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CONSERVATION IMPORTANCE OF HABITAT HETEROGENEITY IN PANNONIAN SANDY FOREST-STEPPES

Summary of Ph.D. dissertation

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NEW SCIENTIFIC RESULTS

- A compositional gradient was arranged along the vegetation cover gradient from closed woodland to open annual grassland. Taxonomic, functional and phylogenetic diversity did not follow the same pattern. An edge effect was detected for species richness, while functional and phylogenetic diversity was higher in woody habitats than in the grasslands.
- The studied habitats were dominated by the stress-tolerant strategy, but this strategy decreased towards the forests and the importance of the competitor strategy showed a reverse trend, whereas the stress-tolerant strategy was supplemented by the R strategy in open grasslands.
- The compositional and CSR strategy gradients were confirmed by the results of the microclimate study and the importance of tree cover in mitigating harsh climatic conditions was demonstrated.
- The results demonstrated the conservation importance of remnant near-natural forest patches compared to plantations and evaluated three main plantation types in terms of native, non-native species, conservation, taxonomic, functional and phylogenetic diversity, resulting in clear suggestions for nature conservation and forestry.
- A comparative study with Deliblato Sands confirmed the existence of edges in sandy forest steppe based on species composition and prevalently edge-related diagnostic species, but did not confirm the existence of edge effects for Deliblato, probably due to the high species richness of grasslands in the area.

1. Introduction

The alternative stable state hypothesis suggests that in certain ecosystems, two or more states (e.g. forest and grassland) can coexist 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). Eurasian forest-steppes, representing an ecosystem with alternative stable states, constitute a transitional zone between closed-canopy forests and grasslands, spanning from the Pannonian region to the Russian and Chinese Far East (Erdős et al., 2018a). The vast majority of previous research and practical efforts in nature conservation have concentrated on either the grassland or forest state separately (e.g., Török et al., 2014, Dieler et al., 2017, Ónodi et al., 2021, Reis et al., 2021), but the combined study of differently-sized forest and grassland patches of various types, and especially an intricate network of differently exposed edges, is under-researched.

The various habitat types in the forest-steppe ecosystem may possess distinct features, which can have profound implications for conservation strategies. For instance, in the sandy forest-steppes of the Pannonian region, the most species-rich habitats are forest edges, while grasslands host the highest number of protected and rare species (Erdős et al., 2018b). The limited number of studies that considered different habitat types solely focused on taxonomic diversity, overlooking other aspects of diversity, such as functional or phylogenetic diversity measures (Bátori et al., 2018, Erdős et al., 2018b, Chytrý et al., 2022).

Understanding the mechanisms of assembly and the influencing factors allows ecologists to anticipate the success of invasions or the responses of communities to environmental changes at local, regional, or global levels (Cavender-Bares et al., 2009). The ecological strategy based on traits (i.e., traits that are directly connected to the CSR strategies) may be used to provide information about the primary drivers that determine community composition (Grime and Pierce, 2012). Currently, knowledge of CSR strategies is still unknown in forest-steppe ecosystems, which may limit understanding of habitat heterogeneity.

Microclimate has a significant effect on vegetation, but the knowledge of microclimate variables in forest-grassland mosaics is still rather limited. Up to now, microclimate parameters were only measured for a very short period, typically 24 hours on a single summer day (Erdős et al., 2014c, 2018b, Bátori et al., 2014; Tölgyesi et al., 2018; Milošević et al., 2020). Moreover, earlier studies usually did not take into account the full variety of forest-grassland mosaics: some works disregarded the edge habitat (e.g., Tölgyesi et al., 2018; Milošević et al., 2020), while others restricted their attention to small forest patches and a single type of grassland (e.g., Erdős et al., 2014c; Süle et al., 2020). Thus, it is necessary to measure long-term microclimate conditions in a broader spectrum of near-natural forest-steppe habitats.

Tree plantations are widespread in Pannonian forest-steppe landscapes (Molnár et al., 2012; Wesche et al., 2016; Erdős et al., 2018a), but their impact on forest-steppe vegetation remains unknown. Knowing how well the plantations can provide habitats for native species, particularly those that are rare and endangered, is crucial for conservation objectives. Also, a better understanding of what extent tree plantations of various species can substitute near-natural forests in terms of different aspects of diversity (taxonomic, functional and phylogenetic) is necessary.

Although studies of edges and the two adjacent habitats in forest-grassland mosaics are increasing, our knowledge regarding how composition, taxonomic, edge-related species, functional, and phylogenetic diversity patterns change across edges is very limited.

2. Aims and study questions

2.1. General aim and specific objectives

The general aim of this doctoral research was to provide information on the habitat heterogeneity of sandy forest-steppes to support the conservation of this ecosystem in the Pannonian region. Based on the general aim, the specific objectives were to reveal:

- how species composition, as well as taxonomic, functional, and phylogenetic diversity, vary in eight connected habitat types (large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, closed perennial grasslands, open perennial grasslands, and open annual grasslands) found in a sandy forest-steppe ecosystem (**study 1**);
- what the dominant CSR strategies and assembly processes of the eight habitats of sandy forest-steppes are (**study 2**);
- What the microclimate conditions of seven common habitat types (large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, open perennial grasslands, and open annual grasslands) throughout the vegetation period are in a sandy forest-steppe ecosystem (**study 3**);
- how the species composition, diversity, and ecological value of near-natural forests differ from those of various types of tree plantations (native deciduous, non-native evergreen, and non-native deciduous) in a region whose natural forests were transformed to tree plantations (**study 4**);
- how the species composition and diversity of edge habitats (i.e., north-facing forest edges and south-facing forest edges) are related to those of two habitat interiors (i.e., forests and grasslands) in two forest-steppe ecosystems in the Pannonian region (forest-steppes in the Kiskunság Sand Ridge, Hungary and the Deliblato Sands, Serbia) (**study 5**).

2.2. Study questions

In order to clarify the specific objective of each study, the specific questions were the following in each study:

- **Study 1:** (1) Is there a compositional gradient from large forest patches to open annual grasslands in a sandy forest-steppe ecosystem when eight habitats (large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, closed perennial grasslands, open perennial grasslands, and open annual grasslands) are considered together? (2) Do edges have their own species that are rare in other habitats? (3) Does taxonomic diversity peak at forest edges, and gradually decrease both towards forest patches and grasslands? (4) Do functional and phylogenetic diversity have a similar pattern with taxonomic diversity?
- **Study 2:** (1) Taking into account the eight habitats mentioned above, is community composition driven by competitive exclusion in the more productive environment of forest

patches? (2) Is stress (i.e., environmental filtering) the most important driver under the harsher conditions of open grasslands? (3) Which habitats are most affected by disturbance?

- **Study 3:** (1) How do air temperature and humidity differ among the studied habitats (large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, open perennial grasslands, and open annual grasslands) during the growing season from April to October? (2) Which habitats are more stressed to vegetation growth in terms of vapor pressure deficit?
- **Study 4:** (1) How distinct or overlapping is the species composition of the four studied habitats (i.e. near-natural forests, native deciduous, non-native evergreen, and non-native deciduous tree plantations)? (2) How do taxonomic, functional, and phylogenetic diversity indices vary among the four habitat types? (3) What is the ecological value of the studied habitats in terms of protected, endemic, and red-listed species and naturalness status?
- **Study 5:** (1) Does the species composition of the edges (i.e., north-facing forest edges and south-facing forest edges) differ from the two habitat interiors (i.e., forests and grasslands)? (2) Do edge-related species (i.e. species that favor edge habitats and are rare or absent in habitat interiors) exist? (3) Do taxonomic, functional, and phylogenetic diversity of the edges differ from those of the forests and grasslands?

3. Literature overview

3.1. Definition of forest-steppes

Forest-steppes are considered the most diverse and dynamic biomes in temperate regions (Sottile et al., 2015; Erdős et al., 2018a). According to Erdős et al. (2018a), forest-steppes are defined as natural and near-natural ecosystems that pose differently-sized forest patches (e.g. small, medium, and large forests) interspersed with grasslands (e.g., open and closed grasslands) in the temperate zone. From 10% to 70% is covered by arboreal components and at least 10% is covered by vascular plants in the grassland component. Forest-steppe has a wide range of names such as "open woodland", "wooded-steppe", "sparse arid woodland" and "steppe forest" (Erdős et al., 2018a).

3.2. Main regions of forest-steppes

Forest-steppes are distributed in North America (e.g., Nuzzo, 1986; Anderson et al., 1999; Leach and Givnish, 1999; Fowler and Beckage, 2020), South America (e.g., Aguiar and Sala, 1994; Sottile et al., 2015) and Eurasia (e.g., Erdős et al., 2018a; 2019a). The following is a basic description of the main regions where forest-steppes can be found.

3.2.1. Forest-steppes in North America

Based on the climate conditions, savannas vary in ecological features, and not all of them may be classified as forest-steppes. For example, tropical and subtropical savannas occurring in Africa and Australia are not regarded as forest-steppes. However, savannas in North America can be considered as forest-steppes, as they represent a woodland-grassland mosaic under temperate climate conditions, spreading from south-central Canada to northern Mexico (e.g., Fowler and Beckage, 2020). Apart from savannas, Pinyon-Juniper woodland and Aspen parklands are also other types of forest-steppes in North America. To the best of our knowledge, forest-steppes in North America may be classified into five primary types as follows:

a. Midwestern oak Savannas

These savannas are located in Ohio, Indiana, Michigan, Illinois, Wisconsin, Minnesota, Missouri, and Iowa (Bray, 1958; Madany, 1981; Nuzzo, 1986, Betz and Lamp, 1990; Ko and Reich, 1993; Anderson et al., 1999; Brock and Brock, 2004; Ebinger et al., 2006; Karnitz and Asbjornsen, 2006; Jackson, 2009; Phillippe et al., 2008, 2011; Dey and Kabrick, 2015) (Fig. 1a). The total area had a sharp reduction of 99.88%. In 1985, only 2,607 hectares of high-quality oak savannas were found in the Midwest (Nuzzo, 1986). Midwestern oak savannas are one of the most important forest-steppes in North America (Nuzzo, 1986; Dey and Kabrick, 2015).

This region has a humid continental climate (Wall and Parrish, 2014), with warm summers and cold winters. The annual rainfall averages 780-980 mm, with the most precipitation from May to June (115-124 mm). The mean annual temperature is 8.5-9.9 ^{o}C, the hottest and coldest months are July (average 22.3-23.6 ^{o}C) and January (average from -7.9 to -5.7 ^{o}C), respectively. The number of frost-free days registers 161-174 (Ko and Reich, 1993; Ebinger et al., 2006, Phillippe et al., 2011). Forest-steppes occupy plains, valleys, sand dunes, and rolling hills. The average elevation varies from 180 to 360 m a.s.l. The soils are well-drained, fine-textured and acidic with low fertility (Madany, 1981; Nuzzo, 1986; Anderson et al., 1999).

Forest patches are dominated by oak trees, including *Quercus macrocarpa*, *Q. alba*, *Q. velutina*, and *Q. ellipsoidalis*. The native shrubs include *Cornus alterniflora, Lonicera canadensis, L. reticulate, Prunus americana,* and *Salix exigua*. In the Midwest, there are two types of grasses (cool- and warm-season grasses). The warm-season grasses can be called "prairie grasses", with some common species such as *Andropogon gerardii, Bouteloua curtipendula, Panicum virgatum, Schizachyrium scoparium, Sorghastrum nutans, Spartina pectinate,* and *Sporobolus heterolepis*. Meanwhile, the cool grasses are known as "savanna grasses". The dominant species are *Bromus kalmia, Calamagrostis canadensis, Elymus canadensis, Koeleria macrantha,* and *Stipa spartea.*

b. California oak savannas

They are primarily found in the California Central Valley, coastal California, Transverse Ranges, Sierra Nevada foothills, and Peninsular Ranges (Anderson et al., 1999; Fowler and Beckage, 2020; Tyler and Stahlheber, 2020) (Fig. 1a). The total area of these savannas is about 3 million ha (Tyler and Stahlheber, 2020).

Forest-steppes occupy multiple terrains (valley floors, alluvial terraces, slopes, and some high mountains), with elevation from 60-700 m a.s.l. This leads to various soil types such as rich loams, rocky, sand, and slopes (Tyler and Stahlheber, 2020). This region is characterized by the Mediterranean climate, with cool and wet winters but hot and dry summers. 90% of rainfall falls in the winter and early spring (from December to March), with a total annual precipitation of 400-800 mm. However, the drought period is varied from February to November. The annual temperature averages 14-17 ^{o}C (Tyler and Stahlheber, 2020).

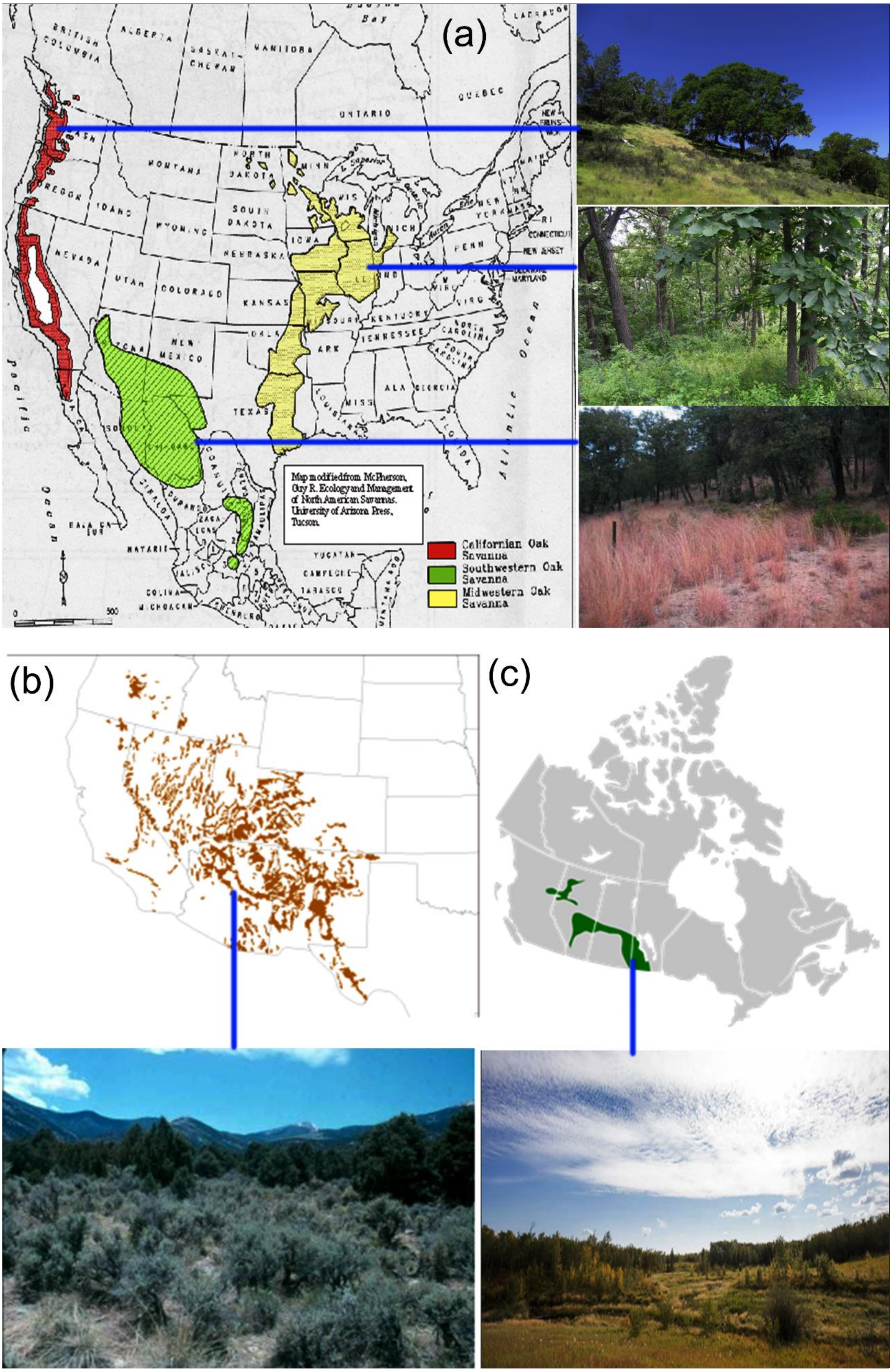

Figure 1. Examples of main types of forest-steppes in North America: (a) oak savannas, (b) Pinyon-Juniper Woodland and (c) Aspen parklands

(Source of figure: Brock, 2010; Nature Conservancy of Canada, 2019; Fowler and Beckage, 2020; Wrangle, 2020)

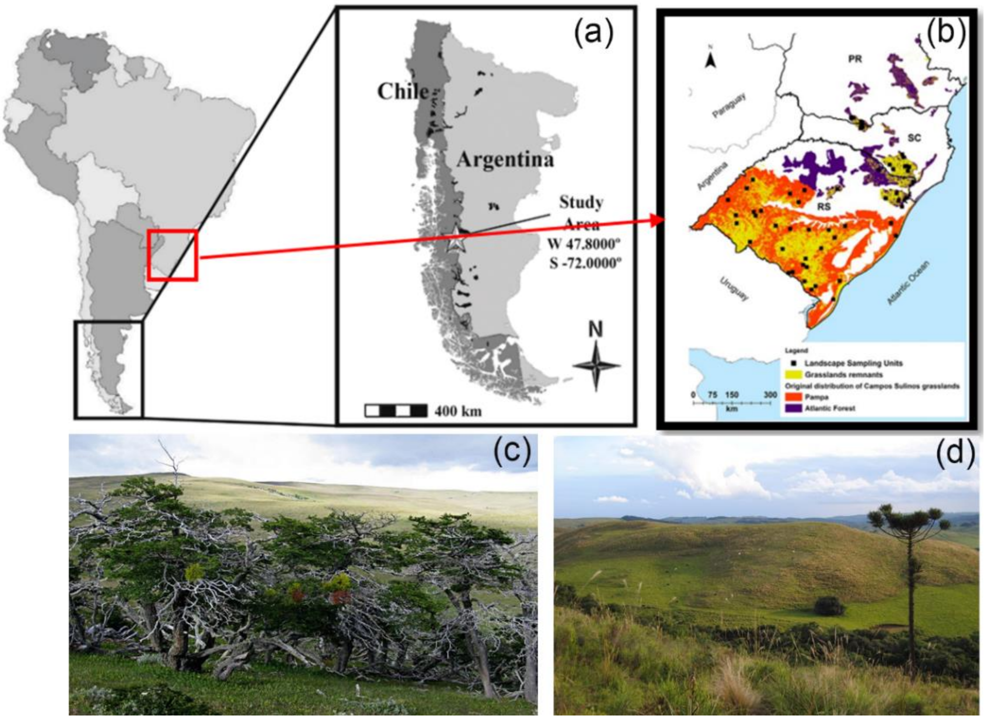

Figure 2. Examples of forest-steppes in South America: *Nothofagus* forest-steppes in Panagonia (a, c) and *Araucaria* forest-steppes in Southern Brazil (b, d)
(Source of figure: Elbroch and Wittmer, 2013; Veldman et al., 2015; Andrade et al., 2018; Vettese et al., 2020)

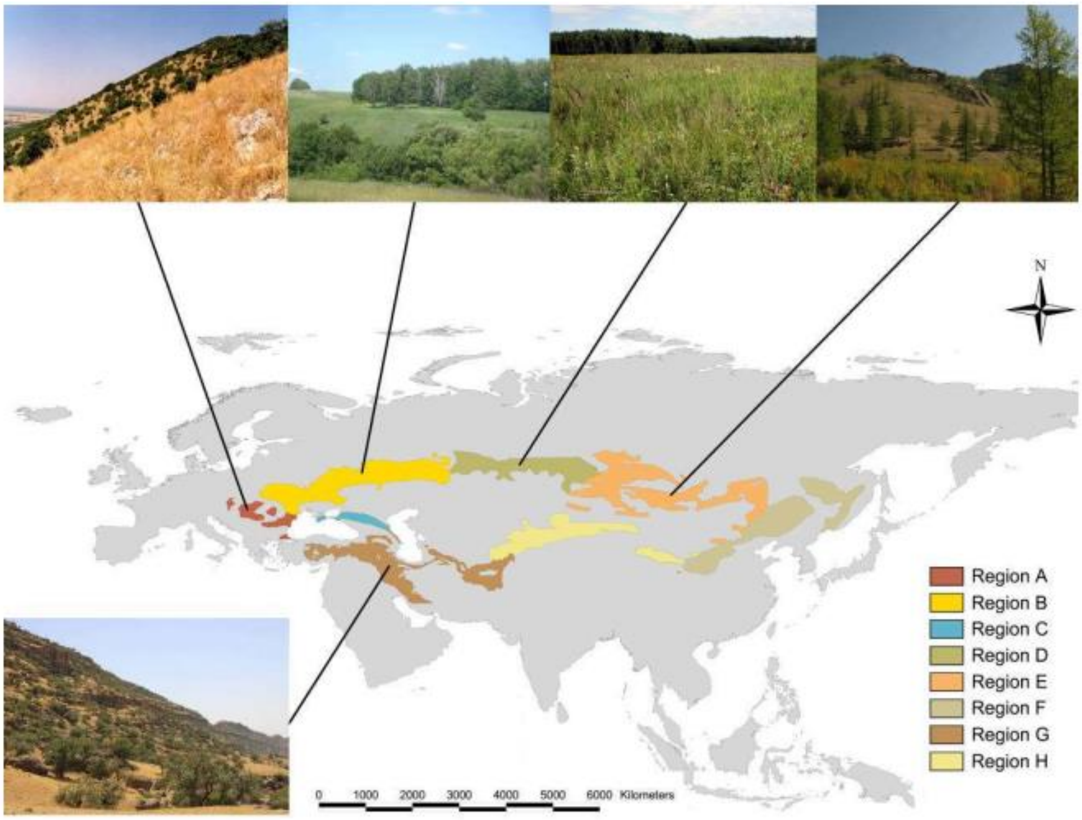

Figure 3. Forest-steppes in Eurasia (Source of figure: Erdős et al., 2019a)
Note: Region A: Southeast Europe, Region B: East Europe, Region C: North Caucasus and Crimea, Region D: west Siberia and north Kazakhstan, Region E: Inner Asia, Region F: Far East, Region G: Middle East, Region H: Southwestern Inner Asia and Central Asia

The oak trees are dominant species in the forest patches, with five different species (*Quercus douglasii, Q. lobate, Q. engelmannii, Q. agrifolia* and *Q. wislizeni* var. *wislizeni*). Other tree species also appear such as *Pinus sabiniana* and *Aesculus californica*. The most common native species in grasslands include *Stipa pulchra, Koeleria macrantha, Elymus elymoides, Poa secunda,* and *Bromus carinatus.* Currently, most of grassland stands are degraded and dominated by the alien species (e.g., *Bromus hordeaceus, B. diandrus, B. madritensis, Festuca myuros, Hordeum murinum, Aegilops triuncialis, Centaurea solstitialis, Carduus pycnocephalus* and *Silybum marianum*).

c. Southwest oak savannas

These savannas are found in mountainous regions of Arizona, New Mexico, and northern Mexico (McClaran and McPherson, 1999; Brock, 2010; Fowler and Beckage, 2020) (Fig. 1a). According to McClaran and McPherson (1999), southwest oak savannas occupy an area of 1.5 million ha. Grasslands with scattered oak trees are located in the foothills and slopes up to 80% (elevation from 1100-2200 m a.s.l.) (McClaran and McPherson, 1999; Brock, 2010). The soils are shallow and rocky, and they are broken into two main types (Aridisols and Mollisols). The climate in this region is hot and dry, with air temperatures in the summer season exceeding 35 ^{o}C. However, freezing temperatures occur during the winter seasons (McClaran and McPherson, 1999). The mean annual temperature is 12-17 ^{o}C, and the rainfall averages 322-600 mm (McClaran and McPherson, 1999; Sheppard et al., 2002).

