *Journal of Vegetation Science.*

Appendix S3. Statistical results of the pairwise comparisons of unweighted components C, S, and R. Plant community abbreviations are according to the caption of Appendix S1.

Pair	Component C		Component S		Component R	
	t	p	t	p	t	p
LF-MF	2.917	0.103	-1.868	1.000	0.505	1.000
LF-SF	9.089	<0.001	-7.431	<0.001	3.397	<0.05
LF-NE	10.753	<0.001	-8.637	<0.001	3.832	<0.01
LF-SE	13.730	<0.001	-7.577	<0.001	0.833	1.000
LF-CG	17.649	<0.001	-9.878	<0.001	1.231	1.000
LF-OP	27.732	<0.001	-10.632	<0.001	-3.830	<0.01
LF-OA	29.558	<0.001	-11.292	<0.001	-4.123	<0.01
MF-SF	6.292	<0.001	-5.676	<0.001	2.952	0.093
MF-NE	7.990	<0.001	-6.908	<0.001	3.397	<0.05
MF-SE	11.031	<0.001	-5.825	<0.001	0.333	1.000
MF-CG	15.188	<0.001	-8.288	<0.001	0.774	1.000
MF-OP	25.328	<0.001	-8.946	<0.001	-4.430	<0.001
MF-OA	27.049	<0.001	-9.582	<0.001	-4.681	<0.001
SF-NE	1.706	1.000	-1.237	1.000	0.446	1.000
SF-SE	4.758	<0.001	-0.149	1.000	-2.629	0.247
SF-CG	9.387	<0.001	-3.039	0.070	-1.968	1.000
SF-OP	19.113	<0.001	-3.282	<0.05	-7.412	<0.001

SF-OA	20.988	<0.001	-4.076	<0.01	-7.570	<0.001
NE-SE	3.052	0.067	1.087	1.000	-3.076	0.062
NE-CG	7.806	<0.001	-1.894	1.000	-2.381	0.494
NE-OP	17.407	<0.001	-2.046	1.000	-7.858	<0.001
NE-OA	19.331	<0.001	-2.876	0.118	-8.004	<0.001
SE-CG	4.977	<0.001	-2.901	0.109	0.467	1.000
SE-OP	14.355	<0.001	-3.133	0.051	-4.782	<0.001
SE-OA	16.365	<0.001	-3.932	<0.01	-5.019	<0.001
CG-OP	8.329	<0.001	-0.001	1.000	-4.896	<0.001
CG-OA	10.432	<0.001	-0.834	1.000	-5.156	<0.001
OP-OA	2.417	0.448	-0.890	1.000	-0.378	1.000

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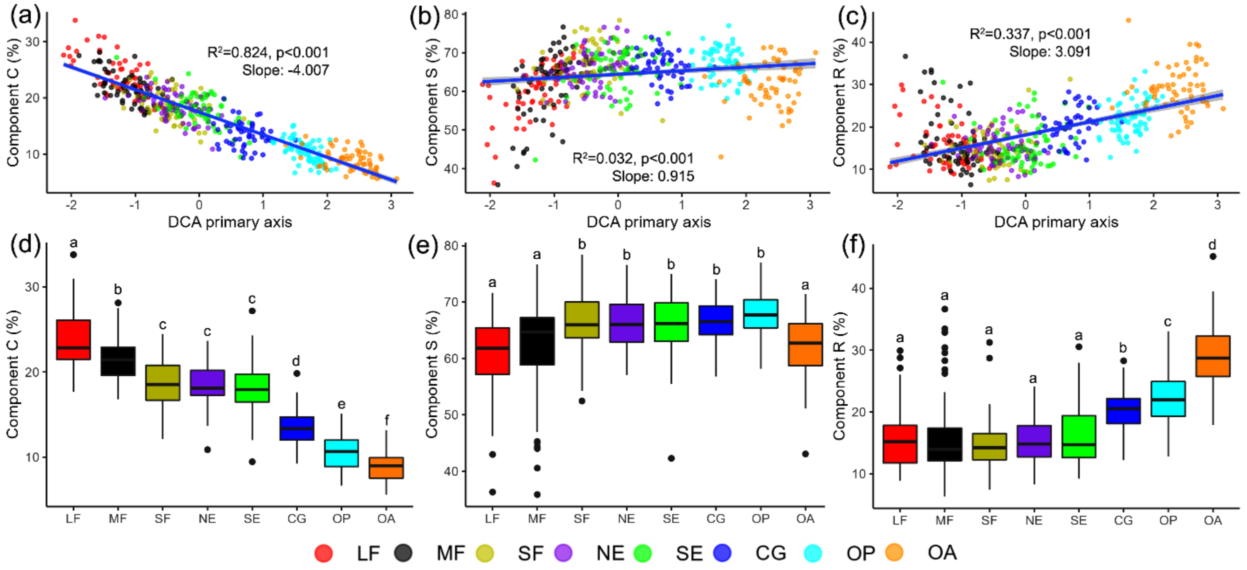

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Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics

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ABSTRACT

Forest-grassland mosaics are widespread features at the interface between tree- and grass-dominated ecosystems. However, the importance of habitat heterogeneity in these mosaics is not fully appreciated, and the contribution of individual woody and herbaceous habitats to the overall conservation value of the mosaic is unclear. We distinguished six main habitats in the forest-grassland mosaics of the Kiskunság Sand Ridge (Hungary) and compared the species composition, species richness, Shannon diversity, naturalness, selected structural features, environmental variables, and the number of protected, endemic, red-listed and specialist species of the plant communities. Each habitat had species that were absent or rare elsewhere. Grasslands had the highest conservation importance in most respects. North-facing forest edges had the highest species richness, while south-facing edges were primarily important for tree recruitment. Among the forest habitats, small forest patches were the most valuable, while large and medium forest patches had the lowest conservation importance. We showed that the current single-habitat focus of both research and conservation in the studied forest-grassland mosaics is not justified. Instead, an integrated view of the entire mosaic is necessary. Management practices and restoration projects should promote habitat heterogeneity, e.g., by assisting tree and shrub establishment and survival in grasslands. The legislative background should recognize the existence of fine-scale forest-grassland mosaics, which are neither grasslands nor forests, but a mixture.

1. Introduction

The intensification of land-use practices and the resulting habitat homogenization pose major challenges for current conservation (Ernst et al., 2017; Foley et al., 2005; Rembold et al., 2017; Stoate et al., 2001). Likewise, land abandonment often leads to homogenization (Bergmeier et al., 2010; Plieninger et al., 2015; Ernst et al., 2017). Generally, heterogeneous areas are expected to contain more niches and, consequently, more species than homogeneous areas (Bazzaz, 1975; Chesson, 2000; Tilman, 1982). In fact, spatial heterogeneity seems necessary for the maintenance of biodiversity, ecosystem services, and endangered species (Armengot et al., 2012; Dorresteijn et al., 2015; Valkó et al., 2012). Thus, from a conservation perspective, the presence of various habitat patches in close proximity is considered beneficial (Jakobsson and Lindborg, 2015; Tölgyesi et al., 2017).

Habitat heterogeneity and its conservation implications are relatively well studied in agricultural and agroforestry landscapes (e.g., Bennett et al., 2006; Benton et al., 2003; Jakobsson and Lindborg, 2015; Lee and Martin, 2017; Manning et al., 2006; Moreno et al., 2017; Plieninger et al., 2015; Stoate et al., 2001; Tscharntke et al., 2005). Unfortunately, the importance of habitat heterogeneity for conservation has received less attention in natural mosaics at the interfaces of tree- and grass-dominated biomes (cf. Tews et al., 2004).

Forest-grassland mosaics typically consist of numerous types of forest and grassland patches of various sizes, as well as intervening edge communities, with strongly different physiognomies and environmental conditions (Breshears, 2006; Schultz, 2005). In such mosaics, appropriate conservation actions and adequate management strategies require an integrated view of the complex ecosystem (Luza et al., 2014).

Forest-grassland mosaics represent high conservation significance (Erdős et al., 2018; Prevedello et al., 2018). However, in Eastern Europe, most of these mosaics have been transformed to croplands or non-native tree plantations, while the remaining fragments are threatened by different forms of homogenization (Wesche et al., 2016). In some regions, the spontaneous or human-induced spread of woody species may result in the disappearance of grassland habitats. At the

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same time, woody habitats are diminishing in other regions due to the combined effects of climate change, sinking groundwater level, and fire (Molnár, 1998; Wesche et al., 2016).

The conservation importance of habitat heterogeneity in the natural forest-grassland mosaics of Eastern Europe is, as yet, not fully appreciated. Ecological studies have typically focused on either the grassland or the forest component separately, disregarding the mosaic character (Erdős et al., 2015). The same bias exists in conservation practice. For example, restoration efforts usually aim to reconstruct only one of the components (e.g., Filatova and Zolotukhin, 2002; Halassy et al., 2016; Szitár et al., 2016; Török et al., 2014). Projects that intend to restore entire mosaic complexes (i.e., both woody and herbaceous components) are scarce (Török et al., 2017). While grazing and mowing are traditional and effective tools in both restoration and conservation management, changes in land-use in the form of either intensification (e.g., overgrazing, mechanized mowing) or abandonment may reduce heterogeneity and may thus have a detrimental effect on these complex systems (Bergmeier et al., 2010; Öllerer, 2014; Tölgyesi et al., 2017).

In this study, our aim was to explore the contribution of individual woody and herbaceous habitats to the overall conservation value of the entire mosaic. Our questions were the following: (1) If we aim to protect the entire species pool of the mosaic, is it sufficient to conserve one or a few keystone habitats, or is it necessary to conserve all of them? (2) What is the importance of individual habitats in terms of conservation-related characteristics (species richness, diversity, the number of species with special conservation relevance, naturalness, tree size-classes and recruitment, adventives)? (3) How does environmental heterogeneity support the observed vegetation pattern?

2. Material and methods

2.1. Study area

The study was conducted in the Kiskunság Sand Ridge, which is a lowland area between the Danube and Tisza rivers in Hungary. Three study sites were selected: Tatárszentgyörgy (N 47°02′, E 19°22′), Fülöpháza (N 46°52′, E 19°25′), and Bócsa (N 46°41′, E 19°27′) (Fig. 1a). All three sites are part of the Natura 2000 network of protected areas, and the Fülöpháza and Bócsa sites belong to the Kiskunság National Park. The mean annual temperature is 10.3–10.5 °C, and the mean annual precipitation is 520–550 mm (Tölgyesi et al., 2016). The study sites are characterized by stabilized calcareous sand dunes and interdune depressions that are covered by humus-poor sandy soils with low water retention capacities (Várallyay, 1993).

The vegetation is a mosaic of woody and herbaceous components (Fig. 1b). The open perennial sand grassland (*Festucetum vaginatae*, Natura 2000 category: 6260, *Pannonic sand steppes, a habitat of community importance in the European Union) is the most widespread natural herbaceous community of the study sites. The total cover of vascular plants usually varies between 40 and 70%, and the rest of the area is covered by mosses, lichens, or bare sand. The dominant species are *Festuca vaginata*, *Stipa borysthenica*, and *S. capillata*, while *Alkanna tinctoria*, *Dianthus serotinus*, *Euphorbia segueriana*, *Fumana procumbens*, and *Poa bulbosa* are also common.

Patches of the juniper-poplar forest (*Junipero-Populetum albae*, Natura 2000 category: 91N0, Pannonic inland sand dune thicket) are scattered in the grassland. The canopy layer has a cover of 40–60% and is co-dominated by 10–15 m tall *Populus alba* and *P.* × *canescens* individuals. The shrub layer cover varies between 5 and 80% with heights of 1–5 m, and is composed of *Berberis vulgaris*, *Crataegus monogyna*, *Juniperus communis*, and *Ligustrum vulgare*. The most common species in the herb layer include *Anthriscus cerefolium*, *Asparagus officinalis*, *Carex liparicarpos*, *Cynoglossum officinale*, *Poa angustifolia*, and tree and shrub seedlings. Some xeric species, such as *Eryngium campestre*, *Festuca rupicola*, and *Potentilla arenaria*, are mainly found under canopy gaps. The sizes of the forest patches range from a few individual trees (approx. 50 m^2) to a few hectares, although patches larger than 1 ha are rare.

The study sites were extensively grazed till the end of the 19th century. In the 20th century, the Fülöpháza and the Bócsa sites were used for military exercises, which stopped in 1974 (Biró et al., 2013; Kertész et al., 2017). Currently the level of anthropogenic disturbances is very low (strictly regulated tourism and research). There is strong evidence that the mosaic character is a result of climatic features and soil characteristics, and the grassland component persists even without grazing or other forms of disturbances (Bodrogközy, 1982; Erdős et al., 2015; Fekete, 1992). Both the position and the extent of the studied habitat patches are relatively stable at a decadal time-scale: grassland-to-forest or forest-to-grassland transitions are rare and occur very slowly (Erdős et al., 2015; Fekete, 1992).

2.2. Sampling design

Based on previous research (Erdős et al., 2015), six habitat types were distinguished in the present study: large forest patches (> 0.5 ha), medium forest patches (0.2–0.4 ha), small forest patches (< 0.1 ha), north-facing forest edges, south-facing forest edges, and grasslands. Patches were selected randomly for the study. Plots within the individual patches were placed so as to ensure representativeness and avoid degraded areas such as road or path margins and plantations. Edge plots were established in more or less straight peripheral zones of forest patches > 0.2 ha outward from the outermost tree trunks but still under the canopy. We sampled a total of 90 permanent plots (3 sites × 6 habitats × 5 replicates). Plot size was 25 m^2 (2 m × 12.5 m at edges, 5 m × 5 m elsewhere). The sizes and shapes of the plots were determined according to the local circumstances: the size was small enough to sample even the smallest forest patches but large enough for a standard coenological relevé, whereas the elongated form of the edge plots ensured that they did not extend into the forest or grassland interiors.

Within each plot, the percent covers of all vascular plant species in all vegetation layers were visually estimated in April (spring aspect) and July (summer aspect) 2016. Visual estimations were done by the same person in all plots. Of the spring and summer cover values, for each species, the largest value was used for subsequent data analyses.

All individual trees were inventoried in the plots, and the diameter at breast height (DBH) was measured for trees taller than 1.3 m.

As potential environmental drivers of vegetation in the different habitats, microclimate variables and soil moisture content were measured in 30 plots (6 habitats × 5 replicates) at the Fülöpháza site. Among the three study sites, Fülöpháza lies in the middle, in an almost equal distance from the other two sites. Air temperature (°C) and relative air humidity (%) were measured synchronously for 24 h at 25 cm above the ground surface in the centre of each plot using MCC USB-502 data loggers (Measurement Computing Corp). Microclimate loggers were housed in naturally ventilated radiation shields to avoid direct solar radiation, and the logging interval was set to 1 min. Measurements occurred from 3 to 4 August under clear weather conditions. Soil moisture values were measured in the upper 20 cm layer on 26 July using a FieldScout TDR300 Soil Moisture Meter (Spectrum Technologies Inc.). Five measurements were carried out for each plot, which were then averaged.

2.3. Data analyses

To assess the compositional relations of the six habitat types, we performed a non-metric multidimensional scaling (NMDS) using Bray-Curtis distance on the square root transformed cover scores. We conducted the analysis with one to six axes and found that using three or more axes caused only slight and linear decreases of the stress factors compared with the two-dimensional solution, so we decided to use only two axes. The analysis was performed in R 3.4.3 (R Core Team, 2017) using the ‘metaMDS’ function of the *vegan* package (Oksanen et al.,

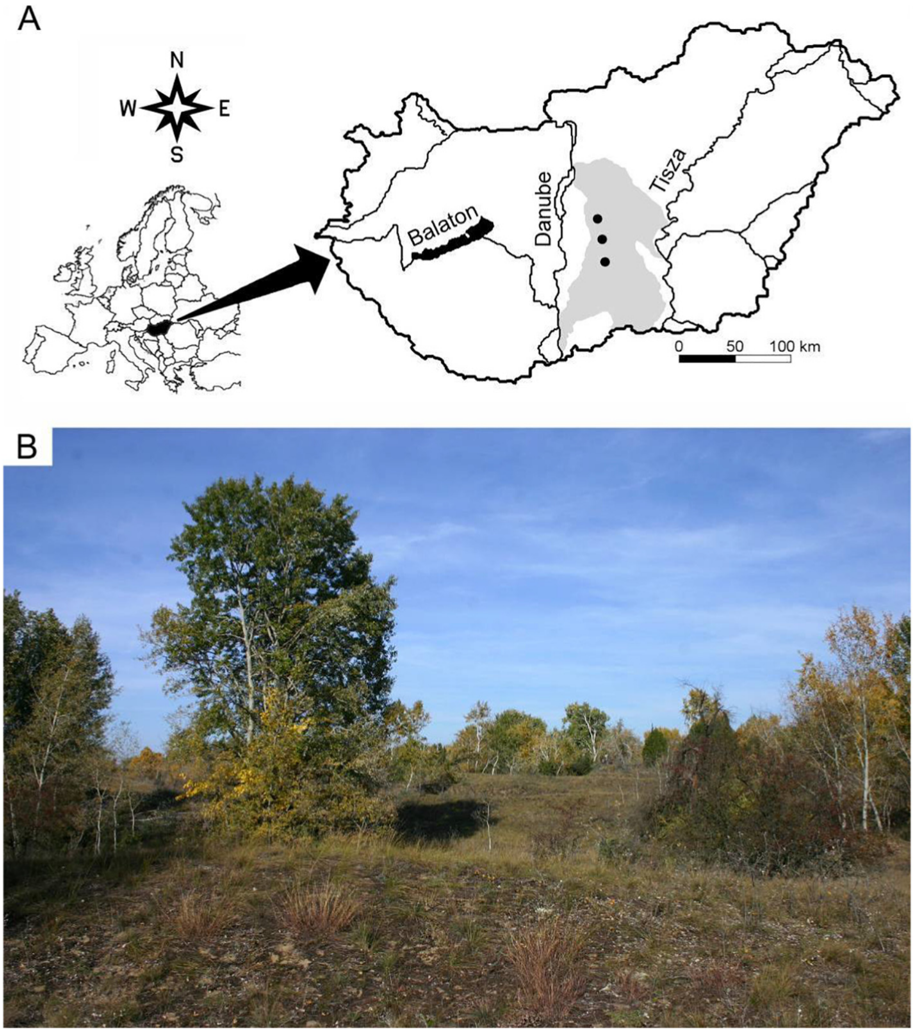

Fig. 1. (a) Locations of the Kiskunság Sand Ridge (grey) between the Danube and Tisza rivers in Hungary and the three study sites (black dots); from north to south: Tatárszentgyörgy, Fülöpháza, Bócsa. (b) Mosaic of woody and herbaceous vegetation at the Fülöpháza site.

2016).

To identify the species that prefer one specific habitat type and are absent or rare in other habitats, we performed a diagnostic species analysis. The phi coefficient was applied as an indicator of the fidelity of a species to certain habitats (Chytrý et al., 2002). The phi coefficient varies between -1 and $+1$; higher values reflect higher diagnostic values. In this study, species with phi values > 0.200 were considered. Significant ($P < 0.01$) diagnostic species were identified by applying Fisher's exact test. Analyses were performed with JUICE 7.0.45 (Tichý, 2002).

Species richness and Shannon diversity were computed for each plot, and the per plot number of species with special conservation relevance was also enumerated, which included all protected, endemic, red-listed and specialist species and was based on Borhidi (1995), Király (2007), and the Database of Hungarian Natural Values (www.termeszetvedelem.hu). As a numeric descriptor of habitat naturalness, we used the relative naturalness indicator values of Borhidi (1995), defined for the Hungarian flora. Naturalness indicator values are defined along an ordinal scale and reflect the observed tolerances of species against habitat degradation. Species that tend to be related to natural habitats have higher values, while species that are more frequent in degraded sites have lower values. Despite some criticism, bioindication in general and naturalness indicators in particular have solid theoretical bases and obvious practical advantages (Diekmann, 2003). Earlier analyses have shown that mean naturalness values are able to indicate habitat naturalness/degradation (Erdős et al., 2017; Sengl et al., 2016, 2017). Here, we calculated the unweighted mean value for each plot, as it is more efficient in site indication than cover-weighted approaches (Tölgyesi et al., 2014).

The species richness, Shannon diversity, number of species with special conservation relevance, and naturalness values were analysed in the R environment with linear mixed-effects models. Site was included as the random factor and habitat was the fixed factor. We used a Poisson error term for the count data (species richness and the number of species with special conservation relevance) and assumed a Gaussian distribution for the continuous variables (Shannon diversity and mean naturalness value). We used the 'glmer' function of the *lme4* package (Bates et al., 2015) for the former situation, and the 'lme' function of the *nlme* package (Pinheiro et al., 2016) for the latter one. The full models were tested for significance with analysis of variance, and if the model explained a significant proportion of the variability, we considered pairwise comparisons of the levels of the fixed factor. To account for multiple comparisons, we adjusted the resulting *P* values with the false discovery rate (FDR) method.

The size-class distribution of the trees was studied using 5 cm diameter classes. The distributions were compared with the Kolmogorov-Smirnov test. Stand characteristics, such as the mean and maximum DBH and number of trees per ha, were calculated for both native and adventive species. The nativeness or adventiveness of the tree species was defined according to Király (2009), as shown in Table A1.

Using the collected microclimate data, we calculated the following variables: mean daily air temperature, mean daytime air temperature, mean nighttime air temperature, mean daily relative air humidity, mean daytime relative air humidity, and mean nighttime relative air humidity. Daytime was defined here as the interval from 7:01 a.m. to 7:00 p.m., while nighttime was the interval from 7:01 p.m. to 7:00 a.m.

To assess the relationships between environmental variables and vegetation pattern, we conducted a distance-based redundancy analysis (dbRDA) in the R environment using the 'capscale' function of the *vegan* package (Oksanen et al., 2016). The ordination was performed using Bray-Curtis distance on the square root transformed species cover scores. For a preliminary dbRDA model, we included seven environmental variables (all six microclimatic variables mentioned above, and soil moisture) and calculated the variance inflation factor (VIF) of each variable to check for multicollinearity. We then removed the variable with the highest VIF and recreated the model. We continued this step-by-step refinement until every VIF was less than five. Finally, we retained only daily mean temperature, nighttime mean temperature, daily mean relative humidity, and mean soil moisture. To find the best model using any of these four explanatory variables, we used the forward selection method ('ordistep' function). We tested the final dbRDA model and the effect of each explanatory variable for significance with analysis of variance using 1000 permutations each.

The plant species names follow Király (2009), while the plant community names are according to Borhidi et al. (2012).

3. Results

We found a total of 182 plant species in the 90 plots. The NMDS ordination indicated a well-defined gradient in the following sequence: large forest patches – medium forest patches – small forest patches and north-facing edges – south-facing edges – grasslands (Fig. 2). Most groups overlapped considerably (especially small forest patches and north-facing edges), but grasslands were distinct from the other habitats.

The significant ($P < 0.01$) diagnostic species of the six habitats are shown in Table A2. Large forest patches had seven diagnostic species, mostly native shrubs (e.g., *Cornus sanguinea*, *Prunus spinosa*). Two native shrubs (*Crataegus monogyna*, *Berberis vulgaris*) were identified as diagnostic species for medium forest patches. Seven species were significantly associated with small forest patches, most of which were herbs (e.g., *Solanum dulcamara*, *Eryngium campestre*). North-facing edges had ten diagnostic species (e.g., *Carlina vulgaris*, *Polygala comosa*). South-facing edges also had ten diagnostic species (e.g., *Koeleria glauca*, *Poa bulbosa*), of which they shared four species with the grassland habitat. Twenty species were associated with grasslands (e.g., *Alkanna tinctoria*, *Fumana procumbens*).

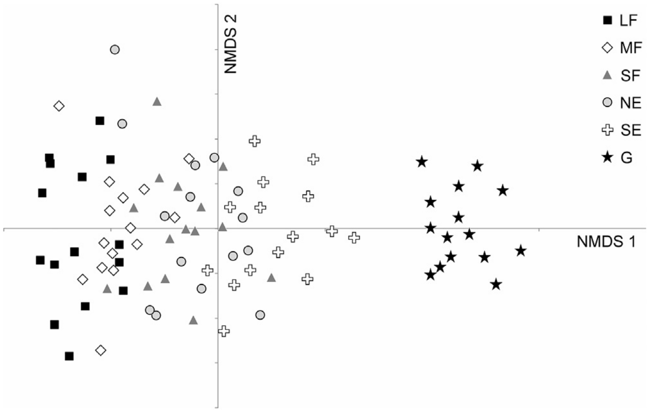

Fig. 2. NMDS ordination scattergram of the 90 relevés. Stress factor: 0.149; $R^2_{NMDS2} = 0.820$, $R^2_{NMDS1} = 0.035$. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

Habitat type had significant effects on species richness ($\chi^2 = 70.62$, $P < 0.001$), Shannon diversity ($\chi^2 = 12.31$, $P = 0.031$), the number of species with special conservation relevance ($\chi^2 = 129.16$, $P < 0.001$), and the mean naturalness value ($\chi^2 = 70.84$, $P < 0.001$). Considering the pairwise comparisons (Table A3), north-facing edges had the highest species richness followed by south-facing edges (Fig. 3a). Species richness was lowest in large and medium forest patches, while grasslands and small forest patches had intermediate species richness. There were no significant differences among the Shannon diversities of the different habitats, although north-facing edges and south-facing edges seemed to have somewhat higher Shannon diversity values than large, medium, and small forest patches (Fig. 3b). These differences were significant in only the uncorrected set of *P* values. The number of species with special conservation relevance showed a gradually increasing trend from the large forest patches towards the grasslands (Fig. 3c). A similar pattern was detected for the mean naturalness values (Fig. 3d).

Recruitment of native trees (mainly *Populus alba* and *P.* × *canescens*, to a much lesser degree *Quercus robur*) seemed to occur in mainly the south-facing edges and to a lesser degree in the north-facing edges and grasslands (Fig. 4, Table 1). In contrast, the recruitment of adventive trees (e.g., *Ailanthus altissima*, *Celtis occidentalis*, *Padus serotina*, and *Robinia pseudoacacia*) was concentrated in the forest interiors of all patch sizes and north-facing edges, while it was rare in the south-facing edges and completely absent in grasslands. The numbers of larger native trees (DBH > 5 cm) were almost equal in large, medium, and small forest patches, while adventive trees with DBH > 5 cm were present in only large forest patches. Large native trees (DBH > 50 cm) were present in mainly large and medium forest patches and to a lesser degree in small forest patches. Adventive tree species were not able to develop to large sizes in any of the studied habitats. According to the Kolmogorov-Smirnov tests (Table 2), the six habitats formed two groups: large, medium, and small forest patches were similar to one another, but differed significantly from the other three habitats (north-facing edges, south-facing edges, and grasslands).

The results of the environmental measurements are shown in Table A4. The best dbRDA model contained all four explanatory variables that were retained (daily mean temperature, nighttime mean temperature, daily mean relative humidity, and soil moisture), and it was significant ($R^2 = 0.276$, $F = 3.76$, $P < 0.001$). Although three of the variables were retained during variable selection, they had nonsignificant effects (nighttime mean temperature: $F = 1.28$, $P = 0.214$, daily mean humidity: $F = 0.98$, $P = 0.394$, and soil moisture: $F = 1.67$, $P = 0.099$), and only daily mean temperature had a significant effect ($F = 2.81$, $P = 0.019$). The dbRDA biplot (Fig. 5) indicated that woody (forest and edge) and non-woody (grassland) habitats were separated according to daily mean temperature, with higher values pointing towards the grassland. Interestingly, soil moisture, although having only a marginally significant effect, explained the distribution of the woody habitat types in the ordination space.

4. Discussion

4.1. Compositional differences among habitats

The composition of the studied habitats formed a gradient from large forest patches to grasslands. However, species turnover was not continuous, and two well-defined groups emerged. The first group contained the grassland habitat, which had the most distinct species composition and the highest number of diagnostic species, suggesting that the grassland species pool is poorly represented in other habitats. The second group consisted of all other (woody) habitats with partly overlapping species compositions and fewer diagnostic species. This most basic distinction (woody vs. herbaceous habitats) defines the

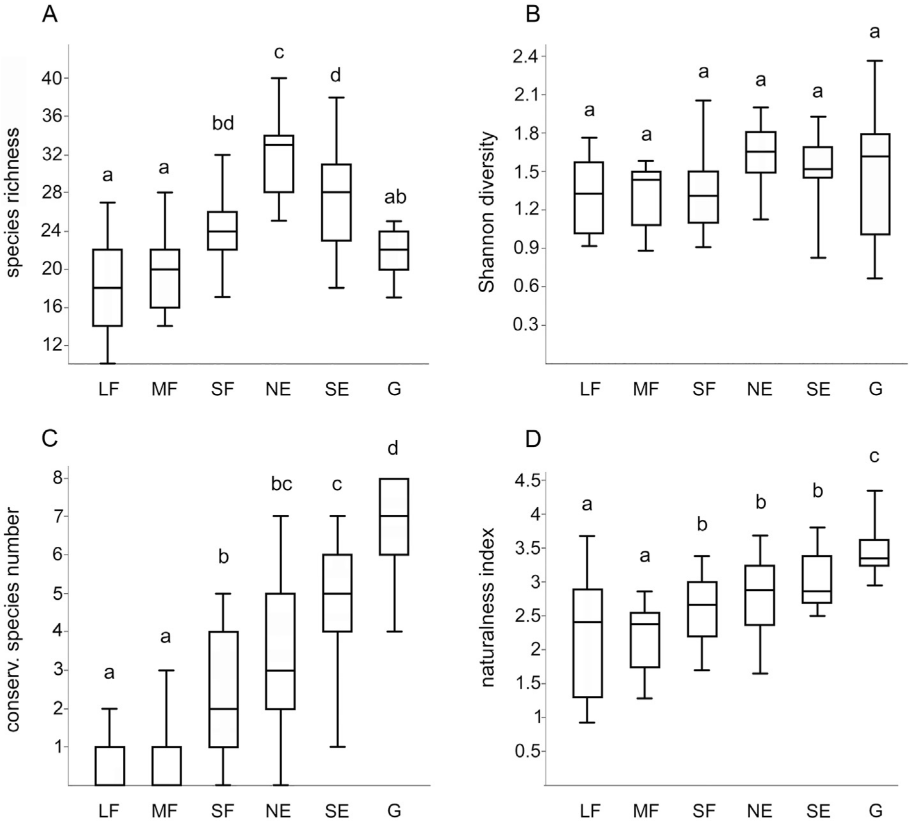

Fig. 3. Species richness (A), Shannon diversity (B), the number of species with special conservation importance (C), and mean naturalness values (D) of the six habitats. Different letters above the boxes indicate significant differences. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

minimum conservation requirement in the studied ecosystem: To represent a considerable proportion of the species pool of the landscape, it is necessary to preserve both the grassland and at least some of the woody habitats.

Given its relatively large variation, the woody habitat group may be further subdivided into edge-like habitats (small forest patches, north-facing edges, and south-facing edges) and forests with core areas (large forest patches and medium forest patches). To achieve a higher landscape-level diversity, it is recommended to conserve at least some edge-like habitats and some forest patches with core areas. However, our results emphasize that all six habitats have their typical species composition and species that are significantly concentrated within each of them. Thus, all habitats deserve special consideration in conservation policy and practice if we aim to protect the highest possible proportion of the species pool.

Until very recently, between-habitat compositional differences have received surprisingly little attention in Eastern European forest-grassland mosaics, where conservation efforts usually focus on only the grassland component (Erdős et al., 2013). In line with the results of Bátori et al. (2018), Kelemen et al. (2017) and Tölgyesi et al. (2017), our study revealed low redundancy between the woody and herbaceous components, which calls for increased efforts to conserve forest habitats in the studied ecosystem.

4.2. *Conservation-related characteristics of the habitats*

One of our most important findings was that the six habitats in the studied ecosystem had strongly different conservation-related characteristics. Grasslands had the highest per plot number of species with special conservation relevance (protected, endemic, red-listed, and specialist species). Similarly, in a mosaic of oak forests and xeric grasslands, Molnár (1998) found that grasslands contained more specialist species than either forest interiors or forest edges. Our results show that the grassland habitat had the highest naturalness. In addition, adventive tree seedlings were completely absent from grasslands, which is in good agreement with earlier studies that indicated low invasibility of undisturbed sand grasslands in the region (Bagi, 2008; Csecserits et al., 2016; Szigetvári, 2002). The conservation importance of the grassland habitat is probably further enhanced by other taxa that were not analysed in this study. For example, sandy grasslands are rich in mosses and lichens, including the endemic species *Cladonia magyarica* (Borhidi et al., 2012).

In our study, edges (especially north-facing ones) had the highest species richness, which is in line with the edge-effect theory (Risser, 1995). Similarly, forest edges were proven to be quite species-rich in other natural and near-natural mosaics in Eastern Europe (Erdős et al., 2013; Molnár, 1998), Asia (Bátori et al., 2018), and South America (de Casenave et al., 1995; Pinder and Rosso, 1998). In addition to hosting high fine-scale species richness, edges play an important role in tree recruitment: The number of native tree seedlings and saplings was the highest in south-facing edges, but it was also considerable in north-facing ones. Thus, forest edges may play a crucial role in the dynamics of forest-grassland mosaics (Erdős et al., 2015).

Forest patches of different sizes may be substantially dissimilar in several respects, although most earlier studies have been conducted in anthropogenic mosaics (e.g., Carranza et al., 2012; Gignac and Dale, 2007; Kolb and Diekmann, 2005; Rosati et al., 2010). In the fine-scale natural mosaics of Hungary, forest patches are usually very small (typically up to a few hectares) (Wesche et al., 2016). The small range of forest patch sizes may explain why forest patches of different sizes have received little attention. Interestingly, despite this small variation in size (the lower threshold of the large forest category was only 0.5 ha in our study), considerable differences were found among small forest patches on the one hand, and medium and large forest patches on the other.

Small forest patches had significantly higher species richness, more species of special conservation interest, and higher naturalness than large and medium forest patches. The differences in stand

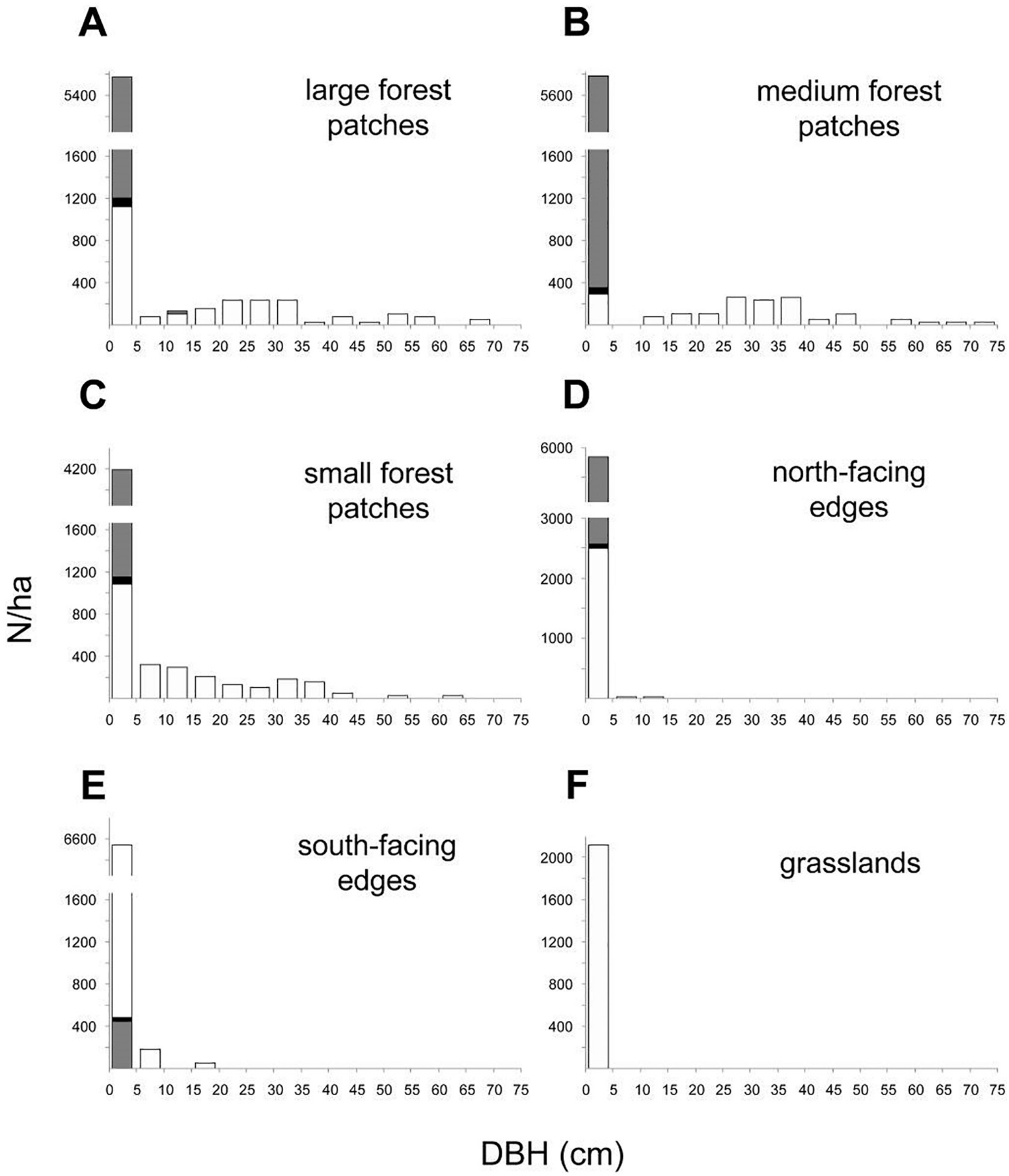

Fig. 4. DBH class distribution of *Populus alba* + *P.* × *canescens* (white), other native trees (black), and adventive trees (grey) in large forest patches (A), medium forest patches (B), small forest patches (C), north-facing edges (D), south-facing edges (E), and grasslands (F).