Emory oak *(Quercus emoryi)* is the most frequent species in the forest patches (McClaran and McPherson, 1999; Brock, 2010). However, mixed oak communities are also represented in this region with some common species (*Quercus arizoni, Q. oblongifol, Q. gris, Juniperus deppeana, J. monosperma, J. scopulorum* and *Pinus cembroides)*. Perennial bunchgrasses and forb species are characteristic in the herb layer. The grasslands are composed of *Andropogon cirratu, Bouteloua curtipendula, Eragrostis intermedia, Leptochloa dubi, Piptochaetium fimbriatum, Sitanion hystrix, Tripsacum lanceolatu,* and *Helianthus petiolaris* (McClaran and McPherson, 1999).

d. Western North American Pinyon-Juniper Woodland

These ecosystems are found in the foothills of western North American mountains (Rocky Mountains, the Basin and Range region, Cascade Mountains, Sierra Nevada, and Sierra Madre Occidental of Mexico) (Rust, 1997; West, 1999; Fowler and Beckage, 2020; Wrangle, 2020) (Fig. 1b). The elevation varies from 1200 to 2600 m. The vegetation grows on multi-terrains (foothill terraces, lower mountain slopes, mesas, and rocky plateaus). The bedrock is characterized by various types: basalt, granite, limestone, pumice, sandstone, shale, and tuff. The annual precipitation ranges from 300 to 400 mm. Temperatures are strongly affected by elevation and fluctuate from -18 °C to 38 °C (Wrangle, 2020).

The important species of juniper are *Juniper osteosperma, J. monosperma, J. occidentalis, J. deppeana, J. scopulorum* and *J. californica.* In addition, pine trees *(Pinus edulis, P. monophylla* and *P. cembroides)* co-dominate in these regions (Rust, 1997; Fowler and Beckage, 2020). Some common shrubs appear such as *Artemisia tridentate, Purshia tridentate, Chrysothamnus* spp., *Ericameria* spp., and *Cercocarpus* spp. The herbaceous plants include *Festuca idahensis, Pseudoroegneria spicata, Achnatherum* spp., *Bouteloua curtipendula,* *B. hirsute, B. eriopoda, B. gracilis, Muhlenbergia pauciflora, M. setifolia, Poa secunda, P. fendleriana* and *Bromus tectorum)* (Fowler and Beckage, 2020; Wrangle, 2020).

e. Aspen parklands

The location of these ecosystems is South-Central Canada (Alberta, Saskatchewan, and Manitoba) (Asamoah et al., 2004; Nature Conservancy of Canada, 2019; Fowler and Beckage, 2020) (Fig. 1c). The rolling topography and fertile soils are important characteristics in this region. The climate is continental (Asamoah et al., 2004), with cool-to-warm summers and cold winters. The mean annual temperature is approximately 1.5 ºC. The mean summer and winter temperatures are about 15 ºC and -12.5 ºC, respectively. The mean annual rainfall ranges between 400 and 500 mm.

Populus tremuloides is the dominant species in this region. *Populus balsamifera* also co-occurs in forest patches. *Pinus banksiana* occurs in the north, and *Quercus macrocarpa* can be found in the southeast. Some common shrubs are *Corylus cornuta, Symphoricarpos albus, Salix bebbiana,* and *Prunus pensylvanica.* Grasslands are dominated by *Festuca hallii, Hesperostipa curtiseta, Elymus albicans, E. trachycaulus* and *Koeleria macrantha*. The most important forbs include *Achillea millefolium* and *Pulsatilla patens* (Nature Conservancy of Canada, 2019).

3.2.2. Forest-steppes in South America

a. Forest-steppe in Patagonia

These forest-steppes are found in Northern Patagonia in Chile and Southern Patagonia between Chile and Argentina (Kitzberger, 2012; Sottile et al., 2015) (Fig. 2a). They are located in an elevation from 1100-1600 m a.s.l. The annual temperature and rainfall fluctuate between 4-8 ºC and 300-1400 mm, respectively.

Nothofagus dombeyi and *N. pumilio* are dominant in forest patches. Some other common species are *Nothofagus alpina, N. obliqua, N. antarctica, Fitzroya cupressoides, Araucaria araucana, Austrocedrus chilensis, Chusquea culeou, Drimys winteri, Maytenus magellanica,* and *Maytenus boaria*. The most important shrub species are *Lomatia hirsuta, Embothrium coccinueum, Diostea juncea, Schinus patagonicus, Gaultheria mucronata,* and *Berberis microphylla*. *Stipa speciosa, Festuca pallescens, Empetrum rubrum, Pinguicula antarctica, Arachnites uniflora, Mulinum spinousum, Senecio filaginoides, Symphyotrichum vahlii, Acaena pinnatifida,* and *Vicia nigricans* are primary species in the grasslands (Kitzberger, 2012; Sottile et al., 2015).

b. Forest-steppes in southern Brazil

Forest-steppes are located in the highland plateau of southern Brazil (Paraná, Santa Catarina, and Rio Grande do Sul states) which is part of the area known as Campos Sulinos (Luza et al., 2014; Andrade et al., 2016; Iriarte and Behling, 2017; Andrade et al., 2018; Külkamp et al., 2018; Overbeck et al., 2018) (Fig. 2b). The elevations of these steppe-forests are approximately 400 m a.s.l, characterized by shallow soils (Andrade et al., 2018). The average annual temperature and precipitation are 11-20 ºC and 1000-2200 mm, respectively (Andrade et al., 2018; Overbeck et al., 2018).

The vegetation is covered by steppe and *Araucaria* forests. *Araucaria angustifolia* has the highest abundance in forest patches. *Araucaria* forests are composed of *Araucaria angustifolia, Drymis brasiliensis, Ilex paraguayensis, Mimosa scabrella, Podocarpus lambertii,* and *Symplocos uniflora*.

The grassland is formed by *Andropogon lateralis, A. gerardii, Axonopus ramboi, Solanum mauritianum, Tibouchina urbanii, Calea phyllolepis, Mikania paranensis, Schizachyrium scoparium, S. tenerum, Axonopus pellitus, A. affini, Rhynchospora flexuosa, Paspalum maculosum, P. notatum, Scleria distans, Baccharis subtropicalis, Sorghastrum nutans,* and *S. pellitum* (Iriarte and Behling, 2017; Andrade et al., 2018; Overbeck et al., 2018).

3.2.3. Forest-steppes in Eurasia

Following the report of Erdős et al. (2018a), Eurasian forest-steppes are divided into 8 main regions (Fig. 3).

a. Southeast Europe

Forest-steppes in this region are primarily found in Hungary, northeast Austria, south Slovakia, the southeast Czech Republic, Romania, northeast Croatia, north and northeast Serbia, southwest Ukraine, south Moldova, Turkey-in-Europe, north and southeast Bulgaria, and northeast Greece. They are influenced by mediterranean climate, with the mean annual temperature and precipitation of 9-13.5 °C and 420-600 mm, respectively. Forest-steppe mosaics are the most common on plains, but they can also be found on hills and mountains (Erdős et al., 2018a).

Forest patches are constituted by oak trees (*Quercus robur, Q. cerris, Q. frainetto, Q. petraea,* and *Q. pubescens*) co-occuring with other trees such as *Populus alba, Acer tataricum, Fraxinus ornus, Carpinus orientalis,* and *Tilia tomentosa.* The presence of *Astragalus onobrychis, Chrysopogon gryllus, Festuca vaginata, F. rupicola, Fragaria viridis, Stipa capillata, Salvia austriaca, S. nemorosa* and *S. nutans* is characteristic in grasslands.

b. East Europe

Forest-steppes are reported from Moldova, northeast Romania, southwest Russia, southeast Poland, and Ukraine. The temperate continental and mediterranean climate have a strong effect on the forest-steppes. The average annual temperature ranges between 3 and 9 ^{o}C, while the average annual rainfall ranges from 400 to 600 mm. Forest-steppes can be found in the elevation from 90 to 500 m.s.l. (Erdős et al., 2018a).

The stands of forest patches are mainly characterized by *Acer platanoides, Betula pendula, Fraxinus excelsior, Quercus robur, Tilia cordata, Populus tremula,* and *Ulmus glabra*. The common species in grasslands are *Koeleria macrantha, Festuca valesiaca, Fragaria viridis, Filipendula vulgaris, Ranunculus polyanthemos, Poa angustifolia, Salvia nutans, S. pratensis, Stipa pennata, S. capillata, S. pulcherrima, S. zalesskii, Trifolium montanum,* and *Teucrium chamaedrys*.

c. North Caucasus and Crimea

This region is strongly influenced by the Mediterranean climate, with an average annual temperature of 9.5-12 ^{o}C and a mean annual rainfall of 300–770 mm. Forest-steppes cover large regions from sea level to around 600 m a.s.l. (Erdős et al., 2018a).

Trees such as *Acer campestre, Arbutus andrachne, Carpinus betulus, Juniperus excelsa, Quercus robur, Q. petraea, Tilia dasystyla, Pyrus communis, P. elaeagrifolia, Pistacia atlantica,* and *Ulmus procera* form forest patches in this region. Meanwhile, grassland is marked by herb species such as *Festuca rupicola, Phleum phleoides, Adonis vernalis, Paeonia tenuifolia, Stipa capillata, S. pennata, S. pontica,* and *S. pulcherrima.*

d. West Siberia and north Kazakhstan

In this region, continental climate strongly influences the vegetation in forest-steppes. The mean annual temperature is low (1-4.5 ^{o}C), while the mean annual precipitation varies from 270 to 610 mm. A major part of forest-steppes are found in elevations from 100-400 m a.s.l. (Erdős et al., 2018a).

The dominant species of forest patches are *Betula pubescens, B. pendula, Pinus sylvestris,* and *Populus tremula,* while grasslands are mainly composed of *Artemisia pontica, A. glauca, Festuca valesiaca, F. rupicola, Filipendula vulgaris, Fragaria viridis, Helictotrichon hookeri, Gypsophila paniculata, Lathyrus pisiformis, Poa angustifolia, Phlomoides tuberosa, Phleum phleoides, Potentilla incana, Pimpinella saxifraga, Stipa pennata, S. capillata, S. zalesskii, S. tirsa, Scorzonera ensifolia,* and *Vicia cracca*.

e. Inner Asia

The mosaics of forest-steppes are primarily located in mountainous areas (the Altai Mountains, the Sayan Mountains, the Transbaikal Mountains, the Tarbagatai Mountains, the Saur Mountains, the Khangai Mountains, the Khentei Mountains), Baikal area, and Inner Mongolia. The elevation varies from 200 to 2400 m a.s.l. The climate is ultracontinental: temperature ranges between -6 °C and +5 °C on an annual basis, and the average annual precipitation ranges from 210 to 550 mm (Erdős et al., 2018a).

Betula platyphylla, B. pendula, Larix gmelinii, L. sibirica, Pinus sylvestris, and *Ulmus pumila* are typical species of forest patches. Grasslands are mainly formed by the following species: *Agropyron cristatum, Achnatherum sibiricum, Artemisia frigida, Cleistogenes squarrosa, Carex pediformis, Cymbaria daurica, Festuca lenensis, F. valesiaca, Leymus chinensis, Poa attenuata, Nepeta multifida, Stellera chamaejasme, Stipa krylovii,* and *S. baicalensis.*

f. Far East

This area includes West Manchuria, the Greater Khingan Range's southernmost parts, China's Loess Plateau in the east, the Khanka Lowland, the southwest Sihote Alin, and the Amur Lowland. This region's forest-steppes can be found on a variety of terrains and at a variety of altitudes. The east of this region is influenced by monsoonal circulation, but the western parts are affected by continental climate. The average annual temperature varies between 1°C and +14 °C. The average annual precipitation ranges from 360 to 650 mm (Erdős et al., 2018a).

The forest interiors are characterized by high number of oak trees *(Quercus mongolica).* Additionally, other tree species such as *Betula platyphylla, B. dahurica,* and *Tilia amurensis* are also abundant. The most frequent species in grassland are *Bothriochloa ischaemum, Arundinella hirta, Cymbaria daurica, Calamagrostis epigejos, Leymus chinensis, Filifolium sibiricum, Poa pratensis, Stipa bungeana, S. baicalensis, S. pennata,* and *S. grandis.*

g. *Middle East*

This region encompasses the Caucasus (southern and eastern parts), Anatolia's middle area, the east and southeast of Anatolia, and mountainous areas (the Abdulaziz Mountains, the Zagros Mountains, the Persian Plateau, the Alborz Mountains, the Kopet Dag, the Badkhyz Mountains, and the central Afghan Mountains). Forest-steppes can be found on hills and mountains with elevations from 200 to 3000 m a.s.l. The mediterranean climate has a major impact on forest-steppe, with a mean annual temperature of 10.5 - 17.0 °C and mean annual precipitation of 270 - 860 mm (Erdős et al., 2018a).

The typical species in forest patches are *Juniperus foetidissima, J. excelsa, Pinus sylvestris, P. nigra, Pistacia vera, P. atlantica, Pyrus elaeagrifolia, Prunus dulcis, Quercus robur, Q. brantii, Q. ithaburensis, Q. infectoria, Q. macranthera, Q. pubescens,* and *Q. petraea.* Grasslands are composed of *Astragalus lycius, Astragalus angustifolius, Agropyron cristatum, Bothriochloa ischaemum*, *Chrysopogon gryllus, Festuca valesiaca*, *Koeleria macrantha*, *Poa bulbosa*, *Seriphidium sieberi*, *S. fragrans*, *Stipa barbata*, *S. arabica*, *S. capillata*, *S. pulcherrima,* and *S. lessingiana.*

h. *Southwestern Inner Asia and Central Asia*

The forest-steppes mainly occur in mountain regions (the Pamir Mountains, the Alai Mountains, the Tian Shan, the Qilian Mountains, and the Helan Mountains). Forest-steppes in this area are located at elevations from 800 to 3,500 m a.s.l., and are strongly influenced by continental climate. However, the western parts of the region are characterized by mediterranean influences. The average annual temperature varies between 0 and 12°C, while the average yearly rainfall is from 380 to 600 mm (Erdős et al., 2018a).

Forest patches (mainly *Juniperus* species, *Juglans regia*, *Punica granatum*, *Malus sieversii* and *Pistacia* varieties) and grasslands (*Bothriochloa ischaemum*, *Hordeum bulbosum*, *Ferula tenuisecta*, *Thinopyrum intermedium,* and *Poa bulbosa*) form forest-steppes in the western part of the region. In the eastern part of the region, there is an expositional forest-steppe, meaning that forest patches (composed of *Betula pendula*, *Larix sibirica*, *Populus tremula*, *Picea crassifolia*, *P. schrenkiana*, *P. crassifolia*, *P. asperata*, and *Ulmus glaucescens*) are typical on north-facing slopes, while grasslands grow on south-facing slopes (composed of *Artemisia lagopus*, *A. frigida*, *Ajania fruticulosa*, *Agropyron cristatum*, *Cleistogenes squarrosa*, *Festuca valesiaca*, *Koeleria macrantha*, *Oryzopsis chinensis*, *Ptilagrostis pelliotii*, *Stipa breviflora*, *S. capillata*, and *S. przewalskyi*). Slopes of other aspects may be occupied by both forest or grassland, depending on the local circumstances.

3.3. Main types of forest-steppes in Hungary

In Hungary, the area of forest-steppes has changed dramatically over the last two centuries (Molnár et al., 2012). The total area of forest-steppes had a sharp decline from 3,700,000 ha to 250,738 ha, with 5.5% natural stands, 38% semi-natural stands, 46% moderately degraded stands, and 10% strongly degraded stands (Molnár et al., 2012). Gálhidy et al. (2011) has a similar report that only a few thousand hectares of forest-steppes are left at best, and most of them are in a significantly deteriorated state. Forest steppes in Hungary are divided into four main groups: sandy forest-steppe, open loess forest-steppe, open salt forest-steppe, and rocky forest-steppes (Illyés and Bölöni, 2007; Gálhidy et al., 2011; Molnár et al., 2012; Erdős et al., 2011; 2012; 2013a; 2014a,b). Below is a description of Hungary's primary forest-steppe categories.

3.3.1. Sandy forest-steppes

Sandy regions are mainly distributed between the Danube and Tisza rivers and a small part of eastern Hungary (Fig. 4). Historically, sandy areas were primarily devoid of trees, but during the 19th century, woodlands extended in open and closed steppes due to partly the outcome of afforestation and partly spontaneous process related to decreasing frequency of overgrazing (Molnár et al., 2012; Erdős et al., 2015). During the successional process in the sandy region, open and closed steppe stands form mosaics with *Quercus* forest-steppes or *Juniperis-Populus* forest-steppes (Molnár et al., 2012). Therefore, the vegetation of sandy forest-steppes is classified into four primary categories: open sand steppes, closed sand steppes, *Quercus* forest-steppes, and *Juniperus-Populus* forest-steppes (Fig. 4). The section of this dissertation under “study area” included a detailed description of the vegetation of sandy forest-steppes.

The total area of sandy forest-steppes is nearly 42,000 ha, reduced by 96.7% in comparison to the original sandy forest-steppes (Molnár et al., 2012). Sandy forest-steppes became one of the most vulnerable habitat types at the end of the 20th century (Gálhidy et al., 2011; Molnár et al., 2012). They belong to the critically endangered (CE) category, according to the IUCN classification (Gálhidy et al., 2011). In the coming decades, the forest-steppes on sand are predicted to completely disappear in Hungary (Molnár et al., 2012), emphasizing the necessary to conserve the rest of the sandy forest-steppes.

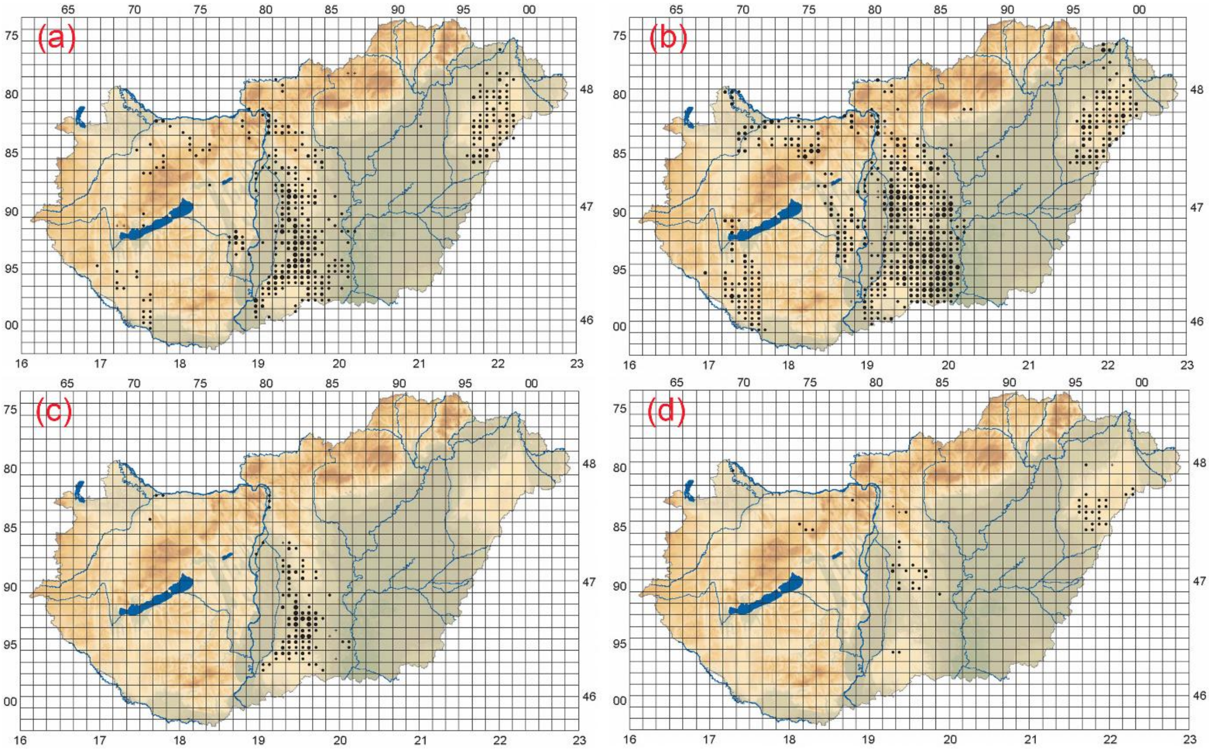

Figure 4. Distribution and the main vegetation types of sandy forest-steppes in Hungary (black dots): (a) open sand steppes, (b) closed sand steppes, (c) *Juniperus-Populus* forest-steppes, and (d) *Quercus* forest-steppes. Source of figure: MÉTA webpage (https://novenyzetiterkep.hu/)

3.3.2. Loess forest-steppes

25,198 ha of loess forest-steppe can be found in Hungary (Molnár et al., 2012). The vegetation can be divided into four categories: Closed steppes on chernozem soil, Open steppes on loess and clay cliffs, *Quercus* steppe woodlands on chernozem soil, and Steppe thickets (Fig. 5).

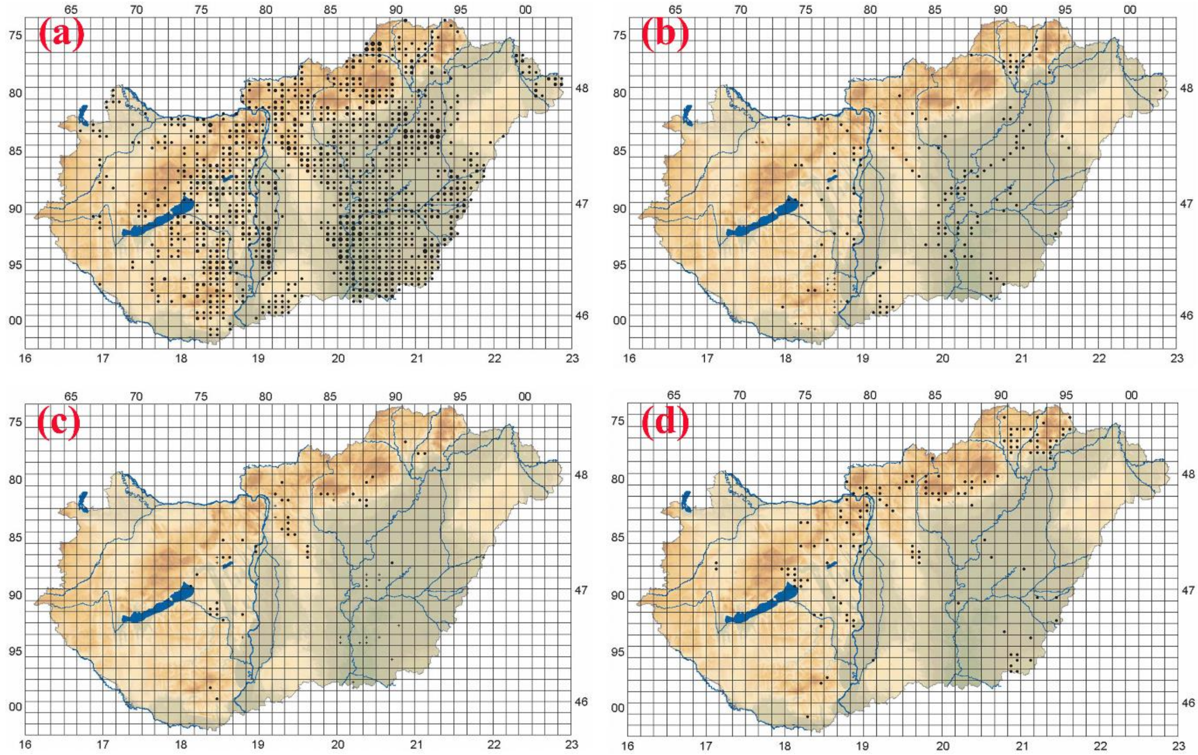

Figure 5. Distribution and the main vegetation types of loess forest-steppe in Hungary (black dots): (a) Closed steppes on chernozem soil, (b) Open steppes on loess and clay cliffs, (c) *Quercus* steppe Woodlands on chernozem soil, and (d) Steppe thickets. Source of figure: MÉTA webpage (https://novenyzetiterkep.hu/)

– Closed steppes are dominated by *Festuca rupicola*. Some common taxa are *Allium paniculatum*, *Bothriochloa ischaemum, Fragaria viridis, Poa angustifolia*, *Plantago media*, *Stipa capillata*, *Salvia austriaca*, *Ranunculus polyanthemos*, and *Viola ambigua.*

– Open steppes (*Artemisia* steppes) are dominated by *Kochia prostrata* and *Agropyron pectiniforme*. Some other species are also important such as *Allium sphaerocephalon, Bassia sedoides, Bothriochloa ischaemum, Bromus tectorum, Iris pumila, Linum austriacum, Poa bulbosa, Stipa capillata* and *Xeranthemum annuum.*

– Small oak forests *(Quercus pubescens* and *Q. robur)* combined with shrub and herb layer, formed Steppe Woodland of *Quercus*. The other typical species are *Buglossoides purpurocaerulea, Carex humilis, Festuca rupicola, Ligustrum vulgare, Prunus spinosa, Pyrus pyraster, Peucedanum cervaria, Polygonatum odoratum, Stipa capillata, Ulmus minor* and *Viburnum lantana.*

– Steppe thickets are composed of herbs (*Adonis vernalis, Brachypodium pinnatum, Festuca rupicola, Fragaria viridis, Iris variegata,* and *Vinca herbacea*) and shrubs *(Crataegus monogyna, Prunus tenella, Prunus fruticose,* and *Rosa* species).

3.3.3. Saline forest-steppe

The saline forest-steppe has a total area of approximately 183,550 ha (Molnár et al., 2012). The vegetation can be distinguished into seven categories: *Artemisia* steppes, *Achillea* steppes, Saline meadows, Tall herb meadow steppes, *Puccinellia* meadows, the annual vegetation of saline-flats and mud-flats, and *Quercus* steppe woodlands (Fig. 6).

– *Artemisia* steppes on solonetz soil are dominated by *Artemisia santonicum* and *Festuca pseudovina*. The other typical species are *Allium vineale, Bupleurum tenuissimum, Hordeum hystrix, Lotus tenuis, Plantago schwarzenbergiana, Poa bulbosa, Scilla autumnalis,* and *Veronica arvensis.*

– *Achillea* steppes on solonetz soil are dominated by *Festuca pseudovina*, *Achillea setacea* and *A. collina*. Other common species are *Bupleurum tenuissimum, Carex stenophylla, Cynodon dactylon, Euphorbia cyparissias, Koeleria cristata, Limonium gmelini, Poa angustifolia, Plantago lanceolata, Scleranthus annuus, Ranunculus pedatus,* and *Trifolium fragiferum.*

– Saline meadows on solonetz soil are characterized by the presence of species such as *Alopecurus pratensis, Agrostis stolonifera, Beckmannia eruciformis, Elymus repens, Plantago schwarzenbergiana,* and *Ranunculus lateriflorus*, while those on solonchak soil are formed by herbs such as *Achillea asplenifolia, Carex distans, Juncus gerardii, Festuca arundinacea, Linum perenne,* and *Taraxacum bessarabicum.*

– Herb meadow steppes on solonetz soils are constituted by herb species *Artemisia pontica, Alopecurus pratensis, Dianthus pontederae, Festuca rupicola, F. pratensis, Iris spuria, Plantago schwarzenbergiana, Seseli varium,* and *Viscaria vulgaris.*

– *Puccinellia* meadows and the annual vegetation of saline-flats and mud-flats are marked by the frequent occurrence of herbs *Atriplex littoralis, Bassia sedoides, Chenopodium chenopodioides, Cyperus pannonicus, Myosurus minimus, Puccinellia limosa, Plantago maritima, Salicornia prostrata, Spergularia media, S. salina* and *Suaeda maritima.*

– *Quercus* steppe woodlands on saline soils are formed by pedunculate oak *(Quercus robur)*. The common shrub species include *Crataegus monogyna, Ligustrum vulgare, Prunus spinosa,* and *Pyrus pyraster.* The typical species in steppes are *Brachypodium sylvaticum, Carex melanostachya, Doronicum hungaricum, Poa nemoralis, Scilla vindobonensis,* and *Serratula tinctoria.*

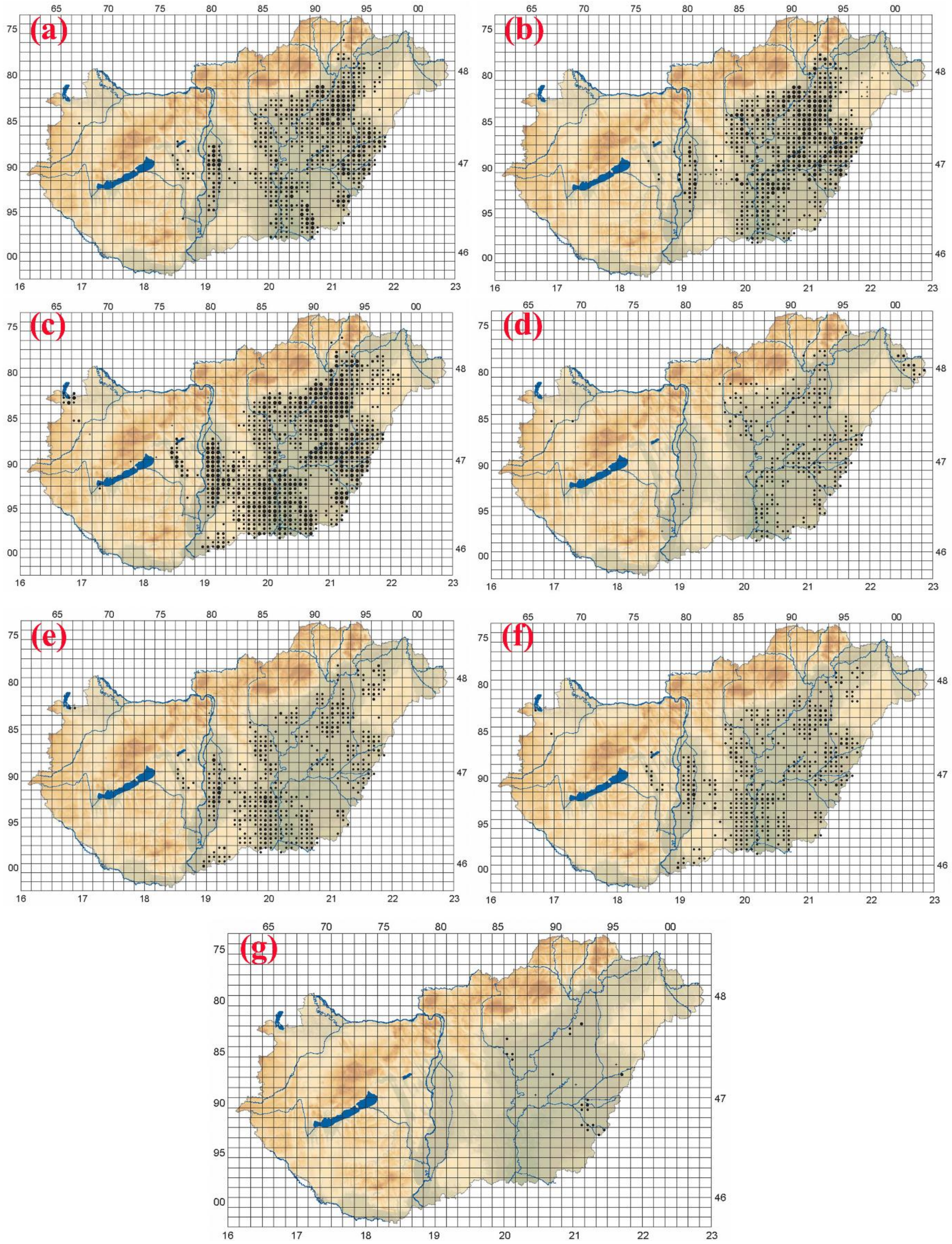

Figure 6. Distribution and the main vegetation of saline forest-steppe in Hungary (black dots): (a) *Artemisia* steppes, (b) *Achillea* steppes, (c) Saline meadows, (d) Tall herb meadow steppes, (e) *Puccinellia* meadows, (f) the annual vegetation of saline-flats and mud-flats, and (g) Steppe Woodlands of *Quercus*. Source of figure: MÉTA webpage (https://novenyzetiterkep.hu/)

3.3.4. Rocky forest-steppes

Rocky forest-steppes in Hungary occur in the North Hungarian Mountains, the Transdanubian Mountain, the Villány Mountains, and the Mecsek Mountains (Illyés and Bölöni, 2007; Bölöni et al., 2008; Molnár et al., 2008a; Erdős et al., 2011, 2012, 2013a; 2014a,b; Bátori et al., 2022) (Fig. 7). The vegetation is primarily found on bedrocks that consist of limestone and dolomite and are partly covered by loess. Forest-steppes are mainly situated in foothill (<400 m a.s.l.) and submontane (400–750 m asl), but they also can be found in montane zones (>750 m asl) (Bátori et al., 2022). The mean annual temperature and precipitation are 8.8-10.5 ^{o}C and 670-723 mm, respectively (Erdős et al., 2011, 2013a).

In rocky forest-steppes, the most frequent tree species are *Quercus pubescens* and *Fraxinus ornus*. The common shrubs include *Crataegus monogyna*, *Cotinus coggygria*, and *Viburnum lantana*, while typical species of the herb layer are *Adonis vernalis*, *Artemisia alba*, *Chrysopogon gryllus*, *Dianthus giganteiformis*, *Festuca rupicola*, *Orlaya grandiflora*, *Pulsatilla grandis*, *Stipa capillata*, *S. pulcherrima*, and *Teucrium chamaedrys*.

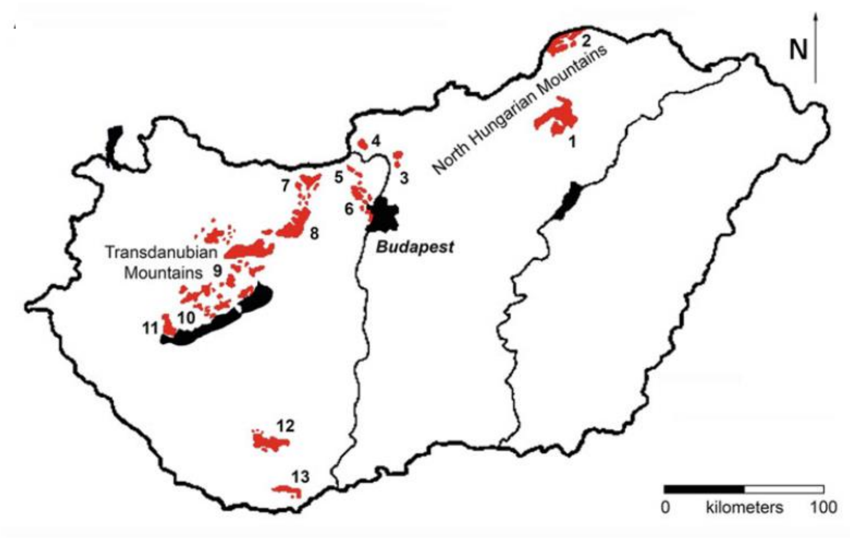

Figure 7. Locations of rocky forest-steppes in Hungary. North Hungarian Mts: Bükk Mts (1) and Aggtelek Karst (2); Transdanubian Mts: southwestern Cserhát Mts (3), southern Börzsöny Mts (4), Pilis Mts (5), Buda Mts (6), Gerecse Mts (7), Vértes Mts (8), Bakony Mts (9), Balaton Upland (10) and Keszthely Mts (11); Mecsek (12) and Villány Mts (13) (Source of figure: Bátori et al., 2022)

3.4. Non-native and native tree plantations and their diversity patterns

Tree plantations are expanding to meet the need for timber and fuelwood (Cubbage et al., 2010), and they may be an essential strategy for ecosystem and environmental services, including carbon sequestration, habitats for forest-adapted species, phytoremediation as well as soil and water stabilization (Albert et al., 2021; Benye et al., 2021; Hynes et al., 2021). These 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). In Hungary, 6.3% of forest area (i.e., 130,000 hectares) is tree plantations (Forest Europe, 2020).

A wide range of studies has revealed that tree plantations have poor biodiversity and a simple composition, structure, and function (Biró et al., 2008; Chen and Cao, 2014; Hynes et al., 2021, Rédei et al., 2020). Additionally, they also have a high abundance of non-native species (Csecserits et al., 2016; Medvecká et al., 2018; Slabejová et al., 2019) that invade semi-natural and natural habitats, resulting in population decline and at the end extinction of many endangered plant species (Vítková et al., 2017). In some cases, however, studies have demonstrated that tree plantations can contain a diverse range of plant species (Brockerhoff et al., 2003; Cusack and Montagnini, 2004; Butler et al., 2008) and host some endangered or protected species (Arrieta and Suárez, 2006; Bremer and Farley, 2010). From the conservation viewpoint, plantations with several tree species have greater biodiversity than monocultures (Barsoum et al., 2016), while native tree plantations have a higher level of biodiversity than exotic plantations (Bremer and Farley, 2010; Rédei et al., 2020).

In Hungary, tree plantations are increasing rapidly for economic purpose, and they have extended to sandy forest-steppes as well (Molnár et al., 2012; Csecserits et al., 2016). These plantations span over large areas and are in continuous contact with grasslands as well as natural and near-natural forests. Typical tree species planted in plantations include non-native *(Robinia pseudoacacia, Pinus nigra, Pinus sylvestris)* and native trees *(Populus alba* and *Quercus robur)* (Csecserits et al., 2016; Vítková et al., 2017; Nicolescu et al., 2018). An earlier study found that the species richness is different in various plantations of this region (Rédei et al., 2020). For instance, the total species richness in the plantations of black locust was the lowest, but that was not different among plantations of oak, poplar, and pine plantations. Furthermore, the richness of forest species was the highest in oak plantations and the lowest in alien poplar ones. The number of grassland species, however, was the highest in exotic poplar plantations, whereas black locust and oak plantations were the lowest. The richness of native weed and alien species did not differ among various tree plantations. Diversity pattern (species richness) in tree plantations has been studied (Csecserits et al., 2016; Rédei et al., 2020), but 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).

3.5. Biodiversity patterns and ecological characteristics of forest-steppes

3.5.1. Biodiversity patterns: taxonomic, functional and phylogenetic diverity

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 (Fig. 8a). 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; i.e., several states of the continuum can be found in a single landscape. While macroclimate is the same for all these habitats, considerable secondary (microclimatic and soil) 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 (Erdős et al., 2018b, 2020). Thus, the gradient of varying vegetation cover may correspond to multiple environmental gradients (Fig. 8b), which may create the biodiversity feature of forest-steppe.

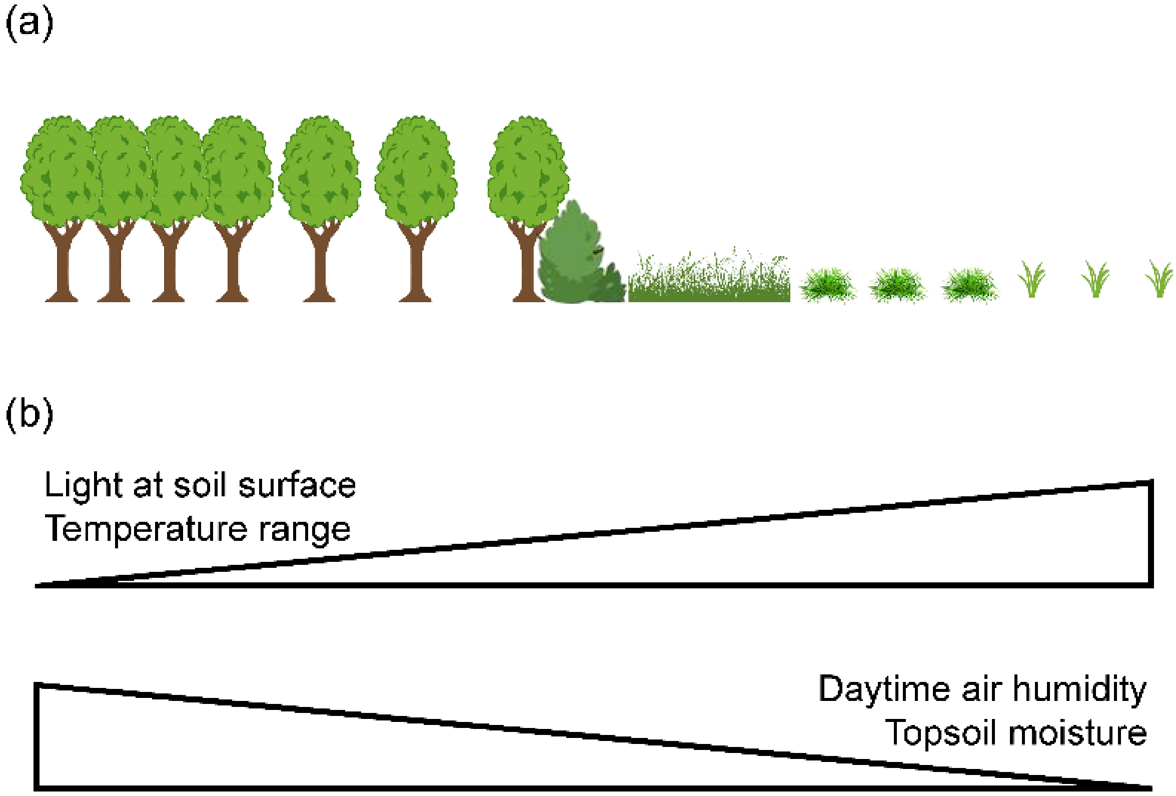

Figure 8. (a) Gradient of vegetation cover, ranging from closed-canopy forests to sparse grasslands, (b) environmental gradients caused by the vegetation gradient.