Table 1
Stand characteristics of the six habitats. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

	LF	MF	SF	NE	SE	G
DBH < 5 cm						
N/ha native trees	1200.0	346.7	1146.7	2560.0	6080.0	2106.7
N/ha adventive trees	4373.3	5440.0	3040.0	3280.0	453.3	–
DBH > 5 cm						
N/ha native trees	1440.0	1360.0	1520.0	53.3	240.0	–
N/ha adventive trees	26.7	–	–	–	–	–
mean DBH (cm)	30.3	33.9	22.0	8.3	7.9	–
DBH > 50 cm						
N/ha native trees	240.0	133.3	53.3	–	–	–
N/ha adventive trees	–	–	–	–	–	–
max. DBH (cm)	68.4	70.0	62.7	10.5	16.9	–

Table 2
Results of the Kolmogorov-Smirnov tests for the six habitats regarding DBH class distribution. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

D*P*	LF	MF	SF	NE	SE	G
LF		0.994	0.968	< **0.001**	**0.001**	< **0.001**
MF	0.13		0.849	< **0.001**	**0.002**	< **0.001**
SF	0.13	0.20		**0.010**	**0.013**	< **0.001**
NE	0.67	0.67	0.53		0.863	0.735
SE	0.67	0.67	0.53	0.13		0.724
G	0.80	0.80	0.67	0.13	0.13	

Significant differences are highlighted in bold.

characteristics were less pronounced, although the number of large trees (DBH > 50 cm) in small forests was low compared to the numbers in medium and large forest patches. Medium and large forest patches had low species richness, only a few species of special

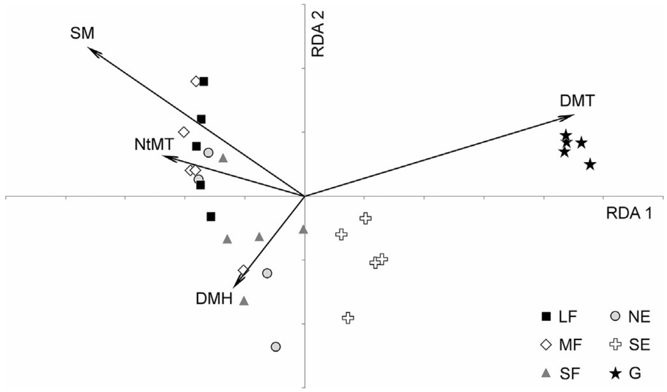

Fig. 5. Biplot of the dbRDA of the six main habitats in Fülöpháza. Constrained inertia: 37.6, unconstrained inertia: 62.4%; eigenvalues of the first and second axes: 2.170 and 0.256, respectively. DMT: daily mean temperature, DMH: daily mean relative humidity, NtMT: nighttime mean temperature, SM: soil moisture; LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

conservation relevance, and low naturalness values. In addition, large and medium forest patches hosted the largest proportions of adventive trees; thus, these forests should be regarded as potential invasion hot-spots. Csecserits et al. (2016) identified the following habitats as invasion hot-spots in our study region: tree plantations, agricultural habitats, old-fields, and oak forests. Pándi et al. (2014) concluded that abandoned farms are invasion centres. From these sources, adventive species with good dispersal abilities can easily reach all six habitat types evaluated in this study, but they probably have the best establishment chances in relatively humid and cool habitats such as medium and large forest patches.

Medium and large forest patches seemed to have relatively low conservation importance. However, they added structural characteristics to the landscape that small forest patches lacked. The noticeable number of native shrubs and large trees (DBH > 50 cm) should be considered important from a conservation perspective. For example, large trees provide habitat for several protected animals, including insects (e.g., *Aegosoma scabricorne* and *Oryctes nasicornis*) and birds (e.g., *Coracias garrulus* and other cavity-nesting birds) (Foit et al., 2016; Gaskó, 2009). It should also be kept in mind that the existence of edges depends on forest patches of sufficient size.

4.3. Environmental heterogeneity

Environmental parameters are expected to differ between woody and herbaceous patches in mosaic ecosystems (e.g., Breshears, 2006; Schmidt et al., 2017). In our study, the daily mean temperature differed significantly between woody and herbaceous habitats, while soil moisture showed conspicuous differences among the different woody habitats. Although the causal relations between vegetation and the environment are complex, it may be assumed that trees modify their environment in a way that has a profound effect on the herb layer (cf. Scholes and Archer, 1997). This moderating effect is expected to be especially strong in harsh environments (Callaway and Walker, 1997) such as the semi-arid Kiskunság Sand Ridge.

Soil moisture and daily mean and daytime mean air humidity were higher in the forest patches than in the grasslands, while the daily mean and daytime mean temperature were lower, and the maxima and minima of both temperature and humidity were less extreme in the forest patches. Thus, conserving woody habitats is important for creating environments that are suitable for mesic plants that would be unable to survive in the dry grassland component of the mosaic. This role of trees and groves is predicted to become increasingly important with ongoing climate change (Manning et al., 2009).

4.4. Conclusions and implications for conservation policy and practice

Our study implies that maintaining habitat heterogeneity through the protection of various habitats is of crucial conservation importance. Some habitats have outstanding species richness, some possess high resistance against invasion, and others are important mainly for tree recruitment or structural reasons. In addition, all habitats have characteristic species compositions with species that are absent or rare elsewhere.

In concordance with the findings of Török et al. (2017) and Weking et al. (2016), our study suggests that it is not sufficient to focus on either the grassland or the forest components in conservation-oriented research and practice. Rather, an integrated view of the entire mosaic is urgently needed. For example, the establishment of native trees should be promoted in areas where they have been reduced through cutting, overgrazing or fire (e.g., by deploying safe sites for seedlings). Management practices should be adapted to support native tree recruitment (e.g., by decreasing grazing pressure). During restoration projects, the reconstruction of forest patches should be of high priority.

Inappropriate legislation is a possible explanation why the complexity of forest-grassland mosaics has been neglected in both research and management in Eastern Europe (Babai et al., 2015; Hartel et al., 2013; Korotchenko and Peregrym, 2012; Tölgyesi et al., 2017; Varga et al., 2016). From a legal perspective, an area may be treated as either forest or grassland, but not as a mosaic of both. These two categories (i.e., forest and grassland) do not match reality in Eastern Europe, where the natural vegetation of large areas is actually a mosaic of woody and herbaceous patches.

Adapting conservation policy and practice to fit the complexity of forest-grassland mosaics may be a difficult task; however, there is no alternative if the natural values of these unique ecosystems are to be conserved.

Statement of competing interests

The authors have no competing interests to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.07.029.

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Table A1. Native and adventive tree species (defined according to Király, 2009) found in the 90 plots.

Native tree species
Acer campestre
Populus alba
Populus × canescens
Quercus robur
Adventive tree species
Ailanthus altissima
Amorpha fruticosa
Armeniaca vulgaris
Celtis occidentalis
Elaeagnus angustifolia
Gleditsia triacanthos
Juglans regia
Morus alba
Padus serotina
Pinus nigra
Robinia pseudoacacia

Table A2. Significant (P < 0.01) diagnostic species of the six habitats with phi coefficients > 0.200. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

	LF	MF	SF	NE	SE	G
Cornus sanguine	0.409					
Robinia pseudoacacia	0.358					
Brachypodium sylvaticum	0.341					
Rubus caesius	0.323					
Prunus spinosa	0.312					
Rhamnus catharticus	0.243					
Crataegus monogyna	0.226	0.226				
Berberis vulgaris		0.258	0.258			
Solanum dulcamara			0.403			
Chenopodium album			0.341			
Silene otites			0.323			
Eryngium campestre			0.261			
Asparagus officinalis			0.251			
Poa angustifolia			0.241	0.294		
Carlina vulgaris				0.492		
Viola rupestris				0.456		
Teucrium chamaedrys				0.452		
Leontodon hispidus				0.425		
Polygala comosa				0.341		
Taraxacum laevigatum agg.				0.312		
Pimpinella saxifrage				0.268		
Scabiosa ochroleuca				0.268		
Potentilla arenaria				0.344	0.289	
Thesium ramosum					0.408	
Carex stenophylla					0.341	
Verbascum lychnitis					0.332	
Bothriochloa ischaemum					0.296	
Koeleria glauca					0.268	
Poa bulbosa					0.416	0.349
Arenaria serpyllifolia					0.394	0.394
Stipa borysthenica+capillata					0.339	0.339
Festuca vaginata					0.243	0.347
Alkanna tinctoria						0.738
Erophila verna						0.738
Kochia laniflora						0.730
Holosteum umbellatum						0.664
Secale sylvestre						0.638
Crepis rhoeadifolia						0.628
Silene conica						0.536
Centaurea arenaria						0.528
Polygonum arenarium						0.480
Fumana procumbens						0.462
Euphorbia seguieriana						0.438

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Artemisia campestris	0.409
Bromus squarrosus	0.409
Medicago minima	0.368
Syrenia cana	0.368
Cerastium semidecandrum	0.358

Table A3. Statistical results of the pairwise comparisons of species number, Shannon diversity, number of species with special conservation importance, and mean naturalness values of the habitats. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

	Species number		Shannon diversity		Conserv. species number		Naturalness	
	z	p	t	p	z	p	t	p
LF vs MF	0.62	0.534	0.09	0.924	0.69	0.493	-0.17	0.863
LF vs SF	3.24	**0.002**	0.23	0.924	3.85	**<0.001**	2.13	**0.049**
LF vs NE	6.83	**<0.001**	2.74	0.070	4.87	**<0.001**	3.15	**0.004**
LF vs SE	4.65	**<0.001**	1.77	0.288	5.81	**<0.001**	4.12	**<0.001**
LF vs G	1.66	0.132	1.33	0.354	6.93	**<0.001**	6.87	**<0.001**
MF vs SF	2.63	**0.015**	0.13	0.924	3.44	**<0.001**	2.31	**0.036**
MF vs NE	6.24	**<0.001**	2.65	0.070	4.61	**<0.001**	3.33	**0.002**
MF vs SE	4.05	**<0.001**	1.68	0.288	5.71	**<0.001**	4.29	**<0.001**
MF vs G	1.04	0.319	1.23	0.370	7.02	**<0.001**	7.04	**<0.001**
SF vs NE	3.68	**<0.001**	2.52	0.070	1.6	0.118	1.02	0.359
SF vs SE	1.44	0.174	1.55	0.313	3.24	**0.001**	1.98	0.064
SF vs G	-1.60	0.139	1.10	0.413	5.37	**<0.001**	4.73	**<0.001**
NE vs SE	-2.26	**0.036**	-0.97	0.460	1.72	0.098	0.96	0.362
NE vs G	-5.25	**<0.001**	-1.42	0.345	4.04	**<0.001**	3.71	**<0.001**
SE vs G	-3.02	**0.004**	-0.45	0.816	2.43	**0.018**	2.75	**0.012**

Table A4. Measured environmental parameters (T: air temperature, H: relative air humidity, SM: soil moisture) in the six habitats at the Fülöpháza site, calculated from five replicates from each habitat. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

	LF	MF	SF	NE	SE	G
T (daily mean) (°C)	26.7	27.0	27.2	26.2	27.5	28.5
T (daytime mean) (°C)	32.3	33.0	33.7	31.5	35.0	36.9
T (nighttime mean) (°C)	21.0	21.0	20.7	20.9	20.1	20.2
T (maximum) (°C)	37.4	37.7	38.9	37.7	43.2	42.2
T (minimum) (°C)	17.6	17.6	17.1	17.8	16.8	16.6
H (daily mean) (%)	63.2	62.7	62.3	63.9	62.2	61.1
H (daytime mean) (%)	48.3	46.6	45.1	51.7	43.4	38.3
H (nighttime mean) (%)	78.1	78.8	79.5	76.2	81.1	83.9
H (max) (%)	89.5	89.7	91.5	89.8	92.6	95.2
H (min) (%)	29.8	29.0	28.6	30.9	23.2	23.7
SM (%)	10.2	11.6	9.3	11.1	8.4	7.0

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Plant composition and diversity at edges in a semi-natural forest–grassland mosaic

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Abstract As key components of landscapes, edges have received considerable scientific attention in anthropogenic ecosystems. However, edges in natural and semi-natural forest–grassland mosaics have received less attention, despite the fact that they cover a considerable proportion of these mosaic ecosystems. We studied forest edges in a semi-natural forest–grassland mosaic ecosystem of the Samobor Mountains (Croatia). Our aim was to compare the species composition, diversity and ecological indicator values of forest edges to those of the interior parts of the adjacent forest and grassland habitats. The vegetation was studied in 80 plots established in forest patch interiors, north-facing forest edges, south-facing forest edges and grassland interiors. We found that edges had a unique species composition, containing species from both the forest and the grassland interiors plus their own edge-related species (i.e. species that significantly preferred the edge habitat). These local edge-related species did not correspond to regionally-identified edge-related species. Compared to the forest and the grassland interiors, we revealed increased species richness in north-facing edges but not in south-facing edges. The mean light availability and nutrient supply indicator values of the edges were intermediate between those of the forest interiors and the grasslands. The mean soil moisture indicator values of the edges were similar to those of the grasslands. Our results show that edges form a unique component of forest–grassland mosaics, and they contribute considerably to landscape complexity, which should be taken into account during conservation decisions and habitat management.

Keywords Ecological boundary · Ecotone · Edge effect · Edge-related species · Forest edge · Habitat heterogeneity

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Introduction

Edges have received considerable attention in the ecological literature, as they are key structural and functional components of landscapes (Risser 1995; Cadenasso et al. 2003a; Ries et al. 2004, 2017; Yarrow and Marín 2007; Hufkens et al. 2009; Kolasa 2014). Edges influence the flow of organisms, materials and energy (Cadenasso et al. 2003b); influence population interactions (Fagan et al. 1999) and may serve as habitats or conduits for many species (Forman and Moore 1992).

Edges situated between forest and grassland ecosystems belong to the most conspicuous edge types (Forman and Moore 1992; Risser 1995; Cadenasso et al. 2003b). With accelerating forest fragmentation and an associated increase in edge proportion, forest edges have received considerable scientific attention in anthropogenic ecosystems (Merriam and Wegner 1992; Harper et al. 2005; Peters et al. 2006; Tokuoka et al. 2011; Dodonov et al. 2013; Haddad et al. 2015). For example, forest edges adjacent to clear-cuts (e.g. Chen et al. 1992; Euskirchen et al. 2001; Burton 2002; Harper and Macdonald 2002) or arable fields (e.g. Fraver 1994; Honnay et al. 2002; Devlaeminck et al. 2005) have been in the focus of ecological research. However, forest edges also play an important role in natural and semi-natural ecosystems, yet edges in these systems have received less attention in previous studies (but see Müller et al. 2012; Ibanez et al. 2013; Dislich and Mantovani 2016; Harper et al. 2018).

In Central and Southeast Europe, mosaic habitats consisting of alternating forest and grassland patches are an important component of landscapes, especially under relatively harsh conditions such as sand dunes and south-facing rocky slopes (Horvat et al. 1974; Öllerer 2014; Erdős et al. 2018a). A considerable proportion of these mosaic ecosystems, including extensively used pastures and pastures that have been abandoned recently, are semi-natural, i.e. modified by human activity but still dominated by native species that establish and reproduce spontaneously (Sjörs 1986).

Semi-natural landscapes in general and extensive pastures in particular have an outstanding conservation importance as they contain a large diversity of plants, including several rare species (Horvat et al. 1974; Ellenberg 1988; Bergmeier et al. 2010). It seems highly likely that the notable species diversity and natural value of forest–grassland mosaics are strongly connected to their high habitat heterogeneity, i.e. the presence of structurally very different patches in small proximity (e.g. Erdős et al. 2018b; Tölgyesi et al. 2018). Currently, however, the habitat heterogeneity of semi-natural forest–grassland mosaics is rapidly diminishing through different forms of homogenisation: overgrazing and intensification result in the disappearance of the forest component, while afforestation, the spread of invasive trees and the cessation of grazing threaten the survival of the grassland component (Bergmeier et al. 2010; Erdős et al. 2018b). It seems certain that a better understanding of the importance of habitat heterogeneity could contribute to a more efficient conservation of these valuable ecosystems.

Extensive and recently abandoned pastures typically have a fine-scale mosaic, that is, both the forest and the grassland patches are small (Horvat et al. 1974; Bergmeier et al. 2010; Erdős et al. 2011, 2018b; Borhidi et al. 2012). Consequently, the proportion of edge habitats is considerable, and they may have a disproportionately high conservation importance (Kent et al. 1997).

Edges have been proposed to have their own characteristic species composition, supporting species from both habitat interiors plus so-called edge-related species (i.e. species that tend to be concentrated within habitat edges) (Odum 1971; di Castri and Hansen 1992; Risser 1995; Kent et al. 1997). This has important conservation implications, as edge-related species, if they exist, would undoubtedly increase species richness at the landscape and regional scales (Naiman et al. 1988). Unfortunately, field studies are scarce, and the majority of them did not use any significance test to identify edge-related species (Lloyd et al. 2000; Baker et al. 2002).

Edges with different orientations tend to differ regarding environmental conditions (Chen et al. 1995; Gehlhausen et al. 2000; Ries et al. 2004; Heithecker and Halpern 2007), and consequently, regarding species composition (Dierschke 1974), which may contribute to a further increase in landscape- or regional-scale diversity. However, these differences remain poorly understood in semi-natural forest–grassland mosaics.

From a nature conservation perspective, edges may also be extremely important components of landscapes because their habitat-scale diversity is sometimes expected to be greater than that of either of the two adjacent habitat interiors (Odum 1971; Pianka 1983; Risser 1995; Kent et al. 1997). However, Ries et al. (2017) pointed out that this should not be considered a general phenomenon. Van der Maarel (1990) suggested that only blurred edges with stable environmental conditions have higher diversity than patch interiors, while abrupt edges with fluctuating environmental conditions (i.e. strong microclimatic variations in time) have lower diversity. Some field evidence shows that edge diversity may be intermediate between the diversities of the two habitat interiors (Walker et al. 2003; Erdős et al. 2011). The results of Łuczaj and Sadowska (1997) emphasise that edge diversity may vary considerably among different taxonomic groups. So far, generalisations have been rather difficult because of the limited number of case studies, especially for semi-natural systems (Harper et al. 2005; Kark and van Rensburg 2006).

In spite of the important role edges presumably play in these complex semi-natural mosaic ecosystems, their properties have been addressed by a surprisingly low number of studies. Our aim was to investigate forest edges in a semi-natural mosaic ecosystem with no current management activity, where small forest patches are embedded in a grassland matrix. We studied north- and south-facing forest edges in relation to the neighbouring forest and grassland habitats. Our specific questions were as follows: (1) Do edges have a specific species composition that differs from the habitat interiors? (2) Do edges possess their own edge-related species that significantly prefer edge habitats? (3) Do edges have larger per plot species richness and Shannon diversity than forest and grassland interiors? (4) Is the proportion of phytosociological preference groups different between habitat interiors and edges? (5) Are the mean ecological indicator values of edges and habitat interiors different? (6) Are north-facing and south-facing edges different regarding the above characteristics?

Materials and methods

Study area

Our study was conducted in the Samobor Mountains (northwest Croatia), which form a transition between the Alps, the Dinarides and the Carpathian Basin (Trinajstić 1995). We chose a south-facing slope (N45°48′02″, E15°38′30″) west of the town of Samobor. The elevation is 370–410 m asl, the bedrock is dolomite and the soil is rendzina (Mayer and Vrbek 1995; Trinajstić 1995). The mean annual temperature in Samobor is 11 °C, and the mean annual precipitation is 1015 mm, most of which falls in June and October–November (Mayer and Vrbek 1995). The natural vegetation of the study site consists of xeric forests. As a result of human impact (grazing and mowing), these forests have developed into a mosaic of xeric forest patches and dry grasslands (Horvat et al. 1974) (Fig. 1). The size of the forest patches usually varies between ca. 0.02 and 0.2 ha. Due to the high number of protected and rare species, these mosaics have extreme conservation importance but are diminishing as pastures and meadows are abandoned.

The forest component of the vegetation mosaic in the study site is represented by the calcareous pubescent oak – hophornbeam forest *Querco-Ostryetum carpinifoliae*. This is a thermophilous community distributed in the western Balkan Peninsula, preferring the south-facing slopes of mountains and hills (Horvat et al. 1974). The canopy layer has a cover of 60–80% and is co-dominated by flower ash (*Fraxinus ornus*), hophornbeam (*Ostrya carpinifolia*) and pubescent oak (*Quercus pubescens*). The shrub layer cover varies between 10 and 50% and is primarily composed of common dogwood (*Cornus sanguinea*), common buckthorn (*Rhamnus cathartica*) and wayfarer (*Viburnum lantana*). The most common species in the herb layer include branched St Bernard's-lily (*Anthericum ramosum*), upright brome (*Bromus erectus*), blue sedge (*Carex flacca*), winter heath (*Erica herbacea*) and angular Solomon's seal (*Polygonatum odoratum*). The grassland component is formed by the upright brome—hoary plantain grassland community *Bromo erecto-Plantaginetum mediae*, a meso-xerophytic basiphilous grassland of the western Balkans (Horvat et al. 1974). The dominant species are branched St Bernard's-lily (*A. ramosum*), upright brome (*Bromus erectus*), winter heath (*E. herbacea*), cypress spurge (*Euphorbia cyparissias*), hog's fennel (*Peucedanum oreoselinum*), wall germander (*Teucrium chamaedrys*) and broad-leaved thyme (*Thymus pulegioides*).

The study site was used as an extensively managed pasture, but grazing stopped in the 1980s. Currently there is no land-use or management activity.

Fig. 1 The forest-edge-grassland complex at the study site in the Samobor Mountains

Species names are used according to The Plant List (www.theplantlist.org), and plant community names follow the nomenclature of Trinajstić (2008).

Field work

Twenty forest patches were selected for the study. For all patches, four 2 m × 1 m plots were established in the following arrangement, corresponding to four different habitats: one plot in the forest patch interior, one plot in the north-facing forest edge, one plot in the south-facing forest edge and one plot in the neighbouring grassland. We thus used a total of 80 plots (20 patches × 4 habitats). The minimum distance between neighbouring patches was 75 m, while the distance between the neighbouring plots in the four habitats belonging to the same patch was 10–15 m. An edge was defined as the zone outside of the outermost tree trunks but still under the canopy. Forest edges in similar ecosystems are usually very narrow (Jakucs 1972; Erdős et al. 2011, 2014); thus, using small and elongated plots ensured that the plots fit into the edges. The cover of all vascular plant species of all vegetation layers was visually estimated in May 2017. As the canopy layer was low (typically 4–5 m, sometimes even less), and it merged with the shrub layer, the shrub and the canopy layers were treated jointly in this work.

Data analysis

To study the compositional differences among the four habitats, detrended correspondence analysis (DCA) (Hill and Gauch 1980) was performed on square root-transformed cover scores. The analysis was carried out in the R environment (R Core Team 2018) using the 'decorana' function of the *vegan* package (Oksanen et al. 2018).

We prepared a Venn diagram to show the number of species that are restricted to a single habitat and the number of species that are present in two or more habitats. We used the online Venn diagram generator of the Bioinformatics and Systems Biology Group of the Department of Plant Systems Biology, Ghent University (https://bioinformatics.psb.ugent.be/webtools/Venn/).

We also statistically identified diagnostic species, i.e. species that preferentially occur in certain habitats and are absent or rare in the other habitats (Barkman 1989). For this purpose, we used the phi coefficient, which has been shown to be an appropriate indicator of species' concentrations in certain habitats (Chytrý et al. 2002; Tichý and Chytrý 2006). The phi coefficient compares the observed frequencies of a species within a given community with frequencies that would be expected if the species was randomly distributed. The coefficient varies between − 1 and + 1; higher values reflect higher diagnostic values. Significant diagnostic species were identified with Fisher's exact test. We used JUICE 7.0.45 software (Tichý 2002) for the calculations.

Species number and Shannon diversity were computed for each plot. To examine whether there were any significant differences between the habitats, we applied the Friedman test using the 'friedman.test' function of the *stats* package (R Core Team 2018). The individual patches were used as blocking factor in the analyses. For the post-hoc pairwise comparisons of the habitats, the Nemenyi test was used with the 'posthoc.friedman.nemenyi.test' function of the *PMCMRv4.3* package (Pohlert 2014).

All species were classified into phytosociological preference groups according to Borhidi (1995) and the Flora Croatica Database (https://hirc.botanic.hr/fcd/). Frequency distributions were calculated for each habitat, which were then compared using Pearson's chi-square test with the 'chisq.test' function of the *stats* package (R Core Team 2018). For the post-hoc pairwise comparisons of the frequency distributions of the habitats, we used the 'pairwiseNominalIndependence' function of the *rcompanion* package (Mangiafico 2018).

We also calculated the mean ecological indicator values for soil moisture, light availability and nutrient supply for each plot. We used the indicator values of Pignatti (2005), which are based on the values of Ellenberg et al. (1992) but extended for southern Europe. Earlier field measurements have shown that ecological indicator values are able to provide reliable estimates of site conditions (e.g. Schaffers and Sýkora 2000; Dzwonko 2001; Tölgyesi et al. 2014). It has been shown that mean ecological indicator values perform well and have a solid theoretical basis (ter Braak and Gremmen 1987; Diekmann 2003). The Friedman test was used to examine differences among the habitats, using the 'friedman.test' function of the *stats* package (R Core Team 2018), while the Nemenyi test was used for post-hoc comparisons, using the 'posthoc.friedman.nemenyi.test' function of the *PMCMRv4.3* package (Pohlert 2014).

Results

We found a total of 131 plant species in the 80 plots (species cover values for all plots can be found in the Online Resource 1). North-facing edges had 93 species, south-facing edges had 88 species, while 88 species occurred in the forests, and 61 species in the grasslands.

According to the DCA ordination, forest plots and grassland plots formed two well-distinguishable groups (Fig. 2). Edge plots were situated in an intermediate position. North-facing edges and south-facing edges overlapped considerably in the ordination space.

A large number of species occurred in all four studied habitats (39 species) (Fig. 3). Somewhat fewer species were shared among forests, north-facing edges and south-facing edges (16 species) or between forests and north-facing edges (10 species). The number of species restricted to north-facing edges (14 species) or forests (12 species) was also considerable.

Forests had 16 diagnostic species, while grasslands had 11 diagnostic species (Table 1). The number of diagnostic species in north-facing and south-facing edges was 10 and 5, respectively. Notably, the diagnostic species of edges had rather low fidelity values. Among the significant diagnostic species of north-facing edges, there was only one species (*Peucedanum cervaria*) that is regionally regarded as edge-related. The situation was similar for south-facing edges, since *Peucedanum oreoselinum* was the only diagnostic species known for its regional affinity to edges. However, in our study, this species was also diagnostic for grasslands.

Habitat type had a significant influence on per plot species number according to the Friedman test ($\chi^2 = 13.338$, df = 3 , $p < 0.01$). As shown by the post-hoc tests, north-facing edges were the most species rich, while forests and grasslands had significantly lower per plot species numbers (Fig. 4a). South-facing edges did not differ significantly from any other habitat, although they seemed to be more species rich than habitat interiors.

Habitat type significantly influenced Shannon diversity, as indicated by the Friedman test ($\chi^2 = 14.460$, df = 3, $p < 0.01$). The post-hoc comparisons showed that forests had the lowest Shannon diversity values, north-facing edges and grasslands

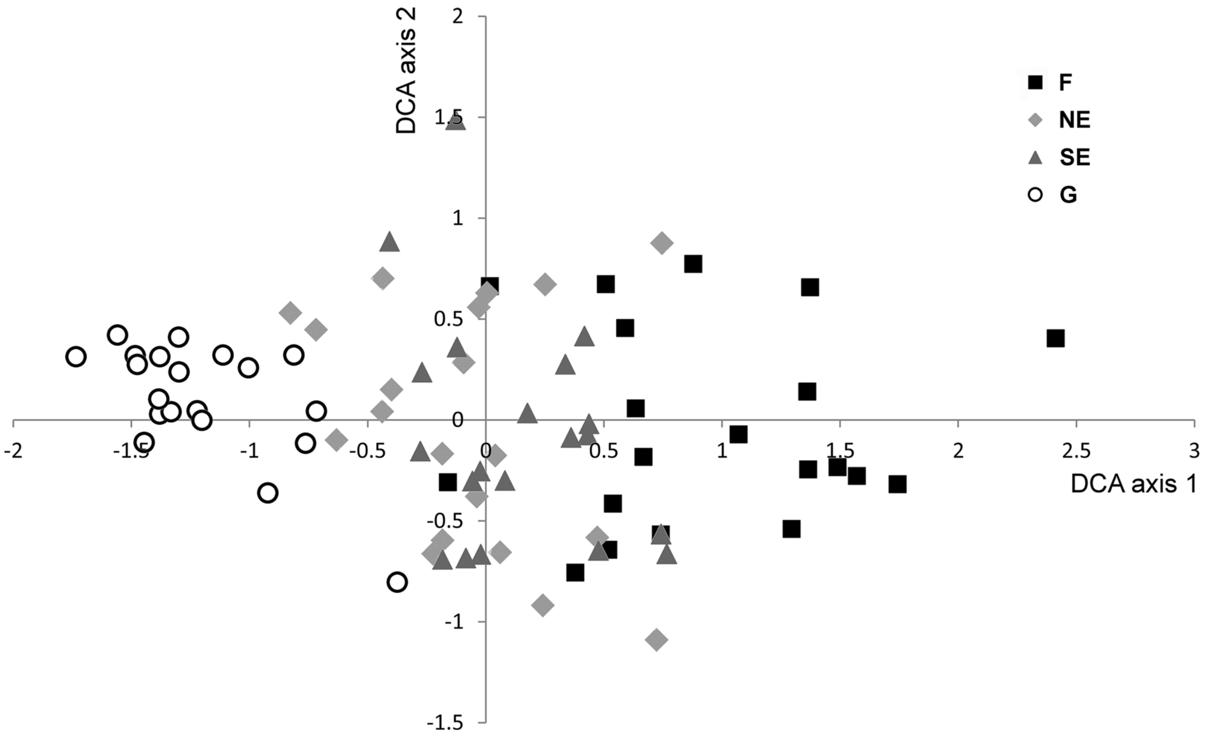

Fig. 2 DCA ordination scattergram of the 80 plots. *F* forest, *NE* north-facing edge, *SE* south-facing edge, *G* grassland. Eigenvalues of the first and second axes were 0.503 and 0.418, respectively

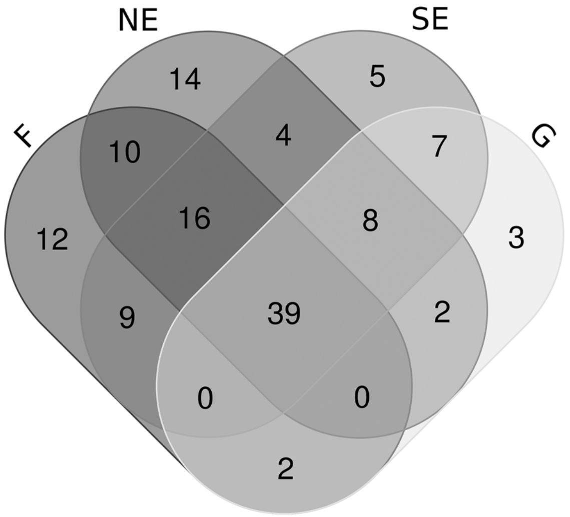

Fig. 3 Venn diagram of all species found in the study plots, according to their habitats. *F* forest, *NE* north-facing edge, *SE* south-facing edge, *G* grassland

were significantly more diverse, while south-facing edges were intermediate (Fig. 4b).

There were significant differences among the frequency distributions of the phytosociological preference groups in the four habitat types, as shown by Pearson's chi-square test ($\chi^2 = 209.43$, df = 18, $p < 0.001$). The post-hoc tests revealed no significant differences between north-facing edges and south-facing edges, while the other habitats differed significantly from one another (Fig. 5). The forest habitat was dominated by species of mesic and xeric forests and scrubs, while species of mesic and xeric grasslands were more typical than other types of species in the grassland habitat. Edges were generally intermediate: the proportion of species of mesic and xeric forests and scrubs was lower than in the forest interior but higher than in the grassland interior, while the reverse pattern was true for the species of mesic and xeric grasslands.

Mean ecological indicator values differed significantly among the four habitats, as shown by the Friedman test (soil moisture: $\chi^2 = 33.603$, df = 3, $p < 0.001$, light availability: $\chi^2 = 48.780$, df = 3, $p < 0.001$, nutrient supply: $\chi^2 = 39.780$, df = 3, $p < 0.001$). According to the post-hoc tests, forests

Table 1 Diagnostic species of the four studied habitats with fidelity values and regional phytosociological preferences

	F	NE	SE	G	Phytosociological preference
Lonicera caprifolium	0.524***				M + X forest
Hedera helix	0.522***				M + X forest
Cornus sanguinea	0.443***				Indiff
Dioscorea communis	0.418***				M + X forest
Primula vulgaris	0.393**				M forest
Mercurialis ovata	0.384**				X forest
Campanula persicifolia	0.343**				M + X forest
Sorbus aria	0.342**				Indiff
Cephalanthera damasonium	0.328*				M + X forest
Viburnum lantana	0.328*				X forest
Ligustrum vulgare	0.293*				M + X forest
Rosa canina	0.274*				Scrub
Quercus cerris	0.265*				X forest
Fraxinus ornus	0.254*	0.254*			X forest
Viola hirta	0.246*				Edge
Quercus pubescens	0.229*	0.229*	0.300**		X forest
Koeleria pyramidata		0.303**		0.303**	X forest
Hypochaeris maculate		0.274*			X grassland
Leontodon incanus		0.272*			X grassland
Lotus corniculatus		0.265*			Indiff
Peucedanum cervaria		0.265*			Edge
Brachypodium pinnatum		0.242*			X grassland
Ostrya carpinifolia		0.231*			X forest
Carex flacca		0.222*			Indiff
Euphorbia cyparissias			0.322**	0.322**	Indiff
Hypericum perforatum			0.265*		Indiff
Prunus avium			0.251*		M forest
Peucedanum oreoselinum			0.217*	0.217*	Edge
Globularia punctata				0.613***	X grassland
Anthyllis vulneraria				0.449***	X grassland
Thymus pulegioides				0.435***	M grassland
Helianthemum nummularium				0.419***	X grassland
Bromus erectus				0.412***	X grassland
Scabiosa columbaria				0.311**	X grassland
Carex caryophyllea				0.295**	Indiff
Silene vulgaris				0.291*	Indiff

F forest, *NE* north-facing edge, *SE* south-facing edge, *G* grassland, *edge* species of edges, *M forest* species of mesic forests, *M grassland* species of mesic grasslands, *M + X forest* species of mesic and xeric forests, *indiff* species occurring in woody and non-woody habitats, *scrub* species of scrubs, *X forest* species of xeric forests, *X grassland* species of xeric grasslands

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

had significantly higher moisture values than the other three habitats (Fig. 6a). Forests had the lowest and grassland the highest light indicator values, while edges were intermediate (Fig. 6b). Forests proved to have the highest nutrient values, while grasslands were nutrient-poor, edges being intermediate (Fig. 6c).

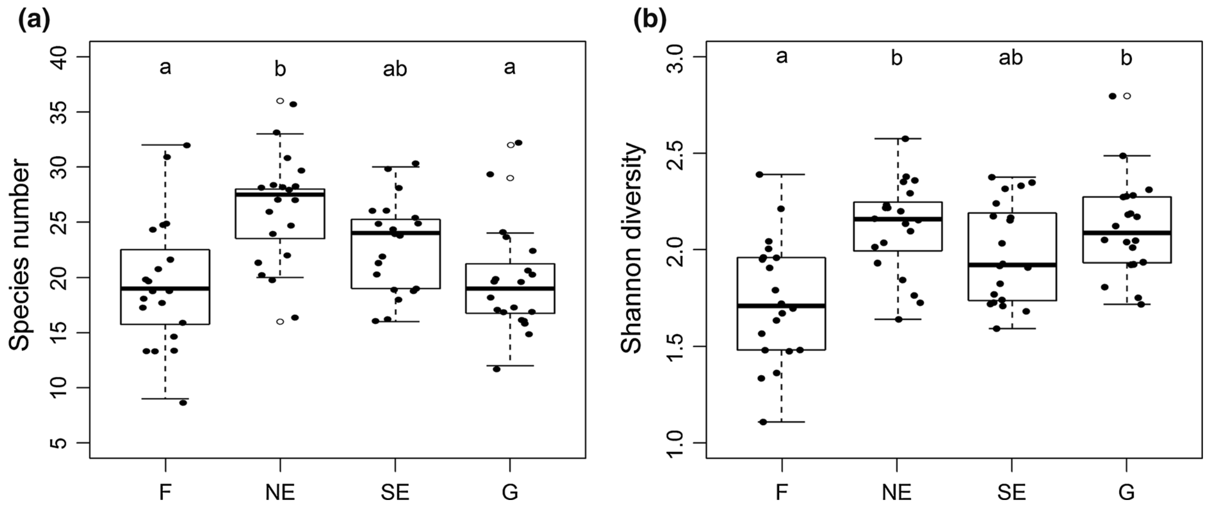

Fig. 4 Species number (**a**) and Shannon diversity (**b**) of the four studied habitats. Boxes not sharing a letter are significantly different. *F* forest, *NE* north-facing edge, *SE* south-facing edge, *G* grassland

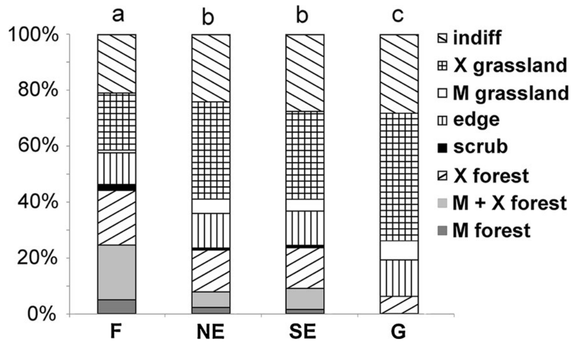

Fig. 5 Frequency distributions of phytosociological preference categories in the four studied habitats. Habitats not sharing a letter are significantly different. *F* forest, *NE* north-facing edge, *SE* south-facing edge, *G* grassland. *Indiff* species occurring in woody and non-woody habitats, *X grassland* species of xeric grasslands, *M grassland* species of mesic grasslands, *edge* species of edges, *scrub* species of scrubs, *X forest* species of xeric forests, *M + X forest* species of mesic and xeric forests, *M forest* species of mesic forests

Discussion

Our analyses showed that edges have a plant species composition that clearly differs from that of both the forest and grassland habitats, although overlaps do exist. Similar results for specific edge compositions were reported from other xeric forest–grassland mosaics such as the sandy forest-steppes of the Carpathian Basin (Erdős et al. 2013, 2014), Argentina's semi-arid Chaco forests (de Casenave et al. 1995), savannas in southern Brazil (Müller et al. 2012), African semi-natural savanna landscapes (Hennenberg et al. 2005) and Kazakh forest-steppes (Bátori et al. 2018). Thus, based on species composition, it seems justifiable to treat edges as separate communities in all the abovementioned study areas. However, different patterns also exist. For example, the species composition of edges may be very similar to that of forest interiors, as was the case in the xeric scrub of the Brazilian Caatinga (Santos and Santos 2008). Alternatively, edge composition may be similar to the composition of grassland interiors, as was shown by Erdős et al. (2011) in a xeric rocky scrubland in the Carpathian Basin.

Edges in our study area hosted both forest-related and grassland-related species. This result, however, was also obtained for the forest and grassland habitats (i.e. grassland-related species occurred in the forests, and some forest-related species were found in the grasslands). This fact may be explained by the fine-scale mosaic pattern of the study area (Horvat et al. 1974; Vukelić 2012): forest patches are so small that their total area is affected by the neighbouring grasslands; because the forest patches have a relatively dry and warm microclimate, colonisation by grassland species can occur. Similarly, the small grassland patches are probably influenced by the canopy of the nearby trees, and therefore, some forest species can easily extend into grasslands (Baker et al. 2013).

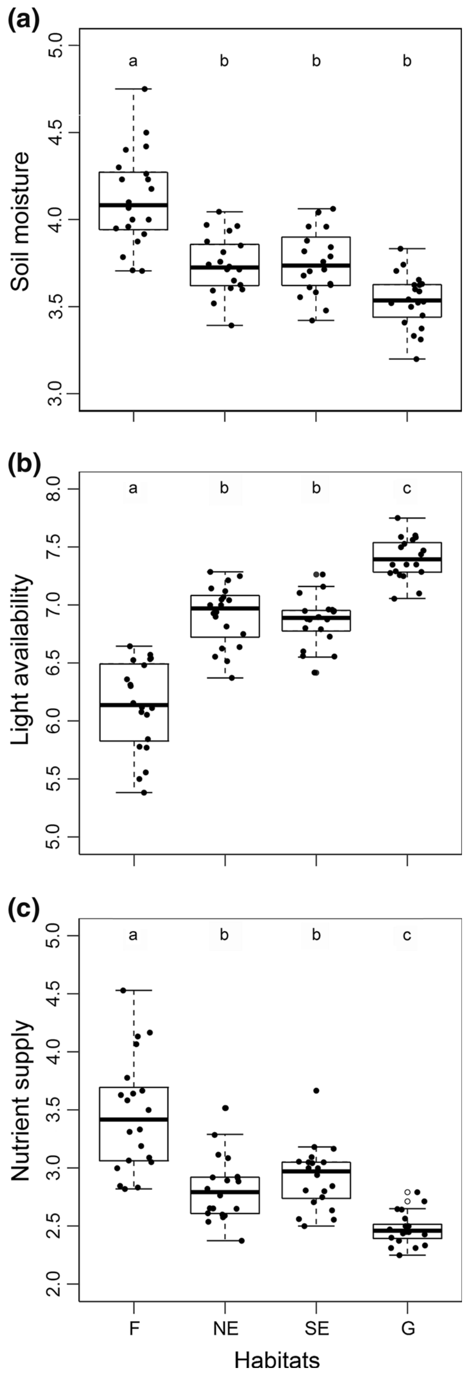

Fig. 6 Mean ecological indicator values of the four habitats for soil moisture (**a**), light availability (**b**) and nutrient supply (**c**). *F* forest, *NE* north-facing edge, *SE* south-facing edge, *G* grassland

As predicted by the edge effect theory (e.g. Risser 1995; Kent et al. 1997), edges had their own species, i.e. species that were significantly concentrated in edges. Interestingly, species that are regarded as edge related in regional phytosociological databases were under-represented among the significant edge diagnostic species identified in our study area. This result indicates that local edge species do not necessarily correspond to regional edge species (Lloyd et al. 2000; Erdős et al. 2013). Some species that are common outside of edges in a given region may be restricted to edges locally, provided that only edges have an appropriate combination of environmental factors in that specific location.

Per plot species richness was highest in north-facing edges, followed by south-facing edges; however, south-facing edges were not significantly different from the forest and grassland habitats. The Shannon diversity of north-facing edges was higher than that of forests but did not differ significantly from that of grasslands, while the diversity of south-facing edges did not differ significantly from any of the other studied habitats. Increased species richness has also been found in similar xeric forest–grassland mosaics in Eastern Europe (Molnár 1998; Erdős et al. 2013, 2014), Asia (Bátori et al. 2018) and South America (de Casenave et al. 1995).

The total (i.e. pooled) species number was highest in north-facing edges and slightly lower in south-facing edges and forests, while it was lowest in grasslands (Fig. 7). In an earlier study conducted in the Carpathian Basin, Erdős et al. (2013) also found that the total species number was highest in the edge habitat. However, grasslands in that study were almost as species rich as edges, while forests were particularly species poor, which is in contrast to the species richness patterns of the Samobor Mountains revealed in our present study. One possible explanation for these differences may be found in biogeographic patterns. The Samobor Mountains belong to the zone of deciduous forests, where grasslands were formed by human activity in historical times (Ellenberg 1988). This pattern explains why the species pool of forests exceeds that of grasslands. In contrast, substantial parts of the Carpathian Basin belong to the forest-steppe belt (Magyari et al. 2010), where grasslands are natural and have a much longer history, resulting in a considerably larger species pool.

According to the ecological indicator values, edges had mostly intermediate environmental conditions between the forest and the grassland habitats (Fig. 7), which is in line with earlier studies based on direct

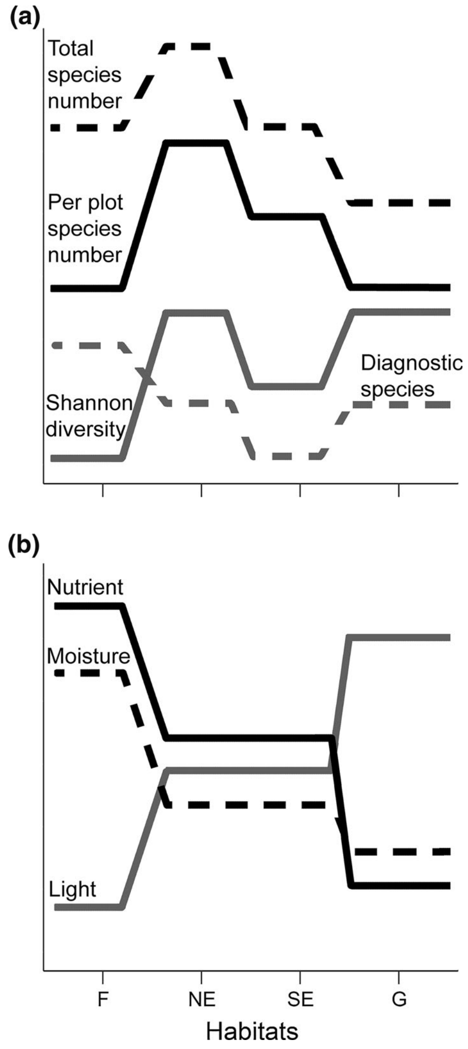

Fig. 7 Schematic representation of the main results of the study for **a** species number and diversity and **b** ecological indicator values. *St* total species number, *Sp* per plot species number, *D* number of diagnostic species, *H* Shannon diversity, *M* soil moisture indicator values, *L* light availability indicator values, *N* nutrient supply indicator values, *F* forest, *NE* north-facing edge, *SE* south-facing edge, *G* grassland

measurements (e.g. Cadenasso et al. 1997; Heithecker and Halpern 2007; Erdős et al. 2014) or ecological indication (e.g. Erdős et al. 2013; Palo et al. 2013).

We found moderate differences between north-facing and south-facing edges regarding species composition, while no significant differences were revealed regarding species richness, Shannon diversity, phytosociological preference groups and mean ecological indicator values. Some earlier studies suggested that there may be considerable differences between differently exposed edges in terms of abiotic factors (Ries et al. 2004; Wicklein et al. 2012), species richness (Fraver 1994; Erdős et al. 2013, 2018a, 2018b) and species composition (Brothers and Spingarn 1992; Fraver 1994). However, the study of Erdős et al. (2011), conducted in a recently abandoned pasture with a fine-scale forest–grassland mosaic found no significant differences between differently exposed slopes, which is in line with our current results.

In sum, we found that edges have a unique species composition, supporting species from both habitat interiors plus their own edge-related species. These edge-related species did not correspond to regionally-identified edge-related species. We found evidence for increased species richness in north-facing edges (Fig. 7), while this was not true for south-facing edges. Our findings support the notion that edges should be recognised as a special component of forest–grassland mosaics, which has important conservation implications. In many forest–grassland mosaics of Europe, land abandonment results in succession and gradual development into forest or shrubland (Ellenberg 1988). This process is considered undesirable, as grasslands represent high conservation value (Dengler et al. 2014; Valkó et al. 2018). It is clear, however, that if the mosaic character is lost with ongoing succession, not only the grassland but also the edge component will disappear. As shown by our results, edges contribute considerably to the compositional and structural complexity of the landscape. Thus, forest–grassland mosaics should be preserved not only because of grasslands but also because of edges.

The re-establishment of traditional low-intensity, extensive agricultural practises has been suggested as an appropriate management tool to preserve semi-natural grasslands in many European landscapes (Ostermann 1998). The historical land-use of our study area in the Samobor Mts is grazing. It has been shown that in such cases grazing is the best option, as many species are adapted to the specific disturbance dynamics of grazing (Römermann et al. 2009). Unfortunately, grazing may not be an economically viable solution any more. While mowing and mulching may be less favourable from a nature conservation perspective, they are usually considered acceptable alternatives in calcareous grasslands, as they are easier to implement and are able to maintain the mosaic character of the habitat (Kahmen et al. 2002; Moog et al. 2002; Wallis de Vries et al. 2002).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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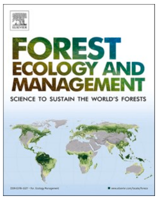

Non-native tree plantations are weak substitutes for near-natural forests regarding plant diversity and ecological value

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ABSTRACT

While near-natural forest stands are dramatically diminishing, monoculture tree plantations are rapidly spreading globally, including the eastern part of Central Europe. Tree plantations are regarded as simplified and species-poor ecosystems, but their functional and phylogenetic diversity and ecological value are still mostly unknown. In the present study, we investigated near-natural poplar forests and the three most common tree plantation types (native deciduous *Populus alba*, non-native evergreen *Pinus nigra*, and non-native deciduous *Robinia pseudoacacia* plantations) in the Kiskunság Sand Ridge, central Hungary. Our aim was to find out how different the species composition of the studied habitats is, how taxonomic, functional, and phylogenetic diversity vary among the four habitat types (i.e., near-natural forests and three types of plantations), and what the ecological value of the studied habitats is. We found that the four habitat types had significantly different species compositions. Although each habitat contained some diagnostic species, near-natural forests had the highest number of diagnostic species. While many of the diagnostic species of near-natural forests were native shrubs, tree plantations had many weeds and non-native herbs as diagnostic species. Near-natural forests had the highest per plot richness of native species and the lowest richness of non-natives. Shannon diversity, functional diversity and phylogenetic diversity were higher in the near-natural forests and two types of plantations (*Populus* and *Pinus*) compared to *Robinia* plantations. Based on naturalness indicator values, near-natural forests were the least degraded and *Robinia* plantations were the most degraded. Near-natural forests contained the most species of high conservation importance. Overall, near-natural forests proved to be much more valuable from an ecological and conservation perspective than any of the studied plantations; conservation and restoration programs should therefore focus on this type of habitat. Among the plantations, *Populus alba* plantations are the best substitute option in most respects, although they harbored a relatively high number of non-native species. We suggest that the native *Populus alba* should be preferred to non-native tree species when plantations are established. In addition, decreasing the extent of *Pinus* and *Robinia* plantations is essential on the long run if we aim to maintain the ecological integrity of the region.

1. Introduction

Tree plantations are often viewed as a solution to the increasing demand for timber and fuelwood and as an opportunity to counteract anthropogenic carbon emission (Cubbage et al., 2010, Paquette and Messier, 2010; Bastin et al., 2019; Tölgyesi et al., 2022). These

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plantations usually replace natural vegetation or are established on former agricultural areas, abandoned and/or degraded land (Brockerhoff et al., 2008; Pawson et al., 2013). Tree plantations are defined as “intensively managed forests, mainly composed of one or two tree species, native or exotic, of equal age, planted with regular spacing and mainly established for productive purposes” (FAO, 2020). Globally, these plantations account for about 3 % of all tree-covered areas (approximately 131 million hectares) (FAO, 2020) but their area is growing at a rate of about 2–3 million ha annually (FAO and UNEP., 2020). In Europe, tree plantations cover around 3.8 % of the forest area (about 8.1 million hectares), and nearly 52.8 % of these plantations comprise non-native species (Forest Europe, 2020).

Compared to natural and near-natural forests, tree plantations are regarded as simplified ecosystems with a low ecological value (Michelsen et al., 1996; Biró et al., 2008; Chen and Cao, 2014; Habel et al., 2018; Rédei et al., 2020; Hynes et al., 2021), and they have been shown to serve as invasion hotspots in the landscape (Csecserits et al., 2016; Medvecká et al., 2018; Slabejová et al., 2019). Also, the relatively young age of tree plantations compared to the older natural and near-natural forests may negatively affect their biodiversity and ecosystem services (e.g., Bremer and Farley, 2010; Wilson et al., 2017; Hua et al., 2022). Nevertheless, some evidence shows that tree plantations can also provide important ecosystem services, offer valuable habitat for certain threatened species, and may support conservation efforts in specific cases via reducing edge effects or increasing connectivity in severely fragmented landscapes (Brockerhoff et al., 2008; Pawson et al., 2013; Irwin et al., 2014; Albert et al., 2021; Hynes et al., 2021; Molnár et al., 2022).

Tree plantations, especially monocultures, tend to decrease plant species richness as well as the richness of several other taxa (Chaudhary et al., 2016; Habel et al., 2018; Rédei et al., 2020; Seifert et al., 2022). However, this pattern should not be considered a general phenomenon. For instance, in the study of Slabejová et al. (2019) it was found that the species richness in *Robinia pseudoacacia* plantations was not significantly different from that of floodplain forests and oak forests, but was higher than that of oak-hornbeam forests.

However, species richness and other simple measures of taxonomic diversity represent only one aspect of biodiversity. It has been recognized that functional diversity (i.e., the variability in functional traits of organisms) and phylogenetic diversity (the divergence of evolutionary lineages within a community) provide important additional information about an ecosystem’s properties (Díaz and Cabido, 2001; Díaz et al., 2006, Cadotte et al., 2009; Srivastava et al., 2012; Staab et al., 2021). Functional and phylogenetic diversity influence ecosystem processes, dynamics, stability, and ecosystem services (Scherer-Lorenzen, 2008; Cavender-Bares et al., 2009; Cadotte et al., 2011). Though high taxonomic diversity sometimes entails high functional and phylogenetic diversity (e.g., Cadotte et al., 2009; Swenson et al., 2012), a growing body of evidence shows that this is not always the case (e.g., Díaz and Cabido, 2001; Losos, 2008; Bernard-Verdier et al., 2013; Purschke et al., 2013; Doxa et al., 2020).

There has been a sharp decline in natural and near-natural forests and a rapid spread of tree plantations in the eastern part of Central Europe during the last two centuries (e.g., Biró et al., 2013; Popovici et al., 2013). However, it is largely unknown to what extent tree plantations of various species can substitute near-natural forests in terms of different aspects of diversity (taxonomic, functional, and phylogenetic). In this study, our aim was to compare the species composition, diversity, and ecological value of near-natural forests with those of various types of tree plantations (native deciduous, non-native evergreen, and non-native deciduous) in a region that has lost most of its natural forests to tree plantations. Our specific questions were the following: (i) How distinct or overlapping is the species composition of the studied habitats? (ii) How do taxonomic, functional, and phylogenetic diversity indices vary among the four habitat types? (iii) What is the ecological value of the studied habitats in terms of protected, endemic, and red listed species and naturalness status?

2. Materials and methods

2.1. Study area

The study was performed in the Kiskunság Sand Ridge, a lowland region in the center of the Pannonian biogeographic region between the rivers Danube and Tisza in Hungary (Fig. 1A). The climate of the area is sub-continental with sub-Mediterranean influences. The monthly mean temperature ranges from − 1.8 °C in January to 21 °C in July (annual mean temperature of 10.4 °C), while the mean annual rainfall is 500–550 mm (Kovács-Láng et al., 2000). The study area is made up of calcareous sand dunes, characterized by humus-poor sandy soils with low water retention capacity (Várallyay, 1993).

The natural vegetation of the study area is a mosaic of dry grassland and forest patches. Today these mosaics are embedded in a matrix of tree plantations and agricultural areas (Fig. 1B). The most typical (near-) natural forest type is the poplar forest *Junipero-Populetum albae*, which ranges in size from a few dozen square meters to a few hectares. Its canopy is composed primarily of 10–15 m tall *Populus alba* trees, with a total canopy cover of 50–80 % (Fig. 1C). The layer of shrubs is mainly formed by *Berberis vulgaris*, *Crataegus monogyna*, *Juniperus communis*, *Ligustrum vulgare*, and *Rhamnus catharticus* with cover values of 5–80 % and height of 1–5 m. The herb layer is primarily composed of *Anthriscus cerefolium*, *Asparagus officinalis*, *Carex liparicarpos*, *Calamagrostis epigeios*, and *Poa angustifolia*. The area of near-natural forests has shrunk dramatically during the previous centuries (Biró, 2008), and currently they occur mostly in protected forest-steppe mosaics with no wood production or forestry management activity, except for the occasional removal of non-native invasive tree individuals. In this study we define near-natural forests as spontaneous stands in protected areas, dominated by native species and devoid of visible signs of recent human impact.

In contrast to near-natural forests, tree plantations are widespread throughout the study region. The three most common types of plantations are those of the native deciduous white poplar (*Populus alba*), the non-native deciduous black locust (*Robinia pseudoacacia*), and the non-native evergreen Austrian pine (*Pinus nigra*) (Biró et al., 2013; Rédei et al., 2020).

Populus alba plantations typically have a canopy cover of ca. 50–70 % (Fig. 1D). The shrub layer is usually sparse (0–25 % cover) and mainly formed by *Crataegus monogyna*, *Padus serotina*, and *Robinia pseudoacacia*. The most common species in the herb layer are *Asclepias syriaca*, *Calamagrostis epigeios*, *Cynoglossum officinale*, *Poa angustifolia*, and *Taraxacum laevigatum*.

Pinus nigra plantations are usually characterized by a canopy cover of 50–60 % (Fig. 1E). Their shrub layer (total cover of 0–20 %) is constituted by *Berberis vulgaris*, *Crataegus monogyna*, and *Celtis occidentalis*. The herb layer is usually composed of *Asclepias syriaca, Poa angustifolia*, *Taraxacum laevigatum*, and *Silene alba*.

Robinia pseudoacacia plantations (Fig. 1F) have canopy cover values of ca 60–80 %. The shrub layer is very sparse (0–10 % cover), its typical species include *Ailanthus altissima* and *Crataegus monogyna*. In the herb layer, the dominant species is *Bromus sterilis*. Other typical species are *Anthriscus cerefolium*, *Elymus hispidus*, *Galium aparine*, and *Lamium amplexicaule*.

2.2. Field sampling

We selected nine sites where near-natural forests and the three most typical tree plantation types were present in close proximity to ensure that biotic and abiotic conditions are similar, but not too close to avoid potential autocorrelation effects. The sites were as follows: Fülöpháza (N 46°52′; E 19°25′), Orgovány (N 46°47′; E 19°28′), Bócsa (N 46°41′; E 19°28′); Bodoglár (N 46°31′; E 19°37′), Tázlár (N 46°31′; E 19°30′), Imrehegy (N 46°29′; E 19°22′), Pirtó (N 46°28′; E 19°26′), Négyestelep

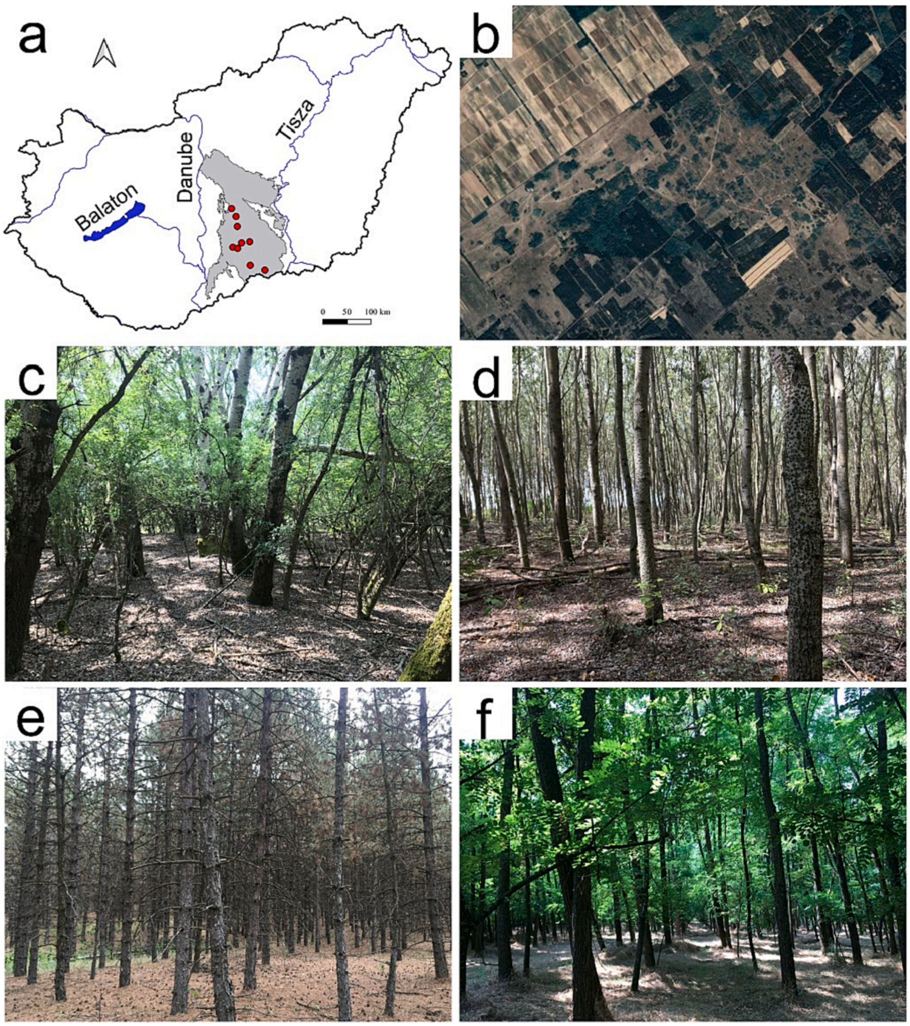

Fig. 1. (A) The nine study sites (indicated by red dots) in the Kiskunság Sand Ridge (gray area), Hungary; (B) satellite photo of a typical landscape in the Kiskunság, with protected near-natural poplar forest patches (in the center and towards the south), surrounded by tree plantations and agricultural areas; (C) near-natural poplar forest; (D) plantation of the native *Populus alba*; (E) plantation of the non-native *Pinus nigra*; (F) plantation of the non-native *Robinia pseudoacacia*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(N 46°17′; E 19°35′), and Ásotthalom (N 46°13′; E 19°47′).

At each site, four habitat types were sampled: near-natural poplar forests, plantations of native *Populus alba*, plantations of non-native *Pinus nigra*, and plantations of non-native *Robinia pseudoacacia*. Sampling was carried out in mature forests and even-aged tree plantations (DBH > 10 cm). Near-natural forests were sampled in protected areas, whereas plantations were sampled in the immediate proximity outside the protected areas, with similar environmental factors, on the same soil type. Only those near-natural stands were sampled that were > 0.2 ha to ensure that the studied plantations and near-natural stands are of comparable sizes. All sampled stands of the three plantation types had the same management type: they were created after deep-ploughing, and mechanical weed control was used for the initial five years, after which there was no further management. This is the most wide-spread management for plantations in the region (Rédei et al., 2020).

To sample the vegetation, we used 5 m × 5 m plots in the interior of the habitats where there was no sign of edge effect. We visually estimated the percentage cover of all vascular plant species within each plot in spring (April–May) and summer (July–August), and then we combined the spring and summer cover values for data analyses by using the larger value for each species. In this study, we only considered the shrub and herb layers. A total of 175 plots were sampled (40 plots in *Pinus nigra* plantations and 45 plots in each of the other habitat types; the distribution of plots across sites and habitats is shown in Table S1, while additional information on the four habitat types is provided in Table S2). The minimum distance among the plots was 200 m to avoid spatial autocorrelation. Plant species names follow Király (2009), and plant association names are used according to Borhidi et al. (2012).

2.3. *Data analyses*

To compare the species composition of the four habitat types, we performed non-metric multidimensional scaling (NMDS), using Bray-Curtis dissimilarity on the square-root transformed cover percentages. A permutational multivariate analysis of variance (PERMANOVA) with 1000 permutations was applied to confirm compositional distinctness among different habitats. The “metaMDS” and “adonis2” functions in the vegan package of R version 4.1.2 were used for NMDS and PERMANOVA, respectively (R Core Team, 2021; Oksanen et al., 2022). If the p-value of PERMANOVA test was lower than 0.05, we used “pairwise.adonis” function in the funfuns package for the pairwise comparisons with p-value adjusted by the Bonferroni method (Trachsel, 2022).

We performed a diagnostic species analysis to identify the species that favor one particular habitat and are absent or rare in other habitats. The phi-coefficient was used as an indicator of fidelity to identify diagnostic species of each habitat (Chytrý et al., 2002). Only species having a phi value higher than 0.2 were considered diagnostic species. We used Fisher’s exact test to reveal significant diagnostic species ($p < 0.001$). The calculations were conducted with JUICE 7.1.30 (Tichý, 2002).

We applied the “diversity” function of the R vegan package to calculate Shannon diversity for each plot (Oksanen et al., 2022). We also calculated the number of non-native and native species per plot.

To quantify functional diversity (FD), we chose Rao’s quadratic entropy (RaoQ), as it is an appropriate measure of functional diversity (Botta-Dukát, 2005; Ricotta, 2005). This approach takes into account both the relative abundances of species and the pairwise functional differences between species. We calculated plot-level Rao's quadratic entropy with the combination of nine traits: start of flowering, flowering duration, specific leaf area (SLA), mean plant height, thousand seed mass, life form, seed dispersal, pollination type, and reproduction type (Table 1). SLA, plant height, and thousand seed mass were selected because they are usually regarded as the most important and ecologically most informative traits of plant strategies (Westoby, 1998). The other traits were related to key ecosystem functions (Weiher et al., 1999). SLA, plant height, thousand seed mass, and flowering duration were log-transformed prior to calculation. The "gawdis" function of the gawdis package in R was used to calculate species dissimilarity because it was designed to compute multi-trait dissimilarity with more uniform contributions from various traits by minimizing the differences in the correlation between the dissimilarity of individual traits (quantitative traits) and categorical or fuzzy coded traits (de Bello et al, 2021a).

As a measure of phylogenetic diversity (PD), Rao's quadratic entropy was selected since it enables robust comparison between phylogenetic and functional diversity within the same conceptual and mathematical framework (Jucker et al., 2013; Swenson, 2014; de Bello et al., 2021b). A phylogenetic tree of the 173 species we recorded was created based on the 74,533-species mega-tree GBOTB.extended.tre (Jin and Qian, 2019). To construct this phylogenetic tree, the nomenclature of plant species (species name, genus name, and family name) was standardized according to The Plant List (2013). Then we used "phylo.maker" function of the V.PhyloMaker package in R version 4.1.2 to create phylogeny under the scenario 3, in which undetermined species were bound to their closest relatives. The final tree is shown in Fig.S1. The "cophenetic" function of the picante package was used to compute phylogenetic distance (Kembel et al., 2010).

Finally, we selected the "rao.diversity" function of the SYNCSA package in order to calculate RaoQ for both FD and PD (Debastiani and Pillar, 2012). Log-transformation of abundance data was used for these analyses (de Bello et al., 2021b).

To assess the naturalness of the habitats (i.e., their position along the natural-degraded continuum), we used the naturalness indicator values of Borhidi (1995). The approach is similar to the ecological indicator values, and rests on the fact that different plant species have different tolerances regarding degradation: while some plants prefer natural or near-natural habitats, others can tolerate or even benefit from degradation (Erdős et al., 2022a). Species associated with natural habitats receive high scores, while species related to degraded areas have low scores. The unweighted mean naturalness value per plot was calculated using the species present in each plot. Although various other approaches exist, it has been shown that they often yield similar results (Erdős et al., 2017) but the unweighted mean is usually more efficient than the calculation based on cover-weighted approaches (Tölgyesi et al., 2014).

We analyzed the number of non-native and native species, Shannon diversity, mean naturalness values, PD and FD with linear mixed-effects models. The fixed factor was habitat, while the random factor was site. We used the "glmmTMB" function of the glmmTMB package to generate the models with Poisson family for count data (the number of non-native and native species), Gaussian family for mean naturalness value, and Gamma family for Shannon diversity, PD and FD (Brooks et al., 2017). To test the linear mixed-effects models, we used analysis of variance (ANOVA), and if the model explained a significant proportion of the variability, we performed all pairwise comparisons of the fixed factor levels and manually adjusted the p-values with the Bonferroni correction by the "emmeans" function in the emmeans package (Lenth, 2022).

A Venn-diagram was created to show how many of the species with high conservation importance (protected, endemic, and red-listed plant species) are restricted to some of the habitats and how many occur in two or more habitats. To identify protected, endemic, and red-listed species, the following sources were used: Database of Hungarian Natural Values (www. termeszetvedelem.hu), FLÓRA database (Horváth et al., 1995), and Király (2007). The Venn diagram was prepared using the online Venn diagram creator of the Ghent University (https://bioinformatics.psb.ugent.be/webtools/Venn/).

Table 1
Details of the nine traits used for the functional diversity analyses.

Trait	Data type	Source
Start of flowering	Nominal with three levels: blooming from early spring (Months 1 to 4); blooming from early summer (Months 5 and 6); blooming from late summer (Months 7 to 9)	Király (2009)
Flowering duration	Numeric (number of months)	Király (2009)
Specific leaf area (SLA)	Numeric (mm^2/mg)	Kleyer et al. (2008); Lhotsky et al. (2016); E-Vojtkó et al. (2020); Gyalus et al. (2022); McIntosh-Buday et al. (2022)
Mean plant height	Numeric (cm)	Király (2009)
Thousand seed mass	Numeric (g)	Török et al. (2013, 2016); Royal Botanic Gardens Kew (2017)
Life-form type	Fuzzy coding with 8 levels: tree and shrub; semishrub; dwarf shrub; hemicryptophyte; geophyte; therophyte; hemitherophyte; epiphyte	Horváth et al. (1995); Király (2009)
Seed dispersal type	Fuzzy coding with 4 levels: anemochor (dispersal by air); rainwash (dispersal on the open soil surface by flowing water during heavy rainstorms); autochor (self-despersal); zoochor (dispersal by animals)	Fitter and Peat (1994); Csontos et al. (2002); Royal Botanic Gardens Kew (2017); USDA Forest Service (2017)
Pollination type	Fuzzy coding with 3 levels: insects; wind; self-pollination	Fitter and Peat (1994); Kühn el al. (2004); USDA Forest Service (2017)
Reproduction type	Fuzzy coding with 2 levels: generative; vegetative	Kühn et al. (2004)

3. Results

A total of 173 plant species were found in the 175 plots. Near-natural forests had the highest total species number (126 species), followed by *Populus alba* plantations (117 species), while *Pinus nigra* and *Robinia pseudoacacia* plantations had 83 species each.

Although there was some slight overlap among the habitat types in the NMDS ordination space (especially between *Populus alba* plantations and *Pinus nigra* plantations) (Fig. 2), the PERMANOVA confirmed highly significant differences between the habitat types ($F = 31.1$, $R^2 = 0.35$, $p = 0.001$). Pairwise comparisons revealed significant habitat differences for all pairs ($p < 0.01$, Table S3).

Significant ($p < 0.001$) diagnostic species are shown in Table 2. Near-natural forests had 20 diagnostic species, all of which were native, and contained many shrubs (e.g., *Berberis vulgaris*, *Ligustrum vulgare*, and *Rhamnus catharticus*). *Populus alba* plantations had 12 diagnostic species, most of which were non-native species (e.g., *Acer negundo, Ambrosia artemisiifolia,* and *Conyza canadensis*). *Setaria viridis* was the only diagnostic species of *Pinus nigra* plantations. *Robinia pseudoacacia* plantations had 13 diagnostic species, among them several native weed species (e.g., *Anthriscus cerefolium*, *Galium aparine*, and *Lamium purpureum*). Interestingly, *Robinia pseudoacacia* plantations also contained some species that are typical of open grasslands (e.g., *Secale sylvestre* and *Viola arvensis*).