The co-occurrence of differently-sized forest and grassland patches of various types, connected by an intricate network of differently exposed edges seems to be of primary importance in supporting high diversity and conservation value. Each of the studied habitats plays an important role in the mosaic forest-steppe ecosystem for a different reason (Bátori et al., 2018; Erdős et al., 2014c, 2018b). When compared to forest interiors or forest edges, grasslands, for example, include more endemic, protected, red-listed, and specialist plant species, as well as mosses and lichens of special conservation importance (Borhidi et al., 2012; Molnár, 1998; Erdős et al., 2018b). Moreover, the highest naturalness are found in the grassland (Erdős et al., 2018b). Forest edges pose the highest species richness and Shannon diversity, especially the north-facing ones (Bátori et al., 2018; Erdős et al., 2013b; 2014c; 2018b). Additionally, forest edges seem to have an important role in native tree recruitment: the highest number of native tree seedlings and saplings is registered in south-facing edges (Erdős et al., 2015; 2018b). Meanwhile, forest patches are necessary to create environments for plants with a demand of mesic temperature or humidity conditions and play important roles in protecting the understorey against extreme events or extreme climate conditions (Erdős et al., 2018b). There are some major variations in forest patches of differing sizes. For example, the species richness, naturalness, and numbers for protected species in small forest patches are higher than those of large and medium forest patches. However, the opposite was true for the number of large trees (Erdős et al., 2015; 2018b).

Ecologists have increasingly recognized that besides taxonomic diversity, functional diversity (i.e., the variability of functional traits of the organisms in an ecosystem) and phylogenetic diversity (i.e., the divergence of evolutionary lineages within a community) may provide valuable insight into the origin and functioning of ecosystems (Tilman, 1997; Díaz and Cabido, 2001; Díaz et al., 2006). Functional diversity greatly influences ecosystem processes, dynamics, and stability, and has an effect on ecosystem goods and services (Scherer-Lorenzen, 2008; Cadotte et al., 2011; Hallett et al., 2017). Some studies conducted at broad spatial scales have shown that plant communities that are more species rich are also more functionally diverse (Swenson et al., 2012; Echeverría-Londoño et al., 2018; Li et al., 2018), 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 (Harper and Macdonald, 2001; Esseen et al., 2016; Franklin et al., 2021). 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, it is expected that 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 (Díaz and Cabido, 2001; Silvertown et al., 2006; Losos, 2008; Bernard-Verdier et al., 2013). Indeed, understanding the relationship of taxonomic diversity, phylogenetic and functional diversity in forest-steppe ecosystem is important both from a theoretical and a practical perspective, and it could contribute to adequate conservation legislation, effective practical habitat management actions, and appropriate restoration efforts. If the same habitat marks a peak in taxonomic, phylogenetic, and functional diversity on the one hand and conservation value in forest-steppe mosaics on the other, the effort for conservation needs to be directed in that habitat. If the peak in diversities appears differently in different habitats, then simultaneous focus on multiple habitats is essential for practical conservation. Therefore, further studies are needed to reveal the diversity patterns and conservation value in multiple habitats of forest-steppes.

3.5.2. CSR strategies

Plant community assembly has long been in 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 on 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 and 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 species 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 CSD-filter (C: competition, S: stress, D: disturbance), 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. Currently, knowledge of Grime's scheme-based filters is still unknown in sandy forest-steppe, which may limit understanding of habitat heterogeneity in this ecosystem.

3.5.3. Relationship between species composition and environment

The abiotic factors vary robustly in different habitats of forest-steppes. Previous studies emphasize that temperature, air humidity, light, and soil moisture differed significantly among the habitats of sandy forest-steppes (Erdős et al., 2013b, 2014c, 2018b, 2020). Among ecological indicator values, mean indicator values for temperature were the highest in grasslands, followed by edges, and the lowest in forests. A similar pattern was observed in the mean indicator values for light availability, but the mean indicator values for soil moisture illustrated an opposite pattern (Erdős et al., 2013b, 2020). The measurements of light, air temperature, air humidity, and soil moisture in the field exhibit trends similar to their corresponding ecological indicator values (Erdős et al., 2018b). The daily variation of the temperature and moisture in the grasslands was extremely great, but less so in the forest interiors (Erdős et al., 2014c, 2018b). Therefore, the range of vapor pressure deficit (VPD) in the grove was smaller than it was in open habitats (Süle et al., 2020). Besides, soil characteristics were different among grassland and forest patches (Tölgyesi et al., 2020). The humus content of the soil is always larger in forest patches than in grasslands (Bodrogközy, 1982).

Environmental variabilities among habitats in the forest-steppe considerably affect vegetation. Grasslands are primarily fitting for xeric species, while forest patches are suitable for mesic species to grow and survive (Erdős et al., 2018b). Additionally, oak regeneration only survived and grew in forest interiors and forest edges, but they were absent in grasslands. This may be related to environmental parameters (Erdős et al., 2021). Environmental conditions in edges were different from the neighboring habitat interiors, resulting in the highest species richness in this habitat (Erdős et al., 2014c, 2018b).

Recently, there have been intensive studies on vegetation-environment relations, with particular attention on the aspects of soil moisture, air humidity, and air temperature patterns. The measurement of environmental parameters in the substantial majority of the earlier investigations limited themselves for only a very short period (typically 24 hours on a selected summer day) (Erdős et al., 2014c, 2018b, Bátori et al., 2014; Tölgyesi et al., 2018; Milošević et al., 2020). Therefore, the most crucial microclimatic conditions may be missed by these short-term assessments. Additionally, microclimatic measurements for a long time from other ecosystems such as transition zones of forest to arable land, harvested forests, temperate forests, tropical forests, and plantations, have been reported (Wright et al., 2010; Ewers and Banks-Leite, 2013; Crockatt and Bebber, 2015; Baker et al., 2016; Schmidt et al., 2019; Slabejová et al., 2019). In order to attain more informed background data about the environmental context of forest-steppes in the Kiskunság Sand Ridge, long-term measurements should be carried out during the growing season of vegetation, from spring to autumn. Furthermore, earlier studies did not take into account the full variety of forest-grassland mosaics: some works disregarded the edge habitat (e.g., Tölgyesi et al., 2018; Milošević et al., 2020), while others restricted their attention to small forest patches and a single type of grassland (e.g., Erdős et al., 2014c; Süle et al., 2020). Thus, measuring microclimate in a broader spectrum of near-natural forest-steppe habitats is necessary to fill the above knowledge gap.

3.5.4. Forest edges

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., 2014c, 2019c).

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., 2014c; 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 and phylogenetic diversity 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.

4. Material and methods

4.1. Study area

4.1.1. The Kiskunság Sand Ridge in Hungary

The Kiskunság Sand Ridge of Hungary (hereafter Kiskunság), which encompasses a significantly large segment of the Great Hungarian Plain, is located between the rivers Danube and Tisza. 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).

Thirteen study sites were selected in the Kiskunság Sand Ridge, as these sites represent all remaining near-natural forest-steppe mosaics larger than 10 ha in the region (Table 1; Fig. 9). All study sites are under legal protection, and are covered with near-natural forest-steppe vegetation (Fig. 10a). 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 document, we define near-natural forests as spontaneous stands in protected areas, dominated by native species and devoid of visible signs of human land-use. The poplar-juniper forest patches (*Junipero-Populetum albae*) have a total canopy cover of ca. 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 meters to ca. one hectare. Large forest patches are able to buffer environmental extremes, while smaller forest patches are considerably influenced by the surrounding grassland habitats (Ylisirniö et al., 2016; Erdős et al., 2018b), which may have a strong influence on species composition. Therefore, we differentiated three forest patch size classes: large forest patches (> 0.5 ha), medium forest patches (0.2–0.4 ha), and small forest patches (< 0.1 ha) (Fig. 10b–d).

Table 1. General information about thirteen study locations in the Kiskunság Sand Ridge (from north to south), Hungary

No.	Site	Coordinates		Protection level	Protected area size (ha)	Note
		Latitude	Longitude			
1	Csévharaszt	N 47°17'	E 19°23'	Nature reserve	105	-
2	Táborfalva	N 47°07'	E 19°23'	Natura 2000	ca. 1000	the sandy habitats only
3	Tatárszentgyörgy	N 47°02'	E 19°22'	Natura 2000	105	the sandy habitats only
4	Fülöpháza$^{(1)(+)}$	N 46°52'	E 19°25'	National park	1992	-
5	Orgovány$^{(+)}$	N 46°47'	E 19°28'	National park	656	the sandy habitats only
6	Bócsa$^{(+)}$	N 46°41'	E 19°28'	National park	11488	-
7	Bodoglár$^{(+)}$	N 46°31'	E 19°37'	Local nature reserve	235	-
8	Tázlár$^{(+)}$	N 46°31'	E 19°30'	Natura 2000	1929	-
9	Imrehegy$^{(+)}$	N 46°29'	E 19°22'	Nature 2000	ca. 450	the unit under study
10	Pirtó$^{(+)}$	N 46°28'	E 19°26'	Nature reserve	591	-
11	Kéleshalom	N 46°23'	E 19°20'	Nature reserve	168	-
12	Négyestelep$^{(+)}$	N 46°17'	E 19°35'	Nature 2000	136	the unit under study
13	Ásotthalom$^{(+)}$	N 46°13'	E 19°47'	Landscape protection area	17.5	-

$^{(1)}$A site was chosen in study 3; $^{(+)}$sites were chosen in study 4

The forest edge was defined as a more or less straight peripheral zone of each forest patch > 0.2 ha reaching out of the outermost trunks of living tree (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., Wicklein et al., 2012; Erdős et al., 2018b). As north- and south-facing edges are expected to show the greatest differences (Ries et al., 2004; Harper et al., 2005), they were included in the study (Fig. 10e–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)* (Fig. 10g) 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)* (Fig. 10h) 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)* (Fig. 10i) 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, Silene conica,* and *Polygonum arenarium.* Spaces among vascular plants are typically covered by mosses.

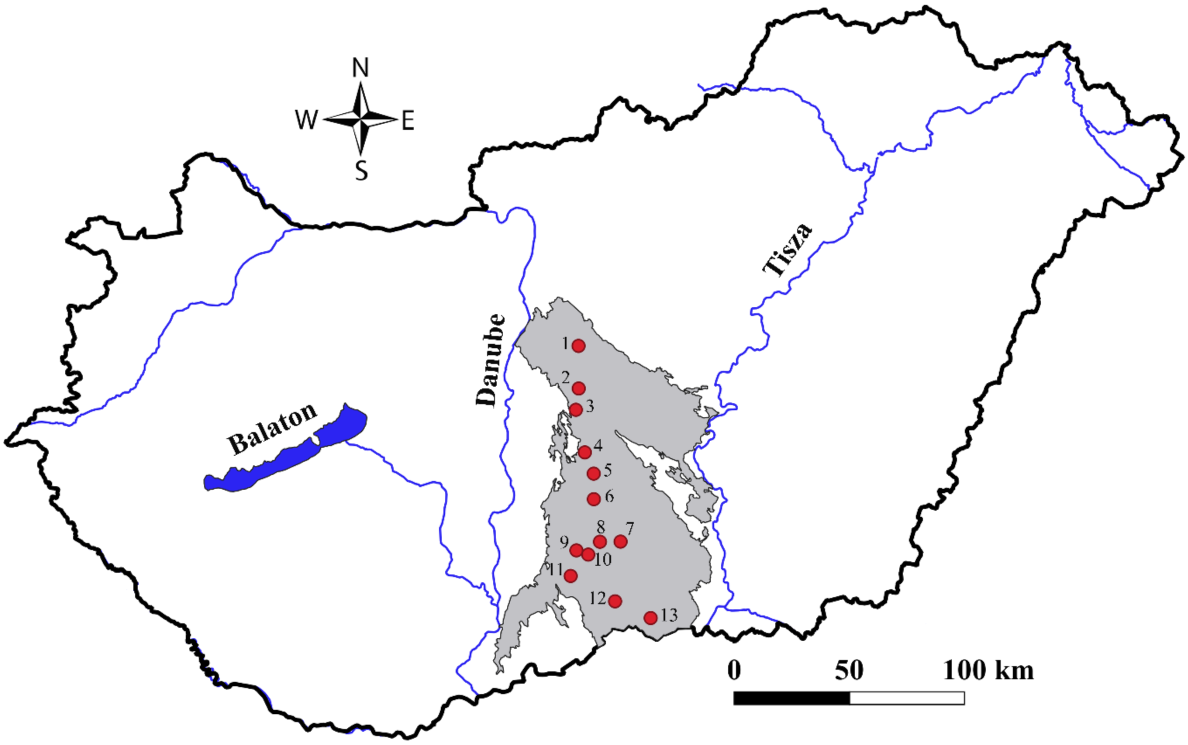

Figure 9. The position of the 13 study sites (red dots) in the Kiskunság Sand Ridge (gray) between the Rivers Danube and Tisza in Hungary. From north to south, the thirdteen sites are as follows: 1: Csévharaszt; 2: Táborfalva; 3: Tatárszentgyörgy; 4: Fülöpháza; 5: Orgovány; 6: Bócsa; 7: Bodoglár; 8: Tázlár; 9: Imrehegy; 10: Pirtó; 11: Kéleshalom; 12: Négyestelep; and 13: Ásotthalom.

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*) that is usually mixed with Scots pine (*Pinus sylvestris*) (Biró et al., 2013; Rédei et al., 2020).

Populus alba plantations typically have a canopy cover of ca. 50-70% (Fig.10j). The shrub layer has a cover of 0–25% 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*.

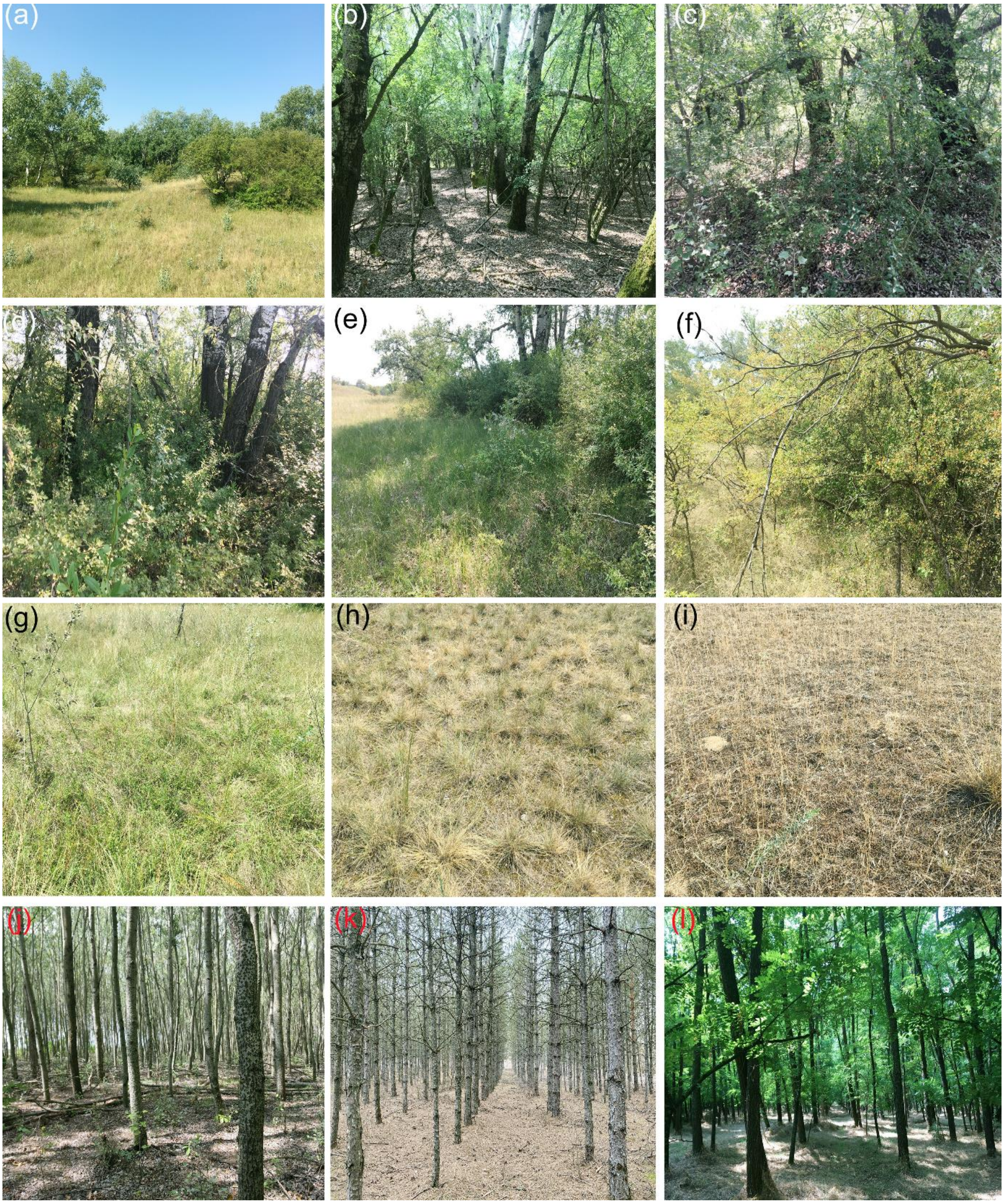

Figure 10. (a) The natural vegetation of the Kiskunság Sand Ridge (Hungary) is forest-steppe, that is, a mosaic of forests and grasslands. The following eight habitat types were found in forest-steppe mosaics: (b) large forest patch, (c) medium forest patch, (d) small forest patch, (e) north-facing forest edge, (f) south-facing forest edge, (g) closed perennial grassland, (h) open perennial grassland and (i) open annual grassland. The forest-steppe mosaics are surrounded by tree plantations as follows: (j) plantation of the native *Populus alba*; (k) plantation of the non-native *Pinus nigra*; and (l) plantation of the non-native *Robinia pseudoacacia*.

Pinus nigra plantations are usually characterized by a canopy cover of 50-60% (Fig.10k). 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.10l) have canopy cover values of ca 60-80%. The shrub layer is very sparse (0–10% cover), its frequent 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*, *E. repens, Galium aparine*, and *Lamium amplexicaule*.

4.1.2. The Deliblato Sands in Serbia

The Deliblato Sands (hereafter 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 (Fig. 11a). The climate is moderate continental; average annual temperature and precipitation are 12.5°C and 664 mm, respectively (Ćuk et al., 2023). This region is composed of slightly undulating stabilized sand dunes of aeolian origin, with humus-poor sandy soils and low water retention capacity (Sipos et al., 2022). The site selected 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. 11b). The grasslands *(Adonido vernalis-Chrysopogonetum grylli)* have 50–95% total cover and are dominated by *Chrysopogon gryllus*, *Festuca rupicola*, *F. valesiaca*, *Stipa borysthenica*, and *S. capillata.* Other common species in grasslands include *Euphorbia seguieriana*, *Phleum phleoides*, *Potentilla arenaria*, and *Thymus pannonicus*. The forests *(Querco-Tilietum tomentosae)* have a height of 15–25 m, a canopy cover of 60–95%, and are co-dominated by *Tilia tomentosa* and *Quercus robur*. The shrub layer covers 30–65% and is primarily composed of *Cornus sanguinea*, *Cotinus coggygria, Ligustrum vulgare*, *Lonicera xylosteum*, *Rhamnus saxatilis* subsp. *tinctoria*, and *Viburnum lantana*. The herbaceous species commonly found in the forest patches include *Alliaria petiolata*, *Convallaria majalis, Corydalis solida*, *Polygonatum odoratum,* and *Viola suavis*.

Plant species nomenclature is based on Király (2009), while plant association names follow Borhidi et al. (2012) for Hungary and Ćuk (2019) for Serbia.

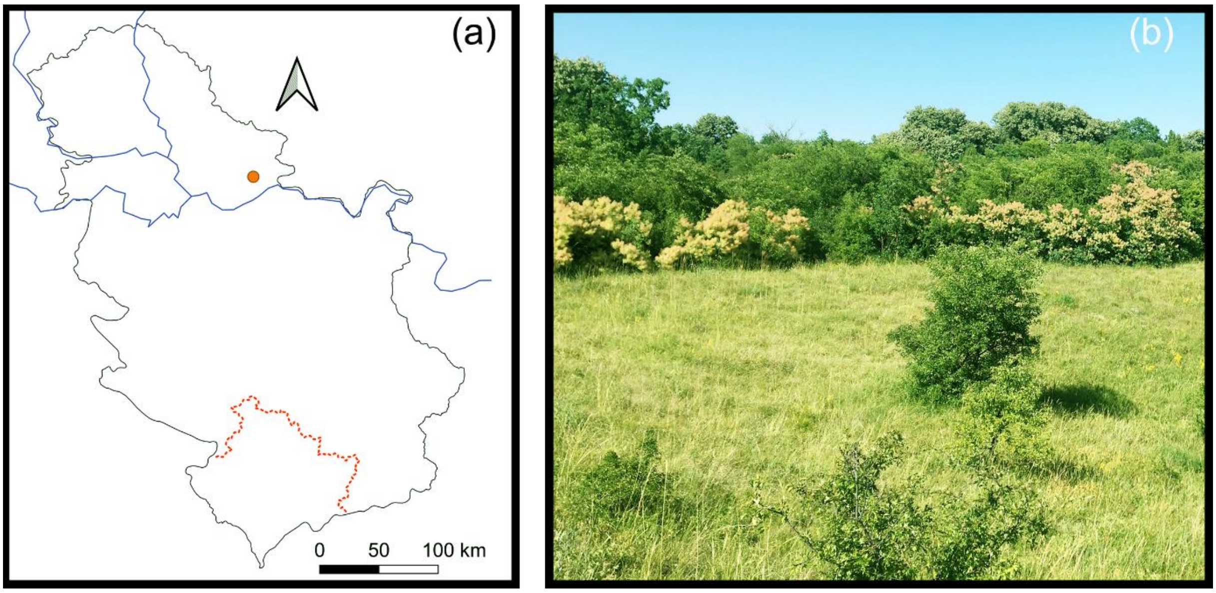

Figure 11. Location of the Deliblato (orange dot) in Serbia (a), and the forest-steppe mosaics in this region (b)

4.2. Field works

4.2.1. Study 1: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity and Study 2: Plant strategies and community assembly rules in forest-grassland mosaics

All thirteen study sites (Table 1, Fig. 9), and eight habitats were included as follows: large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, closed perennial grasslands, open perennial grasslands, and open annual grasslands (Fig. 10). 25-m^2 plots (5 m × 5 m plots for forest interiors and grasslands and 2 m × 12.5 m plots for forest edges (the longer side of the plot parallel with the edge) in order to rule out their extension into the interiors of forests or grasslands) were used, following the design of earlier studies (Erdős et al., 2018b; 2019b; 2020). 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 (the canopy layer comprises trees with a height greater than 5m, the shrub layer consists of trees with a height below 5m, and the herb layer encompasses various herbaceous plants and small woody plants, including tree seedlings, saplings, shrubs, and woody vines, with a height less than 0.5 m) were estimated and included in all analyses. 296 plant species were found, but 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) that they were young or underdeveloped at the time of sampling were excluded from the analyses involving functional and phylogenetic indices, as well as CSR strategy.

4.2.2. Study 3: microclimate in the habitats of a forest-steppe ecosystem

For this study, an area near Fülöpháza, located in the center of the Sand Ridge, has been chosen (Fig. 9). Microclimate measurements were carried out in the seven habitat types described above (i.e., large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, open perennial grasslands, and open annual grasslands). Closed perennial grasslands were not included because they were rare at this site. Three replicates for each habitat type were used. The air temperature (ºC) and relative air humidity (%) were measured once every month in all seven habitats from April to October 2022. They were measured synchronously 20 cm above the ground surface in the center of each habitat for 24 hours (i.e., a day per month) using MCC USB-502 data loggers (Measurement Computing Corporation, Norton, MA, USA). The resolution of the sensors was set to once every minute; therefore, each sensor yielded 1440 temperature and 1440 humidity data records per day. The loggers were placed in naturally ventilated radiation shields in order to avoid direct solar radiation. The sampling occasions were selected under clear weather conditions, but the weather was cloudy during the second daytime periods of July and was rainy during the first couple of hours during September.

4.2.3. Study 4: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity of near-natural forests and tree plantations

Nine study sites were selected 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, Orgovány, Bócsa; Bodoglár, Tázlár, Imrehegy, Pirtó, Négyestelep, and Ásotthalom (Table 1).

At each site, four habitat types were sampled: near-natural poplar forests (forest patches located in forest-steppe mosaics), 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). We chose these plantations because they are the most common. In addition, they represent three broad ecological types: native deciduous, non-native deciduous and non-native evergreen. 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 larger than 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 and shrub 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, 5 m × 5 m plots were used in the interior of the habitats where there was no sign of edge effect. The minimum distance among the plots was 200 m to avoid spatial autocorrelation. The sampling method was the same as applied in our first two studies. 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 S2, while additional information related to cover value of the canopy, shrub, and herb layers, as well as species richness on the four habitat types is provided in Table S3).

4.2.4. Study 5: Forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity

In this study, forest-steppes in the Kiskunság Sand Ridges (forest-steppe mosaics in Bodoglár and Tázlár were chosen, as they are very close to each other) and the Deliblato Sands were selected (Fig. 9 and Fig. 11) The distance between the two study sites is approximately 220 km. Four main habitat types were differentiated at both sites: large forest patches (>0.5 ha), north-facing forest edges, south-facing forest edges, and grasslands. In this study, the grasslands *Festucetum vaginatae* and *Adonido vernalis-Chrysopogonetum grylli* were chosen in the Kiskunság and the Deliblato, respectively. We chose these grasslands because they are common and typical in each region. The peripheral zone of a forest patch > 0.2 ha, 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 four habitat types in the two sites is presented in Table S4). The method to sample the vegetation using 25 m^2-plots is the same as we used in study 1. Four unidentified taxa (*Allium* sp., *Hieracium* sp., *Lathyrus* sp., and *Orobanche* sp.) per 229 species, none of which appeared in >1 of the 80 plots, were not included in the functional and phylogenetic diversity analyses.

4.3. Data analyses

4.3.1. Species composition

To reveal the compositional relation among eight habitat types (i.e., large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, closed perennial grasslands, open perennial grasslands, and open annual grasslands) in study 1, four habitats (i.e., near-natural poplar forests, plantations of native *Populus alba*, plantations of non-native *Pinus nigra,* and plantations of non-native *Robinia pseudoacacia*) in study 4, and four habitats (i.e., large forest patches, north-facing forest edges, south-facing forest edges, and grasslands) in study 5 for the Kiskunság and the Deliblato, 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 (R Core Team, 2021; Oksanen et al., 2022). The "pairwise.adonis" function in the funfuns package was used with p-value adjusted by the Bonferroni method to test the pairwise differences (Trachsel, 2022).

4.3.2. Taxonomic diversity and diagnostic species

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). For study 4, the number and cover of non-native and native species per plot was also calculated. Non-natives were defined according to Borhidi (1995). 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 were identified with Fisher's exact test. We only considered those species that were diagnostic for a single habitat type. The analyses were carried out in JUICE 7.1 (Tichý, 2002).

4.3.3. Functional and phylogenetic diversity

To quantify functional diversity (FD), Rao's quadratic entropy (RaoQ) was used, 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. Plot-level Rao's quadratic entropy was calculated 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 S5). SLA, plant height, and thousand seed mass were selected because they are usually regarded as the most important and the 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. 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. 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). Phylogenetic trees of the 289 species in study 1, 173 species in study 3, and 225 species in study 5 were created based on the 74,533-species mega-tree GBOTB.extended.tre (Jin and Qian, 2019). To construct these phylogenetic trees, the nomenclature of plant species (species name, genus name, and family name) was standardized according to The Plant List (2013). Then "phylo.maker" function of the V.PhyloMaker package in R version 4.1.2 was applied to create phylogeny under the scenario 3, in which undetermined species were bound to their closest relatives. In addition, RaoQ was calculated for all species, it also was applied to compute only angiosperm species in study 1 and study 5. The phylogenetic trees are shown in Fig. S1 for study 1, Fig. S2 for study 3, and Fig. S3 for study 5. The "cophenetic" function of the picante package was used to compute phylogenetic distance (Kembel et al., 2010).

Finally, the "rao.diversity" function of the SYNCSA package was used in order to calculate RaoQ for both FD and PD (Debastiani and 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 standardized effect size of RaoQ (SES.RaoQ) was measured as (observed RaoQ value – mean expected RaoQ values)/standard deviation of expected RaoQ values (de Bello et al., 2021b). The null models for functional indices were generated by permuting the species labels of the trait matrix (999 randomizations) using the R code provided by de Bello et al. (2021b), 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, a two-sided Wilcoxon signed rank test was performed (Bernard-Verdier et al., 2012; Nooten et al., 2021; de Bello et al., 2021b).

4.3.4. 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 C strategy invest resources in increasing leaf area (LA); species with S strategy invest in retaining leaf dry matter content (LDMC); and species with R strategy invest primarily in the ability to increase specific leaf area (SLA) (Pierce et al., 2017). It is widely accepted that these traits strongly represent the leaf economics and plants 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; 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., 2022). However, 8 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.

Every species receives separate values according to the three strategies. For example, a given species may be regarded as primarily C-strategists, but may also have some S or R characteristics. We calculated the strategy (separate C, S, and R percentage 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 to determine 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.

For all habitats, 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 and Ferry, 2018).

4.3.5. Microclimate variables

The following variables were computed from the obtained microclimate data: mean daily air temperature (MDAT), mean daytime air temperature (MDtAT), mean nighttime air temperature (MNtAT), mean daily relative air humidity (MDAH), mean daytime relative air humidity (MDtAH), and mean nighttime relative air humidity (MNtAH). Daytime was defined 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.

(see Bátori et al., 2014; Erdős et al., 2014c, 2018b). These variables were calculated for each replicate.

Vapor pressure deficit (VPD) was selected as the meaningful limiting factor for plant growth and productivity (McDowell et al., 2008; Yuan et al., 2019; Süle et al., 2020). Vascular plants may be stressed if VPD values exceed a certain threshold (Novick et al., 2016; Shamshiri et al., 2018; Süle et al., 2020). This factor (VPD, Pa) was calculated from the air temperature (t, ^{o}C) and relative air humidity (H, %) according to Bolton (1980):

$$VPD = (100 - H) \times 6.112 \times e\hat{}(17.67 \times t/(t + 234.5))$$

In this study, the exceedance rate was analyzed, which is the percentage of VPD values above an appropriate threshold (1.2 or 3.0 kPa) over a 24-h period. This approach can help us better understand the microclimatic conditions that affect vegetation growth (Süle et al., 2020). The limiting threshold for the stress effect was set at 1.2 kPa, as suggested by many previous studies (Novick et al., 2016; Shamshiri et al., 2018; Süle et al., 2020), whereas 3 kPa threshold had a stronger inhibitory effect on plant growth and photosynthesis (Shirke and Pathre, 2004; Shibuya et al., 2018; Süle et al., 2020). A VPD duration curve (DC) was constructed using 1440 VPD values that were averaged over three replicates collected over the period of 24 hours for each habitat per month. This method is similar to the flow duration curve in hydrology and is thoroughly described by Süle et al. (2020). In addition, the DC for each replicate was also calculated. Based on this DC, the exceedance rate was calculated per replicate, which was then used for statistical analysis.

4.3.6. Statistical methods

For study 2, to reveal how ecological strategies (C, S, and R) correlate with the compositional gradient, we used linear regression between plot ordination scores and each strategy (C, S, and R). The models were visually checked using the diagnostic plots. In order to have the plot ordination score, 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 habitat types along the compositional gradient, which provides a continuous number interpretable as "compositional similarity to open grassland" or "compositional dissmimilarity to large forest." We chose DCA ordination instead of NMDS ordination in study 2 to maximize variation to the first axis (see Fig. S4).

A Venn-diagram was created for study 4 related to four habitats (near-natural forest patches, plantations of native *Populus alba*, plantations of non-native *Pinus nigra*, and plantations of non-native *Robinia pseudoacacia*) 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, accessed on September, 2021) for protected species including both protected and strictly protected species, FLÓRA database (Horváth et al., 1995) for endemic species, and Király (2007) for red-listed species. The Venn diagram was prepared using the online Venn diagram creator of the Ghent University (https://bioinformatics.psb.ugent.be/webtools/Venn/).

To assess the naturalness of the habitats in study 4 (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 (i.e., anthropogenic impacts): 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 preferred over the calculation based on cover-weighted approaches (Tölgyesi et al., 2014).

For studies 1, 2, and 4, species richness, Shannon diversity, SES.RaoQ, RaoQ, strategy (C, S, and R), naturalness values, and the cover of native and non-native species 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, Gamma or Gaussian family for continuous variables (Brooks et al., 2017). The assumptions of the models were visually checked using the performance package in R (Lüdecke et al., 2021). 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).

For study 3, the variables related to 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, as well as exceedance rate, were analyzed using general linear models. The fixed factor was the habitat. The “glm” function in R version 4.1.2 was used to build the models with Gaussian family (R Core Team, 2021). The assumptions of the models were checked by visual assessment of diagnostic plots. We then tested the general linear models using analysis of variance (ANOVA) with the “Anova” function in the car package (Fox and Weisberg, 2019). If the model had a significant proportion of variability, we performed all pairwise comparisons of the fixed factor levels using the “emmeans” function in the emmeans package in R (Lenth, 2022). The p-values were adjusted with the false discovery rate (FDR) method.

Regarding study 5, before data analysis, the Shapiro–Wilk normality test and the Bartlett test were applied to determine deviations from normality and homogeneity of variance, respectively. The Kruskal-Wallis test was performed 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 for all studies.

5. Results

5.1. Study 1: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity in forest-grassland mosaics

A total of 296 species were found in 494 plots, with 28 species being non-native and 268 species being native. Large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, closed perennial grasslands, open perennial grasslands, and open annual grasslands had 148, 155, 185, 216, 183, 155, 109, and 108 species, respectively.

5.1.1. Vegetation gradient and diagnostic species

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 (Fig. 12). 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, with the exception of only one pair: large forest patches and medium forest patches ($p > 0.05$; Table S6).

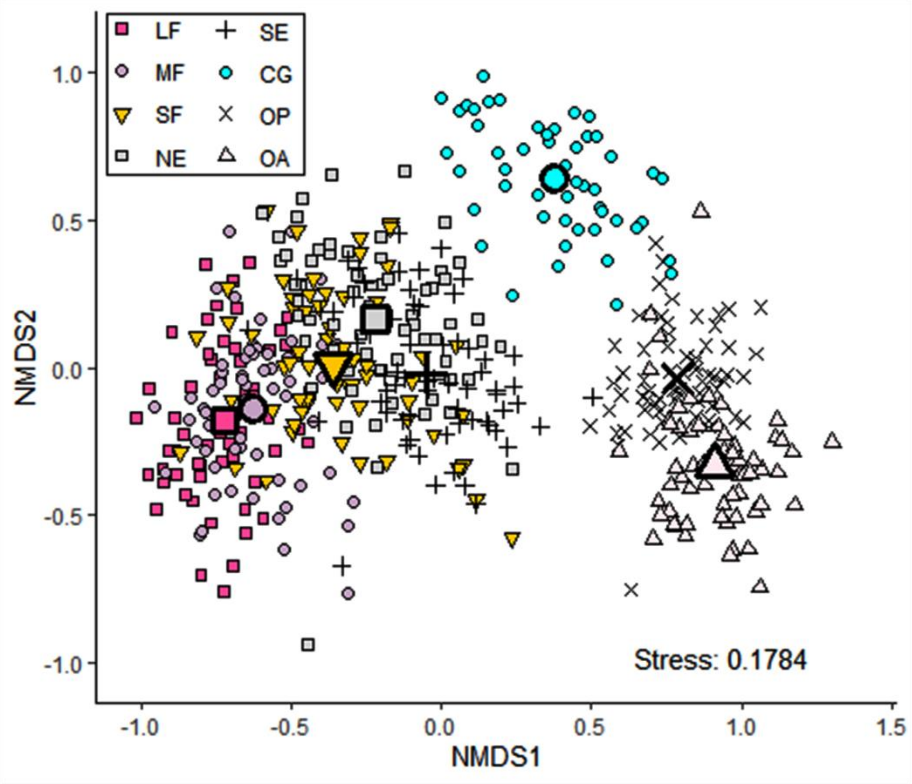

Figure 12. Habitat types along the forest-grassland gradient. Forest, edge and grassland types are placed in accordance with their position along the vegetation openness gradient in the ordination diagram. The NMDS ordination was prepared using square-root transformed cover percentages and Bray–Curtis 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.

The list of diagnostic species related to the eight habitats is presented in Table 2. 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.

Table 2. Diagnostic species of the eight habitats with phi coefficients > 0.200 (p<0.001). 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.

Species	LF	MF	SF	NE	SE	CG	OP	OA
Ailanthus altissima	0.235							
Cornus sanguinea	0.237							
Euonymus europaeus	0.271							
Geum urbanum	0.263							
Robinia pseudoacacia	0.327							
Rubus caesius	0.209							
Stellaria media	0.212							
Taraxacum officinale agg.	0.213							
Lithospermum officinale		0.334						
Padus serotina		0.212						
Vincetoxicum hirundinaria		0.213						
Achillea pannonica				0.259				
Asperula cynanchica				0.279				
Carlina vulgaris				0.429				
Hieracium echioides				0.261				
Leontodon hispidus				0.320				
Medicago falcate				0.307				
Pimpinella saxifraga				0.308				
Pinus nigra				0.238				
Polygala comosa				0.329				
Scabiosa ochroleuca				0.408				
Seseli annuum				0.350				
Solidago virgaurea				0.240				
Tephroseris integrifolia				0.249				
Thesium ramosum				0.307				
Tragopogon floccosus				0.217				
Viola rupestris				0.428				
Chenopodium album					0.268			
Chondrilla juncea					0.215			
Cynodon dactylon					0.282			
Senecio vernalis					0.249			
Allium sphaerocephalon						0.249		
Bothriochloa ischaemum						0.241		
Carex caryophyllea						0.429		

Dianthus pontederae	0.308		
Equisetum ramosissimum	0.257		
Festuca pseudovina	0.214		
Festuca rupicola-valesiaca(1)	0.650		
Filipendula vulgaris	0.237		
Koeleria cristata	0.684		
Ononis spinosa	0.246		
Phleum phleoides	0.359		
Salix rosmarinifolia	0.334		
Saxifraga tridactylites	0.342		
Scirpoides holoschoenus	0.617		
Veronica prostrata	0.223		
Erophila verna		0.708	
Festuca wagneri		0.223	
Koeleria glauca		0.244	
Myosotis stricta		0.296	
Trinia ramosissima		0.217	
Bromus squarrosus			0.601
Bromus tectorum			0.433
Conyza canadensis			0.218
Corispermum canescens			0.327
Linaria genistifolia			0.221
Salsola kali			0.358
Setaria viridis			0.506
Tragus racemosus			0.681
Tribulus terrestris			0.253
Veronica praecox			0.208
Viola arvensis			0.271

(1) These two species were not distinguished due to the challenges of species determination

5.1.2. Taxonomic diversity

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 (Fig. 13a). 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 (Fig. 13b).

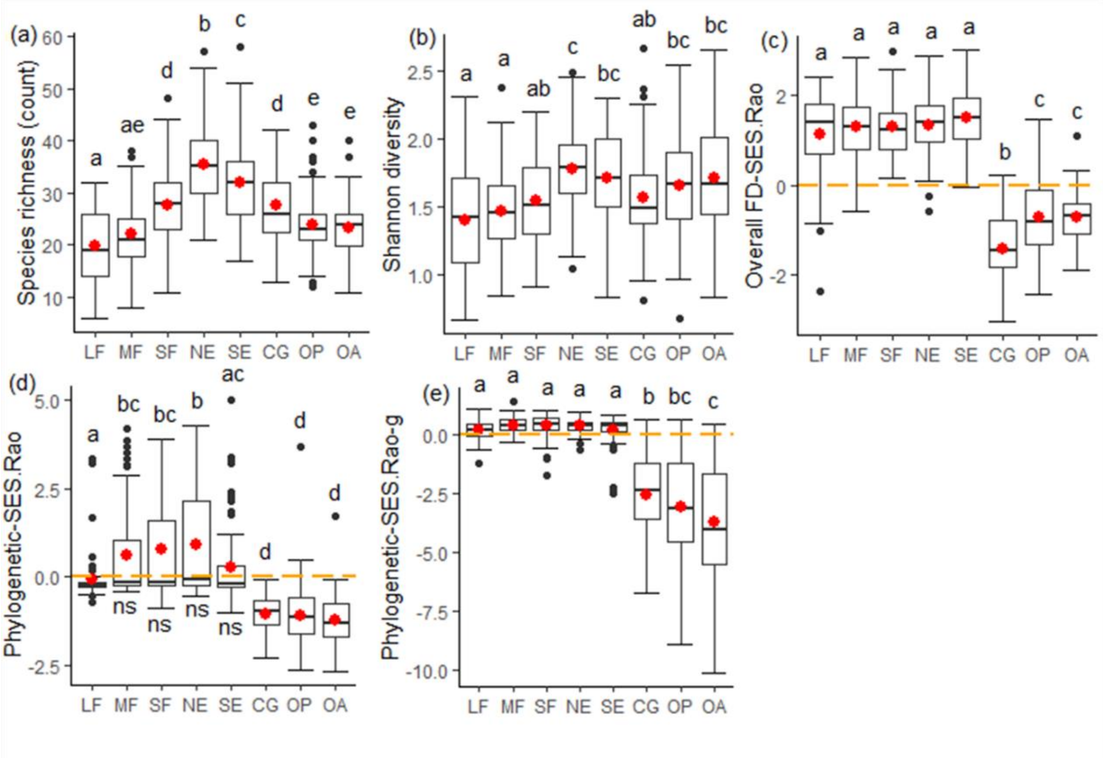

Figure 13. Differences in diversity measures among habitat types. Diversity measures include species richness (a), Shannon diversity (b), standardized effect size of Rao's quadratic entropy (SES.RaoQ) for functional diversity based on all traits (c), SES.RaoQ for phylogenetic diversity (d) and SES.RaoQ for phylogenetic diversity with non-angiosperm species excluded (e). 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. 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).

5.1.3. Functional diversity

Habitat type significantly affected overall functional diversity based on nine functional traits (Table S5) ($\chi^2 = 1266$, $p < 0.001$). Functional diversity was significantly higher in woody habitats (i.e. forests and edges) than in grassland habitats (Fig. 13c). Among the grassland habitats, the lowest functional diversity was found in closed perennial grasslands. Woody habitats were overdispersed, whereas grassland habitats were underdispersed (Fig. 13c; Table S7).

The functional diversity of individual traits was significantly influenced by habitat type (Table 3). The functional diversities of flowering time, seed dispersal, reproduction type and plant height were significantly higher in woody habitats than in grassland habitats (Fig. 14a–d), and a similar result was also observed for the functional diversity of seed mass (Fig. 14g). 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 (Fig. 14d–e). Closed perennial grasslands, open annual grasslands and medium forest patches had the highest functional diversity for SLA (Fig. 14f). 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 (Fig. 14g). 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 edges (Fig. 14h).

Table 3. The ANOVA results of trait-wise functional diversity among habitats.