Habitat type significantly influenced the number of native species

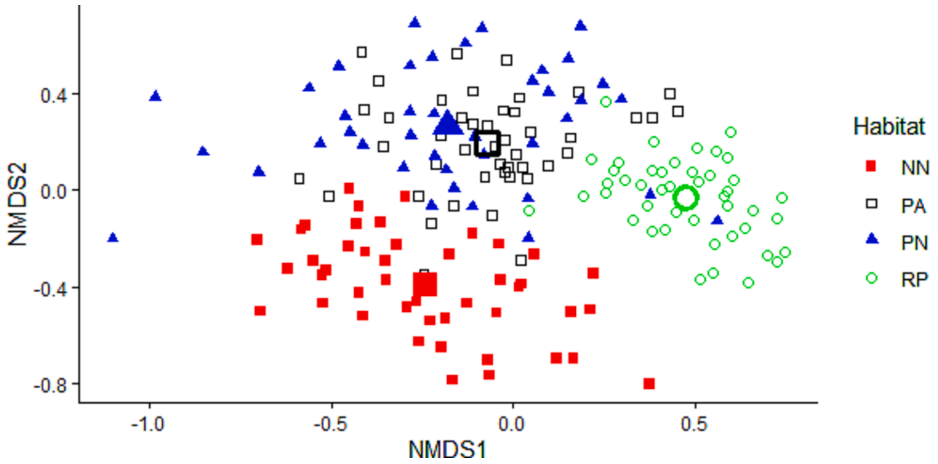

Fig. 2. NMDS ordination scattergram of 175 plots. NN: near-natural poplar forests; PA: plantations of native *Populus alba*; PN: plantations of non-native *Pinus nigra*; RP: plantations of non-native *Robinia pseudoacacia*. Large signs show the centroids for each habitat. Stress = 0.25.

Table 2
Significant ($p < 0.001$) diagnostic species of the four habitats with phi coefficients > 0.200. NN: near-natural poplar forests. PA: plantations of native *Populus alba*; PN: plantations of non-native *Pinus nigra*; RP: plantations of non-native *Robinia pseudoacacia*.

	NN	PA	PN	RP
Rhamnus catharticus	0.621			
Berberis vulgaris	0.614			
Ligustrum vulgare	0.588			
Populus alba	0.443			
Asparagus officinalis	0.409			
Carex liparicarpos	0.407			
Lithospermum officinale	0.388			
Seseli annuum	0.388			
Prunus spinosa	0.373			
Carex flacca	0.360			
Rosa canina agg.	0.335			
Euonymus europaeus	0.334			
Galium verum	0.334			
Hieracium umbellatum	0.322			
Teucrium chamaedrys	0.316			
Juniperus communis	0.315			
Polygonatum odoratum	0.311			
Thymus pannonicus	0.311			
Taraxacum officinale	0.302			
Crataegus monogyna	0.360	0.249		
Poa angustifolia		0.363		
Cynodon dactylon		0.353		
Trifolium repens		0.348		
Dactylis glomerata		0.343		
Ambrosia artemisiifolia		0.335		
Convolvulus arvensis		0.335		
Asclepias syriaca		0.324		
Elymus repens		0.315		
Acer negundo		0.294		
Conyza canadensis		0.272		
Taraxacum laevigatum		0.249		
Setaria viridis			0.267	
Lamium amplexicaule				0.546
Thlaspi perfoliatum				0.510
Secale sylvestre				0.492
Anthriscus cerefolium				0.491
Lamium purpureum				0.455
Geranium molle				0.442
Bromus sterilis				0.395
Ballota nigra				0.309
Viola arvensis				0.303
Galium aparine				0.296
Allium oleraceum				0.288
Juglans regia				0.282
Elymus hispidus				0.278

(chi-squared = 105.3, $p < 0.001$), the number of non-native species (chi-squared = 43.2, $p < 0.001$), Shannon diversity (chi-squared = 43.9, $p < 0.001$), functional diversity (chi-squared = 28.0, $p < 0.001$), and phylogenetic diversity (chi-squared = 43.3, $p < 0.001$). Based on pairwise comparisons (Table S4), near-natural forests contained the highest number of native species, followed by native tree plantations of *Populus alba* (Fig. 3A). The non-native tree plantations had the lowest number of native species. In contrast, the number of non-native species proved to be the lowest in near-natural forests, although it was not significantly different from *Pinus nigra* plantations (Fig. 3B). The number of non-native species was higher in *Populus alba* plantations than in the non-native tree plantations. There were no significant differences among the Shannon diversities of near-natural forest, *Populus alba* plantations and *Pinus nigra* plantations, but they all had higher Shannon diversity than *Robinia pseudoacacia* plantations (Fig. 3C). A similar pattern was observed for functional diversity (Fig. 3D). Phylogenetic diversity was the highest in near-natural forests, but it was not significantly different compared with *Pinus nigra* plantations (Fig. 3E). Phylogenetic diversity was the lowest in plantations of non-native *Robinia pseudoacacia*, while plantations of native *Populus alba* had intermediate phylogenetic diversity.

Habitat type also had significant effects on the mean naturalness value (chi-squared = 208.1, $p < 0.001$). The mean naturalness value was the highest in near-natural forests, and it was the lowest in *Robinia pseudoacacia* plantations, while the other habitats were intermediate (Fig. 3F, Table S4).

We found a total of 14 species with high conservation importance (i.e., protected, endemic, and/or red-listed species). Near-natural poplar forests were the most valuable habitat in this respect, as they harbored 12 of these species, six of which were restricted to this habitat type (e.g. *Dianthus serotinus*, *Epipactis atrorubens*, and *Iris arenaria*). Seven species with high conservation importance were found in *Populus alba* plantations, five in *Pinus nigra* plantations, and only one species in *Robinia pseudoacacia* plantations (Fig. 4).

4. Discussion

4.1. Species composition

The NMDS analysis found that each habitat type had its own species assemblage, although some overlaps do exist (Fig. 2). The differences in species composition can be explained by two sets of factors. First, forestry activities connected to the creation and management of plantations (mechanical site preparation, mechanical weed control during the initial five years, etc.) may be directly responsible for the

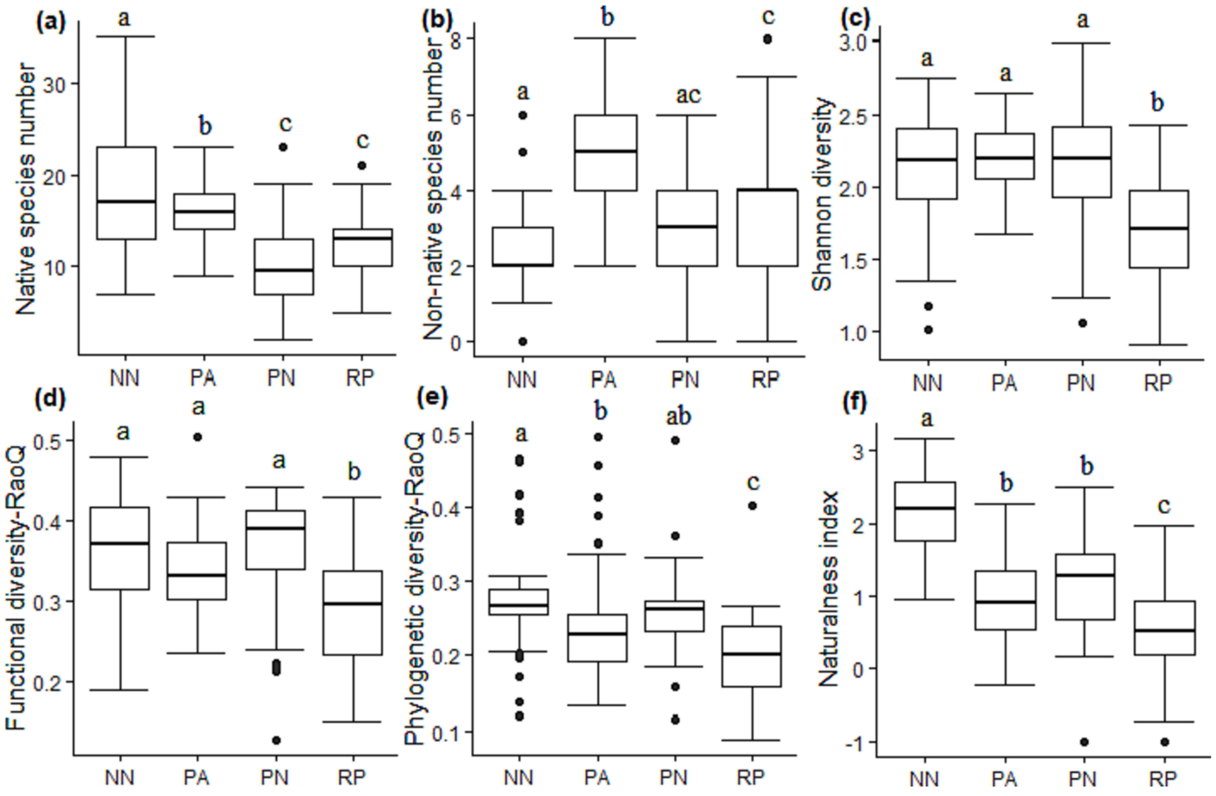

Fig. 3. The number of native species (A), the number of non-native species (B), Shannon diversity (C), functional diversity (D), phylogenetic diversity (E), and the mean naturalness values (F) of the four habitat types. Different letters indicate significant differences ($p < 0.05$). NN: near-natural poplar forests. PA: plantations of native *Populus alba*; PN: plantations of non-native *Pinus nigra*; RP: plantations of non-native *Robinia pseudoacacia*.

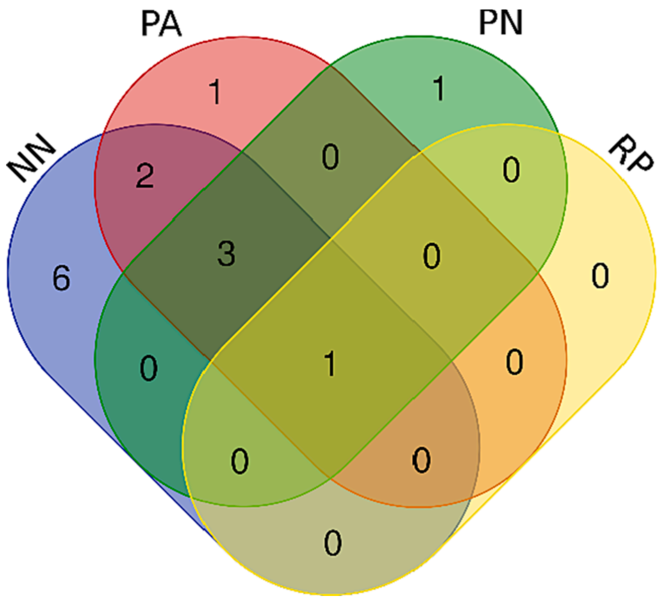

Fig. 4. Venn diagram of species with high conservation importance (protected, endemic, and/or red-listed species) according to their habitat. NN: near-natural poplar forests. PA: plantations of native *Populus alba*; PN: plantations of non-native *Pinus nigra*; RP: plantations of non-native *Robinia pseudoacacia*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

compositional differences between the near-natural forests (without forestry activity) and the tree plantations (Rédei et al., 2020; Tölgyesi et al., 2020). Second, the different dominant species alter their environment differently, which may result in compositional differences. For example, *Pinus* plantations tend to have a deep layer of slowly decaying leaf litter, and lower soil pH than near-natural forests or deciduous plantations (Kováč et al., 2005; Cakir and Makineci, 2013; Mikulová et al., 2019), while *Robinia* plantations significantly increase the *N*-content of the soil (Šibíková et al., 2019; Tölgyesi et al., 2020).

We found that all habitats had some diagnostic species that were significantly concentrated within them while being rare or absent in the other habitats (Table 2). Near-natural forests had the highest number of diagnostic species. Similarly, in the Carpathian Mts and the Carpathian Basin, Slabejová et al. (2019) found that oak-hornbeam forests hosted more diagnostic species than adjacent black locust plantations. Among the diagnostic species of the near-natural forests, there were many shrubs, which shows the negative effects of intensive forestry activities (shrub removal during the initial five years) in tree plantations.

Interestingly, *Robinia pseudoacacia* plantations contained several diagnostic species related to open grasslands. This may be due to the fact that the starting time of leaf expansion of *Robinia pseudoacacia* is typically late, usually from the end of April to early May (Cierjacks et al., 2013; Tölgyesi et al., 2020), probably resulting in light, temperature, and humidity levels comparable to those of grasslands during the spring months. Those species of open grasslands that complete their whole life cycle during spring (e.g., *Lamium amplexicaule*, *Thlaspi perfoliatum*, and *Viola arvensis*) are able to survive in *Robinia* plantations but not in other plantations or near-natural forests. Many of the diagnostic species of *Robinia* plantations were weeds with high *N*-requirements (e.g., *Anthriscus cerefolium*, *Ballota nigra*, and *Galium aparine*), which is probably connected to the *N*-fixing capacity of *Robinia*. Similarly, *Robinia* plantations typically contain many nitrofrequent species throughout Central Europe (Vítková et al., 2017).

Although the number of real forest specialist plant species is relatively low almost everywhere in the Kiskunság Sand Ridge (e.g., Erdős et al., 2013), the diagnostic species of the near-natural poplar forests nevertheless tend to show a higher level of specialization than the three plantation types. For example, *Polygonatum odoratum* and *Thymus pannonicus* are to some degree specialized to xeric forests and dry grasslands, respectively. In contrast, the diagnostic species of the plantations have much wider ecological tolerances.

The compositional differences among the near-natural forests and the three types of tree plantations may have major consequences on ecological functions and ecosystem services. For example, the native shrubs that are significantly related to near-natural forests provide habitat, hiding or nesting place, and food source for several animals from arthropods to birds and mammals, while the same functions and services are compromised in tree plantations due to the rarity of these shrub species. Several non-native plant species have been shown to be significantly related to plantations (especially those of *Populus alba*). These likely have fewer relationships with the native flora and fauna, as they are newcomers with a very short history in the region (e.g., *Ambrosia artemisiifolia* and *Asclepias syriaca*). Consequently, these species may have a disproportionately low contribution to the ecological functions and ecosystem services of their habitat.

4.2. Diversity patterns

In our study, near-natural forests had the highest total (i.e. pooled) species number and the highest per plot number of native species (Fig. 3A). The global analysis of Bremer and Farley (2010) showed that plantations usually decrease plant species richness if they replace primary forests, but often increase species richness if they replace secondary forests. However, it has to be emphasized here that tree plantations usually contain mostly generalist species (i.e., species with wide habitat preferences), while they are very poor in specialist species (e.g., Michelsen et al., 1996; Habel et al., 2018; Rédei et al., 2020). Bremer and Farley (2010) regarded forest stands older than 200 years as primary forest. The near-natural forests of our study fit this definition, as most of them are spontaneous stands probably originating from the early 19th century. Today they have a structure that is assumed to resemble that of primary forests (Erdős et al., 2015). Similarly, Rédei et al. (2020) reported that species richness was higher in near-natural oak and poplar forests than in plantations. Among the three studied plantation types, plantations of the native *Populus alba* had the highest richness of native plant species, which is in good accordance with the findings of Bremer and Farley (2010). Near-natural forests in the region usually show a relatively high level of heterogeneity even at fine spatial scale, which probably entails a higher number of micro-habitats and niches for specialized plants, resulting in higher taxonomic diversity. In contrast, plantations usually seem to be more homogeneous, thus offering a limited number of micro-habitats and niches, and resulting in lower taxonomic diversity.

The lower richness of non-native species of near-natural forests in our study (Fig. 3B) is in line with other studies from Eastern Central Europe (Medvecká et al., 2018; Slabejová et al., 2019; Rédei et al., 2020) as well as with patterns in other regions (Bremer and Farley, 2010). *Populus alba* plantations contained significantly more non-native species than any other habitat type included in our study, lending credence to the biotic acceptance theory (Stohlgren et al., 1999, 2006; Belote et al., 2008), which suggests that high native species richness within a post-disturbance habitat will also promote high non-native species richness.

Compared to the richness of native and non-native species, Shannon diversity showed a slightly different pattern (Fig. 3C). Although *Pinus nigra* plantations had the lowest per plot species richness, their Shannon diversity was relatively high and did not differ from that of near-natural forests and *Populus alba* plantations. One possible explanation is that the few species that occur in *Pinus* plantations reach very low cover values, resulting in high species evenness, which in turn leads to high Shannon diversity. In contrast, Shannon diversity was the lowest in *Robinia pseudoacacia* plantations, probably because the high *N*-content of the soil allows a few nitrofrequent herb species (e.g. *Bromus sterilis* and *Anthriscus cerefolium*) to become dominant.

The low plant species richness of *Pinus* and *Robinia* plantations (accompanied by the dominance of a few plant species in *Robinia* plantations) may have serious consequences for other taxa. For example, these plantations may provide a limited pollen and nectar source for insects, compared to near-natural forests. Similarly, plantations may offer limited food source for herbivores and seed predators.

Our results showed that the functional diversity of near-natural forest did not differ from that of *Populus alba* and *Pinus nigra* plantations, while the functional diversity of *Robinia pseudoacacia* plantations was the lowest (Fig. 3D). Some earlier studies showed that near-natural forests and plantations had similar functional diversities. For example, in Brazil, the functional diversity of native *Araucaria* forests was similar to that of *Araucaria* and *Pinus* plantations (Malysz et al., 2019). Another study in the Solomon Islands found no differences in functional diversity between primary forests, secondary forests, and abandoned monoculture tree plantations (Katovai et al., 2012). Examining ecosystem functions of various habitats across a heterogeneous landscape in Kenya, Habel and Ulrich (2020) found no significant differences between natural forests and non-native plantations. In our case, the number of native species increased along the sequence *Pinus* plantation – *Populus* plantation – near-natural forest (Fig. 3A), while functional diversity remained the same (Fig. 3D). This suggests high functional redundancy in near-natural forests, which is thought to result in greater ecosystem stability and resilience (Biggs et al., 2020).

We found that near-natural forests had the highest and *Robinia pseudoacacia* plantations the lowest phylogenetic diversity (Fig. 3E). Some earlier studies have also indicated that monoculture tree plantations have substantially lower phylogenetic diversity than near-natural and natural forests (Eastern Europe: Piwczyński et al., 2016, South America: Athayde et al., 2015, Asia: Qin et al., 2017; Kusuma et al., 2018). In our study, *Pinus nigra* plantations had the highest phylogenetic diversity among the plantations and although they tended to have lower phylogenetic diversity than near-natural forests, the difference was not significant. This is in good agreement with the study of Piwczyński et al. (2016), who observed that the understory plant communities in natural oak forests had similar phylogenetic diversity to *Pinus sylvestris* plantations.

Low species richness of plantations was usually accompanied by low phylogenetic and functional diversities for several animal taxa, including birds (Almeida et al., 2016; Jacoboski et al., 2016; Pedley et al., 2019), ants (Liu et al., 2016; Martello., 2018), and spiders (Potapov et al., 2020; Junggebauer et al., 2021). Our study, however, indicates that lower plant species richness in plantations does not necessarily entail low functional or phylogenetic diversity, lending support to the view that species richness is not necessarily informative of functional or phylogenetic diversity (e.g., Díaz and Cabido, 2001; Bernard-Verdier et al., 2013; Purschke et al., 2013).

4.3. Ecological value of the studied habitats

The fact that plantations had significantly lower naturalness status than near-natural forests (Fig. 3F) indicates that the establishment and management of plantations result in serious ecosystem degradation, especially in the case of *Robinia* plantations. This finding supports the conceptual model of Brockerhoff et al. (2008), which predicts that the conservation value of forests decreases with increasing management intensity. While plantations may provide some economic benefits, they are clearly undesirable from an ecological point of view.

Our study found that near-natural forests harbored more protected, endemic, and red-listed species than plantations (Fig. 4). This is in good accordance with earlier observations (Cotter et al., 2017; Šibíková et al., 2019; Singh et al., 2021). An important finding is that plantations of the native *Populus alba* had a better capacity to support protected, endemic, and red-listed species than plantations of non-native species. *Robinia* plantations proved to be especially poor in species of high conservation value. This is in line with the results of Deák et al. (2016), who found that most specialist species of high conservation importance could not survive under *Robinia* plantations. The probable reason is that the increased *N*-availability of the soils of *Robinia* plantations favors weedy species of high competitive ability, while it tends to negatively affect more valuable specialist species (Deák et al., 2016).

4.4. *Implications for conservation and forestry*

Our study clearly showed that, from an ecological and conservation perspective, near-natural forests are more valuable than any of the studied plantations: near-natural forests had the highest richness of native species and the lowest richness of non-natives, possessed high Shannon diversity as well as high functional and phylogenetic diversity (Table 3). In addition, they were the least degraded and contained the most species with special conservation importance. Unfortunately, the few remaining near-natural poplar forest stands are severely fragmented in the study region (Molnár et al., 2012; Biró et al., 2018). While most of them are legally protected, their integrity is challenged by the spread of invasive species, including *Robinia pseudoacacia*, *Celtis occidentalis*, and *Padus serotina* (Molnár et al., 2008). Ensuring legal protection for the few stands outside nature reserves is an urgent task. Also, efforts should be made to restore poplar forests on abandoned lands. This would have positive effects beyond the near-natural stands themselves. For example, ecosystem functions may spill over from near-natural forests into nearby agricultural fields or tree plantations (Seifert et al., 2022), enhancing the value of ecosystem functions at the landscape scale.

Among the studied plantations, *Populus alba* plantations proved to be the best option in most respects, although they contained a high number of non-native species (Table 3). Therefore, we conclude that currently, *Populus alba* plantations are the best option among tree plantations. This is in line with earlier studies emphasizing that plantations of native tree species are more valuable from an ecological perspective than those of non-native species (Bremer and Farley, 2010; Dickie et al., 2014; Bazalová et al., 2018).

In our study, *Robinia* plantations performed poorly in almost all respects: they had low native species number, Shannon diversity, functional and phylogenetic diversity, and naturalness value. Although this species has a long history in the region (Vítková et al., 2017), *Robinia* plantations are ecologically undesirable.

Some other studies performed in the region also found that monoculture tree plantations are ecologically weak substitutes for near-natural forests (Table 3). Ónodi et al. (2022) reported that the diversity of bird species was significantly lower in plantations than in near-natural forests. According to Rédei et al. (2020), the number of forest specialist species is significantly lower in plantations than in near-natural forests. Also, plantations have serious negative effects on certain ecosystem properties. For example, Tölgyesi et al. (2020) showed that the humus content of the topsoil was higher in near-natural poplar forests than in *Pinus* or *Robinia* plantations, probably due to the soil disturbance during forestry activities. *Pinus* plantations proved especially harmful to the local and regional water balance, as they desiccated both the lower soil layers and the topsoil, probably as a combined effect of the high precipitation interception of their canopy, the fine root system near the soil surface, and the transpiration during winter (Tölgyesi et al., 2020). In addition, *Pinus nigra* is highly flammable and is therefore associated with serious fire risk (Cseresnyés et al., 2011). This means that the carbon sequestration capacity of *Pinus* plantations is uncertain at best (Erdős et al., 2022b). The increasing severity of drought periods and the rise in temperature predicted for Hungary (Bartholy and Gelybó, 2007; Blanka et al., 2013) is expected to result in a further increase of fire risk associated with *Pinus* plantations. This, in addition to the economic loss, threatens ecosystems and human lives alike.

Table 3
Ecological characteristics of near-natural *Populus alba* forests (NN), plantations of the native *Populus alba* (PA), plantations of the non-native evergreen *Pinus nigra* (PN), and plantations of the non-native deciduous *Robinia pseudoacacia* (RP). Plus signs indicate the ecologically most beneficial, minus signs the least beneficial habitats, while plus/minus signs mean that the effects are intermediate.

	NN	PA	PN	RP	Source
Native species richness	+	+/-	–	–	This study
Non-native species richness	+	–	+/-	+/-	This study
Shannon diversity	+	+	+	–	This study
Functional diversity	+	+	+	–	This study
Phylogenetic diversity	+	+/-	+/-	–	This study
Naturalness	+	+/-	+/-	–	This study
Species with high conservation importance	+	+/-	+/-	–	This study
Richness of forest specialist plants	+	–	–	–	Rédei et al. (2020)
Bird diversity	+(1)	+/-	+/-	+/-	Ónodi et al. (2022)
Soil humus content	+		–	–	Tölgyesi et al. (2020)
Local and regional water balance	+		–	+	Tölgyesi et al. (2022)
Fire risk			–		Cseresnyés et al. (2011)

(1) Mixed oak-poplar forests.

Currently, ca. 35 % (277,662 ha) of the Kiskunság Sand Ridge is covered by forests and tree plantations. Of the forests and plantations, 31 % (86,575 ha) are *Robinia* plantations, ca. 20 % (55,039 ha) are *Pinus* plantations, while only ca. 6 % (17,277 ha) are near-natural *Populus alba* forests (based on the Ecosystem Map of Hungary and the results of a national forest condition assessment using the National Forestry Database, where near-natural forests were more broadly defined than in our current study and included some species-rich plantations; Tanács et al., 2021, 2022). The ecological characteristics discussed above show that the present state of the Kiskunság sand ridge is clearly unsustainable. Thus, we strongly recommend that the remaining unmanaged near-natural poplar stands should be protected and stands should be restored. *Populus alba* should be preferred to non-native tree species whenever the establishment of plantations is unavoidable because of economic or legal reasons. These plantations could serve as buffers around near-natural stands, and as green corridors among protected areas (Brockerhoff et al., 2008). Less intensive forestry, mimicking natural processes, could even increase the ecological value of these plantations while maintaining their commercial value. In addition, some *Populus alba* plantations could be set aside as it is reasonable to assume that, in the long run, their ecological value will increase. Also, selective thinning (rather than clear-cutting) would be beneficial in *Populus alba* plantations, as it would retain a continuous forest with low canopy cover (resembling the naturally low canopy cover of the near-natural forests).

The study region is located within the forest-steppe zone, where forest patches form a mosaic with grasslands (Erdős et al., 2022b). Due to the semi-arid climate and the low water retention capacity of the sandy soils, the creation of plantations in the region is usually only partly successful, as young tree individuals often fail to establish. We suggest that these treeless patches should be set aside without further attempts to plant trees. The resulting openings would mirror the natural vegetation mosaic of the region, potentially allowing the development of near-natural grassland patches. We think that a gradual decrease of the area covered by *Pinus* and *Robinia* plantations is unavoidable on the long run if we are to maintain the ecological integrity of the region.

CRediT authorship contribution statement

Khanh Vu Ho: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **György Kröel-Dulay:** Resources, Writing – review & editing, Funding acquisition. **Csaba Tölgyesi:** Investigation, Writing – review & editing. **Zoltán Bátori:** Investigation, Writing –

review & editing. **Eszter Tanács:** Investigation, Formal analysis, Writing – review & editing. **Miklós Kertész:** Investigation, Writing – review & editing. **Péter Török:** Funding acquisition, Writing – review & editing. **László Erdős:** Conceptualization, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120789.

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Appendix

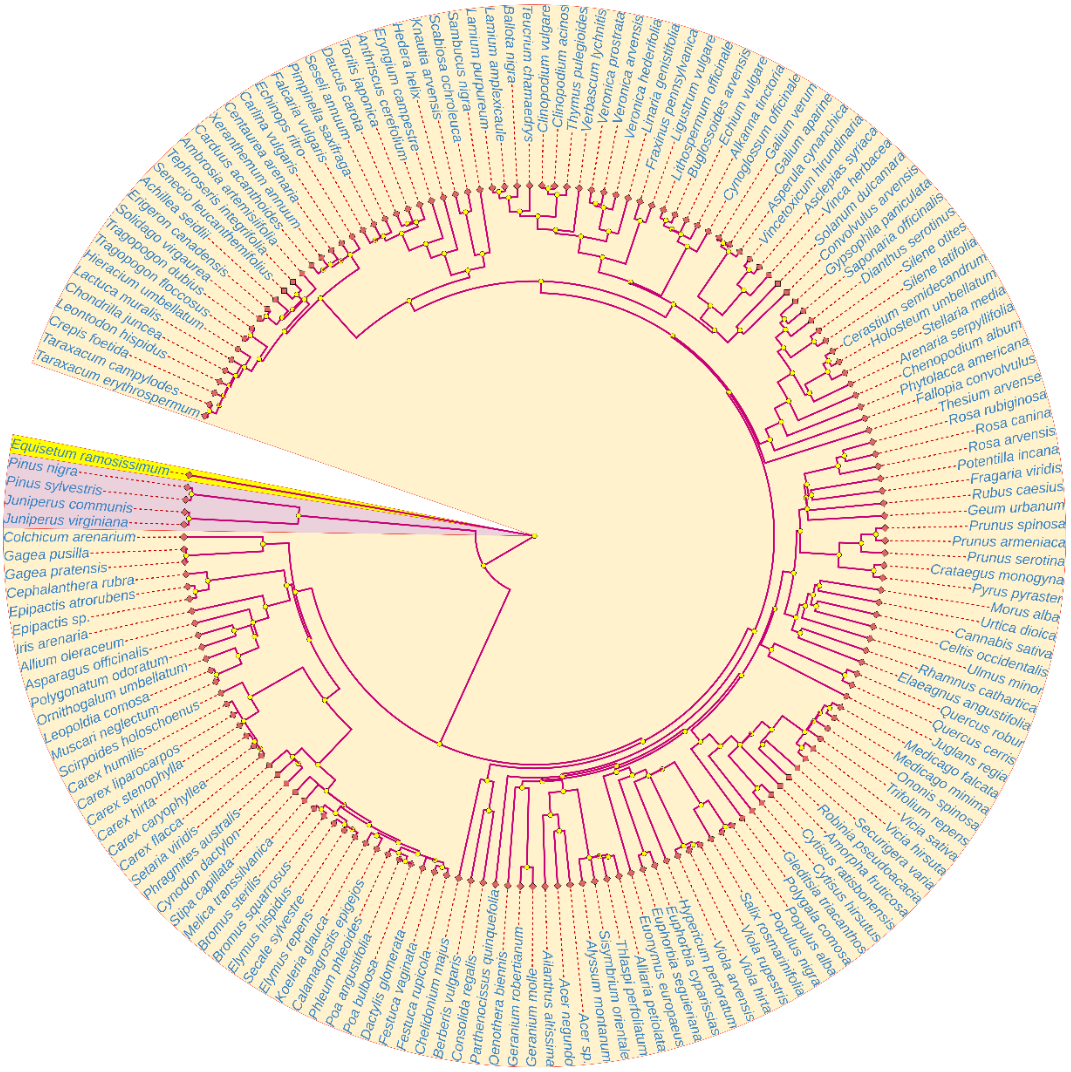

Figure S1. Phylogenetic tree containing 173 species. The yellow zone includes one pteridophyte species, the purple zone includes four gymnosperms species, while the remaining species are angiosperms.

Table S1. The distribution of plots across habitats and sites. Habitat type abbreviations are according to the caption of Figure 2.

Study sites	Number of plots			
	NN	PA	PN	RP
Ásotthalom	5	5	5	5
Bócsa	5	5	5	5
Bodoglár	5	5	5	5
Fülöpháza	5	5	5	5
Imrehegy	5	5	5	5
Négyestelep	5	5	5	5
Orgovány	5	5	-	5
Pirtó	5	5	5	5
Tázlár	5	5	5	5

Table S2. Data on the cover value of the canopy, shrub, and herb layers, as well as species richness (mean ± standard error). NN: near-natural poplar forests (n=45); PA: plantations of native *Populus alba* (n=45)*; PN:* plantations of non-native *Pinus nigra* (n=40); *and RP:* plantations of non-native *Robinia pseudoacacia* (n=45).

Habitat	Mean canopy cover (%)	Mean shrub cover (%)	Mean herb cover (%)	Mean species richness⁽¹⁾
NN	48.1±2.47	53.9±3.14	30.8±3.51	20.5±1.11
PA	58.3±0.82	5.31±1.23	39.0±3.93	20.6±0.48
PN	57.4±0.80	0.83±0.51	8.08±2.54	13.5±0.84
RP	67.7±1.08	1.76±0.39	93.5±4.41	15.9±0.61

(1) Only species in the shrub and herb layers were calculated.

Table S3: Statistical results of the pairwise comparisons of species composition. NN: near-natural poplar forests. PA: plantations of native *Populus alba; PN:* plantations of non-native *Pinus nigra; RP:* plantations of non-native *Robinia pseudoacacia.* p-values were adjusted by the Bonferroni method

Pair	F model	R^2	p
NN-PA	22.5	0.203	0.006
NN-PN	24.8	0.230	0.006
NN-RP	64.4	0.422	0.006
PA-PN	11.5	0.122	0.006
PA-RP	40.5	0.315	0.006
PN-RP	36.6	0.306	0.006

Table S4: Statistical results of the pairwise comparisons of native species number, non-native species number, Shannon diversity, functional diversity, phylogenetic diversity and naturalness value. NN: near-natural poplar forests. PA: plantations of native *Populus alba; PN:* plantations of non-native *Pinus nigra; RP:* plantations of non-native *Robinia pseudoacacia.* p-values were adjusted by the Bonferroni method.

Pair	Native species number		Non-native species number		Shannon diversity	
	t	p	t	p	t	p
NN-PA	2.80	0.034	-6.27	<0.001	1.13	1.000
NN-PN	9.13	<0.001	-2.28	0.142	0.36	1.000
NN-RP	7.11	<0.001	-3.66	0.002	-5.14	<0.001
PA-PN	6.59	<0.001	3.96	<0.001	-0.72	1.000
PA-RP	4.36	<0.001	2.81	0.034	-6.23	<0.001
PN-RP	-2.48	0.084	-1.31	1.000	-5.32	<0.001

Pair	Functional diversity		Phylogenetic diversity		Naturalness value	
	t	p	t	p	t	p
NN-PA	-1.12	1.000	-3.11	0.013	10.3	<0.001
NN-PN	0.54	1.000	-1.25	1.000	8.42	<0.001
NN-RP	-4.51	<0.001	-6.36	<0.001	13.9	<0.001
PA-PN	1.61	0.653	1.67	0.580	-1.55	0.738
PA-RP	-3.42	0.005	-3.37	0.006	3.53	0.003
PN-RP	-4.88	<0.001	-4.85	<0.001	4.95	<0.001

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ORIGINAL PAPER

Oak regeneration at the arid boundary of the temperate deciduous forest biome: insights from a seeding and watering experiment

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Abstract

Previous studies found that pedunculate oak, one of the most widespread and abundant species in European deciduous forests, regenerates in open habitats and forest edges, but not in closed forest interiors. However, these observations usually come from the core areas of the biome, and much less is known about such processes at its arid boundary, where limiting factors may be different. In a full factorial field experiment, we tested the effects of different habitats (grassland, forest edge, forest interior) and increased growing season precipitation on the early regeneration of pedunculate oak in a forest-steppe ecosystem in Central Hungary, at the arid boundary of temperate deciduous forests. In the grassland habitat, seedling emergence was very low, and no seedlings survived by the fourth year. In contrast, seedling emergence was high and similar at forest edges and forest interiors, and was not affected by water addition. Most seedlings survived until the fourth year, with no difference between forest edge and forest interior habitats in numbers, and only minor or transient differences in size. The lack of oak regeneration in the grassland differs from previous reports on successful oak regeneration in open habitats, and may be related to a shift from light limitation to other limiting factors, such as moisture or microclimatic extremes, when moving away from the core of the deciduous forest biome towards its arid boundary. The similar number and performance of seedlings in forest edges and forest interiors may also be related to the decreasing importance of light limitation.

Keywords Pedunculate oak · Quercus robur · Forest-steppe · Seedling emergence · Temperate deciduous forest

Introduction

Temperate deciduous forests characterised by various oak, hornbeam, linden, maple, ash, and beech species cover vast areas in Europe (Schultz 2005). They harbour high species richness at the local scale show high net primary production, and possess considerable carbon sequestration capacity (Pfadenhauer and Klötzli 2014). Though the composition, structure, and abiotic parameters of these forests are well studied (Pfadenhauer and Klötzli 2014), considerable debates regarding their dynamics still exist (e.g., Vera 2000; Svenning 2002; Szabó 2009; Gillian 2016). Uncertainties about the dynamics and especially the natural regeneration of temperate deciduous forests are at least partly due to the fact that most of these forests have been heavily modified by human use during the last couple of millennia, severely compromising natural processes (Ellenberg 1988; Walter and Breckle 1989; Schultz 2005; Kirby and Watkins 2015; Gillian 2016).