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

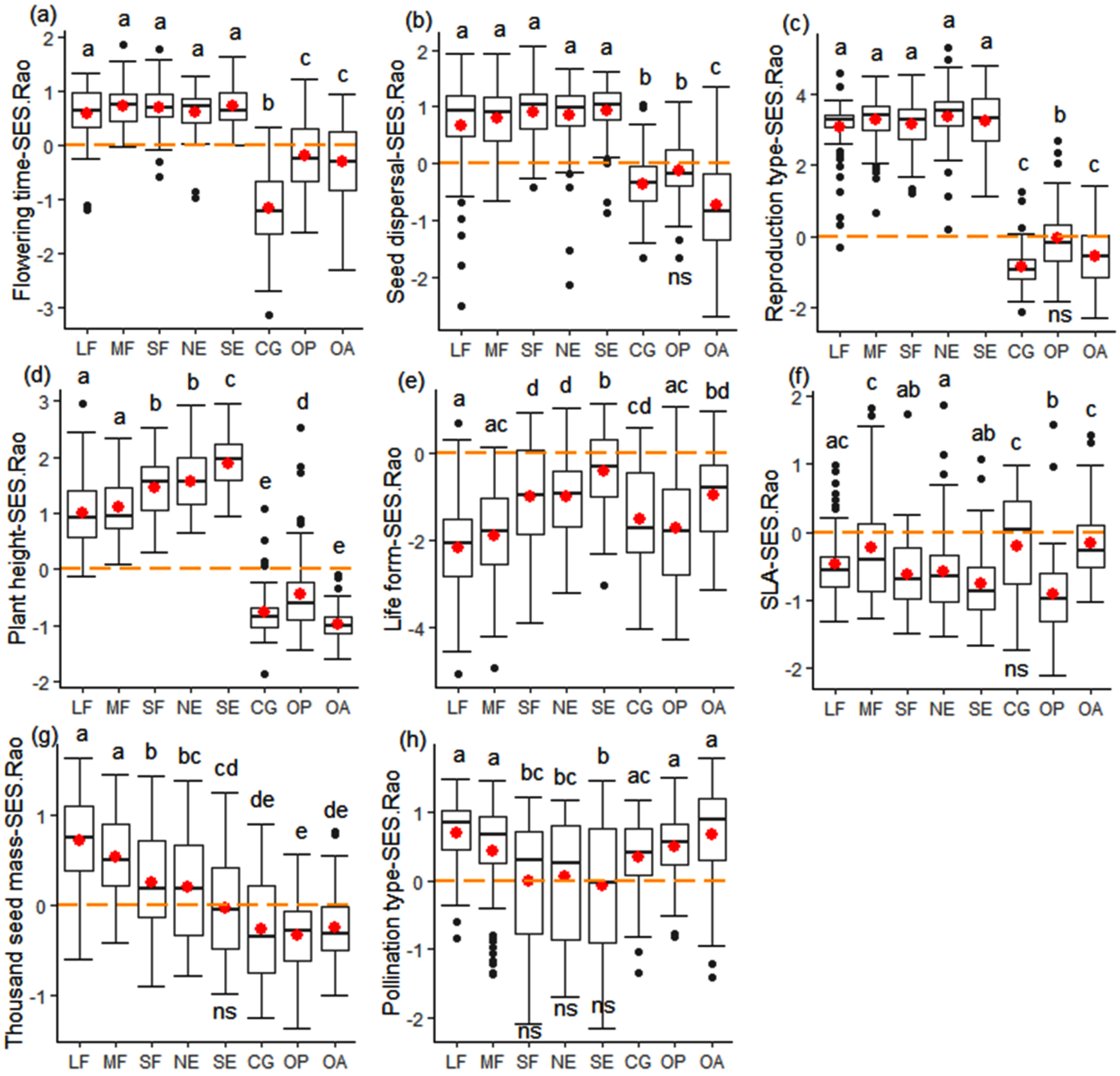

Figure 14. Differences in trait-wise functional diversity among habitat types. Traits include flowering time (a), seed dispersal (b), reproduction type (c), plant height (d), life form (e), specific leaf area (f), thousand seed mass (g) and pollination type (h). LF: large forest patches; MF: medium forest 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. 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).

5.1.4. Phylogenetic diversity

Habitat type had a significant effect on phylogenetic diversity (χ^2 = 319.1, $p < 0.001$). Phylogenetic diversity was significantly higher in woody than in grassland habitats (Fig. 13d). 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 (Fig. 13d; Table S7). All grassland habitats were underdispersed.

If only angiosperms were included in the calculation, habitat type still had a significant effect on phylogenetic diversity (χ^2 = 797.8, $p < 0.001$). Pairwise comparisons revealed significant differences between the woody and the grassland habitats (Fig. 13e). However, there were no significant differences in phylogenetic diversity among the woody habitats. All woody habitats were overdispersed, while all grassland habitats were underdispersed (Fig. 13e; Table S7).

5.2. Study 2: Plant strategies and community assembly rules in forest-grassland mosaics

The ternary plot showing unweighted values revealed that the contribution of mean components S was the highest, ranging from 48.9 to 60.4%, while the smaller contributions were observed from component C (8.98-25.1%) and component R (23.2-30.6%). When taking a closer look (Fig. 15b), a separation between values across habitat 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 (Fig. S5).

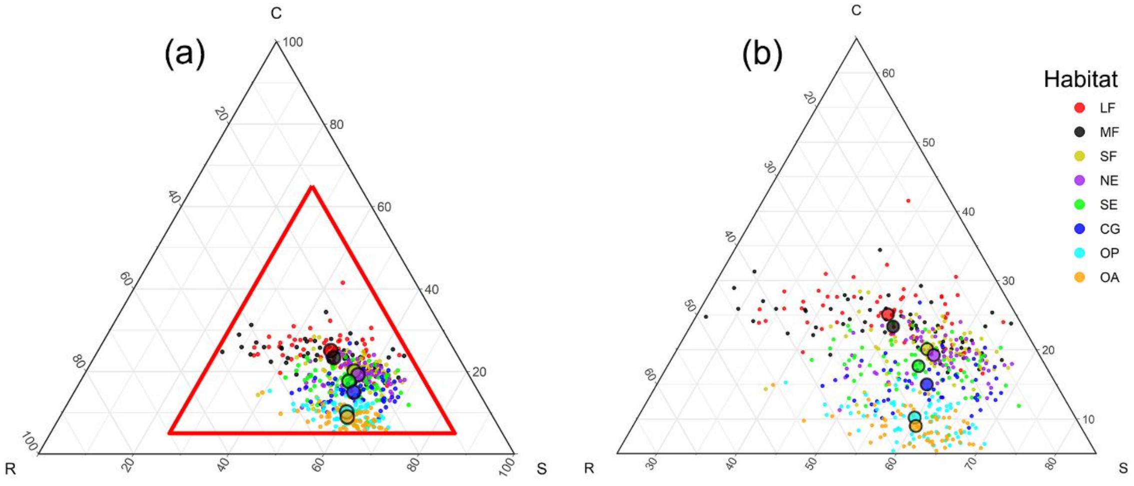

Figure 15. Ternary plots showing unweighted mean values of CSR strategies for the eight habitat types. A red triangle in plot (a) shows the boundaries of plot (b). Larger symbols indicate the mean value for each habitat type. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; CG: closed perennial grasslands; OP: open perennial grasslands; OA: open annual grasslands.

The DCA ordination revealed a compositional gradient along the first DCA axis (Fig. S4). The scores of the sample plots on the primary ordination axis were negatively associated with the C strategy (Fig. 16a) but positively associated with the S strategy (Fig. 16b). A weak but positive relation was observed between R strategy and DCA1 scores (Fig. 16c). The habitat type affected each type of strategy as follows: component C (χ^2 = 1637, p < 0.001), component S (χ^2 = 242, p < 0.001), and component R (χ^2 = 123, p < 0.001). The highest component C was found in large and medium forest patches, which gradually decreased toward the open end of the vegetation gradient (Fig. 16d). Component S depicted a gradually increasing trend from large forest patches to open annual grasslands (Fig. 16e). Open perennial and annual grasslands exhibited the highest component R, whereas north-facing edges displayed the lowest component R (Fig. 16f). Again, patterns were similar with weighted values, although some differences did emerge (Fig. S6). 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.

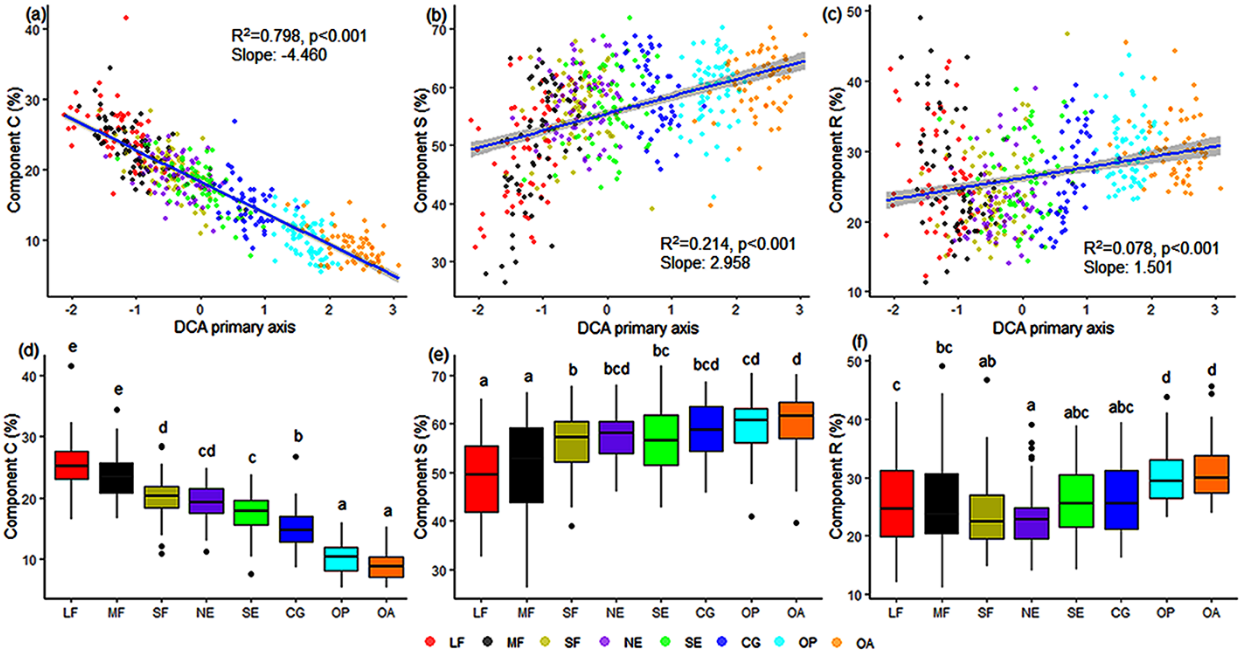

Figure 16. Relationships between plot scores on the primary DCA ordination axis and each unweighted strategy component: (a) C; (b) S, and (c) R; p-value and adjusted R-squared were calculated using linear regression; Slope: the slope value of the regression line; blue line is regression line, and grey 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 habitats. Those that do not share a letter are significantly different at α = 0.05 significance level. 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.

5.3. Study 3: microclimate in the habitats of a forest-steppe ecosystem

5.3.1. Air temperature patterns

The general 24-hour patterns of air temperature were similar in all habitats in each month, with a peak around or slightly after noon and a bottom during nighttime (Fig. 17). The temperature did not differ largely among habitats in April (Fig. 17a), whereas there were larger differences between open grasslands and forests during 24 hours for the other months (Fig. 17b-g). A distinct tendency between differently oriented edges was found. South-facing edges had similar patterns to the grasslands during the daytime, but they were closer to the forests at nighttime. North-facing edges resembled forests during the whole day. A similar pattern was observed for the seven-month average (Fig. 17h). Temperatures among habitats did not vary largely in the last couple of hours of the July measurement, when the weather was cloudy (Fig. 17d), while they fluctuated considerably in the first few hours of the September measurement, when the weather was rainy (Fig. 17f).

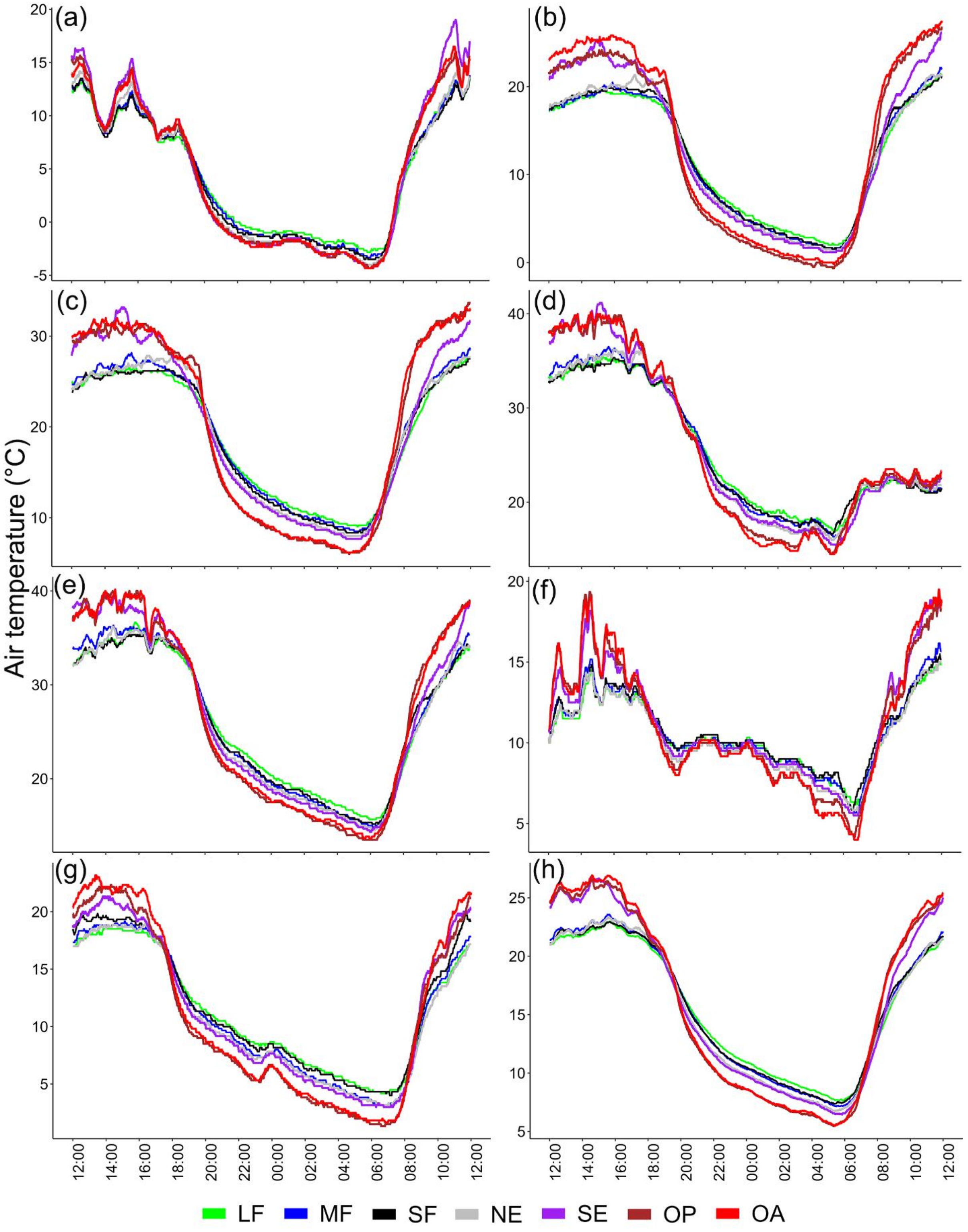

Figure 17. Air temperature values for the various habitat types over a 24-hour period. The values for each minute are averaged over three replicates. The air temperature values were measured for the following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; OP: open perennial grasslands; OA: open annual grasslands.

The mean daily air temperatures were very similar among the habitats in most measured months, but the daytime and nighttime values were significantly different among the habitats in each month (Fig. 18a-g). The diurnal range values were remarkably large in all habitats, but the largest values were observed in open perennial and open annual grasslands. The mean daytime air temperature was the highest in south-facing edges and open grasslands, while the mean nighttime air temperature was the lowest in the open grasslands (Fig. 18). For the seven-month averaged values, there was an increasing trend of daytime air temperatures along the vegetation gradient, while the opposite trend was seen for the nighttime air temperatures (Fig. 18h).

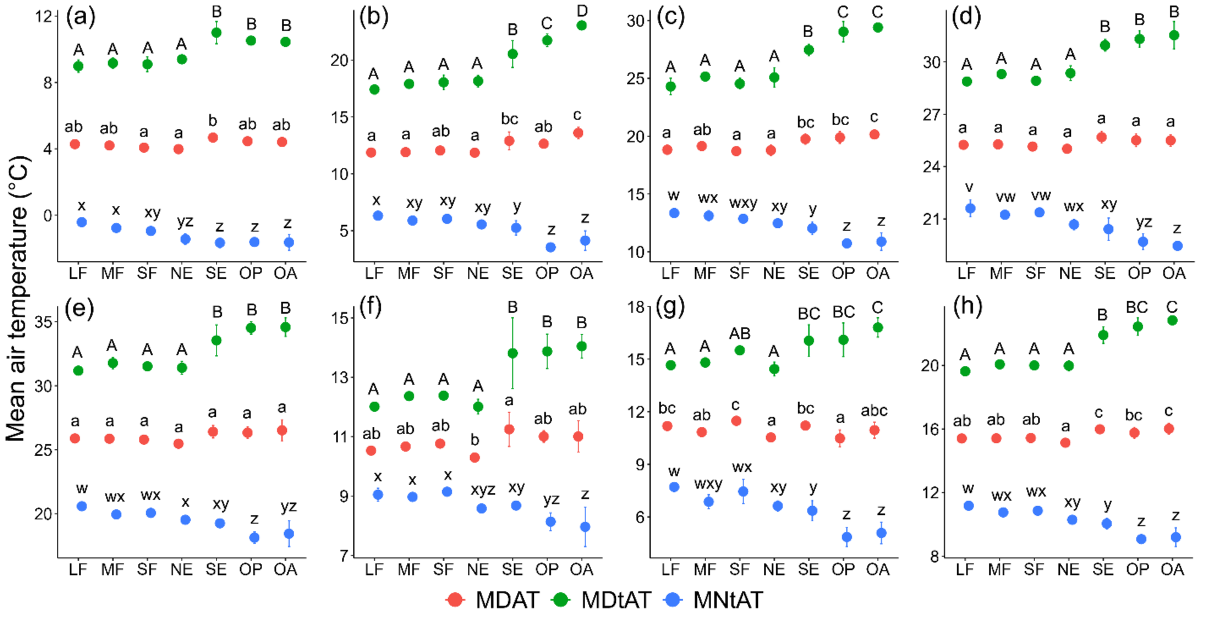

Figure 18. Mean daily, daytime, and nighttime air temperature values of the habitat types (mean ± standard deviation). The values are averaged over three replicates (large dots). The mean air temperature values were measured for the following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; OP: open perennial grasslands; OA: open annual grasslands. Different letters indicate significant differences among habitats. MDAT: mean daily air temperature; MDtAT: mean daytime air temperature; MNtAT: mean nighttime air temperature.

5.3.2. Relative air humidity patterns

The 24-hour patterns of relative air humidity showed the opposite trend compared to air temperature (Fig. 19). In April, the values of relative air humidity measured at the same time were quite similar among habitats, although south-facing edges seemed to have somewhat lower relative air humidity than the other habitats at nighttime (Fig. 19a). From May to October, the driest habitats were south-facing edges, open perennial grasslands, and open annual grasslands during the daytime (Fig. 19b-g). However, open perennial grasslands (and sometimes north-facing edges) were the most humid during the nighttime. This pattern was true for the seven-month mean (Fig. 19h). The values of air humidity remained high during the second daytime period of July (Fig. 19d), whereas humidity fluctuated significantly in the first couple hours of April and September (Fig. 19a, f).

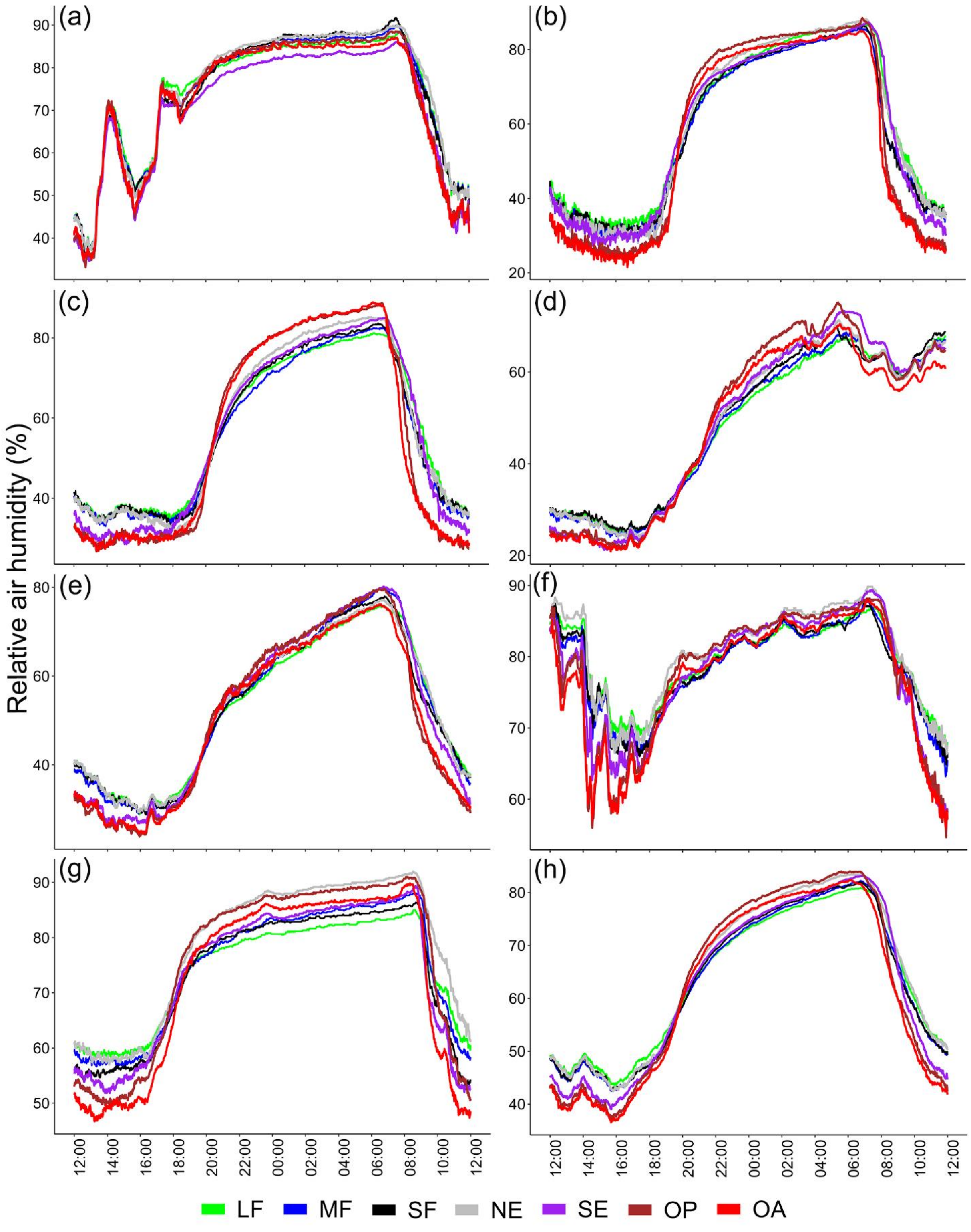

Figure 19. Relative air humidity values for the various habitat types over a 24-hour period. The values for each minute are averaged over three replicates. The relative air humidity values were measured for the following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; OP: open perennial grasslands; OA: open annual grasslands.

Mean daily air humidity, with the exception of May, did not differ significantly among habitats (Fig. 20). A similar pattern was also revealed for the mean nighttime air humidity values, but a peak was shown at open perennial grasslands in June and July (Fig. 20c, d). Regarding mean daytime air humidity, open grasslands were the driest habitats in most months, followed by south-facing edges (Fig. 20a-g). For the seven-month averaged values, both open grassland types had the lowest daytime air humidity, while open perennial grasslands had the highest air humidity at night (Fig. 20h). Rain generated a very similar but more pronounced jittering in the air humidity data as in the air temperature in September.

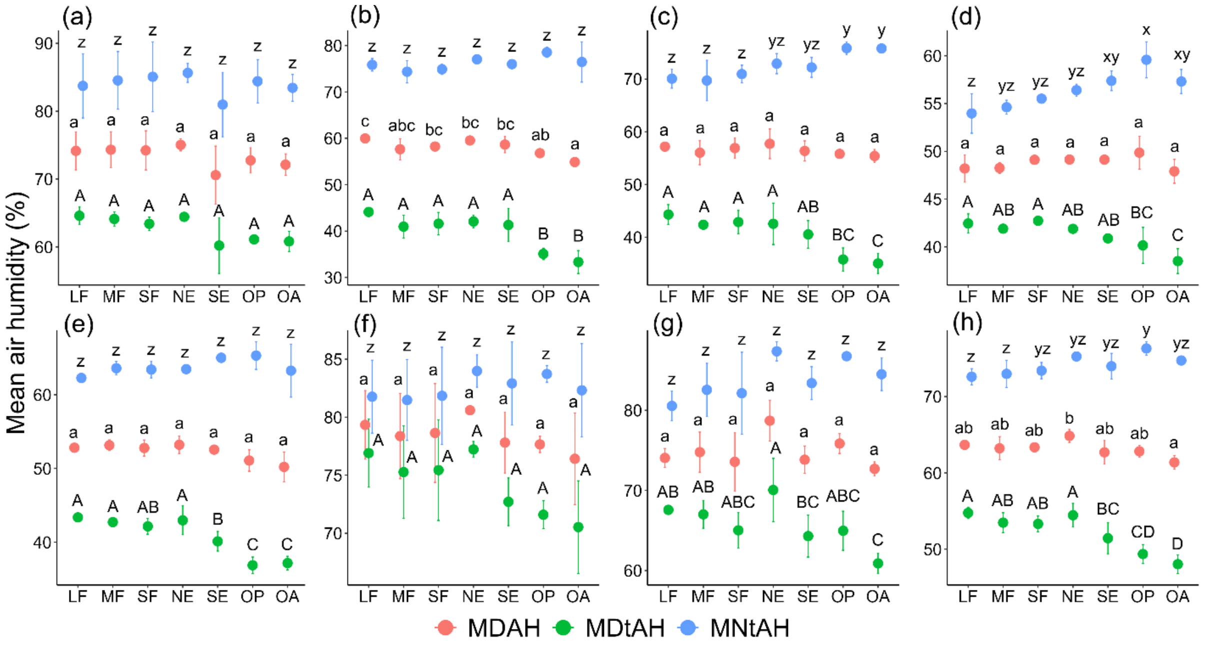

Figure 20. Mean daily, daytime, and nighttime air humidity values of the habitat types (mean ± standard deviation). The values are averaged over three replicates (large dots). The mean air humidity values were measured for the following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; OP: open perennial grasslands; OA: open annual grasslands. Different letters indicate significant differences among habitats. MDAH: mean daily air humidity; MDtAH: mean daytime air humidity; MNtAH: mean nighttime air humidity.

5.3.3. The patterns of vapor pressure deficit (VPD)

The VPD values calculated over 24-hours for each month and the seven-month average were quite high around noon but quite low during the nighttime (Fig. 21a-h). During the daytime, the VPD values of the woody habitats (i.e., forests and edges) were consistently lower than those of open grasslands, with the exception of April. The south-facing edges had higher VPD values than other woody habitats and had a similar trend to grasslands, while north-facing edges seemed similar to forest interiors. The VPD values were extremely high in the summer season, especially in July and August. There were no large differences among habitats at nighttime. A prominent effect of rain and cloudy sky on air temperature and relative air humidity was observed in July and September, which also affected the 24h patterns of VPD (Fig. 21d, f).

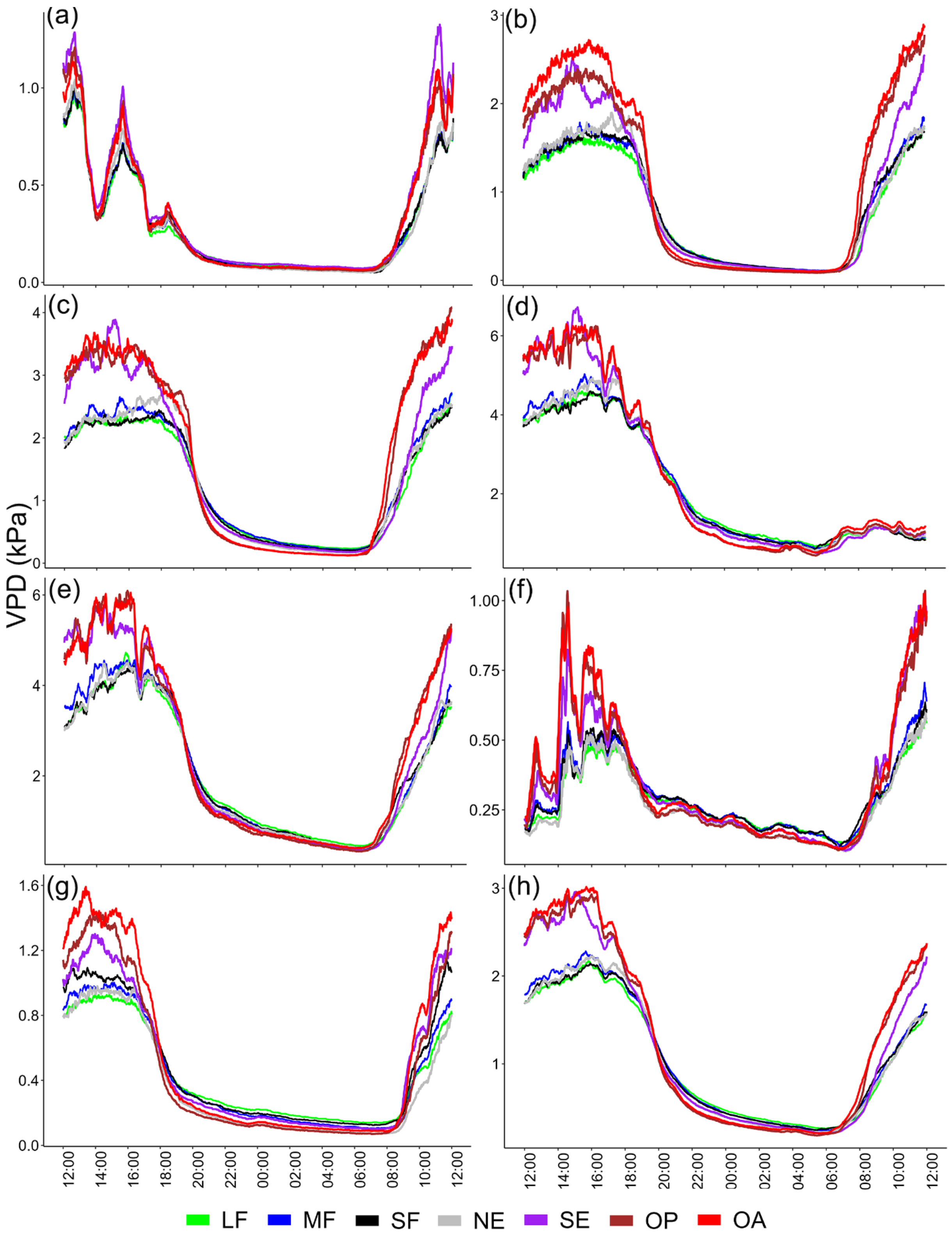

Figure 21. VPD values for the various habitat types over a 24-hour period. The values for each minute are averaged over three replicates. The VPD values were measured for the following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; OP: open perennial grasslands; OA: open annual grasslands.

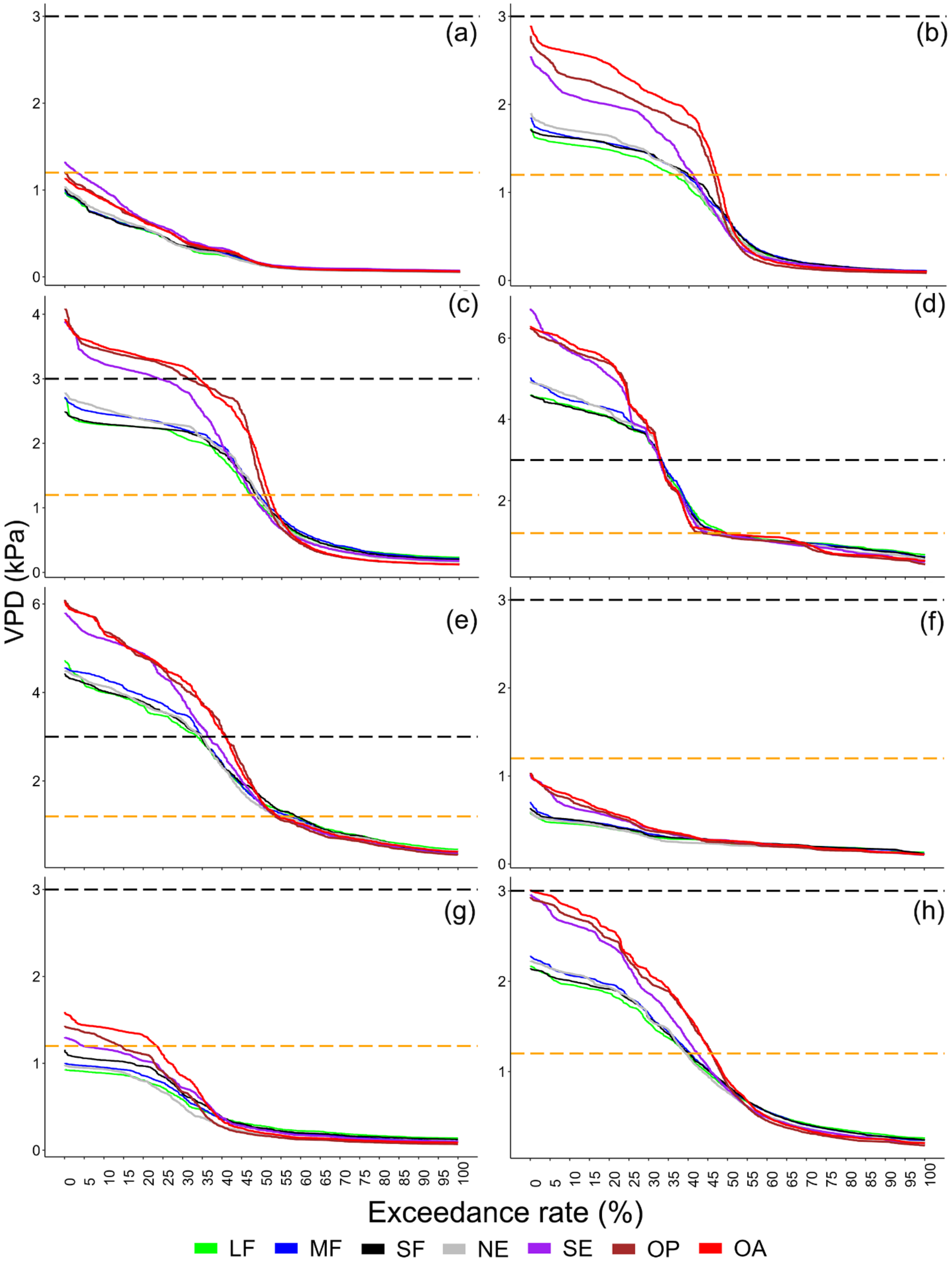

Figure 22. VPD duration curves for habitat types from a 24-hour measurement period each month: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. The VPD values for each minute are averaged over three replicates. The orange dashed line indicates the 1.2 kPa physiological threshold; the black dashed line indicates the 3.0 kPa threshold, above which the exceedance rates significantly diversified. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; OP: open perennial grasslands; OA: open annual grasslands.

Based on the VPD duration curves (Fig. 22), it was found that VPD values exceeded the 1.2 kPa stress threshold for all habitats from May to August. In October, south-facing edges and open grasslands had VPD values higher than 1.2 kPa, but with a low exceedance rate from 4.64% to 23.3%. In terms of the 3 kPa threshold, the summer season seemed critical, with open grasslands and south-facing edges having higher exceedance rates than other habitats. For the seven-month average VPD values, the exceedance rate for 1.2 kPa varied between 39.3 and 46.0% in the studied habitats, while the exceedance rate for 3 kPa was less than 1%, with open annual grasslands having the highest value (Fig. 22h).

Exceedance rate was significantly different among habitats from May to October, except for July and September (Fig. 23). The study revealed that the exceedance rate was very low in April and September (Fig. 23a, f). In May, the most stressed habitats were open grasslands at a 1.2 kPa physiological threshold (Fig. 23b). For June, open grasslands were the most stressed, followed by south-facing edges at a 3 kPa limiting threshold (Fig. 23c). Interestingly, all habitats were very stressed and were thus not significantly different among habitats in July at both limiting thresholds (Fig. 23d), while open grasslands were the harshest habitats in August at the 3 kPa threshold and in October at 1.2 kPa threshold, respectively (Fig. 23e, g). Regarding the averaged values for seven months, open grasslands were the most stressed to plant growth, followed by south-facing edges only at the 1.2 kPa threshold (Fig. 23h).

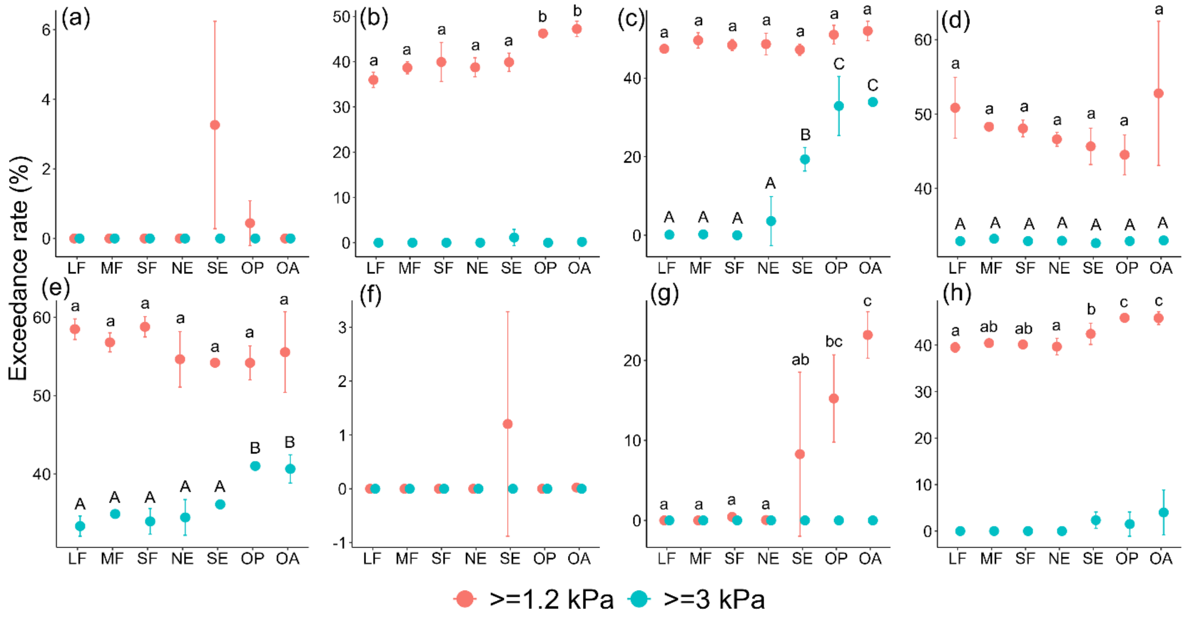

Figure 23. Exceedance rate (%) for vapor pressure deficit values above 1.2 kPa and above 3.0 kPa (mean ± standard deviation). The values are averaged over three replicates (large dots). LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; OP: open perennial grasslands; OA: open annual grasslands. Different letters indicate significant differences among habitats. Exceedance rate for each month: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. Due to the 5% lower mean exceedance rate and data with many zeros, statistical analysis was not applied for the exceedance rate above 1.2 kPa in April and September, and it was not used for the exceedance rate above 3 kPa in April, May, September, October, and seven-month average.

5.4. Study 4: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity of near-natural forests and tree plantations

5.4.1. Species composition and diagnostic species

When we compared species composition among four habitats (near-natural poplar forests *Populus alba*, *Pinus nirga*, and *Robinia pseudoacacia* plantations), we found some slight overlap among the habitat types in the NMDS ordination space (especially between *Populus alba* plantations and *Pinus nigra* plantations) (Fig. 24). However, 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 S8).

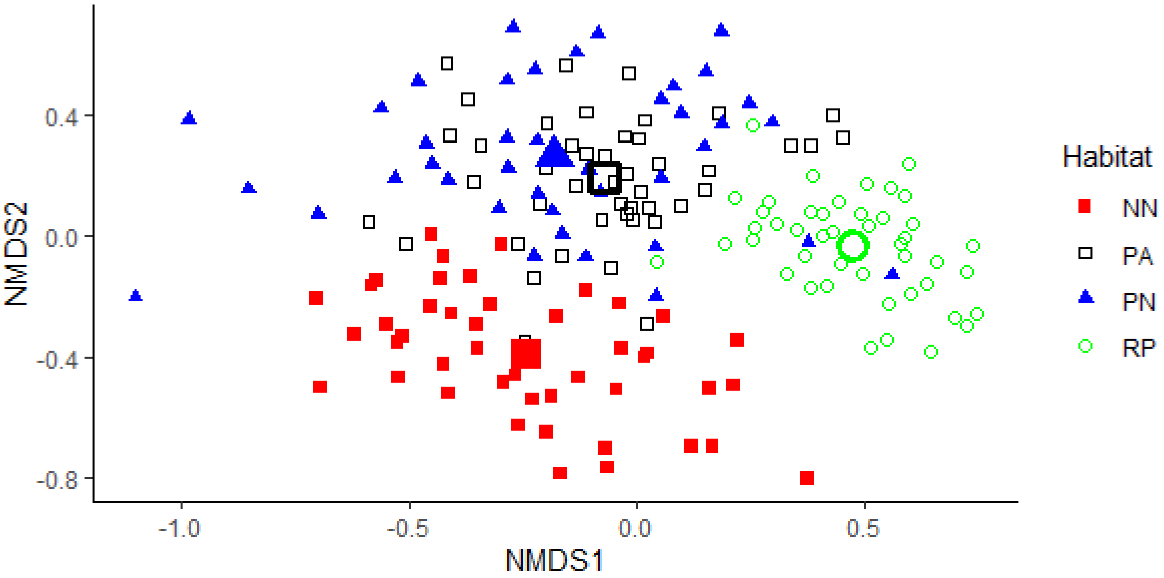

Figure 24. NMDS ordination scattergram of 175 plots. NN: near-natural poplar forests; PA: plantations of native *Populus alba*; PN: plantations of non-native *Pinus nigra*; RP: plantations of non-native *Robinia pseudoacacia*. Large signs show the centroids for each habitat. Stress = 0.25.

Significant ($p<0.001$) diagnostic species are shown in Table 4. Near-natural forests had 19 diagnostic species, all of which were native, and contained many shrubs (e.g., *Berberis vulgaris*, *Ligustrum vulgare*, and *Rhamnus catharticus*). *Populus alba* plantations had 11 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 disturbed grasslands or arable fields (e.g., *Secale sylvestre* and *Viola arvensis*).

Table 4. Diagnostic species of the four habitats with phi coefficients > 0.200 (p<0.001). 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			
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

5.4.2. Taxonomic, functional, and phylogenetic diversity indices

A total of 173 plant species were found in the 175 plots, exclusively in the shrub and herb layers, without a canopy layer. The following results are for these species only. 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.

Habitat type significantly influenced the number of native species (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). Near-natural forests contained the highest number of native species, followed by native tree plantations of *Populus alba* (Fig. 25a). 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. 25b). The number of non-native species was the highest in *Populus alba* 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. 25c). A similar pattern was observed for functional diversity (Fig. 25d). Phylogenetic diversity was the highest in near-natural forests, but it was not significantly different compared with *Pinus nigra* plantations (Fig. 25e). Phylogenetic diversity was the lowest in plantations of non-native *Robinia pseudoacacia*, while plantations of native *Populus alba* had intermediate phylogenetic diversity.