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Pedunculate oak (*Quercus robur*) is one of the most important tree species in European temperate deciduous forests, dominating lowland forests in a huge belt from Britain to the Ural Mts (Walter and Breckle 1989; Bohn et al. 2004). However, it has been recognised that the natural regeneration of this species is frequently deficient (Shaw Shaw 1968a, b; Reif and Gärtner 2007; Annighöfer et al. 2015). It is well-known that pedunculate oak is a light-demanding species (Annighöfer et al. 2015; Leuschner and Ellenberg 2018). Therefore, its regeneration depends on open or semi-open sites with relatively high light availability, such as forest edges, hedges, shelterwoods, openings, and grasslands, and it is not successful in forest interiors (Reif and Gärtner 2007; Leuschner and Ellenberg 2018; reviewed by Bobiec et al. 2018).

Besides light availability, other key factors influencing the regeneration of pedunculate oak include water supply, competition from ground vegetation, zoochory, grazing and browsing (Vander Wall 2001; Annighöfer et al. 2015, Schäfer et al. 2019). Water supply is a critical factor during oak germination and seedling development (Dreyer et al. 1991, Bobiec et al. 2018). While water scarcity is relatively rare in Western Europe and in partially shaded habitats, its effect may be much more important in drier regions and in open habitats (Löf et al. 1998; Reif and Gärtner 2007). Competition heavily influences the survival of seedlings (Jensen and Löf 2017), but it may be reduced in sites where the herb layer is sparse or where ungulates open up the dense sward (Reif and Gärtner 2007). Grazing and browsing can affect seedling survival and performance negatively, but the nutrient reserves of the cotyledon enable oak seedlings to withstand a certain level of defoliation (Frost and Rydin 1997), while thorny shrubs and the high abundance of other, more palatable species can protect oak seedlings from grazing and browsing (Bakker et al. 2004; Jensen et al. 2012). To sum it up, an area ideal for pedunculate oak regeneration has been described as providing sufficient moisture and consisting of a mosaic of forests, thickets, shrubs, solitary trees, grasslands, and the ecotones between these habitats (Vera 2000; Bakker et al. 2004; Bobiec et al. 2018).

Biome boundaries are regions where several species reach their distributional limits, and there is a major shift in the physiognomy of the vegetation (Walter 1985; Gosz and Sharpe 1989, Neilson 1993; Peters et al. 2006, Pinto-Ledezma et al. 2018). In these transitional zones, patches from both adjoining biomes form a mosaic pattern. Constraints operating in the transitional zones are typically different from those operating within the core areas of the biomes (Gosz and Sharpe 1989; Risser 1995). In addition, species that are dominant in the core area of the biome may become limited to specific habitats (with special microclimates) towards the biome boundary (Gosz 1992, 1993; Neilson 1993). Environmental changes, including climate change, are likely to substantially affect biome boundaries (Gosz and Sharpe 1989; Allen and Breshears 1998, Frelich and Reich 2010). Germination and establishment may be critically affected, resulting in altered dynamic processes in biome boundaries (Gosz 1992; Risser 1995; Erdős et al. 2018a).

The forest-steppe zone is at the arid boundary of the temperate deciduous forest biome: as, largely due to climatic constraints, closed-canopy forests open up and gradually give way to grasslands, a mosaic of woody and herbaceous habitats emerges (Wesche et al. 2016; Erdős et al. 2018a). Pedunculate oak is a major constituent not only in the deciduous forest biome of Europe, but also in these mosaic ecosystems (Molnár et al. 2012; Erdős et al. 2018a). While the regeneration of pedunculate oak has been intensively studied within the core areas of the deciduous forest biome, oak regeneration patterns at the arid boundary of the biome are mostly unstudied (Bobiec et al. 2018).

In this study, our objective was to understand the effects of different habitats (forest interior, forest edge, and grassland) and watering on oak germination and early seedling performance. The experimental area lies at the arid boundary of the deciduous forest biome, where growing season precipitation strongly constrains woody vegetation, therefore, we expected that the natural regeneration of oak heavily depends on the amount of precipitation. Accordingly, our hypothesis was that oak seedling emergence and growth would be positively affected by water addition, especially in grasslands, where evapotranspiration and thus water limitation is highest. Furthermore, in line with previous studies, we also hypothesised that seedling emergence and performance would be high in grasslands (only when watered) and in forest edges, but lower and declining through time in forest interiors, because of light limitation.

Materials and methods

Study area

The Kiskunság Sand Ridge in Central Hungary lies at the arid boundary of the temperate deciduous forest biome. The area is the most arid part of the Carpathian Basin, with a mean annual temperature of 10.5 °C (17.4 °C in the growing season from April to September), and a mean annual precipitation of 530 mm (310 mm in the growing season) (Dövényi 2010). The area is characterised by stabilised calcareous sand dunes, with humus-poor sandy soils (Várallyay 1993). Due to a combination of semiarid climate and coarse-textured sandy soil, forests open up and the potential vegetation is forest-steppe, with both forests and grasslands being natural and permanent elements of the landscape, and forming a mosaic (Erdős et al. 2018a).

Pedunculate oak, a characteristic species of the temperate deciduous forests, is also present in this forest-steppe mosaic (Rédei et al. 2020), although its abundance is highly variable and is strongly affected by land use in the past centuries (Biró et al 2013, Erdős et al. 2015). The study area is located near Fülöpháza, Central Hungary; N 46°52', E 19°25') (Fig. 1a), where pedunculate oak is currently relatively rare, most likely due to previous land use, but the species is a typical component in several forest-steppe areas in the region.

The forest component of the vegetation mosaic at the study area is represented by the juniper-poplar forest *Junipero-Populetum albae*. The canopy layer is formed mainly by 12–15 m tall *Populus alba* individuals. For trees with DBH over 5 cm, stand density is 1450 trees/ha (Erdős et al. 2018b). The shrub layer is dominated by *Juniperus communis* and *Crataegus monogyna*. The most frequent species of the herb layer are *Asparagus officinalis*, *Carex flacca*, *C. liparicarpos*, *Poa angustifolia*, and the seedlings of trees and shrubs.

Among the various grassland communities of the study area, the open perennial sand grassland *Festucetum vaginatae* is the most widespread. Its dominant species are *Festuca vaginata*, *Stipa borysthenica*, and *S. capillata*, while *Alkanna tinctoria*, *Dianthus serotinus*, *Euphorbia seguieriana*, *Fumana procumbens*, and *Poa bulbosa* are also common.

The contact zones of the forest patches and the grasslands host specific edge communities with various shrubs (e.g. *Berberis vulgaris*, *Crataegus monogyna*, *Juniperus communis*) and a high density of *Populus alba* saplings. The most frequent and abundant species of the herb layer include *Calamagrostis epigeios*, *Festuca rupicola*, *Pimpinella saxifraga*, and *Taraxacum laevigatum*.

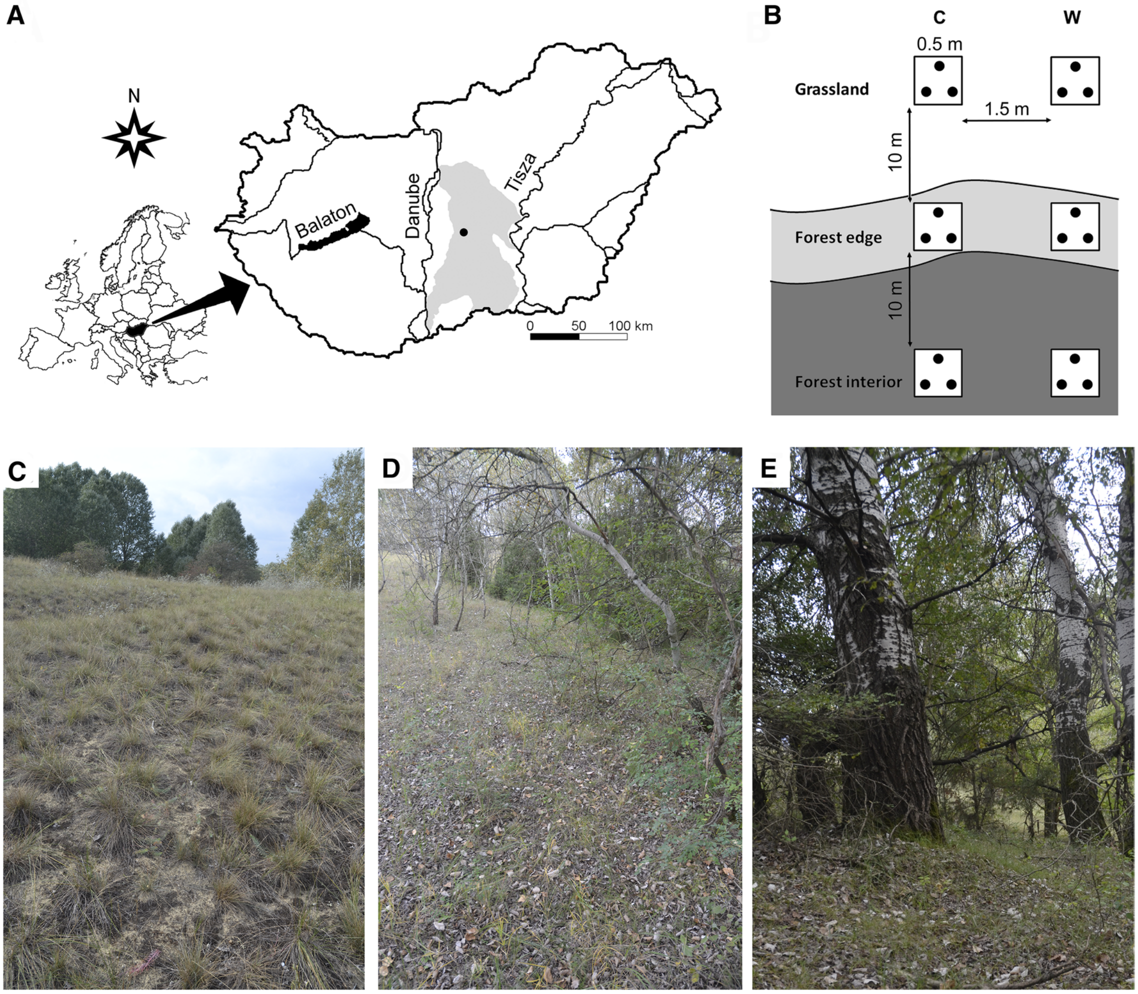


Fig. 1 The position of the study area (black dot) in the Kiskunság Sand Ridge (grey shading) (**a**), the experimental design with oak acorns (black dots) in the 0.5 m×0.5 m plots in the three habitats under study (C: control plots, W: watered plots) (**b**), the grassland habitat (**c**), the forest edge habitat (**d**), and the forest interior habitat (**e**)

The study area belongs to the Kiskunság National Park; it is strictly protected, and every major human activity except research and controlled tourism has been banned since 1975. The browsing pressure by native ungulates (mostly roe deer) is relatively low, but no particular study assessed this issue in the region. The study area is part of the KISKUN Long-term Ecological Research platform (KISKUN LTER, https://deims.org/124f227a-787d-4378-bc29-aa94f29e1732).

The plant species names follow Király (2009), while the plant community names are used according to Borhidi et al. (2012).

Experimental design

Quercus robur acorns were collected in October 2015 from a nearby patch of seed producing oaks. To exclude acorns with reduced viability, we carried out visual inspection and a float test. The float test is reliable in identifying aborted, diseased, insect-infested or otherwise damaged acorns (Gribko and Jones 1995).

Sixteen sites were selected within a ca. 400 m × 1100 m area in a natural forest-grassland mosaic. For each site, three habitats were defined: forest interior (within the forest patch, 10 m from the forest edge), forest edge (the zone outside of the outermost tree trunks but still under the canopy, on the northern side of forest patches), and grassland (a neighbouring treeless area, 10 m from the edge). At each habitat, two 0.5 m × 0.5 m plots were designated in a row parallel to the forest edge. Within both plots, three acorns were planted at a depth of 2 cm in November 2015 (Fig. 1b-e). A total of 288 acorns was used in the experiment (16 sites × 3 habitats × 2 plots × 3 acorns).

At each site and habitat, we applied two precipitation treatments in the two plots: one plot received ambient precipitation (control), while the other plot received additional watering ten times between 5 April and 6 September in their first year (2016). Watering was started in April, because temperature is low until March (ca. 6 °C mean temperature in March) and no water limitation occurs during wintertime. For watering, we used rainwater collected nearby, and the amount added corresponded to 15 mm precipitation each time, resulting in a total of 150 mm watering during the year. The additional watering was 36.5% of the natural precipitation in the growing season and 20.2% of the yearly precipitation in 2016.

Seedlings were individually censused every two or 3 weeks in the first year. The performance of the seedlings was measured near the end of the growing season of the first and the fourth years (19 September 2016 and 25 September 2019, respectively), by registering the following parameters for each plot: (1) the number of living seedlings, (2) the number of leaves per living seedling, and (3) the height of the living seedlings.

During the growing season of 2016, we measured the volumetric soil moisture content of the upper 20 cm every 2 or 3 weeks from 5 April till 6 September, using FieldScout TDR300 Soil Moisture Meter (Spectrum Technologies Inc). Since soil texture is very similar across the different vegetation types in the study area including grasslands and woodlands (Kröel-Dulay et al. 2019), soil water content is a good measure of soil water availability for plants in the different habitats. We measured soil water content before watering at each site and 5 h after watering in three a priori chosen sites. These two measurements aimed at assessing the longer (ca. 2-week-long) and the short-term (right after watering) effects of watering on the soil moisture content. For each 0.5 m × 0.5 m plot, three measurements were done and then averaged. Means for the whole growing season were calculated for each plot.

The Leaf Area Index (LAI) of the woody canopy was estimated above the herbaceous layer (25 cm) using a LAI 2000 Plant Canopy Analyser instrument (LI-COR, Inc., Lincoln, Nebraska). The measurements were conducted in each plot at peak canopy coverage, 30 July 2016, under clear weather conditions. The total cover of the herb layer (percentage of the 0.5 m × 0.5 m plot) was estimated visually on 19 September 2016.

Statistical analyses

All statistical analyses were carried out using the R environment version 3.4.3. (R Core Team 2017). We compared the abiotic conditions of the treated and untreated plots in the three habitat types by using linear mixed-effects (LME) models (nlme package; Pinheiro et al. 2017). We built individual models for soil moisture content before and after watering, LAI, and total herb cover. In the models, habitat type and treatment, and their interaction were used as fixed effects, while site was used as a random effect. As the soil water was measured at only three sites after watering, we analysed the short-term effect of watering by using a linear model where habitat type, watering, and site were all used as fixed effects.

A generalised mixed-effects model (GLMM) with binomial distribution was applied to assess seedling numbers. In these models, the germination success or failure of each acorn was treated as a binary response variable, while habitat type and watering were used as fixed variables, and site as a random variable. Individual models were built for each time. As no seedling survived in the grassland till the fourth year, we did not consider the effect of this habitat type in the respective model.

The effect of habitat type and watering treatment on the leaf number and height of the oak seedlings in both 2016 and 2019 were assessed by applying LME models. In these models, we did not consider the grassland habitat type, as too few seedlings survived in the grassland plots (only 4 individuals by the end of 2016 and none till 2019). Leaf numbers and height data were square-root transformed to meet the homogeneity and normality assumptions of the tests.

We made visual assessments of the residual diagnostic plots to check the assumptions of the tests. For post hoc pairwise comparisons, we performed Tukey tests using the multcomp package (Hothorn et al. 2016).

Results

Inherent differences among the studied habitats

The cover of the herb layer was similar in the grassland and the forest edge habitats, while it was much lower in the forest interior habitat (Table 1, Fig. 2a). Note that the cover of the herb layer was relatively low (below 50%) even in the grassland and the forest edge habitats. The LAI of the overstorey vegetation showed marked differences among the habitats, with the lowest value in grasslands, intermediate values at the forest edges, and the highest values in the forest interiors (Fig. 2b). Average growing season soil moisture content was the lowest in grasslands, while it was higher and similar at the forest edge and the forest interior habitats (Fig. 2c, d; control plots).

Table 1 Linear mixed-effects and linear model results of the effects of habitat type, watering on the total cover of the herb layer, soil moisture content before and 5 h after watering, and leaf area index (LAI)

Variables and effects	*df*	*F*	*P*
Total herb cover			
Habitat type	2	16.9	**0.000**
Watering	1	0.9	0.350
Habitat type × watering	2	0.1	0.891
LAI			
Habitat type	2	318.7	**0.000**
Watering	1	1.0	0.344
Habitat type × watering	2	0.2	0.844
Soil moisture content right after watering			
Habitat type	2	66.2	**0.000**
Watering	1	315.1	**0.000**
Site	2	0.3	0.774
Habitat type × watering	2	14.4	**0.001**
Soil moisture content ca. 2 weeks after watering			
Habitat type	2	86.2	**0.000**
Watering	1	12.1	**0.000**
Habitat type × watering	2	2.6	0.080

P values are rounded to three digits

($P<0.05$) values are shown in bold

Effect of watering treatment on soil moisture content

Watering substantially increased soil moisture content in all the three habitats right after watering (Fig. 2c), and some of this effect remained even ca. 2 weeks after watering (before the next watering), although post hoc tests showed that this was only significant in the forest interior habitats (Fig. 2d).

Seedling emergence and survival

Seedling emergence rate was very low in grassland habitats (on average 0.3 acorns germinated out of 3), but was high (on average 2.5 out of 3) and similar in forest edges and forest interiors (Table 2, Fig. 3a). Water addition did not affect the emergence rate (Table 2, Fig. 3a). Even the few seedlings that emerged in grasslands died by the fourth year, September 2019 (Fig. 3c). Seedling number remained high (on average 2) in forest edge and forest interior habitats until September 2019, and was affected neither by habitat (forest edge vs. forest interior) nor by water addition (Table 2, Fig. 3b–c).

Seedling performance

In September 2016, there was no difference in the leaf number of the seedlings between the forest edge and the forest interior habitats (Table 2, Fig. 4a), while in September 2019, seedlings in forest edges had more leaves than seedlings in forest interiors (Table 2, Fig. 4b). Seedlings were taller in the forest interior habitat in 2016 (Fig. 4c), but there was no difference in plant height between the habitats in 2019 (Fig. 4d). Watering had no effect on leaf number and plant height at either time (Table 2, Fig. 4). In general, oak seedlings grew very little from 2016 to 2019, and were still very short and had few leaves at the age of 4 years (Fig. 4).

Discussion

In contrast to our first hypothesis, watering throughout the growing season did not improve oak seedling emergence and subsequent seedling performance, and this was consistent across all habitat types. Oak seedling emergence and seedling survival were extremely low in the grassland habitat, which is in contrast to previous reports from the core areas of the deciduous forest biome, where pedunculate oak most often regenerates in open or semi-open habitats (Bakker et al. 2004; Bobiec et al. 2018). We did not find a negative effect of the forest interiors compared to forest edges

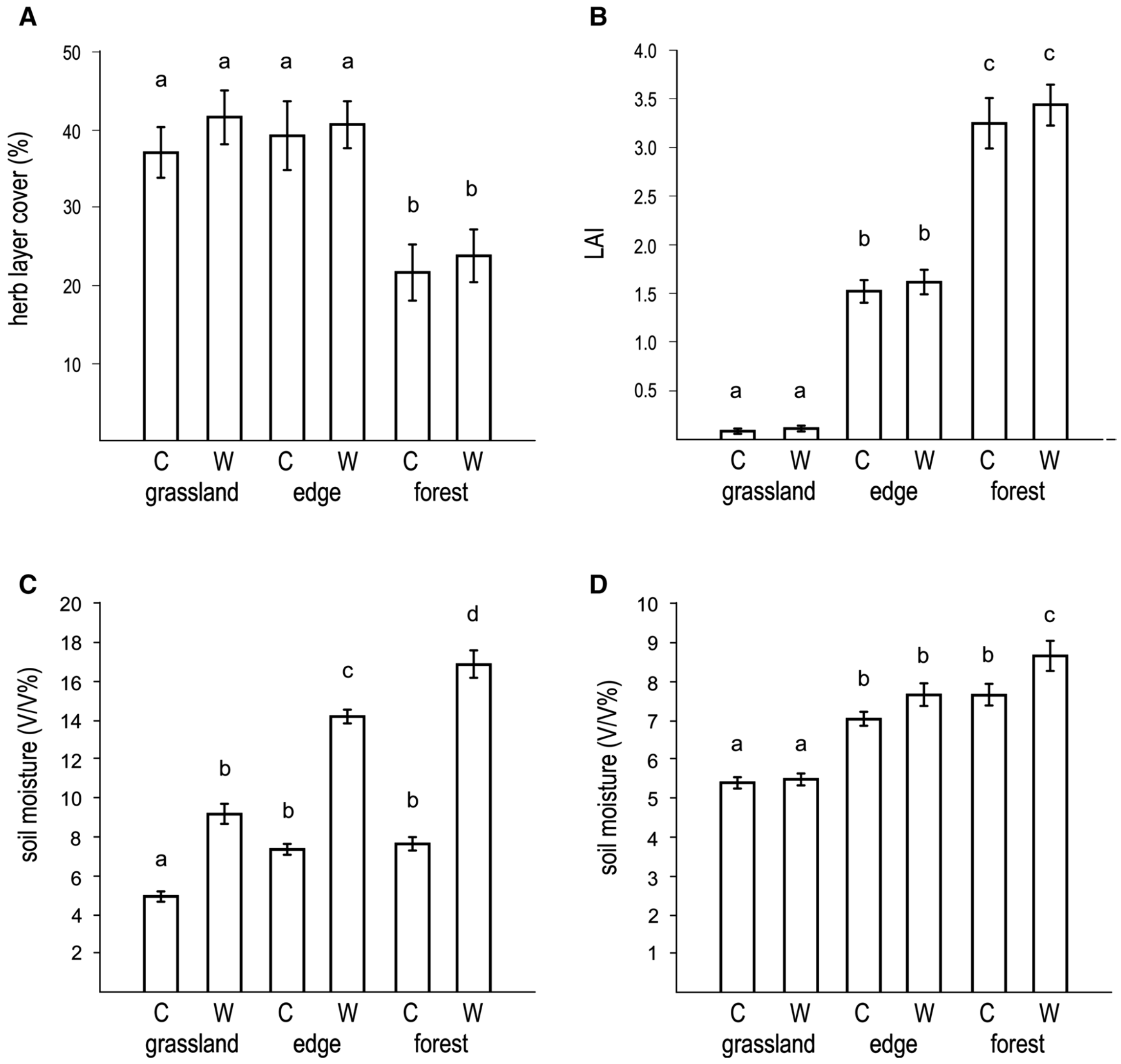


Fig. 2 The cover of the herb layer (**a**), leaf area index (**b**), soil moisture content 5 h after watering (**c**), and soil moisture content 2 weeks after watering (**d**) in the three habitats (grassland, forest edge, and forest interior). C: control plots, W: watered plots

on seedling numbers and performance throughout the four years of the study, while previous studies reported that the shade tolerance of oak seedlings is very low (Lorimer et al. 1994; Welander and Ottosson 1998; Leuschner and Ellenberg 2018). These results suggest that patterns of early oak regeneration at this site at the arid boundary of the temperate deciduous forest biome substantially differ from those previously reported from the core area of the biome. This is most likely related to a shift in oak regeneration from light limitation in the core zone to other limiting factors at the biome boundary.

Effect of watering

Even though we managed to substantially increase soil moisture content during the experiment, excess water had no effect on oak regeneration, which is in striking contrast to our expectation. The pot experiment of van Hees (1997) showed that moist conditions positively affect the height, biomass, and leaf area of *Q. robur* seedlings. The study of Urli et al. (2015) revealed that *Q. robur* seedlings and saplings react sensitively to drought stress in Southwest France and are not able to survive under very dry circumstances. In a Mediterranean mountain environment, Mendoza et al. (2009) found that watering increased the survival of *Q. ilex* and *Q. pyrenaica* seedlings in open and shrubby habitats, while it was not affected under tree canopies, where survival was high even in the absence of watering. In a similar study conducted in Mediterranean ecosystems, Matías et al. (2012a, b) showed that additional watering during the summer is able to increase the survival of *Q. ilex* seedlings in open, shrubby, and forest habitats.

Table 2 Results of generalised linear mixed-effects model and linear mixed-effects models of habitat type and watering treatment on germinated seedling number, leaf number, and plant height

Variables and effects	*df*	Chisq	*P*
Germinated seedlings			
Habitat type	2	34.09	**0.000**
Watering	1	0.04	0.841
Habitat type × watering	2	0.94	0.625
Seedling number in September 2016			
Habitat type	2	28.86	**0.000**
Watering	1	0.01	0.937
Habitat type × watering	2	1.18	0.553
Seedling number in September 2019			
Habitat type	1	0.04	0.832
Watering	1	0.04	0.832
Habitat type × watering	1	0.39	0.532
Leaf number in September 2016			
Habitat type	1	2.44	0.118
Watering	1	0.03	0.872
Habitat type × watering	1	0.45	0.504
Leaf number in September 2019			
Habitat type	1	6.14	**0.013**
Watering	1	0.78	0.378
Habitat type × watering	1	0.24	0.622
Plant height in September 2016			
Habitat type	1	5.60	**0.018**
Watering	1	3.00	0.083
Habitat type × watering	1	0.01	0.937
Plant height in September 2019			
Habitat type	1	0.73	0.393
Watering	1	1.18	0.277
Habitat type × watering	1	0.15	0.703

P values are rounded to three digits

($P<0.05$) values are shown in bold

The lack of response to watering in our experiment may be related to the fact that 2016 was an unusually wet year. Yearly total precipitation in 2016 was 742 mm, compared to the long-term mean of 530 mm; and growing season precipitation was 410 mm, compared to the long-term mean of 310 mm. The fact that even a year of above-average precipitation combined with excess water resulted in very low emergence and no survival in grassland patches suggests that grasslands are truly incapable of supporting oak regeneration in this ecosystem.

In our experiment, watering lasted throughout the growing season, from early April to September. Although we did not assess potential effect of water limitation outside the growing season, the cool temperature combined with usually substantial water in this period (an average 30–50 mm per month, Kovács-Láng et al 2000) makes water limitation unlikely.

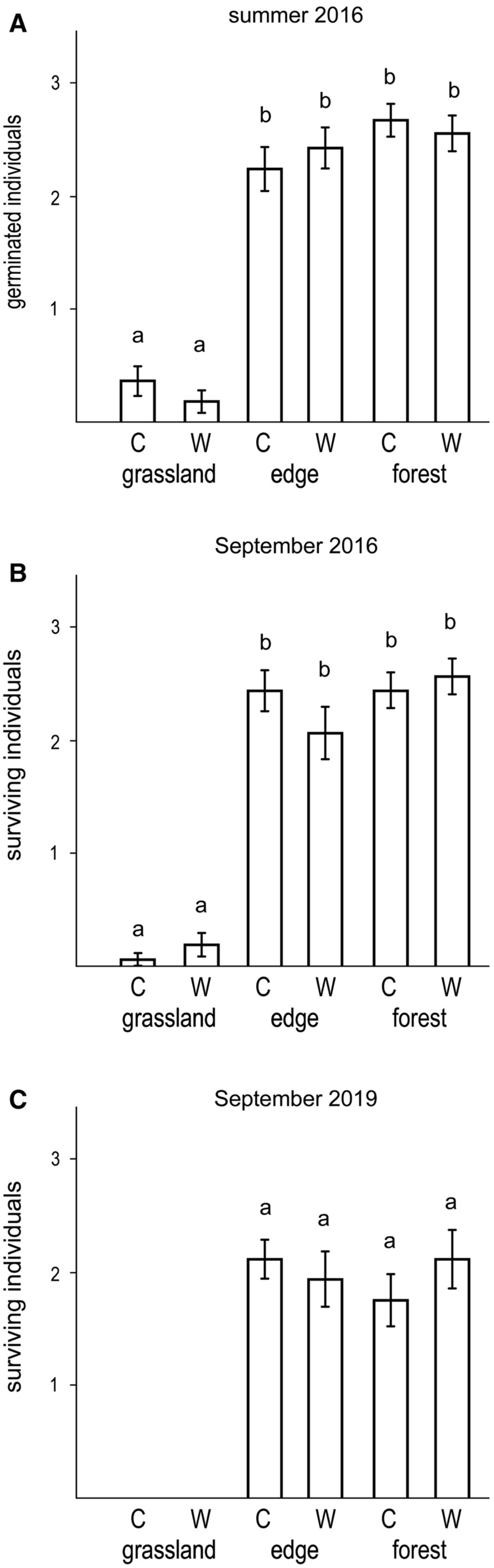
Effect of habitat type

In contrast to our hypothesis that the forest edge would represent the best habitat for seedlings while the grassland (due to drought) and the forest interior (due to shade) habitats would be less suitable, we found that seedling emergence and performance were extremely poor in grasslands while they were high in forest edges and forest interiors. Thus, forest edges and forest interiors proved to be similarly suitable for early oak regeneration, despite the strong differences regarding abiotic parameters in these two habitats. It is possible that increased soil moisture in forest interiors and forest edges compensate seedlings for the shady conditions; a similar compensatory effect has been described by Mellert et al. (2018).

Oak regeneration was absent in the grassland habitat: seedling emergence was extremely low and the few seedlings that did emerge died by September 2019. This finding differs from earlier studies conducted in the temperate deciduous forest biome. For example, Bakker et al. (2004) found that the survival and performance of pedunculate oak seedlings was better in grasslands than in forest interiors in riverine floodplains of western Europe (Germany, the Netherlands, and Great Britain). Similarly, *Q. robur* is able to colonise abandoned ploughlands and pastures as shown in France (Onaindia et al. 2001) and Poland (Bobiec et al. 2011b). The study of Olrik et al. (2012) showed successful colonisation by pedunculate oak in a heathland in Denmark, while oak can occupy abandoned pastures in Poland and Ukraine (Ziobro et al. 2016). In Belgium, several non-woody vegetation types such as grasslands, ruderal fields, and bramble thickets proved to be appropriate for *Q. robur* emergence (Van Uytvanck et al. 2008). Thus, it seems that *Q. robur* can easily regenerate in open (i.e. non-woody) habitats in the core areas of the temperate deciduous forest biome (Bobiec et al. 2018).

However, studies from Mediterranean habitats with oak species other than pedunculate oak indicated that oak regeneration may be limited in open habitats. For example, Mendoza et al. (2009) reported from southern Spain that the seedling survival of two Mediterranean oak species, *Q. ilex* and *Q. pyrenaica*, was the lowest in open habitats, while it was much higher under shrubs and in woodlands. Matías et al. (2012b) found that the emergence of *Q. ilex* was very good in open habitats, but the survival of the seedlings was poor in the same habitat, presumably due to drought stress. Similarly, in southern France, Rousset and Lepart (2000) showed that the germination and survival of *Q. humilis* was

Fig. 3 The number of germinated oak individuals (**a**), individuals that ▸ survived until September 2016 (**b**), and until September 2019 (**c**) in the three habitats (grassland, forest edge, and forest interior). C: control plots, W: watered plots



better under shrubs than in the neighbouring grassland, as shrubs protected the seedlings from drought. In Mediterranean California, the seedling transplantation study of López-Sánchez et al. (2019) revealed that almost all seedlings of *Q. lobata* and *Q. agrifolia* died in the open grassland, while they had significantly higher survival rates under trees and shrubs, where they were more protected from drought stress.

Desiccation is a critical factor during oak germination and seedling growth (Bobiec et al. 2018). Low soil moisture seems to be the most likely cause of poor seedling emergence and performance in the grassland habitat in our study, besides other factors, discussed below. Water limitation is the most prominent ecological constraint in the centre of the Carpathian Basin, with a semi-arid period during the summer months according to the long-term climate records (Borhidi 1993; Kun 2001). In addition, the sandy soils of the study site have very poor water retention capacity (Várallyay 1993), further decreasing water availability. While water limitation is relatively rare in the western and northern parts of Europe (within the core area of the temperate deciduous forest biome) (Reif and Gärtner 2007), it seems to be of primary importance at the arid boundary of the biome. However, the overriding role of water limitations in grasslands could only be proved by a more intense watering treatment (e.g. watering more frequently, or with higher amount, or starting already in autumn).

Competition with ground vegetation is usually considered one of the most important factors limiting oak regeneration (e.g. Vander Wall 2001; Reif and Gärtner 2007; Annighöfer et al. 2015). However, we think it cannot explain the strikingly poor oak regeneration in grasslands. First, the total cover of the herb layer was very low (40% or even less) in the grasslands of the study. Thus, there was ample space for oak seedlings to establish. Second, the cover of the herb layer was similar in the grasslands and the forest edges, yet forest edges had much higher seedling emergence and performance rates.

The poor oak germination and performance of the grassland habitat cannot be explained by browsing or predation either (Bobiec et al. 2018). Browsing pressure is generally low in the area, and we did not see signs of heavy browsing pressure on the seedlings during our regular surveys. Seed predation is also unlikely to differ substantially among the three habitats, due to the small distances (few metres) between the forest interior, forest edge, and grassland plots, and we did not see signs of predation (e.g. soil disturbance).

Further factors potentially limiting oak regeneration include high solar radiation and the lack of a humus layer

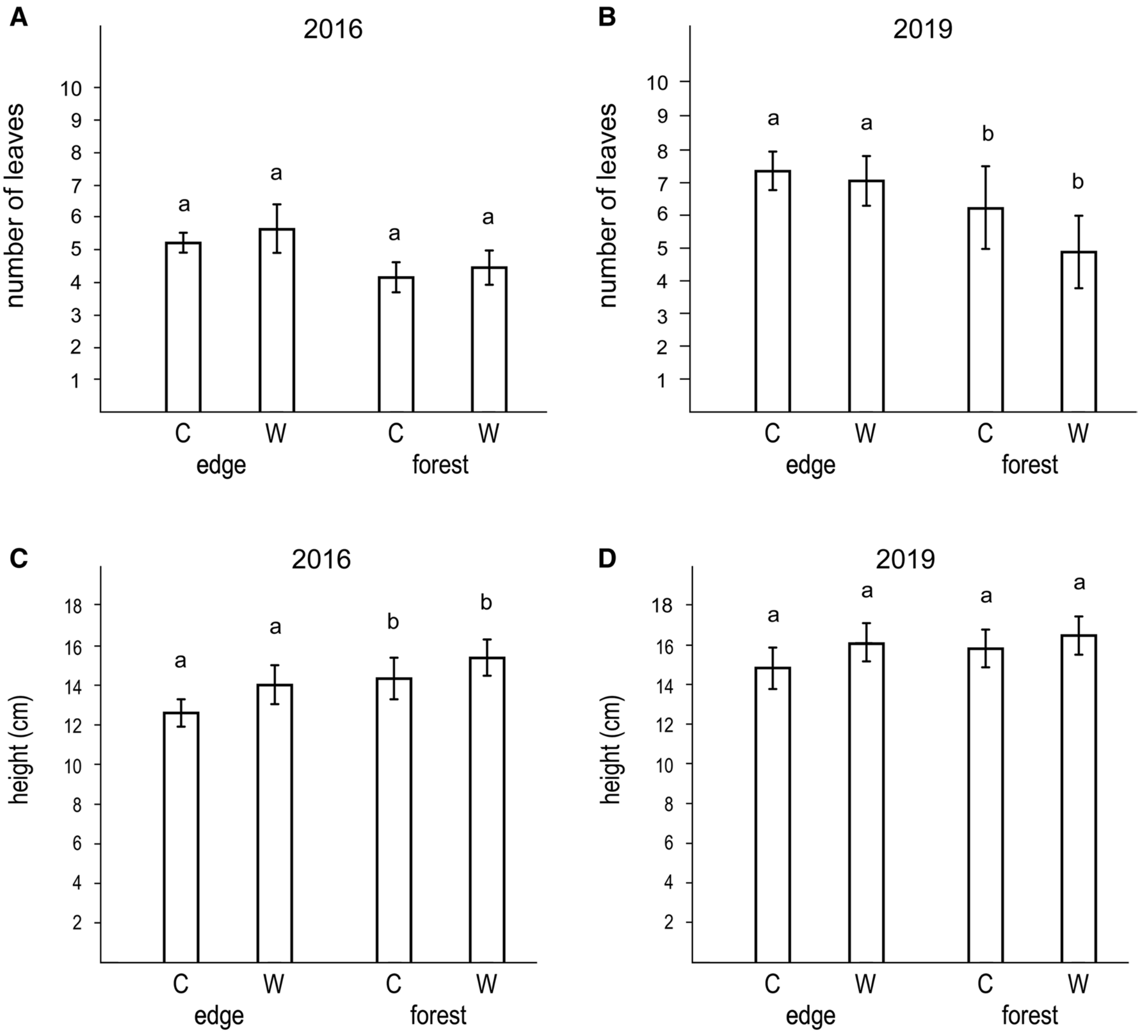


Fig. 4 The number of leaves in September 2016 (**a**), the number of leaves in September 2019 (**b**), the height of the seedlings in September 2016 (**c**), and the height of the seedlings in September 2019 (**d**) in the forest edge and forest interior habitats. C: control plots, W: watered plots

(Nilsson et al. 1996), both of which might have affected seedling emergence and survival in our study. The influence of high solar radiation may be amplified by the very sparse herb layer, and may contribute to the drying of the soil. Regarding the humus layer, the sandy soil of the grassland habitat in the study site is extremely poor in humus: the humus content of the upper 10 cm soil layer can be as low as 0.6%, while it is considerably higher in the forest patches (Bodrogközy 1982; Várallyay 1993; Kröel-Dulay et al. 2019; Tölgyesi et al. 2020).

Microclimatic extremes may also contribute to the poor oak emergence and survival in the grassland habitat. High air temperatures measured near the soil surface in the grassland habitat during summer days (compared to the much cooler forest edges and forest interiors) (e.g. Erdős et al. 2014; Tölgyesi et al. 2020) may damage the tissues and physiological processes of pedunculate oak (Cuza 2018), thus preventing oak regeneration in this habitat.

Our study revealed similarly high early oak regeneration in forest edges and forest interiors. Good oak regeneration within the forest edge habitat fits our hypothesis and is in line with earlier observations regarding habitats optimal for oak regeneration (e.g. Vera 2000; Reif and Gärtner 2007; Bobiec et al. 2018). For example, Herlin and Fry (2000) showed that *Q. robur* is able to establish in forest edges and hedgerows in southern Sweden. Similarly, Bakker et al. (2004) found that edges are optimal habitats for *Q. robur* regeneration throughout northwestern Europe.

We found only small and transient differences between forest edge and forest interior habitats. Seedlings in the forest interiors had fewer leaves than seedlings in forest edges, although the difference was significant only in 2019. This result is in line with earlier studies reporting reduced leaf number in seedlings under shady conditions (e.g. Ziegenhagen and Kausch 1995; Welander and Ottosson 1998). Seedlings were higher in forest interiors than in forest edges in 2016, while no significant difference was found in 2019. Seedlings are usually higher in shady than in sunny habitats (e.g. Ziegenhagen and Kausch 1995; Nilsson et al. 1996; van Hees 1997; Ammer 2003).

The overall similarity of forest interiors and forest edges is surprising given the reported high light requirements of pedunculate oak seedlings. According to Leuschner and Ellenberg (2018), the shade tolerance of *Q. robur* seedlings is very low. Indeed, the regeneration of pedunculate oak depends primarily on non-forest habitats (Bakker et al. 2004; Bobiec et al. 2018). However, it has also been shown that seedlings do tolerate shady conditions during the first few years; that is, their light demand starts to increase only after those initial years (e.g. Welander and Ottosson 1998; Vander Wall 2001; Annighöfer et al. 2015). Von Lüpke and Hauskeller-Bullerjahn (2004) and Bobiec et al. (2011a) found that young oak individuals are increasingly dependent on clearings as they grow up. Ziegenhagen and Kausch (1995) argued that the starch reserves of the young seedlings enable them to survive in shade for a couple of years. Although a negative effect of shading in the forest interiors may easily be seen in the future, the lack of such difference in the first four years is interesting given the above reports on low shade tolerance of pedunculate oak. One possible explanation may be that forest interiors at our site are not as closed as forests in the biome interior (see picture in Fig. 1e). Indeed, the LAI of 3–3.5 measured at our forest interiors is lower than that reported for several temperate oak forests in Europe (e.g. Bréda and Granier 1996; Le Dantec et al. 2000; Soudani et al. 2006; Thimonier et al. 2010). Another explanation for the similar performance of oak seedlings at forest edges and forest interiors is that a factor other than light limits growth. A major candidate in these ecosystems can be soil moisture (Várallyay 1993), which may also explain the extremely small size of the 4-year old oak seedlings (14–16 cm).

Differences in oak regeneration between the core area and the arid boundary of the biome

Towards the arid boundary of the temperate deciduous forest biome, the competitive vigour of the woody lifeforms decreases (Walter and Breckle 1989; Erdős et al. 2018a). As a consequence, forests gradually open up, enabling the emergence of the forest-steppe zone with alternating forest and grassland patches. The poor performance of our seedlings, especially regarding their height, also indicates that conditions are suboptimal for oak regeneration at our site. Seedling height has been reported to reach 13–20 cm after one (Giertych and Suszka 2010; Devetaković et al. 2019), and 30–60 cm after only two growing seasons (Ammer 2003; Cabral and O'Reilly 2008; Andersen 2010).

Conclusions

Our study suggests that oak regeneration pattern in this transitional zone differs markedly from what has been described in the core areas of the temperate deciduous forest biome. When one moves from the core areas of the deciduous forest biome towards the arid boundary of the biome, there seems to be a shift from light limitation to other limiting factors, which prevent oak regeneration in grassland patches and restrict it to forest edges, and, potentially, to forest interiors.

In conclusion, our results emphasise that oak regeneration and thus forest dynamics may be limited by different factors at a biome boundary compared to the biome core. Indeed, the lack of tree regeneration in grassland patches may contribute to the opening up of the closed forest biome, and the emergence of the forest-steppe zone.

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

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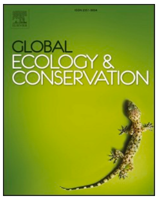

Forest edges revisited: Species composition, edge-related species, taxonomic, functional, and phylogenetic diversity

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ABSTRACT

Although edges are usually considered key areas for biodiversity, previous studies have focused on anthropogenic edges, usually studied edges in relation to forest interiors (disregarding the adjacent non-woody vegetation), and used simple taxonomic indices (without considering functional or phylogenetic aspects). We studied the species composition as well as taxonomic, functional, and phylogenetic diversity of north- and south-facing edges and the two adjacent habitats (forest and grassland) in near-natural forest–grassland mosaics in the Kiskunság Sand Ridge (Hungary) and the Deliblato Sands (Serbia). We found that the species composition of edges was significantly different from that of forests and grasslands, and included species that were rare or absent in habitat interiors. This indicates that the contact of adjacent forest and grassland habitats results in the emergence of a new habitat that deserves scientific attention in its own right. In the Kiskunság, species richness and Shannon diversity were generally higher at edges than in forests

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or grasslands. In the Deliblato, edges were taxonomically not more diverse than grasslands. Thus, increased taxonomic diversity at edges should not be considered a general phenomenon. In the Kiskunság, forests and edges had higher functional diversity than grasslands, while there were no significant differences among the habitats in the Deliblato. It seems that functional diversity is strongly influenced by canopy openness and the traits of the dominant species. The phylogenetic diversity of woody habitats was higher than that of grasslands both in the Kiskunság and the Deliblato, which probably reflects the different evolutionary age of the habitats.

1. Introduction

Vegetation edges or ecotones (i.e., the contact zones between neighboring vegetation types) are important components of spatially heterogeneous landscapes (Harper et al., 2005; Kark and van Rensburg, 2006; Yarrow and Marín, 2007; Dodonov et al., 2013). Edges influence the exchange and redistribution of organisms, materials, and energy between adjacent habitats (Wiens et al., 1985; Ries et al., 2004). In addition, edges can serve as habitat strips (Risser, 1995), regulate population dynamics (Fagan et al., 1999; Peyras et al., 2013), and may also be important from an evolutionary perspective as places of speciation (Kark and van Rensburg, 2006).

The spatial cover and ecological importance of edges is particularly noteworthy in ecosystems that have been fragmented by human activity, but also in ecosystems that are naturally fragmented, showing a mosaic-like arrangement of various habitats. Although anthropogenically created edges have been well-studied in the last few decades (Williams-Linera, 1990; Harper and Macdonald, 2002; Dutoit et al., 2007; Batllori et al., 2009; Dodonov et al., 2013; Czaja et al., 2021), edges between adjacent natural and semi-natural ecosystems have received less attention (Franklin et al., 2021).

Connecting structurally very different habitats, forest edges belong to the most conspicuous ecotone types, and as such, they have been the focus of ecological interest (Risser, 1995; Harper et al., 2005). However, despite the growing body of edge literature, considerable knowledge gaps still exist. For example, it is debated whether forest edges are more similar to the forest or the grassland interior. Some studies have found that the species composition of edges resembles that of forest patches (e.g., Orczewska and Glista, 2005; Santos and Santos, 2008), but contradictory results have also been reported, where edges were more similar to grasslands (Erdős et al., 2011) or were significantly different from both adjacent habitats (Erdős et al., 2014, 2019).

The existence of edge-related species is a related issue. Studies aiming to identify edge-related species are still too scarce and often inconsistent, making generalizations hard or impossible. For example, some earlier studies found species that were significantly related to edges (Erdős et al., 2014; Bátori et al., 2018), while there was weak evidence of edge-related species in other studies (Lloyd et al., 2000; Erdős et al., 2011). Lloyd et al. (2000) cautioned that species that prefer edges should be evaluated carefully, as a species may be edge-related in a given region but may not be related to edges elsewhere.

The edge effect hypothesis is probably the best known, and most intensively discussed, hypothesis in edge research. It contends that taxonomic diversity at edges is higher than in the two adjacent habitat interiors (Odum, 1971; Pianka, 1983; Risser, 1995). However, this pattern may not hold true in all cases. For example, van der Maarel (1990) hypothesized that species diversity may be high in blurred edges under favorable environmental conditions, whereas sharp edges under unstable conditions may support lower diversity than the two adjacent habitats. Similarly, Risser (1995) and Harper and Macdonald (2002) argued that edge diversity may only be higher than that of the forest interior if the edge is old and stable for a long period. Additionally, species diversity in edges may be intermediate, i.e., edges may contain more species than one of the adjacent communities but less species than the other (Stowe et al., 2003; Chytrý et al., 2022). The overwhelming majority of earlier forest edge research only considered forest interiors and edges but disregarded the adjacent habitats (e.g., Gehlhausen et al., 2000; Harper and Macdonald, 2002; Baez and Balslev, 2007), which is a considerable limitation, potentially hindering a correct understanding of ecological edges.

The edge effect hypothesis applies to taxonomic diversity but not to functional or phylogenetic diversity. Functional diversity (i.e., variation in the values of functional traits among organisms) and phylogenetic diversity (i.e., the difference in evolutionary lineages within a community) are important components of biodiversity as they provide information about ecosystem processes, productivity, dynamics, stability, and ecosystem services (Cadotte et al., 2011; Flynn et al., 2011). Some studies indicate that high taxonomic diversity is accompanied by high functional and phylogenetic diversity (e.g., Cadotte et al., 2009; Nagalingum et al., 2015), but contradictory cases have also been reported (e.g., Bernard-Verdier et al., 2013; Doxa et al., 2020). Our knowledge regarding how functional and phylogenetic diversity change across edges is very limited.

Stretching from the Carpathian Basin to the Russian and Chinese Far East, Eurasian forest-steppes are among the most complex non-tropical ecosystems, featuring a mosaic-like arrangement of forest and grassland patches, and edges between them (Chibilyov, 2002; Erdős et al., 2018a). Our aim was to assess how the species composition and diversity of edge habitats are related to those of the forest and grassland interiors in two forest-steppe ecosystems in Central Europe. Specifically, we asked the following questions: i) Does the species composition of the edges differ from the habitat interiors? ii) Do edge-related species (i.e. species that favor edge habitats and are rare or absent in habitat interiors) exist? iii) Do taxonomic, functional, and phylogenetic diversity of the edges differ from those of the forest and grassland interiors?

2. Material and methods

2.1. Study sites

Our study was conducted at two calcareous sandy forest–grassland mosaics of the Carpathian Basin: the Kiskunság Sand Ridge (Hungary; hereafter Kiskunság) in the central part of the Basin, and the Deliblato Sands (Serbia; hereafter Deliblato) at the southernmost edge of the Basin (Fig. 1a, b). Both regions are composed of slightly undulating stabilized sand dunes of aeolian origin, with humus-poor sandy soils and low water retention capacity (Várallyay, 1993; Sipos et al., 2022).

The Kiskunság is a large plain located between the rivers Danube and Tisza in central Hungary. The climate is subcontinental with a sub-Mediterranean influence; mean annual temperature and rainfall are 10.0–10.7 °C and 520–580 mm, respectively (Dövényi, 2010). The site selected for our study is located north of the town of Kiskunhalas (N 46°31'; E 19°37'). The site is covered by near-natural forest–steppe vegetation (Fig. 1c) and is legally protected, with no significant anthropogenic activity. Grasslands exhibit 40–75 % vegetation cover with *Festuca vaginata*, *Stipa borysthenica*, and *S. capillata* as the dominant species. The forest patches have 40–70 % canopy cover and are dominated by 10–15 m tall *Populus alba* trees.

The Deliblato is a sand region in the southeastern part of the Banat region in Serbia, located between the southwestern slopes of the Carpathian Mountains and the Danube River. The climate is moderately continental; average annual temperature and precipitation are 12.5 °C and 664 mm, respectively (Ćuk et al., 2023). The site selected for our study was the Deliblato special nature reserve, southeast of the village of Šušara (N 44°54'; E 21°07'). The natural vegetation is a forest-steppe mosaic (Fig. 1d). The grasslands have 50–95 % total cover and are dominated by *Chrysopogon gryllus*, *Festuca rupicola*, *F. valesiaca*, *Stipa borysthenica*, and *S. capillata*. The forests have a height of 15–25 m, a canopy cover of 60–95 %, and are co-dominated by *Tilia tomentosa* and *Quercus robur*. The distance between the

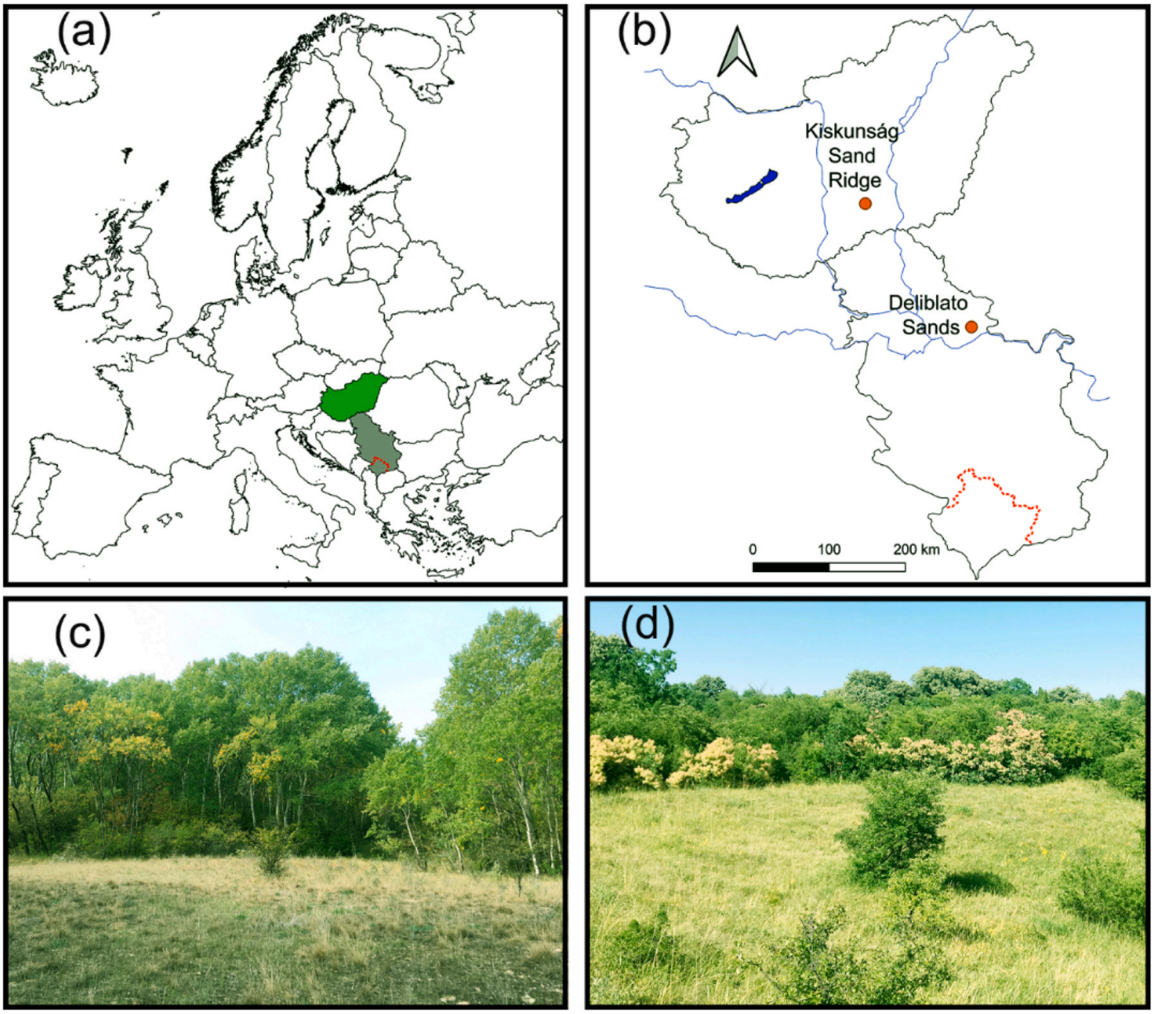

Fig. 1. Location of Hungary (green) and Serbia (gray) in Europe (a). Location of the study sites (orange dots) in Hungary and Serbia (b). Forest–grassland mosaics in the Kiskunság Sand Ridge (c) and the Deliblato Sands (d).

two study sites is approximately 220 km.

2.2. Field sampling

Four main habitat types were differentiated at both sites in this study: forest patches (>0.5 ha), north-facing forest edges, south-facing forest edges, and grasslands. The peripheral zone of a forest patch, away from the outermost tree trunks but still below the tree and/or shrub canopy, was defined as the forest edge. In total, 80 permanent plots were established (4 habitats × 10 replicates × 2 study sites; additional information about the 4 habitat types in the 2 sites is presented in Table S1). We used 5 m × 5 m plots in the forests and grasslands, whereas 2.0 m × 12.5 m plots were used at forest edges to ensure that they did not extend into the forest or grassland interiors. It has been shown that, at the scale used in the present study, results were not affected by plot shape (Keeley and Fotheringham, 2005). The percent cover of each vascular plant species within each plot was visually estimated in spring (April) and summer (July), and the cover values for each species were combined for subsequent data analyses by using the larger value for each species. The names of plant species follow Király (2009). Four unidentified taxa (*Allium* sp., *Hieracium* sp., *Lathyrus* sp., and *Orobanche* sp.), none of which appeared in > 1 of the 80 plots, were not included in the functional and phylogenetic diversity analyses.

2.3. Data analysis

To investigate the species composition of the four habitat types, nonmetric multidimensional scaling (NMDS) was applied to the square root–transformed cover percentages using Bray-Curtis dissimilarity. Two separate NMDS ordinations were performed to compare the habitat structure in the Kiskunság and the Deliblato. Given that overlaps were observed in the ordination space, permutational multivariate analysis of variance (PERMANOVA) and pairwise comparisons with 999 permutations were used to test the compositional differences among the different habitat types at each site. The “metaMDS” and “adonis2” functions in the vegan package and the “pairwise.adonis” function in the funfuns package of R version 4.1.2 were employed for NMDS, PERMANOVA, and pairwise comparisons, respectively (R Core Team, 2021; Oksanen et al., 2022; Trachsel, 2022). We used the Bonferroni method to correct *p*-values in multiple pairwise comparison tests.

To determine the typical species in a target habitat that are rare or absent elsewhere, we identified diagnostic species for the four habitat types in the Kiskunság and the Deliblato, using the phi-coefficient as an indicator of fidelity (Chytrý et al., 2002). Only species with a phi value of > 0.2 were considered diagnostic. Fisher’s exact test was used to determine significant diagnostic species at $p < 0.01$. All calculations were performed using JUICE 7.1.30 software (Tichý, 2002).

The species richness and Shannon diversity of each plot were computed using the “specnumber” and “diversity” functions of the R vegan package, respectively (Oksanen et al., 2022).

We used Rao’s quadratic entropy (RaoQ) to reveal the per plot functional diversity as this index is a suitable measure of functional diversity (Botta-Dukát, 2005; Petchey and Gaston, 2006). The overall (i.e., multi-trait) functional diversity per plot was calculated by considering the contribution of nine traits: flowering start, flowering duration, specific leaf area (SLA), mean plant height, thousand seed mass, life form, seed dispersal, pollination type, and reproduction type (Table S2). In addition, we also calculated functional diversity for each single trait. Two single traits, flowering start and flowering duration, were combined into a trait group called flowering time, the functional diversity of which was also computed. SLA, mean plant height, and thousand seed mass were chosen because they are the most ecologically informative traits (Westoby, 1998), whereas the other traits express critical ecosystem functions (see Weiher et al., 1999). SLA, mean plant height, and thousand seed mass were log-transformed prior to analysis, and the “gawdis” function of the gawdis package in R was applied to determine pairwise functional differences (= species dissimilarity) because it solves the unbalanced contribution of multiple traits and fuzzy-coded traits (de Bello et al., 2021a).

To analyze phylogenetic diversity, we also used RaoQ to ensure that phylogenetic and functional diversity had the same conceptual and mathematical framework (Jucker et al., 2013; Swenson, 2014). We used a published 74,533-species mega-tree (GBOTB.extended.tre) to create a phylogeny of the 225 species found in our study (Jin and Qian, 2019). To build this phylogenetic tree, we standardized plant species nomenclature (family, genus, and species names) based on The Plant List (http://www.theplantlist.org/) and employed the “phylo.maker” function of the V.PhyloMaker package in R using scenario 3, in which unidentified species were tethered to their closest relatives (R Core Team, 2021; Jin and Qian, 2019). The created phylogeny is presented in Fig. S1. As phylogenetic diversity is heavily affected by gymnosperms and pteridophytes, we built an additional tree that excluded all nonangiosperm species (i.e., *Equisetum ramosissimum, Juniperus communis,* and *Pinus nigra*). To compute the matrix of phylogenetic distance, we used the “cophenetic” function of the picante package in R (Kembel et al., 2010). We calculated phylogenetic diversity for two cases: (i) all species, including angiosperms and nonangiosperms, and (ii) only angiosperm species. Finally, the “rao.diversity” function of the SYNCSA package was used to compute RaoQ for functional diversity and phylogenetic diversity (Debastiani and Pillar, 2012).

To remove the impact of species richness on RaoQ and determine whether the habitats are over- or underdispersed, we measured the standardized effect size of RaoQ (SES.RaoQ) using the following equation: (observed RaoQ value–mean expected RaoQ values) / standard deviation of expected RaoQ values (de Bello et al., 2021b). We permuted the species labels in a trait matrix 999 times to create a null model of functional diversity using the R code of de Bello et al. (2021b), and we shuffled the species names on the phylogenetic tree to generate a null model of phylogenetic diversity based on the R code of Swenson (2014). Positive SES values indicate overdispersion (i.e., species are more distant than expected by chance), whereas negative SES values indicate underdispersion (i.e., species are more closely related than expected by chance). A two-sided Wilcoxon signed rank test was applied to determine the statistical significance of SES values relative to the null expectation of SES values (Bernard-Verdier et al., 2012; Nooten et al., 2021).

Before data analysis, we used the Shapiro–Wilk normality test and the Bartlett test to determine deviations from normality and homogeneity of variance, respectively. We used the Kruskal-Wallis test because the data did not meet assumptions of analysis of variance (ANOVA). The differences in the species richness, Shannon diversity, functional and phylogenetic diversity of the four habitat types in two study sites (8 groups = 4 habitats × 2 sites) were tested using the "kruskal.test" function in R. If this test explained a significant proportion of variability, all pairwise comparisons of the habitat types of the two study sites were performed, and the p-values were adjusted using the false discovery rate method via the pairwise.wilcox.test function. P-values of ≤ 0.05 were considered statistically significant.

3. Results

3.1. Species composition and diagnostic species

The NMDS ordinations revealed similar patterns in the Kiskunság and the Deliblato, with edge plots being distinct from forest and grassland plots and placed in an intermediate position (Fig. 2). Although north-facing and south-facing edges overlapped in both sites, the PERMANOVA test revealed significant differences among the habitat types both in the Kiskunság ($F = 13.47$, $R^2 = 0.529$, $p = 0.001$) and the Deliblato ($F = 12.23$, $R^2 = 0.505$, $p = 0.001$). All pairwise comparisons indicated that significant differences existed among habitats ($p < 0.05$; Table S3).

The highest number of diagnostic species was observed in the grasslands, whereas the lowest number was found in the forests and south-facing edges of both the Kiskunság (13, 4, and 4 species, respectively) and the Deliblato (20, 7, and 7 species, respectively). North-facing edges had an intermediate diagnostic species number, with 8 and 11 species in the Kiskunság and the Deliblato, respectively (Tables S4 and S5).

3.2. Taxonomic diversity

Forest patches exhibited the lowest species richness both in the Kiskunság and the Deliblato (Fig. 3a). In the Kiskunság, north-facing edges were the most species-rich, whereas south-facing edges and grasslands had intermediate species richness. Surprisingly, the species richness of edges and grasslands did not differ significantly in the Deliblato, although north-facing edges seemed to be slightly more species rich than the other habitats. The species richness of edges and grasslands was significantly higher in the Deliblato than in the Kiskunság. Somewhat similar patterns were found for Shannon diversity (Fig. 3b), but edges seemed to be less diverse than grasslands in the Deliblato, even though the differences were not significant.

3.3. Functional diversity

The multi-trait functional diversity was significantly higher in woody habitats (forest patches and edges) than in grasslands in the Kiskunság, whereas it was similar among the four habitat types in the Deliblato (Fig. 3c). Woody habitats in the Kiskunság had higher multi-trait functional diversity than those in the Deliblato, but the grasslands of the two sites had similar functional diversity. Only woody habitats of the Kiskunság were functionally overdispersed; all other habitats were functionally underdispersed (Fig. 3c, Table S6).

Regarding the functional diversity of single traits, some common patterns were recognizable at the two sites. In particular, the functional diversity of seed dispersal, reproduction type, and mean plant height were mostly high in woody habitats and low in grasslands (Fig. 4b–d). With a few exceptions in the Deliblato, woody habitats exhibited overdispersion, while grassland habitats exhibited underdispersion or a random pattern for these traits (Table S6). The functional diversity of life form peaked at the edges, and this diversity showed a declining tendency toward neighboring habitats (Fig. 4e). The functional diversity of both SLA and pollination

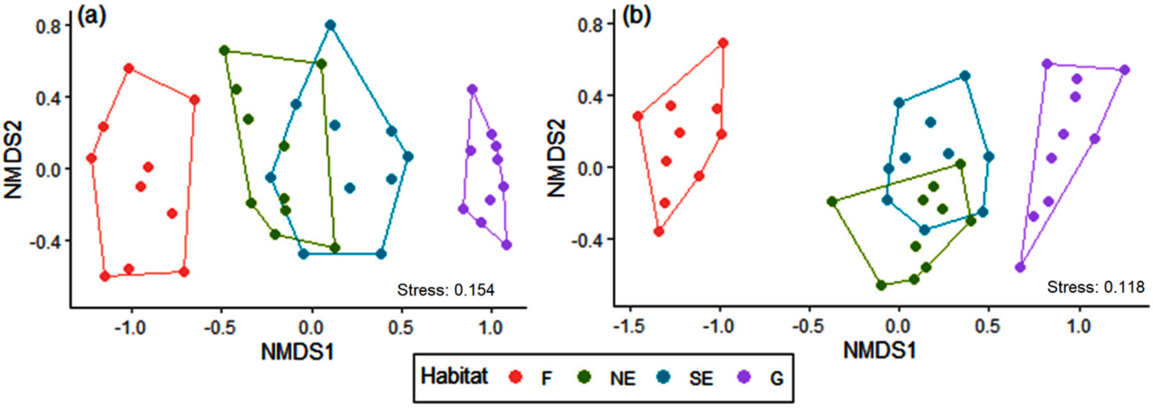

Fig. 2. NMDS ordination diagram of the plots of the Kiskunság (a) and the Deliblato (b) based on the square root–transformed percentage cover data. F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland.

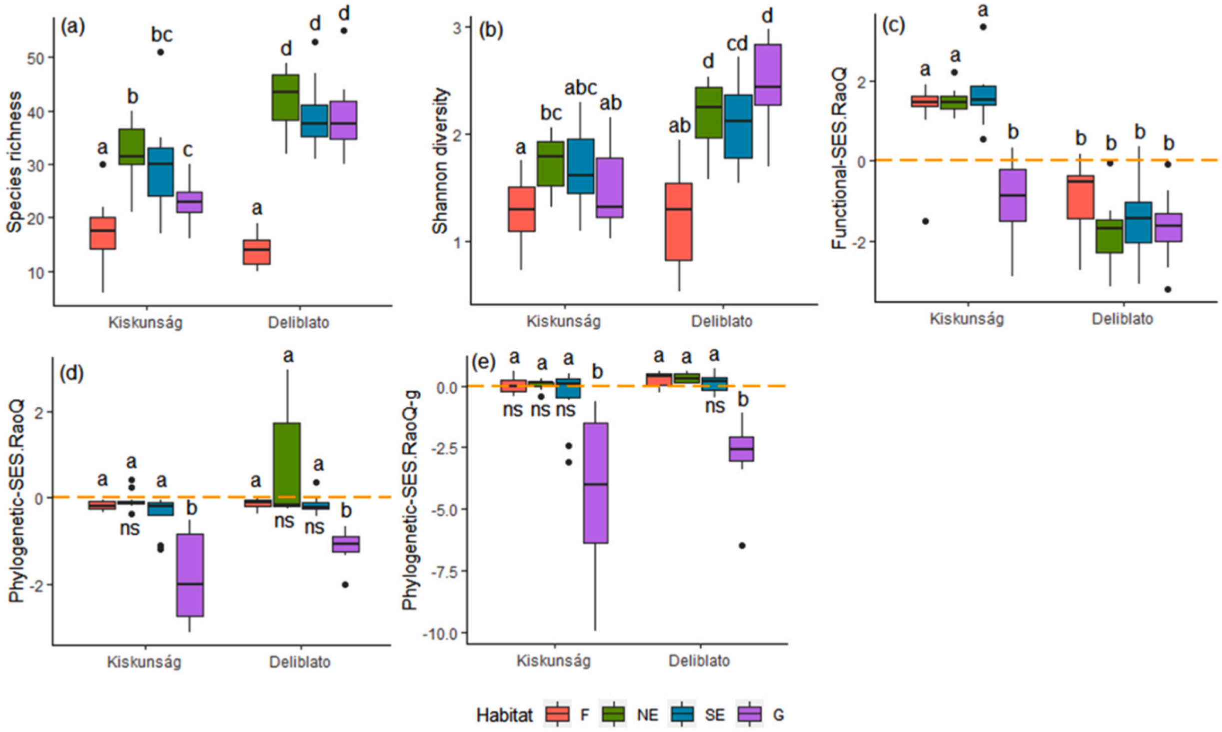

Fig. 3. Species richness (a), Shannon diversity (b), and functional diversity of all traits based on the standardized effect size of Rao's quadratic entropy (SES.RaoQ) (c), phylogenetic diversity of all species (d), phylogenetic diversity of only angiosperm species (e) of the four habitat types in the Kiskunság and the Deliblato. Habitats not sharing a letter are significantly different. F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland. Null model expectation is shown by the dashed horizontal line. Negative SES values indicate underdispersion, whereas positive values indicate overdispersion; "ns" indicates no significant difference (= a random pattern) between observed SES values and the null model expectation (based on a two-sided Wilcoxon signed rank test).

type peaked toward forest patches and grasslands and reached minima at the edges, although between-habitat differences were not always significant (Fig. 4f, h). The SES.RaoQ values of life form and SLA indicated underdispersion in most habitats, whereas these values for pollination type indicated overdispersion in forests and random patterns in most other habitats (Table S6).

We found different patterns of functional diversity for flowering time and thousand seed mass between the Kiskunság and the Deliblato. In the Kiskunság, the functional diversity of flowering time was higher in woody habitats than in grasslands, indicating overdispersion (Fig. 4a, Table S6), whereas the opposite trend was found in the Deliblato. The functional diversity of thousand seed mass gradually decreased from forests toward grasslands in the Kiskunság, whereas no significant difference was found among the four habitat types in the Deliblato (Fig. 4g). Forests in the Kiskunság showed overdispersion, whereas random patterns or underdispersion were found in all other cases (Table S6).

3.4. *Phylogenetic diversity*

The pattern of phylogenetic diversity was similar in the Kiskunság and the Deliblato, i.e., phylogenetic diversity was higher in forests and at edges than in grasslands (Fig. 3d). North-facing edges in both sites were not significantly different from the null model expectation, whereas other habitats, with the exception of south-facing edges in the Deliblato, were underdispersed (Table S6).

A peak was found at the north-facing edges of the Deliblato, although this habitat did not differ significantly from forests and south-facing edges. If only angiosperms were included in the analysis, this peak disappeared. Phylogenetic diversity was still higher in forests and edges than in grasslands (Fig. 3e). All woody habitats showed either overdispersion or random patterns, whereas all grasslands were underdispersed (Table S6).

4. Discussion

4.1. *Species composition and diagnostic species*

We found that the plant species composition of the edges was different from that of the neighboring habitats in both the Kiskunság and the Deliblato (Fig. 2a, b), which therefore seems to be a general pattern in the sandy forest-steppes of the Carpathian Basin. Similar results were reported from Kazakh sandy forest-steppes (Bátori et al., 2018), Croatian rocky forest-steppes (Erdős et al., 2019),

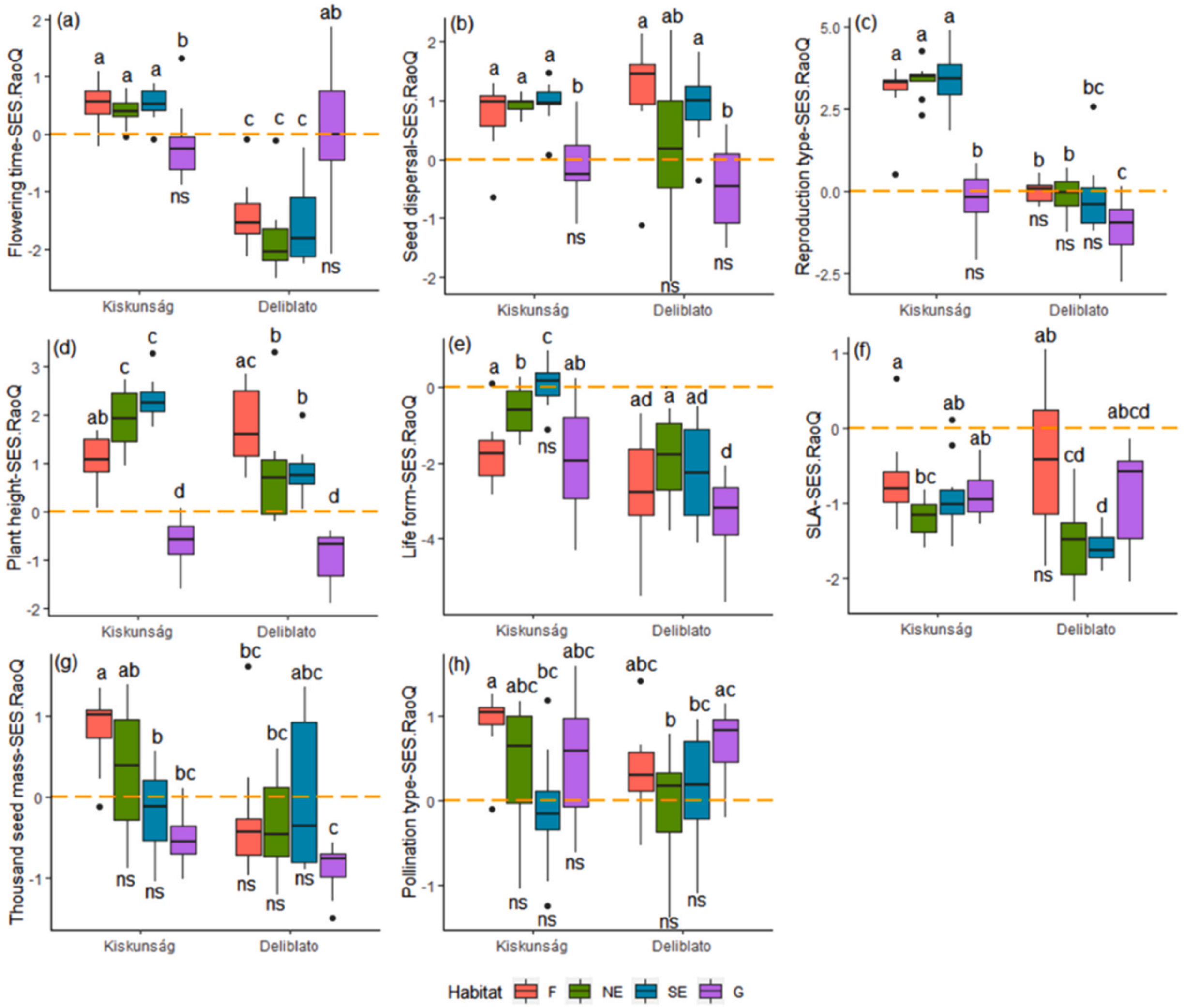

Fig. 4. Functional diversity of single traits. Flowering time (a), seed dispersal (b), reproduction type (c), life form (d), plant height (e), specific leaf area (f), thousand seed mass (g), and pollination type (h). F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland. Habitats not sharing a letter are significantly different. Null model expectation is indicated by a dashed horizontal line. Negative SES values indicate underdispersion; positive SES values indicate overdispersion; "ns" indicates no significant difference (= a random pattern) between the observed SES values and the null model expectation (based on a two-sided Wilcoxon signed rank test).

Brazilian forest-grassland mosaics (Müller et al., 2012), a tropical montane cloud forest in Southeastern Brazil (Santana et al., 2021), and semi-arid Chaco forests in Argentina (de Casenave et al., 1995).

We found that species composition differed significantly between the differently oriented edges (Table S3), which is consistent with the hypothesis of Ries et al. (2004), who suggested that edge response should be different between north- and south-facing edges. One possible explanation is that in the northern temperate zone, south-oriented edges are typically drier and warmer than north-oriented ones owing to increased sunlight exposure (Stoutjesdijk and Barkman, 1992; Heithecker and Halpern, 2007; Bennie et al., 2008). The microclimatic differences are obviously large enough to support significantly different plant communities in our two study sites.

Our analysis revealed that edges had their own diagnostic species rather than only a mixture of species from the interior habitats. This is in agreement with previous studies from sandy forest-steppes (Molnár, 1998; Erdős et al., 2014; Bátori et al., 2018) and other natural or semi-natural forest-grassland mosaics (Hennenberg et al., 2005; Erdős et al., 2019). Our results concerning the species composition and the diagnostic species of the habitats suggest that the contact of the forest and the grassland habitat results in the emergence of a new habitat that deserves scientific attention in its own right. The question whether forest edges should be recognized as separate communities has been debated during the last few decades: while some regarded them as distinct communities, others considered them part of the forest stand or the neighboring grassland (Carni, 2005). Currently, forest edges are viewed as entities in their own right, which is also shown by the fact that they are identified with specific syntaxa, including several alliances within the class *Trifolio-Geranietea sanguinei* (e.g., Borhidi et al., 2012; Mucina et al., 2016). The problems associated with identifying and accurately delineating forest edge communities notwithstanding (e.g., Willner, 2011), we think our results support the view of separate forest edge communities.

The list of diagnostic edge species identified in the present work (Tables S4 and S5) shows remarkable similarities with earlier studies on edges of the region. For example, *Achillea pannonica*, *Carlina vulgaris*, *Festuca rupicola*, and *Seseli annum* proved to be significantly related to forest edges in sandy forest-steppe ecosystems (Erdős et al., 2013, 2014, and 2018b). Regional works list, among others, the following species as typically associated with forest edges: *Anthericum ramosum*, *Dictamnus albus*, *Iris variegata*, *Scabiosa ochroleuca*, and *Thalictrum minus* (Gajić, 1970; Diklić, 1973; Borhidi, 1995). These species indeed had a larger frequency at forest edges in the present work, although the difference did not prove significant, except for *S. ochroleuca* in the Kiskunság. In addition, both the frequency and the cover of the shrubs *Cotinus coggygria* and *Rhamnus saxatilis* ssp. *tinctoria* reached their maxima at forest edges at the Deliblato site. *C. coggygria* forms a similar edge around the xeric shrubforest patches of Hungarian mountain ranges (Jakucs, 1972).

The edge-related species identified in the present work show positive edge response (sensu Ries et al., 2004), i.e., they have increased abundance or frequency at edges. To use a broader categorization, these species are sensitive to edges (Ries and Sisk, 2010). According to Ries et al. (2004) and Ries and Sisk (2010), species preferentially occur at edges if their resources are concentrated there, or if they have complementary resources in the two adjacent habitats. For example, plants related to forest edges may benefit from the increased sunlight availability relative to the forest interior, complemented by increased soil moisture content compared to the grassland interior.

However, no species is expected to react in the same way to various edge types (that is, most species probably show different responses, depending on the type of the edge under study) (Ries and Sisk, 2010; and see also Lloyd et al., 2000). This means that edge-related species identified in the sandy forest-steppe ecosystems of the Carpathian Basin may not be associated with edges in other ecosystems. Those species that did not prove significantly related to any of the studied habitats may be termed edge-insensitive in this specific ecosystem (Ries and Sisk, 2010). Indeed, most reported edge responses are neutral (Ries et al., 2004). However, we think that most of these species do have a definite habitat preference in our case, but they are too rare to show statistically significant responses.

We found notable differences between north-facing and south-facing edges (Fig. 2, Tables S4 and S5). Edge orientation influences the energetic flows at edges, with south-facing edges receiving more sunlight than north-facing ones in the northern hemisphere (Ries et al., 2004). Accordingly, we found a higher number of xeric species at south-facing edges (e.g., *Bromus tectorum* and *Secale sylvestre)*, especially at the Kiskunság site, where edges lacked a protective cover of dense shrubs. At the same time north-facing edges hosted some species that are usually considered forest specialists (e.g., *Solidago virgaurea* and *Viola rupestris)*, or grow in more mesic grasslands (e.g., *Polygala comosa*).

4.2. *Taxonomic diversity*

Forest interiors had the lowest species richness and Shannon diversity in both sites (Fig. 3a, b). Earlier studies in the region (Erdős et al., 2018b, 2023) and in Kazakh forest-steppes (Bátori et al., 2018) have reported similar results; therefore, this seems to be a general phenomenon at the scale of the study (25 m^2).

A likely explanation for low diversity in forest patches is that a few shade-tolerant dominant species exclude the majority of other species beneath the dense canopy of a forest (Mészáros, 1981; Tilman and Pacala, 1993). Additionally, forests host trees with large diameters, implying that fewer vascular plant species will be sampled in a fine-scale plot, potentially leading to low species richness.

In the Kiskunság, edges (especially north-facing ones) had the highest species richness and Shannon diversity (Fig. 3a, b), which is consistent with the edge effect theory (Odum, 1971; Risser, 1995). Similar results were found in other xeric forest-grassland mosaics in Hungary (Erdős et al., 2014, 2023), Croatia (Erdős et al., 2019), and Kazakhstan (Bátori et al., 2018). However, we observed different patterns in the Deliblato, where edges and grasslands had similar species richness and Shannon diversity (Fig. 3a, b), i.e., no edge effect was found in this site. This finding is similar to those reported from rocky (Erdős et al., 2011) and loess forest-steppe (Chytrý et al., 2022) ecosystems and a forest-scrub ecotone (Lloyd et al., 2000). Thus, our results emphasize that the edge effect is not a general phenomenon. The findings of Stowe et al. (2003) and Walker et al. (2003) indicate that the detection of the edge effect may be scale-dependent, i.e., edges may have high species richness at certain scales, while their species richness may not differ from that of habitat interiors at other scales. In a recent study, Chytrý et al. (2022) reported high species richness at forest edges situated on rocky surfaces (andesite, dolomite, and limestone), while this was not the case for forest edges on loess. Thus, Chytrý et al. (2022) concluded that the existence of the edge effect may depend on substrate. Our finding, however, contradicts this view, as we found completely different patterns in the Kiskunság and the Deliblato, despite the similar sand substrate. Also, Chytrý et al. (2022) suggested that the edge effect may depend on the compositional similarity of the contacting forest and grassland habitats: the more different the adjacent habitats are, so the argument runs, the larger the species-pool of the forest edge can be. However, our results do not fit their idea. In our study, differences among the forest and the grassland habitats were more pronounced in the Deliblato (Fig. 2), yet no edge effect could be detected in that ecosystem.

In the Deliblato, species richness and Shannon diversity did not significantly differ between edges and grasslands (Fig. 3a, b), which is apparently in contrast to the edge effect hypothesis. There are several possible explanations why the edge effect was not observed at the Deliblato site. First, most edges in the Deliblato had a dense shrub layer, whereas edges with a dense shrub were not usually observed in the Kiskunság (Table S1). Dense shrubs may exclude many herb species, resulting in reduced diversity relative to that of grasslands. Second, grasslands of the Deliblato are closed (i.e, they have higher total cover values) than those of the sampled grasslands in the Kiskunság. Closed grasslands have been found to be more diverse than open grasslands owing to less harsh environmental conditions (Borhidi et al., 2012; Erdős et al., 2023). Thus, it is possible that the grasslands of the Deliblato are so species-rich that the edges cannot surpass this diversity. Similarly, Labadessa et al. (2017) found that neither species richness nor Shannon diversity nor

Simpson diversity showed a significant increase at the edge of species-rich semi-natural grasslands in Italy. Third, the balance between positive and negative species responses at the edge may also prevent the formation of an observable edge effect, that is, the number of species preferring edges may be offset by the number of species avoiding edges (Ries et al., 2004).

4.3. *Functional diversity*

We found that different patterns of multi-trait functional diversity existed at the two sites: the multi-trait functional diversity of woody habitats was significantly higher than that of the grasslands in the Kiskunság, whereas the multi-trait functional diversity of woody habitats and grasslands did not differ significantly in the Deliblato (Fig. 3c). The stress-dominance hypothesis states that functional diversity will be smaller under harsh conditions because of environmental filtering (Weiher and Keddy, 1995). Grasslands are harsher than forests because they are much more arid and show large temperature extremes, whereas forests are moister and have less extreme temperature conditions (Borhidi et al., 2012; Erdős et al., 2014, 2018b). Therefore, grasslands are predicted to have lower functional diversity than woody habitats. While our findings from the Kiskunság supported the stress-dominance hypothesis, the results from the Deliblato clearly contradicted this view.

Another surprising finding of our study was that the multi-trait functional diversity of woody habitats in the Kiskunság was higher than in the Deliblato (Fig. 3c). One possible explanation for this pattern may be the different openness of the woody habitats in the two sites: the tree/shrub canopy was much more open in the woody habitats in the Kiskunság than in the Deliblato (Table S1). An open canopy may enable the co-existence of species of various heights and life forms, possibly resulting in high functional diversity for these traits (Fig. 4d, e). Different seed masses may be adaptive for plants with different heights, resulting in high functional diversity for this trait (Fig. 4g).

A second explanation for the high functional diversity of the woody habitats in the Kiskunság may be provided by the reproduction type of the dominant species. *Populus alba*, the dominant species in the woody habitats of the Kiskunság, is the only species in our study that reproduces almost exclusively vegetatively. This means that it is functionally very different from all other species, which increases the pairwise functional differences among species, resulting in increased functional diversity for reproduction type (Fig. 4c). When *Populus alba* was removed from the data, the functional diversity for reproduction type was reduced drastically in the Kiskunság woody habitats (Fig. S2). Thus, we conclude that one frequent and dominant species can have a great effect on functional diversity for certain traits.

Lastly, there was higher variability in flowering time in the woody habitats of the Kiskunság than in those of the Deliblato. Particularly, in the Deliblato, the most dominant species started flowering in early summer (May or June), and the flowering duration was only two months. In contrast, these traits were more diverse in the Kiskunság, resulting in higher functional diversity for flowering time (Fig. 4a).

4.4. *Phylogenetic diversity*

Phylogenetic diversity peaked at the north-facing edges in the Deliblato, although this habitat did not differ significantly from the other woody habitats (Fig. 3d). However, if only angiosperm species were included in the analysis of phylogenetic diversity, the peak disappeared (Fig. 3e). This effect was likely caused by *Juniperus communis,* which is a common gymnosperm species at the north-facing edges of Deliblato but was not common at the north-facing edges of the study site in the Kiskunság, where no similar peak appeared. Other non-angiosperm species were rare; therefore, they had little influence on phylogenetic diversity.

The general pattern of phylogenetic diversity was similar in the Kiskunság and the Deliblato, i.e., forests and edges had higher phylogenetic diversity than grasslands. This result is in good agreement with previous findings reported from a Brazilian savanna ecosystem (Gastauer et al., 2017). Procheş et al. (2006), Lososová et al. (2015) and Gerhold et al. (2018) argued that phylogenetic diversity is determined by evolutionary history: evolutionarily old habitats are expected to possess higher phylogenetic diversity than evolutionarily young habitats. Our results seem to confirm this view, as woody habitats have a much longer history in the region (dating back to the Mesozoic) than grassland habitats (dating back only to the late Tertiary) (Lososová et al., 2015).

Some previous studies suggested that low species richness is usually accompanied by low functional and phylogenetic diversity in both plant (Cadotte et al., 2009; Jucker et al., 2013; Selvi et al., 2016) and animal communities (Jacoboski et al., 2016; Martello, 2018; Junggebauer et al., 2021). However, in line with Bernard-Verdier et al. (2013), Bässler et al. (2016), and Doxa et al. (2020), our results emphasize that species richness is not always predictive of functional or phylogenetic diversity.

4.5. *Limitations of the current study*

When evaluating the results of the present work, some considerable limitations of the study have to be taken into account. To ensure comparability, we selected two study sites in relative proximity, but this entails that one has to be careful when drawing general conclusions from this study. This is especially true for functional and phylogenetic diversity, where similar studies along interior-edge-exterior gradients are extremely rare.

Although the two study sites are located in the same biogeographical region and are very similar in terms of climate, soil, vegetation, landscape pattern, and land-use history, there are undoubtable differences between them, which could have influenced the results. For example, the Kiskunság is in the center of the Carpathian Basin, while the Deliblato is near its southern periphery. This small biogeographical difference means that the two sites were differently available to immigrant steppe species during the Holocene through a southeastern and a northwestern corridor (Magyari et al., 2010). In addition, the climate is slightly different, with somewhat higher mean annual temperature and mean annual precipitation at the Deliblato site. Also, there are minor differences in altitude (110–130 m asl for the Kiskunság site and 140–160 m for the Deliblato site). Finally, the species composition and the structure of the vegetation also shows differences. For example, forest patches are typically larger and both the forest canopy and the grassland have larger total cover values in the Deliblato than in the Kiskunság.

5. Conclusions and future directions

Our results showed that forest edges in the study systems had rather distinct species composition and their own set of diagnostic species that avoid habitat interiors. This lends support to the view that forest edge should be considered a community in its own right, rather than a simple mix of the two neighboring communities.

While species richness and Shannon diversity were found to be highest at edges in the Kiskunság, this was not the case in the Deliblato, indicating that the edge effect hypothesis is not a general rule. There is a need for more studies, especially in natural and near-natural ecosystems to discern at which scales and under what circumstances (e.g., soil, edge structure, characteristics of the adjacent vegetation units, etc.) the edge effect hypothesis can be confirmed.

The multi-trait functional diversity was significantly higher in woody habitats (forest patches and edges) than in grasslands in the Kiskunság, while it was similar among the four habitat types in the Deliblato. This clearly contradicts the stress-dominance hypothesis and emphasizes that functional diversity depends on several factors such as canopy openness and the traits of the dominant species. We conclude that it is too early to draw general conclusions on functional diversity patterns across edges.

We found that phylogenetic diversity was higher in woody habitats than in grasslands, which may be explained by the younger evolutionary age of grasslands. Our study showed that taxonomic diversity is not always indicative of functional and phylogenetic diversity.

Our study should be understood as a tentative step to better understand multiple aspects of diversity across edges in near-natural ecosystems. We would like to stress that future works on diversity patterns should include the analysis of functional and phylogenetic diversity.

Ethics statement

Permission to carry out fieldworks in the protected areas was granted by the Pest County Government Office, Department of Environmental Protection, Nature Conservation, and Waste Management, Hungary (permit no. PE/KTFO/1615/2021) and the Ministry of Environmental Protection, Republic of Serbia (permit no. 353–01–1266/2022–04).

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CRediT authorship contribution statement

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Khanh Vu Ho, Mirjana Ćuk, Tijana Šikuljak, Zoltán Bátori, Csaba Tölgyesi, Attila Fűrész, Péter Török, Alida Anna Hábenczyus, Anna Hegyesi, Z. Ladin Coşgun and László Erdős. The first draft of the manuscript was written by Khanh Vu Ho and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Declaration of Competing Interest

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

Data Availability

The datasets generated and analyzed during the current study are available in the Zenodo repository, https://zenodo.org/record/7675504#. ZCNEoPbMKUk.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02625.

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Supporting information

Forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity

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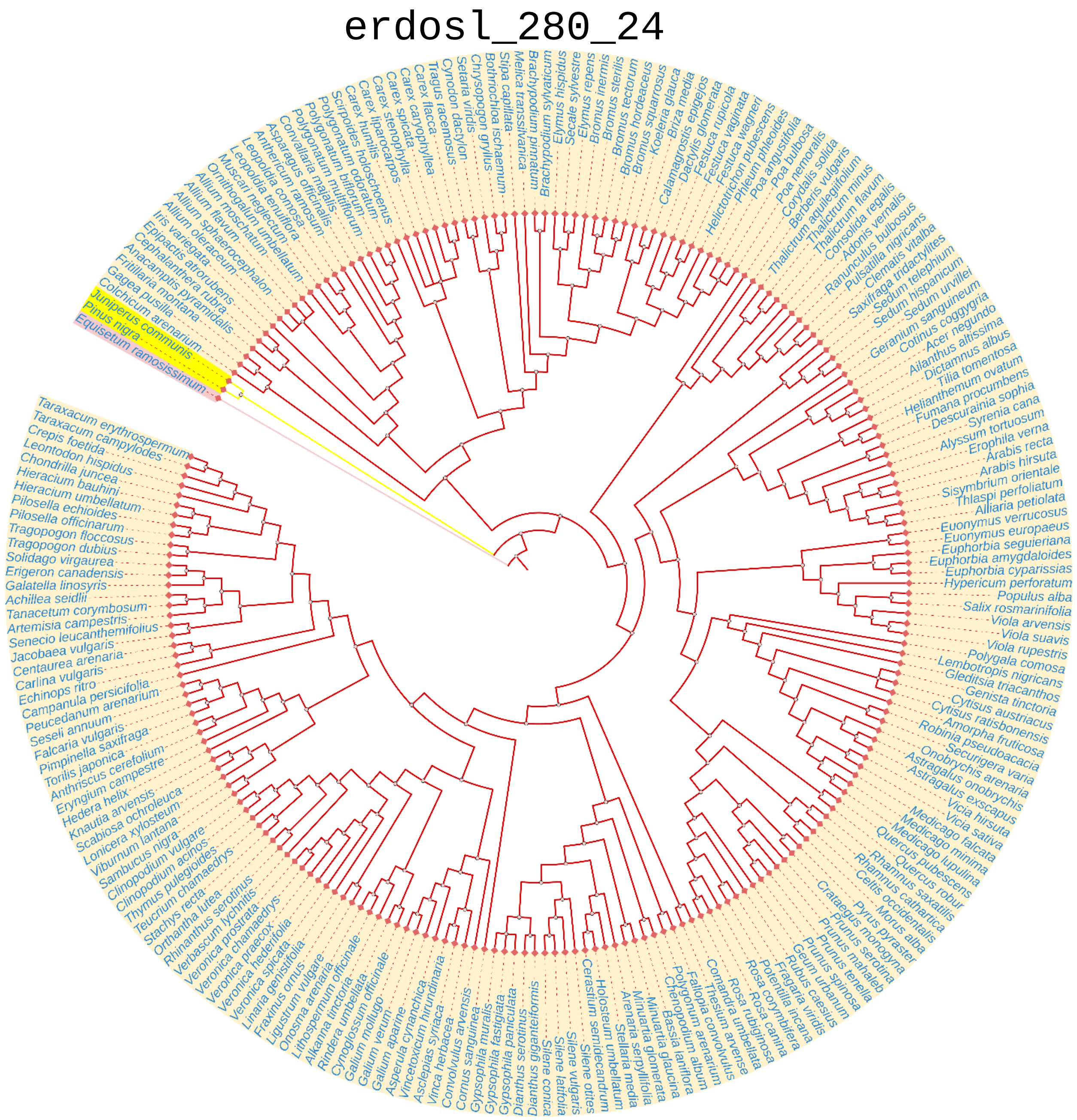

Figure S1. Phylogenetic tree containing 225 species. The purple zone includes one pteridophyte species, the yellow zone includes two gymnosperms species, while the remaining species are angiosperms.

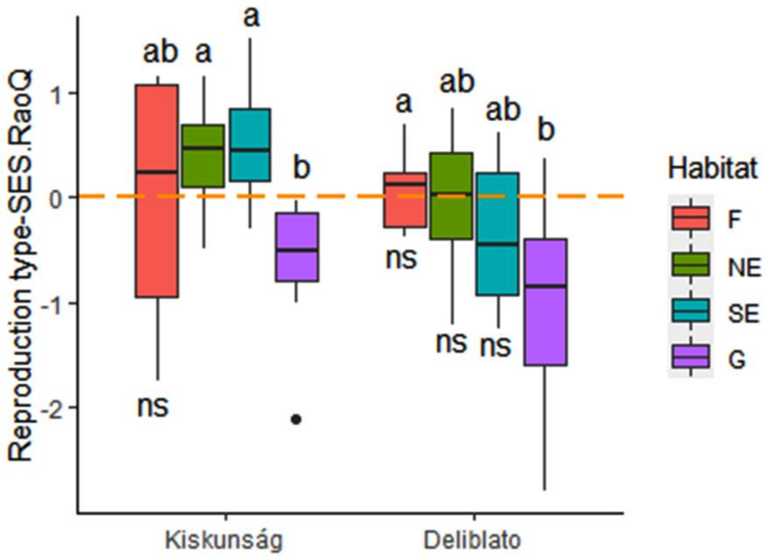

Figure S2. Functional diversity of reproduction type, with *Populus alba*excluded. F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland. Habitats not sharing a letter are significantly different. Null model expectation is indicated by a dashed horizontal line. Negative SES value indicates an underdispersed habitat; positive SES value indicates an overdispersed habitat; "ns" indicates no significant difference (= a random pattern) between the observed SES values and the null model expectation (based on a two-sided Wilcoxon signed rank test).

Table S1. Data on the cover value (%) of the canopy, shrub, and herb layers (mean ± standard error, n=10) in four habitat types in the Kiskunság Sand Ridge and the Deliblato sands. F: forest, NE: north-facing edge, SE: south-facing edge, G: grassland.

	Kiskunság Sand Ridge				Deliblato sands			
	F	NE	SE	G	F	NE	SE	G
Canopy cover	48.5±5.05	41.5±3.07	46.5±6.19	0.00±0.00	78.6±3.00	18.81±6.01	28.5±6.79	0.00±0.00
Shrub cover	58.9±5.24	32.1±7.22	26.3±5.15	0.05±0.05	42.5±4.99	83.1±12.3	87.1±12.6	0.00±0.00
Herb cover	32.0±8.38	52.1±4.55	65.7±5.43	60.1±3.37	27.9±6.07	69.1±6.59	67.4±8.83	75.2±5.55
Total cover	139±9.35	126±4.35	139±11.4	60.1±3.40	149±9.34	171±10.5	183±10.2	75.2±5.55

Table S2. Details of the nine traits used for the functional diversity analyses

Trait	Data type	Source
Flowering start	Nominal with three levels: blooming from early spring (Months 1 to 4); blooming from early summer (Months 5 and 6); blooming from late summer (Months 7 to 9)	Király (2009), Josifović (1970-1977)
Flowering duration	Numeric (number of months)	Király (2009), Josifović (1970-1977)
Specific leaf area (SLA)	Numeric (mm^2/mg)	Kleyer et al. (2008), Lhotsky et al. (2016), E-Vojtkó et al. (2020), Gyalus et al. (2022), McIntosh-Buday et al. (2022)
Mean plant height	Numeric (cm)	Király (2009), Josifović (1970-1977)
Thousand seed mass	Numeric (g)	Török et al. (2013, 2016), Royal Botanic Gardens Kew (2017)
Life-form type	Fuzzy coding with 8 levels: tree and shrub; semishrub; dwarf shrub; hemicryptophyte; geophyte; therophyte; hemitherophyte; epiphyte	Horváth et al. (1995), Király (2009)

Seed dispersal type	Fuzzy coding with 4 levels: anemochor; rainwash; autochor; zoochor	Fitter and Peat (1994); Csontos et al. (2002); Royal Botanic Gardens Kew (2017); USDA Forest Service (2017)
Pollination type	Fuzzy coding with 3 levels: insects; wind; self-pollination	Fitter and Peat (1994); Kühn el al. (2004); USDA Forest Service (2017)
Reproduction type	Fuzzy coding with 2 levels: generative; vegetative	Kühn et al. (2004)

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Table S3. Statistical results of the pairwise comparisons of species composition. F: forest, NE: north-facing edge, SE: south-facing edge, G: grassland.

Pair	Kiskunság Sand Ridge			Deliblato sands		
	F	R2	p-value	F	R2	p-value
F-NE	6.89	0.277	0.006	13.4	0.426	0.006
F-SE	9.97	0.357	0.006	13.6	0.430	0.006
F-G	31.8	0.639	0.006	25.4	0.585	0.006
NE-SE	2.80	0.135	0.012	2.34	0.115	0.036
NE-G	17.4	0.491	0.006	10.9	0.379	0.006

SE-G	11.1	0.381	0.006	9.23	0.339	0.006

Table S4. Significant (P < 0.01) diagnostic species of the four habitats with phi coefficients > 0.200 in the the Kiskunság Sand Ridge. F: forest, NE: north-facing edge, SE: south-facing edge, G: grassland.

Species	F	NE	SE	G
Bromus sterilis	0.565			
Cynoglossum officinale	0.564			
Taraxacum officinale agg.	0.564			
Ligustrum vulgare	0.505			
Thymus pannonicus		0.730		
Carlina vulgaris		0.716		
Pinus nigra		0.642		
Scabiosa ochroleuca		0.617		
Leontodon hispidus		0.584		
Thesium ramosum		0.584		
Viola rupestris		0.566		
Polygala comosa		0.564		
Viola arvensis			0.500	
Bromus tectorum			0.480	
Euphorbia cyparissias			0.480	
Secale sylvestre			0.480	
Fumana procumbens				0.872
Erophila verna				0.854
Holosteum umbellatum				0.775
Polygonum arenarium				0.775
Arenaria serpyllifolia				0.730
Syrenia cana				0.690
Alkanna tinctoria				0.664
Cerastium semidecandrum				0.652
Crepis rhoeadifolia				0.584
Tragus racemosus				0.564
Poa bulbosa				0.521
Bothriochloa ischaemum				0.480
Stipa borysthenica+capillata				0.432

Table S5. Significant ($P < 0.01$) diagnostic species of the four habitats with phi coefficients > 0.200 in the the Deliblato sands. F: forest, NE: north-facing edge, SE: south-facing edge, G: grassland

Species	F	NE	SE	G
Convallaria majalis	0.743			
Cornus sanguinea	0.743			
Viburnum lantana	0.730			
Polygonatum latifolium	0.722			
Lonicera xylosteum	0.694			
Tilia tomentosa	0.505			
Alliaria petiolata	0.500			
Securigera varia		0.775		
Fragaria viridis		0.774		
Rindera umbellata		0.730		
Bromus mollis		0.694		
Viola suavis		0.690		
Solidago virgaurea		0.584		
Achillea pannonica		0.550		
Knautia arvensis		0.480		
Rhamnus saxatilis subsp. tinctoria		0.461	0.461	
Euphorbia cyparissias		0.456	0.456	
Seseli annuum		0.432		
Veronica hederifolia			0.565	
Silene alba			0.564	
Elymus hispidus			0.529	
Chrysopogon gryllus			0.519	
Festuca rupicola+valesiaca			0.432	
Cerastium semidecandrum				0.872
Holosteum umbellatum				0.788
Onobrychis arenaria				0.722
Polygala comosa				0.722
Potentilla arenaria				0.705
Peucedanum arenarium				0.645
Euphorbia seguieriana				0.606
Artemisia campestris				0.566
Centaurea arenaria				0.565
Elymus repens				0.565
Acinos arvensis				0.564
Bothriochloa ischaemum				0.564
Crepis rhoeadifolia				0.564
Galium verum				0.557
Thymus pannonicus				0.531
Asperula cynanchica				0.494
Stipa borysthenica+capillata				0.490
Alyssum tortuosum				0.480
Helianthemum ovatum				0.480
Dianthus pontederae				0.432

Table S6. Statistical results between observed SES.RaoQ values and the null model expectation (two-sided Wilcoxon signed rank test). F: forest, NE: north-facing edge, SE: south-facing edge, G: grassland.

Site	Habitat	SES.RaoQ (FD for all traits)		SES.RaoQ (PD for all species)		SES.RaoQ (PD for only angiosperms)	
		V	P	V	P	V	P
Kiskunság	F	50	0.019	0	0.0019	28	1
	NE	55	0.0019	18	0.375	36	0.432
	SE	55	0.0019	0	0.0019	25	0.846
	G	5	0.019	0	0.0019	0	0.002
Deliblato	F	2	0.006	1	0.0039	48	0.037
	NE	0	0.0019	34	0.556	55	0.002
	SE	2	0.006	10	0.084	35	0.492
	G	0	0.0019	0	0.0019	0	0.002

Table S6 (continued)

Site	Habitat	SES.RaoQ (FD for flowering time)		SES.RaoQ (FD for seed dispersal)		SES.RaoQ (FD for reproduction type)		SES.RaoQ (FD for plant height)	
		V	P	V	p	V	p	V	P
Kiskunság	F	53	0.006	52	0.009	55	0.002	55	0.002
	NE	53	0.006	55	0.002	55	0.002	55	0.002
	SE	54	0.004	55	0.002	55	0.002	55	0.002
	G	16	0.275	22	0.625	23	0.695	3	0.009
Deliblato	F	0	0.002	52	0.009	28	1	55	0.002
	NE	0	0.002	32	0.695	25	0.846	47	0.048
	SE	0	0.002	54	0.004	17	0.322	55	0.002
	G	28	1	12	0.131	1	0.004	0	0.002

Table S6. (continued)

Site	Habitat	SES.RaoQ (FD for life form)		SES.RaoQ (FD for SLA)		SES.RaoQ (FD for seed mass)		SES.RaoQ (FD for pollination type)	
		V	p	V	p	V	p	V	P
Kiskunság	F	1	0.004	3	0.009	54	0.004	54	0.004
	NE	6	0.027	0	0.002	39	0.275	42	0.160
	SE	32	0.695	1	0.004	18	0.375	19	0.432
	G	1	0.004	0	0.002	1	0.004	45	0.084
Deliblato	F	0	0.002	15	0.2324	12	0.131	47	0.049
	NE	0	0.002	0	0.002	11	0.106	30	0.846
	SE	0	0.002	0	0.002	31	0.769	33	0.625
	G	0	0.002	0	0.002	0	0.002	54	0.004

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Research Article

Forest encroachment in Eastern European forest-steppes at a decadal time scale

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Abstract

In the Eurasian forest-steppe, with increasing aridity, the balance between naturally co-existing forest and grassland patches is expected to shift towards grassland dominance in the long run, although feedback mechanisms and changes in land-use may alter this process. In this study, we compared old and recent aerial photographs of Hungarian forest-steppes to find out whether and how the forest proportion and the number of forest patches change at the decadal time scale. The percentage area covered by forest significantly increased in all study sites. The observed forest encroachment may be a legacy from earlier land-use: due to ceased or reduced grazing pressure, forests are invading grasslands until the potential forest cover allowed by climate and soil is reached. The number of forest patches significantly increased at one site (Fülöpháza), while it decreased at two sites (Bugac and Orgovány) and showed no significant change at the fourth site (Tázlár). This indicates that forest encroachment can happen at least in two different ways: through the emergence of new forest patches in the grassland, and through the extension and coalescence of already existing forest patches. Though the present work revealed increasing tree cover at a decadal time scale, the dynamic process should be monitored in the future to see how the vegetation reacts to further aridification. This could help devise a conservation strategy, as the woody/non-woody balance has a profound influence on basic ecosystem properties.

Keywords: forest–grassland dynamics, grazing, semi-open ecosystems, tree–grass ecosystems, woody–herbaceous ecosystems

东欧森林-草原中十年尺度的森林扩张研究

摘要：随着干旱程度的增加，欧亚森林草原地区森林与草地之间的平衡预计会逐渐向草地倾斜。本研究通过比较匈牙利森林草原地区以往和近期的航拍照片，探讨了在10年时间尺度上森林的比例和森林斑块数量是否以及如何发生变化。研究结果显示，所有研究地点的森林覆盖面积百分比显著增加。这种森林扩张可能是早期土地利用的遗留效应：由于放牧压力的消失或减少，森林逐渐侵入草地，直到达到气候

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和土壤条件允许的潜在森林覆盖程度。森林斑块数量在一个研究样点(Fülöpháza)显著增加，而在另外两个研究样点(Bugac 和Orgovány)减少，第四个研究样点(Tázlár)未见显著变化。上述结果表明森林扩张至少可以通过草地中新森林斑块的出现、现有森林斑块的扩展和合并两种不同的方式发生。未来研究仍需继续监测森林动态过程，以便揭示植被如何应对进一步的干旱化。同时，考虑到树木与草本植物之间的平衡对生态系统属性会产生深远影响，长期监测森林动态过程将有助于制定相应的保护策略。

关键词：森林-草地动态，放牧，半开放生态系统，树木-草地生态系统，木本-草本生态系统

INTRODUCTION

Forest–grassland mosaics represent an intermediate state between treeless grasslands and closed-canopy forests (Breshears 2006). Featuring a mosaic of woody and herbaceous components, these ecosystems include open woodlands, tropical and subtropical savannas, the North American prairie-forest ecotone and Eurasian forest-steppes. They cover a considerable proportion of the Earth's terrestrial surface, support high biodiversity, host many endangered and endemic taxa, and provide essential ecosystem services for humans, but are threatened by various anthropogenic effects, such as land-use change, biological invasions and climate change (e.g. Archer 2010; Bond 2019; Erdős *et al.* 2022). To efficiently preserve, restore and manage these ecosystems, we need an in-depth understanding of the balance between woody and herbaceous components and how this is affected by changing abiotic and biotic drivers (House *et al.* 2003).

Recent decades have witnessed considerable changes in the woody/herbaceous proportion in these ecosystems. The increasing dominance of trees and shrubs (usually referred to as woody plant encroachment) is a widespread phenomenon worldwide (e.g. Archer 2010; Briggs *et al.* 2005; García Criado *et al.* 2020; Wang *et al.* 2024), but the reverse process, i.e. the spread of grasslands at the expense of forests, has also been documented (Kharuk *et al.* 2013a, 2013b). The exact causes are not yet fully understood, but changes in climate, modifications in fire regime and/or grazing/browsing pressure, increasing aerial nitrogen deposition, the rise of atmospheric CO_2 concentration, and the spread of invasive woody species have all been suggested as potential drivers (Archer *et al.* 2017; Briggs *et al.* 2005). Shifts in dominance patterns are of utmost ecological importance, as they entail fundamental changes in key ecosystem properties and processes (Archer 2010).

The Eurasian forest-steppe biome is a 9000 km long and, on average, 400 km wide zone extending from the Carpathian Basin (East Central Europe) to the Russian and Chinese Far East (Erdős *et al.* 2022). Situated between temperate or boreal forests and open grasslands, forest-steppes are characterized by a mosaic of relatively distinct forest and grassland patches, the proportion of which is primarily regulated by climate, complemented by topography, soil, herbivores and fire (Erdős *et al.* 2022).

Due to the strong climatic control, forest-steppes are expected to react sensitively to global climate change (Erdős *et al.* 2018). Drought and heat stress can limit tree growth and can eventually lead to tree mortality either directly or through making trees more vulnerable to herbivores and parasites (McDowell *et al.* 2008). With increasing temperature and decreasing summer precipitation, the forest-steppe zone is predicted to shift northwards (Angerer *et al.* 2008; Shvidenko *et al.* 2017; Tchebakova *et al.* 2016), while the forest cover is expected to decrease in current forest-steppe regions (Angerer *et al.* 2008; Dulamsuren *et al.* 2008, 2010; Ishii and Fujita 2013). The decline of woody vegetation has been observed in some forest-steppe ecosystems. For example, in the Kuznetzky Alatau Mountains (at the northern edge of the forest-steppe zone in Siberia), increasing *Pinus sibirica* mortality and decreasing growth have been attributed to drought (Kharuk *et al.* 2013a). Liu *et al.* (2013) found widespread tree mortality and decreased tree growth at Inner Asian forest-steppe sites in response to reduced water availability. Also, decreasing soil moisture and increasing temperature in Siberia during the 20th and early 21st centuries have resulted in *Betula pendula* mortality, especially at stand margins, where the space under the dying trees is quickly occupied by grassland communities (Kharuk *et al.* 2013b). The study of Hickler *et al.* (2012) predicts that the forest-steppes in the centre of the Carpathian Basin will give way to treeless steppes in the long term due to climate change. In the long term, the expansion of grasslands and a parallel decrease in forest cover can be expected in forest-steppe ecosystems if the climate becomes more arid.

However, strong feedbacks between vegetation and the environment tend to stabilize existing forest–grassland patterns and may be able to prevent changes in forest vs. grassland proportion (Erdős *et al.* 2022). Forest patches can modify the below-canopy environment in a way that supports the germination and survival of trees and prevents the establishment of most grassland-related species (Erdős *et al.* 2021; Süle *et al.* 2020; Tölgyesi *et al.* 2018). At the same time, the grassland environment is rather hostile for tree germination and seedling establishment (Dulamsuren *et al.* 2008; Erdős *et al.* 2014). Thus, the proportion of forest and grassland patches may remain constant in spite of the aridification of climate, or may follow climate trends only after a lag phase.

Changes in land-use may further complicate the picture. For example, grazing/browsing pressure from domestic animals is able to constrain woody vegetation in the Eurasian forest-steppe (e.g. Takatsuki *et al.* 2018; Török *et al.* 2018). Forest-steppes used to be grazed by native herbivores, which were replaced by domestic animals (Erdős *et al.* 2022). During the 20th century, grazing ceased in many forest-steppes across Eastern Europe (Török *et al.* 2020), which may result in increasing forest cover in the region.

Fire events (both natural and anthropogenic) may contribute to the stabilization of the existing forest–grassland pattern, as they kill tree seedlings in the grassland component, while wildfires of low to medium intensity do little harm to forest patches (Erdős *et al.* 2022). However, intense fires may reduce or eliminate the woody component, especially if these fires occur frequently.

Despite the large extent and high conservation and economic importance of the Eurasian forest-steppe, studies examining the long-term dynamics of forest-steppe ecosystems are, as yet, very scarce. In this work, we compared old and recent aerial photographs of Hungarian forest-steppe sites. Our aim was to investigate whether and how the forest proportion and the number of forest patches have shifted in forest-steppe ecosystems at the decadal time scale.

MATERIALS AND METHODS

Study sites

We conducted our study in the Kiskunság Sand Ridge in central Hungary (Carpathian Basin, Eastern Europe), a region severely affected by aridification (Rakonczai 2011). The natural vegetation of the region is a mosaic of woody and non-woody habitats (Erdős *et al.* 2018). To select the study sites, all forest-steppe mosaics in the Kiskunság were taken into account, but only those were included in the study (i) for which the land-use history was known and (ii) a period of at least 20 years free of major human interventions could be reliably identified. Sites were not excluded from the analysis if a low level of grazing was present, as grazing constituted a natural part of the forest-steppe dynamics (Erdős *et al.* 2022).

Based on the above criteria, we selected four study areas: Bugac, Fülöpháza, Orgovány and Tázlár (Fig. 1; Table 1). The climate of the sites is sub-continental, with sub-Mediterranean influences; the mean annual temperature varies between 10.2 and 10.5 °C across the sites, while the mean annual precipitation ranges between 520 and 550 mm (1961–1990; Dövényi 2010). The sites experienced significant increases in mean annual temperature between 1971 and 2019, while no significant change could be revealed for annual precipitation (Fig. 2, detailed data are provided in Supplementary Figs S1 and S2). The drying tendency of the climate is exacerbated by local to regional processes such as irrigation from subsurface sources and the establishment of drainage canals (Tölgyesi *et al.* 2021). Moreover, large-scale afforestation, largely with non-native evergreen conifers, further contributes to the aridification of the region (Tölgyesi *et al.* 2023), as evergreen trees, unlike native deciduous ones, evaporate water throughout the year. As a result, water-table depth has dropped considerably during the last few decades (Farkas *et al.* 2017). For example, between 1970 and 2010, the average annual water-table depth sank ca. 2 m in Bócsa (close to our Bugac site) (Rakonczai 2011).

Each site is characterized by stabilized calcareous sand dunes with humus-poor sandy soils that have poor water retention capacity (Várallyay 1993). The vegetation of the sites is a mosaic of forest patches and various grasslands. Forests are dominated by *Populus alba*, while *Festuca vaginata*, *Stipa borysthenica* and *Stipa capillata* co-dominate the most widespread grassland type. Less common grassland types are dominated by *Festuca rupicola*, *Festuca wagneri* or co-dominated by *Secale sylvestre* and *Bromus tectorum*. A more detailed description of the vegetation can be found in Erdős *et al.* (2023).

The Bugac site became legally protected in 1975 as part of the Kiskunság National Park. Grazing ended here around 1930. Wildfires happened in 1976 and 1983 due to nearby military activity, but the areas affected by these fires were excluded from the study.

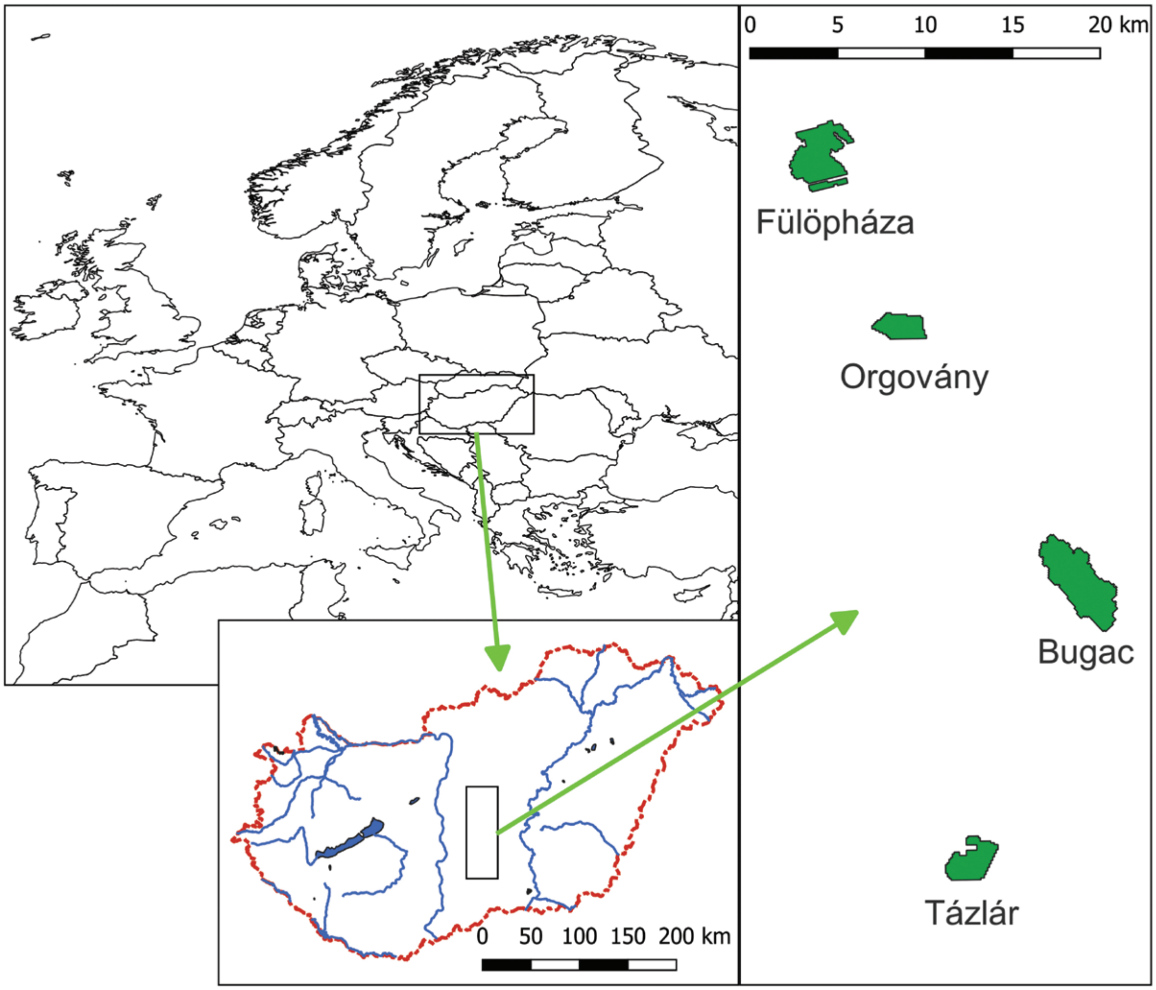

Figure 1: The position of the four study sites in Hungary. Site coordinates are provided in Table 1.

Table 1: Coordinates of the centroids of the study sites, the number of 1 ha cells covering the sites and appropriate for the analyses, the number of selected cells, the dates of the aerial photos and the periods covered by the study

ID	Site	Longitude	Latitude	Number of appropriate cells	Number of selected cells	Archive photo	Recent photo	Period (years)
1	Bugac	E 19.593587°	N 46.657820°	333	10	1976	2009	33
2	Fülöpháza	E 19.406393°	N 46.881320°	451	15	1975	2019	44
3	Orgovány	E 19.464459°	N 46.791246°	343	10	1976	2000	24
4	Tázlár	E 19.508251°	N 46.515596°	468	15	1989	2019	30

A major wildfire in 2012 affected almost the whole area; therefore, our study period ended in 2009, when the last aerial photograph was taken prior to this fire. The Fülöpháza site has been protected since 1975 as part of the Kiskunság National Park. Grazing ended here in the 1970s and no wildfires have happened during the last decades. The Orgovány site has also been protected since 1975 as part of the Kiskunság National Park. A very low grazing was present and there was a major wildfire in 2000. Thus, our study period ended in 2000, when an aerial photograph was taken shortly before the fire. The Tázlár site, which belongs to the Natura 2000 protected area network of the European Union, was occasionally grazed, and no fires occurred here. Restricted forestry such as the removal of invasive trees was present at the sites, but areas affected by this activity were excluded from the analysis.

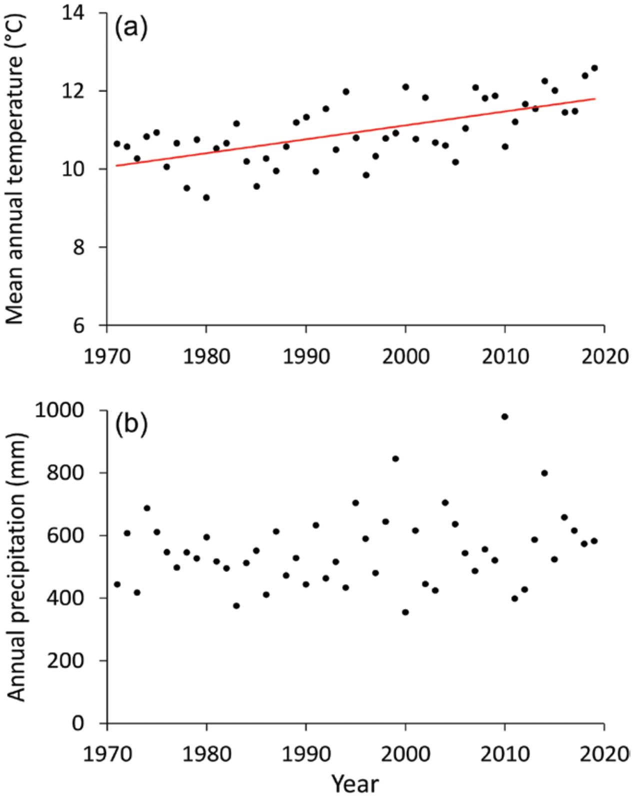

Figure 2: (a) Changes in mean annual temperature averaged across the four study sites between 1971 and 2019 (adjusted $R^2 = 0.40$, $t = 5.72$, $P < 0.001$). (b) Changes in average annual precipitation across the four study sites between 1971 and 2019 (adjusted $R^2 = 0.03$, $t = 1.57$, $P = 0.123$). Data are from the Hungarian Meteorological Survey.

Aerial photograph analyses

For each of the four sites, we identified the periods during which there was no major human disturbance. We then searched for archives and recent aerial photographs of the sites. Our aim was to find archive photos that were taken around the beginning of the intervention-free period, and recent photos towards the end of the intervention-free interval (Table 1).

The archive aerial photos were black and white, while recent photos were in true colour (see Fig. 3 for an example). The aerial photographs were taken during the growing season and depict a leafy state.

The survey was conducted on representative samples of the four study sites. For sampling, the sites were covered with a 1-ha square grid. We selected those parts of the grid that included natural forest-steppe. Thus, plantations and agricultural areas occurring near the edges of the sites were excluded from the sampling. The number of cells covering the study sites is shown in Table 1.

We randomly selected 10 or 15 cells from the grids covering the study sites. In the 1 ha cells, we digitized the extent of the forest vegetation in the archive and the recent photos. Since the pixel size of aerial photos is 0.5 m, the accuracy of the digitization is approx. 1 m. For each cell, two variables were calculated: the proportion of the forest vegetation and the number of forest patches. A forest patch was regarded as separate from other forest patches if its canopy layer was not in contact with any other forest patch (i.e. if it was surrounded by grasslands in all directions). The geospatial procedures were performed in QGIS (QGIS.org 2023).

Statistical analyses

The proportion of the forest vegetation and the number of forest patches were statistically compared between the old and the recent states. The Shapiro–Wilk normality test was used to analyse data distribution. If the data set was normally distributed (forest cover: Bugac and Orgovány, forest patch number: all sites), we evaluated it by paired *t*-test, and if the data distribution was not normal (forest cover: Fülöpháza and Tázlár), we used the Wilcoxon signed-rank test in the coin package (Hothorn *et al.* 2006). Analyses were carried out in R version 4.3.2 (R Core Team 2023).

RESULTS

The percentage area covered by forest significantly increased in all four study sites (Bugac: $t = 5.68$, $P < 0.001$; Fülöpháza: $Z = 3.41$, $P < 0.001$; Orgovány: $t = 8.97$, $P < 0.001$; Tázlár: $Z = 3.24$, $P < 0.001$) (Figs 3 and 4). There were considerable differences among the four sites regarding both the initial forest cover and the change in forest cover during the study periods. The initial forest cover was the lowest at the Fülöpháza site (mean: 1.22%), where it increased more than tenfold during 44 years. The initial forest cover was the highest at the Bugac site, where the mean forest cover increased from 65.68% to 83.23% during 33 years. The Orgovány and the Tázlár sites were between the above two extremes regarding the mean initial forest cover (22.15% and 18.82%, respectively), and the final forest cover values were 46.74% and 32.62%, respectively.

The number of forest patches significantly decreased at two sites (Bugac: $t = -4.42$, $P = 0.02$; Orgovány: $t = -3.27$, $P = 0.01$): at the Bugac site, the

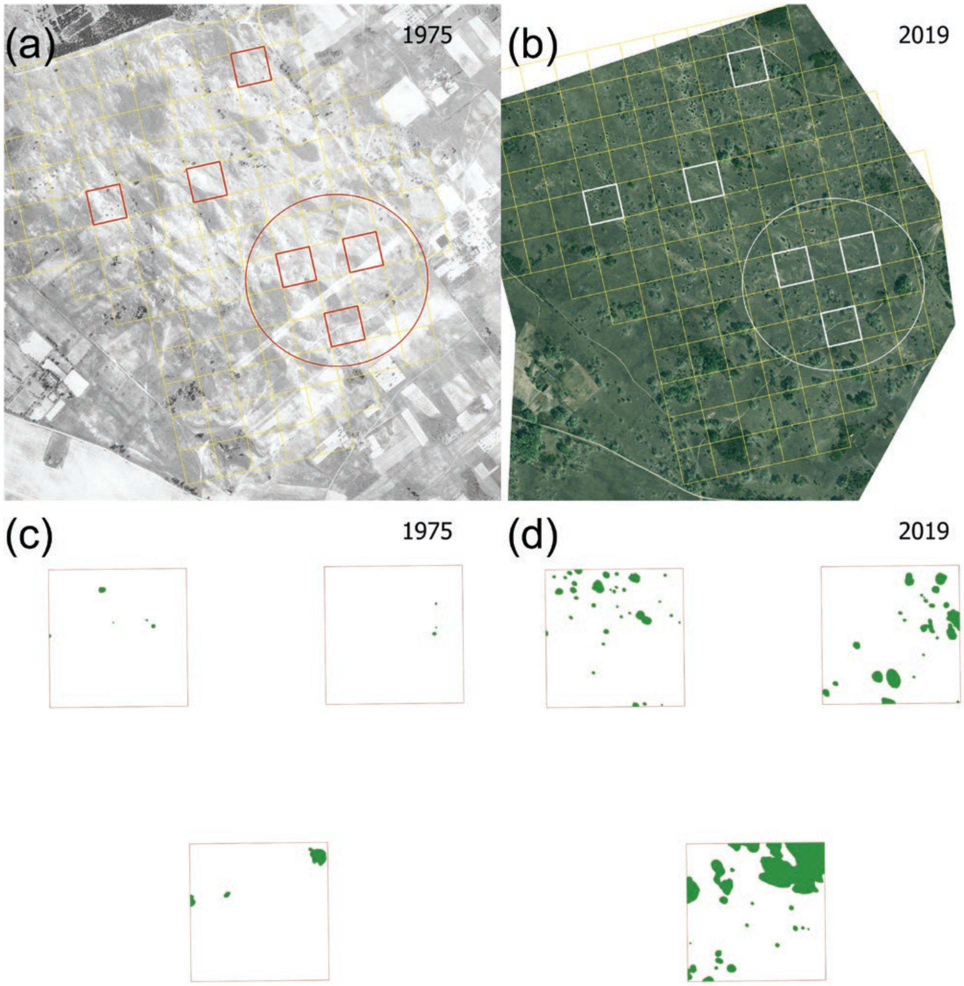

Figure 3: A section of the Fülöpháza site in (a) the old (1975) and (b) the recent (2019) aerial photographs with the grid consisting of 1 ha cells; cells selected for the analyses are highlighted. The lower panels show the extent of forest patches in three cells in the years (c) 1975 and (d) 2019.

mean number of forest patches per 1 ha dropped from 46 to 5.9, while there was a decrease from 41.1 to 20.1 patches at the Orgovány site (Fig. 5). In contrast, there was a significant increase in forest patch number at the Fülöpháza site ($t = 4.39$, $P < 0.001$); here, the mean number of forest patches per 1 ha increased from 6.73 to 20.13. At the Tázlár site, there was no significant change in the number of forest patches ($t = 1.18$, $P = 0.3$).

DISCUSSION

The decadal-scale dynamics of forest–grassland mosaics is an important issue because the balance between the two strongly dissimilar components has a major influence on the overall biodiversity, conservation status and function of these ecosystems (e.g. Ónodi *et al.* 2021; Teleki *et al.* 2020). While there have been several studies in tropical mosaics, the Eurasian forest-steppe is almost entirely unstudied in this respect (but see Liu *et al.* 2021; Teleki *et al.* 2020). A better understanding of how forest-steppes react to changes in the environment or land-use is essential for their effective conservation management and restoration.

We detected increasing forest cover for all of our study sites. This fits worldwide observations on current woody encroachment tendency in several forest–grassland mosaics (e.g. Liu *et al.* 2021; Saintilan and Rogers 2015; Stevens *et al.* 2017). Also, a recent plot resurvey study focussing on the grasslands of the Kiskunság Sand Ridge found that *P. alba*, the dominant tree species of the region, has become significantly more frequent during 17 years, its small individuals being able to spread in grasslands (Erdős *et al.* 2024). We think that there are two possible explanations for the process observed in the forest-steppes of the Kiskunság Sand Ridge.

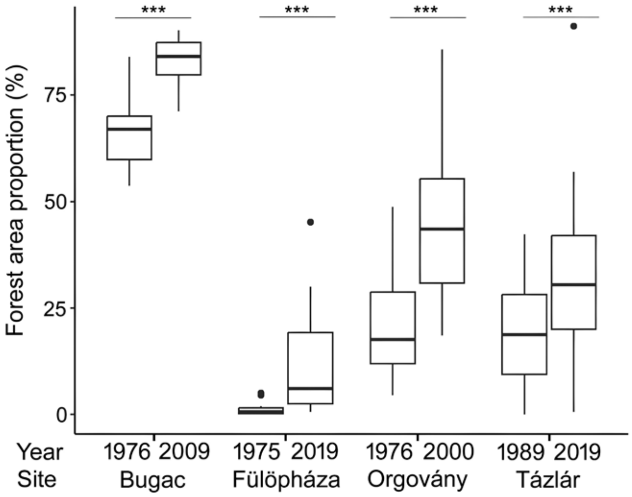

Figure 4: Percentage of forest cover of the 1 ha plots according to the archive and recent aerial photos. ***$P \leq 0.001$.

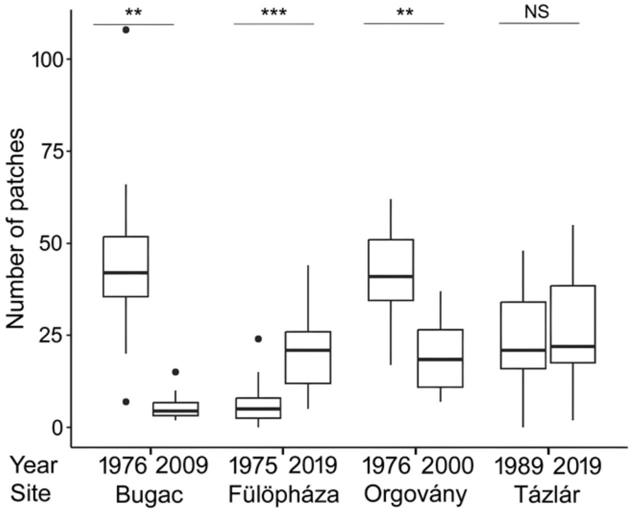

Figure 5: The number of forest patches according to the archive and the recent photos. **$P \leq 0.01$; ***$P \leq 0.001$; NS: $P > 0.05$.

First, increasing temperature (especially in winter) and increasing CO_2 concentration may have a positive impact on forests, provided that water is not limiting (Boisvenue and Running 2006; Way and Oren 2010). Although mean annual temperature shows an increasing trend in our study region, this, as yet, is not accompanied by decreasing annual precipitation (Fig. 2). This climate warming should be favourable for forest growth and associated woody expansion, if water is available for trees in sufficient quantity. Also, it seems that the drop of the water table is not able to reduce forest cover. The dominant tree species of the study sites is *P. alba*, which is known for being able to tolerate extremely hot and dry conditions (Kopecky 1978; Majer 1968). Furthermore, *P. alba* spreads primarily vegetatively, through horizontal roots. The individual trees are able to allocate resources through these roots, which may have a length of 40 m or more (Halupa 1967; Magyar 1961). Thus, trees situated in a very dry micro-environment may receive constant support from trees situated in a better micro-environment such as a dune slack. Also, older trees that reach deeper and moister soil layers are able to provide younger saplings with water. As a result, forest patches are able to withstand a certain level of aridification. Thus, the forest encroachment shown by the present work may indicate that increased temperature and CO_2 concentration shifted the forest–grassland balance towards a more forested landscape (Fig. 6). Forests are spreading until the new (increased) potential forest cover is reached. However, with further increases in temperature, forest encroachment is expected to stop and may even turn into forest retreat: increasing temperature promotes forests only until either the thermal optimum of the dominant tree species is passed, or water availability is compromised (Way and Oren 2010). Simulations show a further increase in temperature and a decrease in precipitation in the Carpathian Basin during the 21st century (Pieczka *et al.* 2011). The largest warming and a significant drop in precipitation are expected for summer, accompanied by more frequent and more intense drought periods (Pongrácz *et al.* 2014). These changes might result in decreasing forest cover in forest-steppe ecosystems.

Second, the current forest encroachment may simply be a legacy from earlier land-use. Two of our study sites were not grazed during the study period (Bugac and Fülöpháza sites), but they had been grazed in earlier times. The other two sites experienced light grazing during the study period (Orgovány and Tázlár sites), but grazing pressure had been almost certainly much higher prior to the study period. In the Eurasian forest-steppe, most large herbivores are either browsers (e.g. goats) or mixed grazers/browsers (e.g. cattle and sheep), and therefore are able to limit forest expansion (Erdős *et al.* 2022). Once grazing ceases or diminishes in a given area, forests are released from this pressure and can invade grasslands until the climatic–edaphic potential of forest cover is reached (Fig. 6).

A closer look at the history of the study sites suggests that the current increase in forest cover may be the result of ceased or reduced grazing. By far the largest initial forest cover (ca. 66%) was revealed at the Bugac site, where grazing ended around 1930. Here, forest

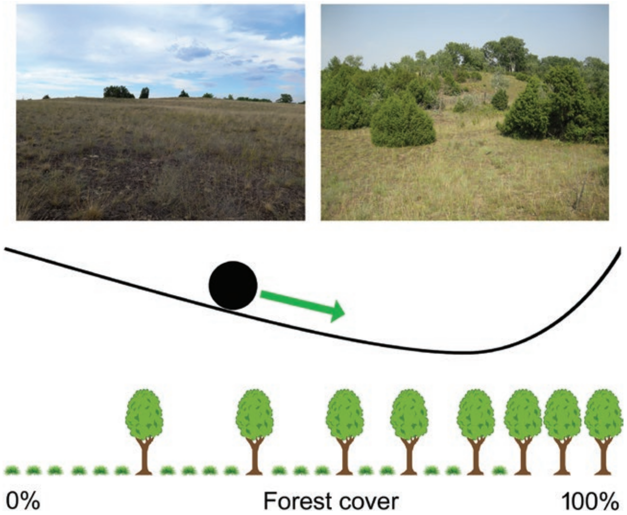

Figure 6: Ball-and-cup model of the forest-steppe ecosystem under study. The current state of the ecosystem is represented by the black ball, while the deepest point of the cup is the equilibrium state allowed by climate and soil. The ecosystem is proceeding towards a higher forest cover either because increased temperature and CO_2 concentration favour woody vegetation or because forests have been released from grazing. The two insets show two states of the ecosystem with lower and higher woody cover.

vegetation had a relatively long time to recover: by the time our old aerial photo was taken in 1976, the fast-growing and rapidly spreading *P. alba* had re-occupied large areas. In contrast, the lowest initial forest cover (ca. 1%) was at the Fülöpháza site, where grazing ended only in the 1970s (i.e. grazing ended around the time when our old aerial photo was taken). Here, the forest had little opportunity to recover.

An earlier study lends further support to our view that the current forest encroachment is actually forest spread after the cessation of grazing. Erdős *et al.* (2015) examined forest–grassland dynamics in a protected forest-steppe in the Kiskunság Sand Ridge, where grazing has been prohibited since 1885. The study revealed a high (ca. 72%) forest cover in 1953, indicating an advanced state of forest recovery.

To sum it up, we believe that the current forest encroachment at the study sites is driven primarily by land-use changes rather than changes in abiotic environmental factors. This is also suggested by the different initial forest cover values between the Bugac and the Fülöpháza sites, which have very similar abiotic environmental factors but time since grazing abandonment differs strongly between them.

Determining the equilibrium forest cover for a given region (i.e. the potential forest cover allowed by climate and soil) is a very important question both from a theoretical and a practical perspective. For example, during restoration programmes, it is essential to have a basic idea of the intended target state. Erdős *et al.* (2015) found that forest cover showed very little increase during a 60-year interval (from ca. 72% to 73%) in a forest-steppe reserve, and they concluded that the forest cover was already close to the potential allowed by climate and soil. Our present work leads to a different conclusion, as we found that forest cover increased well beyond this point at the Bugac site, reaching a mean forest cover of over 83%. However, it has to be noted that grazing and wildfires could considerably reduce forest cover allowed by climate and soil. Unfortunately, very little is known about the natural fire regime in the Eurasian forest-steppe. According to recent literature, fire-free intervals varied from a few years to several centuries during the Holocene (Erdős *et al.* 2022); how much they limited forest cover remains unknown. Similarly, our knowledge about the density of native herbivores that were once widespread in the forest-steppe is so limited that we can only speculate about how strongly they used to limit forest cover. Also, it should be noted that there may be variations in potential forest cover according to climatic or soil variations among individual sites (Kovács-Láng *et al.* 2000).

There was a marked increase in the number of forest patches at the Fülöpháza site, while the reverse process occurred at the Bugac and the Orgovány sites. This shows that forest encroachment can happen at least in two different ways. First, new forest patches can emerge in the grassland, and this seems typical at sites where the initial forest cover is low. Second, existing forest patches extend their area and coalesce, which is more typical at sites that have a higher initial forest cover.

While the cessation of grazing and browsing is suggested to play a prime role in current forest encroachment in our study system, other driving forces are at work in other similar ecosystems of the world. In North American prairies, fire suppression is regarded as the main cause behind increasing woody plant cover, which view is supported by ample empirical evidence (e.g. Helser 2010; Miller *et al.* 2017; Ratajczak *et al.* 2014). Interestingly, in sharp contrast to our results, grazing seems to increase woody cover in some North American prairie ecosystems. For example, in the Kansas tallgrass prairie, grazing was shown to decrease fuel load, which leads to reduced mortality of woody plants caused by fire, resulting in increased *Juniperus virginiana* dominance (Briggs *et al.* 2002). Modifications in climate have also been shown to potentially increase woody plant cover. In the southern Canadian prairie-forest ecotone, *Pinus contorta* encroachment into *Festuca campestris* grassland was found to be driven by the lack of fire, increasing spring temperature, and increasing autumn precipitation (Widenmaier and Strong 2010). All this suggests that forest encroachment has regionally different causes, depending, among others, on climatic conditions or the fire susceptibility of the dominant woody plants.

Forest encroachment and an associated upward shift of the treeline are happening in mountainous regions all around the globe (Holtmeier and Broll 2007). In most cases, the primary driver of the process is land abandonment (mostly the cessation of grazing) rather than climate warming (e.g. Aakala *et al.* 2014; Ameztegui *et al.* 2016; Holtmeier and Broll 2007; Schickhoff *et al.* 2015). This is similar to our findings, which also suggest a prominent role of land-use legacy in a very different environmental setting, indicating that forest encroachment may be the result of the release from grazing/browsing pressure.

Unfortunately, very few forest-steppes have survived in Hungary, and there are even fewer for which the land-use history is sufficiently known to exclude the possibility of major human interventions during the last couple of decades. A possible future avenue for our work is to carry out similar studies in other sandy forest-steppes in the Eastern European region and beyond, within a larger context of the Eurasian forest-steppe biome. Another possibility is to make similar analyses on forest-steppe ecosystems growing on other types of bedrock. Forest-steppe mosaics on loess have been completely destroyed in the region, but there are still some forest-steppes on rocky surfaces, where similar studies may provide valuable information on decadal-scale dynamics. Also, studying tree growth and regeneration in the forest interiors, forest edges and grasslands could provide useful information on dynamic processes in the forest-steppes of the Eastern European region.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Changes in mean annual temperature at the four study sites separately, between 1971 and 2019.

Figure S2: Changes in average annual precipitation at the four study sites separately, between 1971 and 2019.

Authors' Contributions

László Erdős: conceptualisation (lead), funding acquisition (lead), investigation (supporting), methodology (supporting), project administration (lead), supervision (lead), writing – original draft preparation (lead), writing – review & editing (lead); Gábor Ónodi: investigation (supporting), writing – original draft preparation (supporting), writing – review & editing (supporting); Csaba Tölgyesi: investigation (supporting), methodology (supporting), writing – original draft preparation (supporting), writing – review & editing (supporting); György Kröel-Dulay: investigation (supporting), writing – original draft preparation (supporting), writing – review & editing (supporting) Zoltán Bátori: investigation (supporting), writing – original draft preparation (supporting), writing – review & editing (supporting); Eszter Aradi: investigation (supporting), writing – original draft preparation (supporting), writing – review & editing (supporting); Péter Török: funding acquisition (lead), writing – original draft preparation (supporting), writing – review & editing (supporting); Khanh Vu Ho: investigation (lead), methodology (lead), writing – original draft preparation (lead), writing – review & editing (lead); Indri Puspitasari: investigation (lead), methodology (lead), writing – original draft preparation (lead), writing – review & editing (supporting); László Körmöczi: investigation (lead), methodology (lead), project administration (supporting), writing – original draft preparation (lead), writing – review & editing (lead).

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Conflict of interest statement. The authors declare that they have no conflict of interest.

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Supplementary Material

Figure S1: Changes in mean annual temperature at the four study sites separately, between 1971 and 2019. (a) Bugac (adjusted $R^2 = 0.393$, $t = 5.66$, $P < 0.001$), (b) Fülöpháza (adjusted $R^2 = 0.406$, $t = 5.81$, $P < 0.001$), (c) Orgovány (adjusted $R^2 = 0.398$, $t = 5.72$, $P < 0.001$) and (d) Tázlár (adjusted $R^2 = 0.392$, $t = 5.65$, $P < 0.001$). Data are from the Hungarian Meteorological Survey.

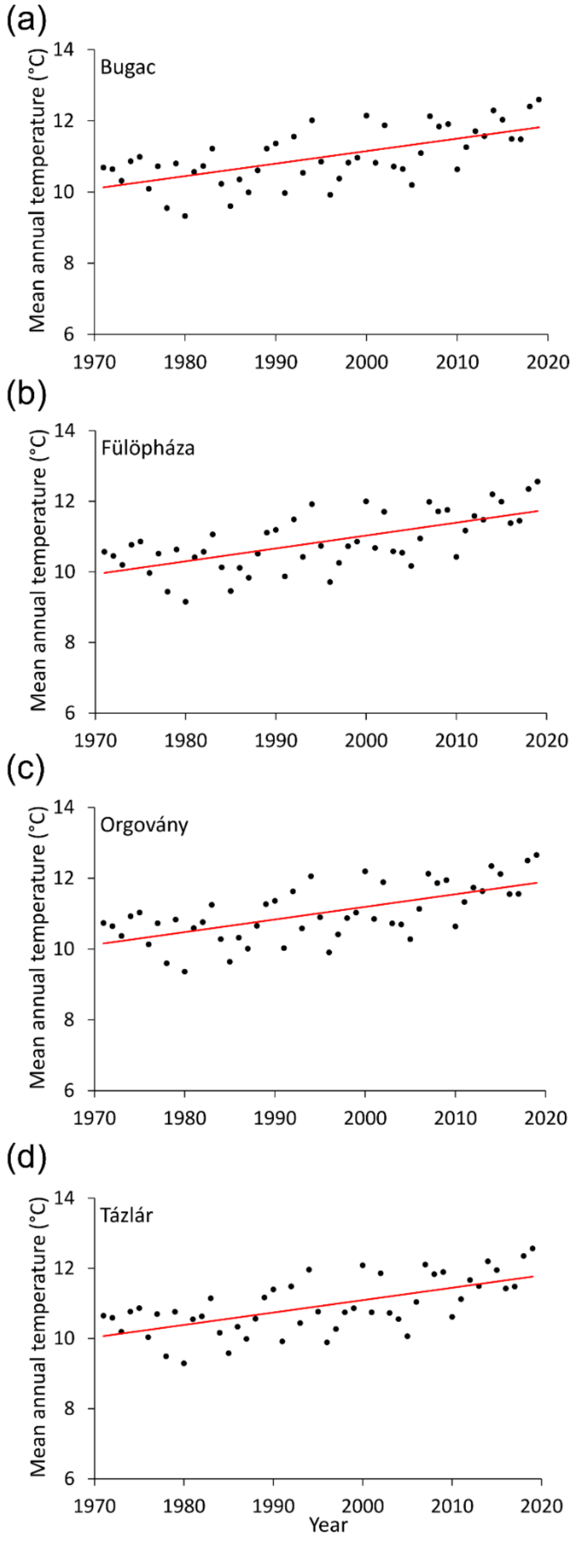

Figure S2: Changes in average annual precipitation at the four study sites separately, between 1971 and 2019. (a) Bugac (adjusted $R^2 = 0.032$, $t = 1.6$, $P = 0.116$), (b) Fülöpháza (adjusted $R^2 = 0.048$, $t = 1.85$, $P = 0.071$), (c) Orgovány (adjusted $R^2 = 0.039$, $t = 1.73$, $P = 0.091$) and (d) Tázlár (adjusted $R^2 = 0.003$, $t = 1.06$, $P = 0.289$). Data are from the Hungarian Meteorological Survey.