Habitat types also impacted the cover of native species (chi-squared=459, p<0.001) and the cover of non-native species (chi-squared=12.6, p<0.005). Near-natural forests and *Robinia pseudoacacia* plantations had the highest cover of native species, followed by *Populus alba* plantations (Fig. S7a). The lowest cover of native species was observed in *Pinus nirga* plantations. Meanwhile, the cover of non-native species was the highest in *Populus alba* plantations and lowest in *Pinus nirga* plantations (Fig. S7b). It was intermediate in the other habitats.

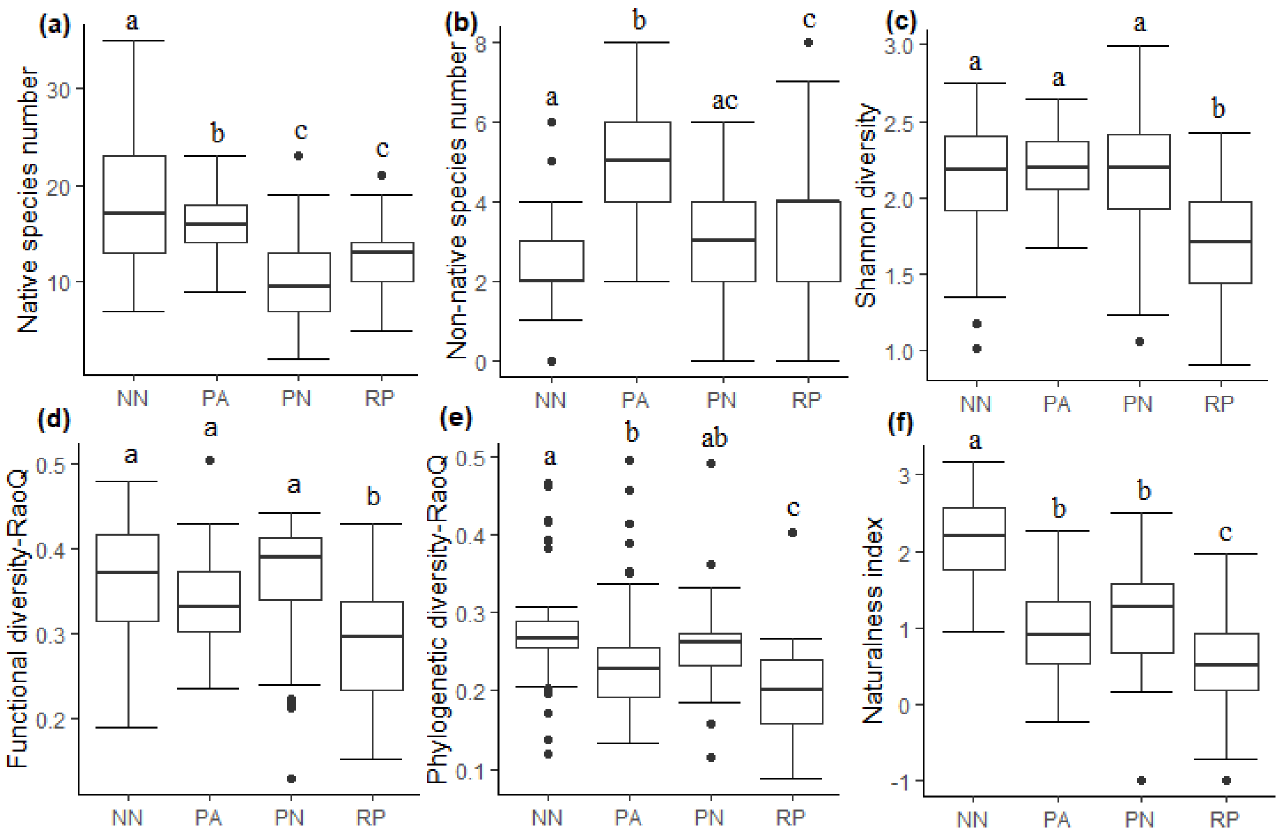

Figure 25. The number of native species (a), the number of non-native species (b), Shannon diversity (c), functional diversity (d), phylogenetic diversity (e), and the mean naturalness values (f) of the four habitat types. Different letters indicate significant differences ($p<0.05$). NN: near-natural poplar forests. PA: plantations of native *Populus alba*; PN: plantations of non-native *Pinus nigra*; RP: plantations of non-native *Robinia pseudoacacia*.

5.4.3. Conservation values

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. 25f).

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. 26). The list of these species is presented in Table S9.

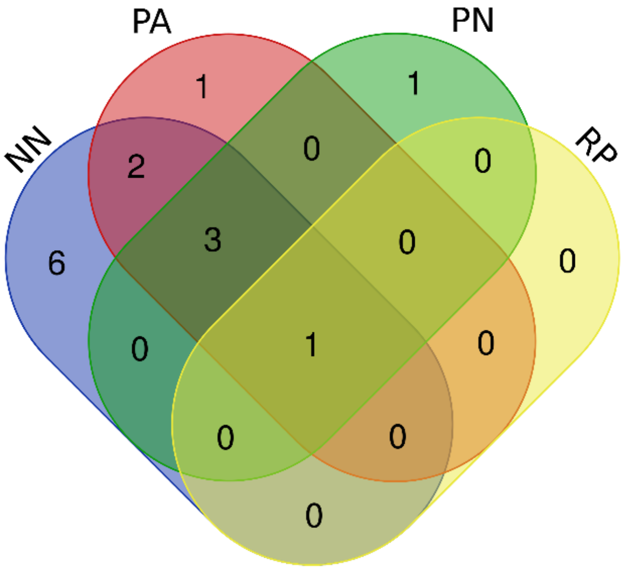

Figure 26. Venn diagram of species with high conservation importance (protected, endemic, and/or red-listed species) according to their habitat. NN: near-natural poplar forests. PA: plantations of native *Populus alba*; PN: plantations of non-native *Pinus nigra*; RP: plantations of non-native *Robinia pseudoacacia*.

5.5. Study 5: Forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity.

5.5.1. 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. 27). 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 S10).

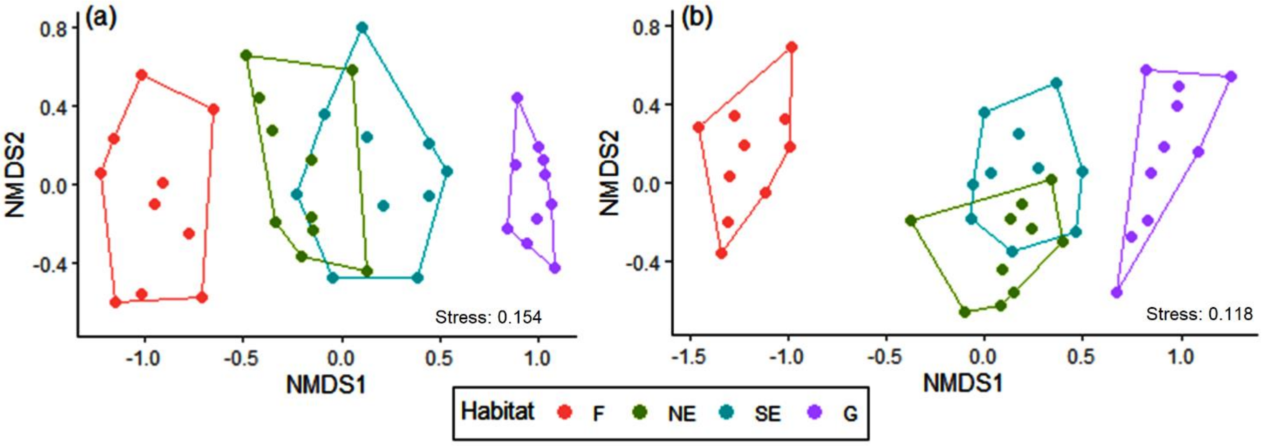

Figure 27. NMDS ordination diagram of the plots of the Kiskunság (a) and the Deliblato (b) based on the square root–transformed percentage cover data. F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland.

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 5 species, respectively). North-facing edges had an intermediate diagnostic species number, with 8 and 9 species in the Kiskunság and the Deliblato, respectively (Tables 5 and 6).

Table 5. Diagnostic species of the four habitats with phi coefficients > 0.200 in the Kiskunság Sand Ridge ($p < 0.01$). 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 6. Diagnostic species of the four habitats with phi coefficients > 0.200 in the Deliblato sands (p < 0.01). 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		
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

5.5.2. Taxonomic diversity

Forest patches exhibited the lowest species richness both in the Kiskunság and the Deliblato (Fig. 28a). 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. 28b), but edges seemed to be less diverse than grasslands in the Deliblato, even though the differences were not significant.

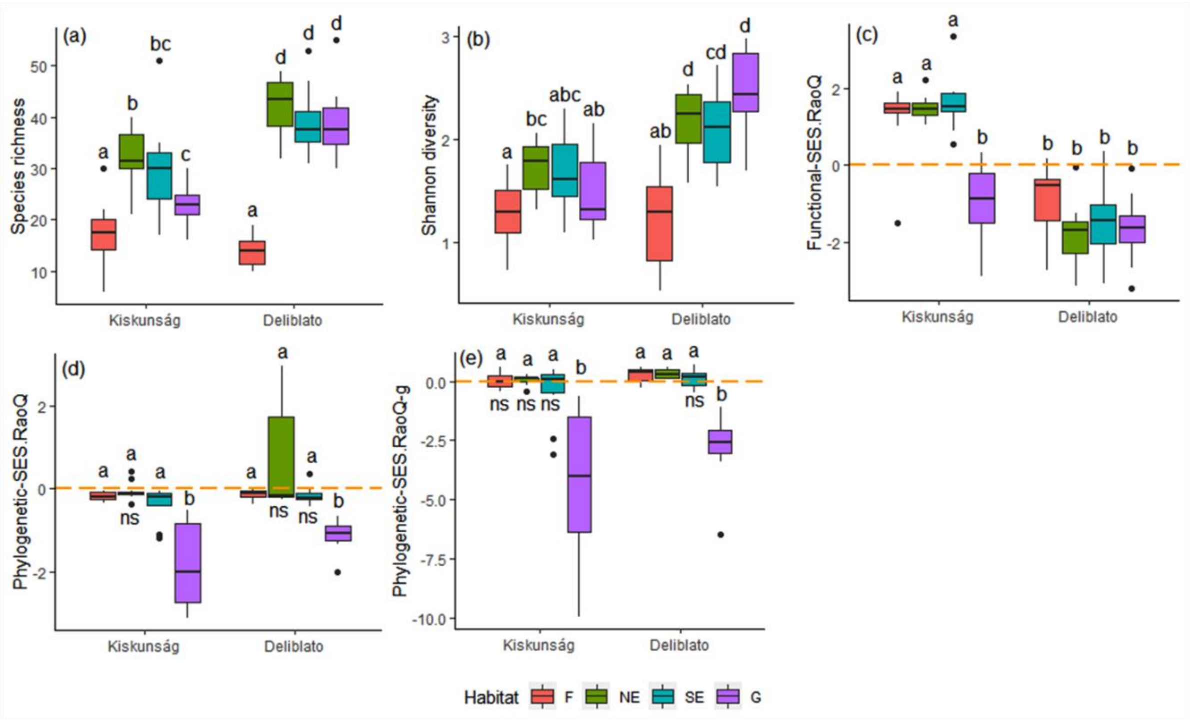

Figure 28. Species richness (a), Shannon diversity (b), and functional diversity of all traits based on the standardized effect size of Rao's quadratic entropy (SES.RaoQ) (c), phylogenetic diversity of all species (d), phylogenetic diversity of only angiosperm species (e) of the four habitat types in 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).

5.5.3. 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. 28c). 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. 28c, Table S11).

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. 29b–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 S11). The functional diversity of life form peaked at the edges, and this diversity showed a declining tendency toward neighboring habitats, especially in the Kiskunság (Fig. 29e). The functional diversity of both SLA and pollination type peaked toward forest patches and grasslands and reached minima at the edges, although between-habitat differences were not always significant (Fig. 29f, 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 S11).

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. 29a, Table S11), 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. 29g). Forests in the Kiskunság showed overdispersion, whereas random patterns or underdispersion were found in all other cases (Table S11).

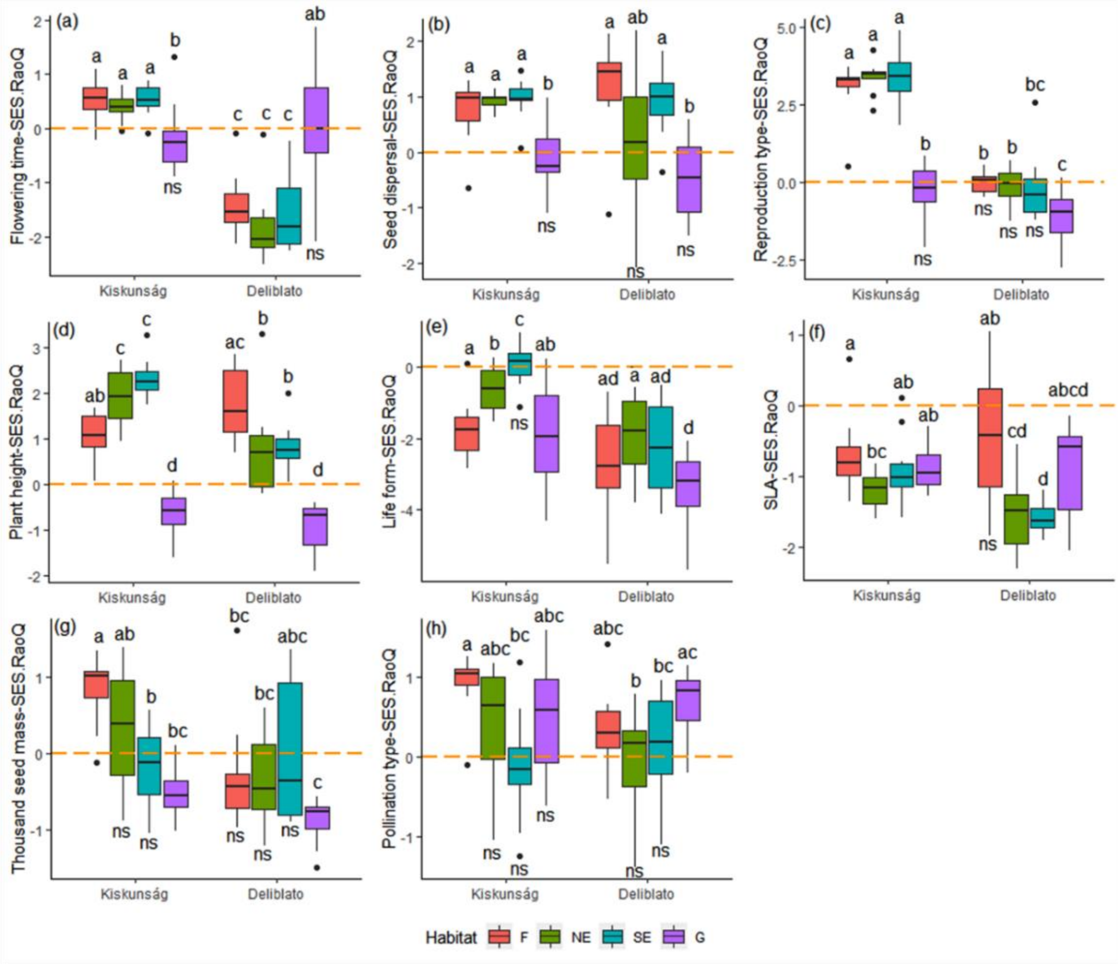

Figure 29. Functional diversity of single traits. Flowering time (a), seed dispersal (b), reproduction type (c), life form (d), plant height (e), specific leaf area (f), thousand seed mass (g), and pollination type (h). F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland. Habitats not 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).

5.5.4. 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. 28d). 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 S11).

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. 28e). All woody habitats showed either overdispersion or random patterns, whereas all grasslands were underdispersed (Table S11).

6. Discussion

6.1. Study 1: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity in forest-grassland mosaics

6.1.1. Vegetation gradient and edge-species

Many ecosystems with alternative stable states are mosaics of differently sized forest patches and one or more types of grassland. Our present study indicated a compositional gradient as follows: large forest patches – medium forest patches – small forest patches – north-facing edges – south-facing edges – closed perennial grasslands – open perennial grasslands and open annual grasslands (Fig. 12), which lead to an environmental harshness gradient in the Kiskunság's sandy forest-steppes (see Study 3). Forest patches are known to reduce environmental harshness (e.g., increase the humus and moisture content of the upper soil and mitigate daily temperature extremes), 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 et al., 2018b; 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 neighboring 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 (Fig. 12). Among the grassland habitats, open perennial grasslands and open annual grasslands were situated at the end of the compositional gradient. This likely reflects their harsh conditions (Bodrogközy, 1982, also see microclimate conditions in Study 3), while the environmental factors of closed perennial grasslands are less harsh (Borhidi et al., 2012). Our study indicates that, despite the considerable compositional overlaps, the eight habitat types are sufficiently distinct to grant all of them special attention in ecological studies and conservation practice.

Our results confirmed the existence of edge-species: we were able to identify species that preferred either north-facing or south-facing edges while they were rare in habitat interiors (Table 2). 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., 2019c). Many edge-related species in the present study, however, are also frequent in disturbed or open habitats. Indentifying edge-related species for generalization proves challenging. Some earlier studies, for example, found species that were significantly related to edges (Erdős et al., 2014; Bátori et al., 2018), while other studies found only weak evidence of edge-related species (Lloyd et al., 2000; Erdős et al., 2011). As a result, species that prefer edges should be evaluated carefully, as a species may be edge-related in one region but not in another (Lloyd et al., 2000).

6.1.2. Taxonomic diversity

Our results showed that species richness peaked at the middle of the compositional gradient and gradually decreased towards both ends (Fig. 13a). 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., 2019c; Molnár, 1998; Pinder and 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). Thus, the high species richness at the middle of the gradient is at least partly due to edge-species.

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 and Macdonald, 2002) and is in good accordance with our results, as all the edges included in the present work were old, undisturbed and stable. In contrast, sharp edges under unstable conditions may support lower species richness (van der Maarel, 1990). Therefore, we emphasize that certain characteristics of forest edges determine the species diversity within edges. Compared to species richness, Shannon diversity showed a slightly different pattern (Fig. 13b). Shannon diversity, similar to species richness, was high at the edges (at the middle of the gradient), but 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.

6.1.3. 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 (Fig. 13a–c). Contrary to species richness and Shannon diversity, functional diversity was significantly higher in woody habitats (forests and edges) than in grasslands (Fig. 13c). 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 (Fig. 14a–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 and Oldeland, 2019), which is in accordance with our results, as grassland habitats are characterised by stronger environmental stress (e.g. soil moisture, temperature) than woody habitats (Bodrogközy, 1982; Erdős et al., 2014c, and Study 3).

Competition for light in the woody habitats leads to a multilayered structure and results in high functional diversity of mean plant height (Fig. 14d). 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 fewer strategies 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 and 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 and 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 and Keddy, 1995). This may have resulted in a higher functional diversity at the sampling scale, especially south-facing edges, 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 (Fig. 14d) and life form (Fig. 14e). This reflects the diverse structural features of the edges and edge-like habitats, which harbor 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, old and stable, 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. Therefore, we suggest exploring a new research direction that involves comparing the vegetation of “old” and “new” edges to investigate their functional differences.

Grasslands had low overall functional diversity values (Fig. 13c), 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 (Fig. 14f). 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 *Secale sylvestre*) have high SLAs. This indicates that two distinct functional strategies coexist in closed grasslands and open annual grasslands (cf. Bernard-Verdier et al., 2012). The functional diversity of pollination type proved to be high in open perennial and open annual grasslands (Fig. 14h). 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), as well as along dry grassland-wetland gradients (Lhotsky et al., 2016b). 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 systemspecific 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.

6.1.4. Phylogenetic diversity

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 (Fig. 13d–e). The difference was probably caused by *Juniperus communis*, by far the most frequent nonangiosperm 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 (Fig. 13d). This difference did not disappear if nonangiosperm species were excluded from the analysis (Fig. 13e), 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.

6.2. Study 2: Plant strategies and community assembly rules in forest-grassland mosaics

In the framework of the CSR theory (Grime and 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.

Generally, each habitat type was dominated by the stress-tolerator strategy (Fig. 15a), 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 less than 350 mm in some years to over 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 habitat type examined in the present work was dominated by the stress-tolerator strategy, ecological strategies differed markedly among the studied habitat types (Fig. 15b and 16). This is similar to the finding of Rosenfield et al. (2019), who revealed distinct plant strategies along a relatively short gradient across forest types (i.e., rainforests, seasonal forests, *Araucaria* forests and Pampean forests) 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 towards 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) 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, 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), Adler et al. (2013) and Lhotsky et al. (2016b), 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 towards the harsh end (in our case, grasslands) and competition getting more important towards the more productive end of the gradient (in our case, forests). Our results also fit the findings of Dayrell et al. (2018), who reported from

Southeast Brazil that 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 (Fig. S6), the importance of stress was further emphasized, as component S was high along the full gradient, and differences were only moderate among the habitats. 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 towards the endpoints 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.

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 habitat 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, i.e., 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. In closed grasslands, there is probably an 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 for light but more competition for water. 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, R strategy was only weakly related to DCA1 scores (Fig. 16c) and played the most important role in the open grassland types (Fig. 16f). 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 (Figure S6). 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 and Shipley, 2017; Pierce et al., 2017). Open annual grasslands (OA) usually emerge as a result of disturbance, most often wind erosion or trampling of grazers and browsers or extreme droughts

(Fekete, 1992; Borhidi et al., 2012; Mojzes et al., 2021), although identifying the exact disturbance agents needs further research.

According to the cover-weighted analyses, the ruderal strategy has a relatively important role in the large and medium forest patches. This may reflect some anthropogenic influence. Although the study sites are legally protected now, forest patches were affected by human activity earlier, which may still have an effect on these habitats. Also, the presence of grazing and/or browsing animals may add to the greater role ruderals play in these habitats.

To sum it up, the stress-tolerant strategy was dominant in all habitat types, but it lost some importance towards large and medium forests as competition increased (Fig. 30). The stress-tolerant strategy was supplemented by the R strategy in open grasslands.

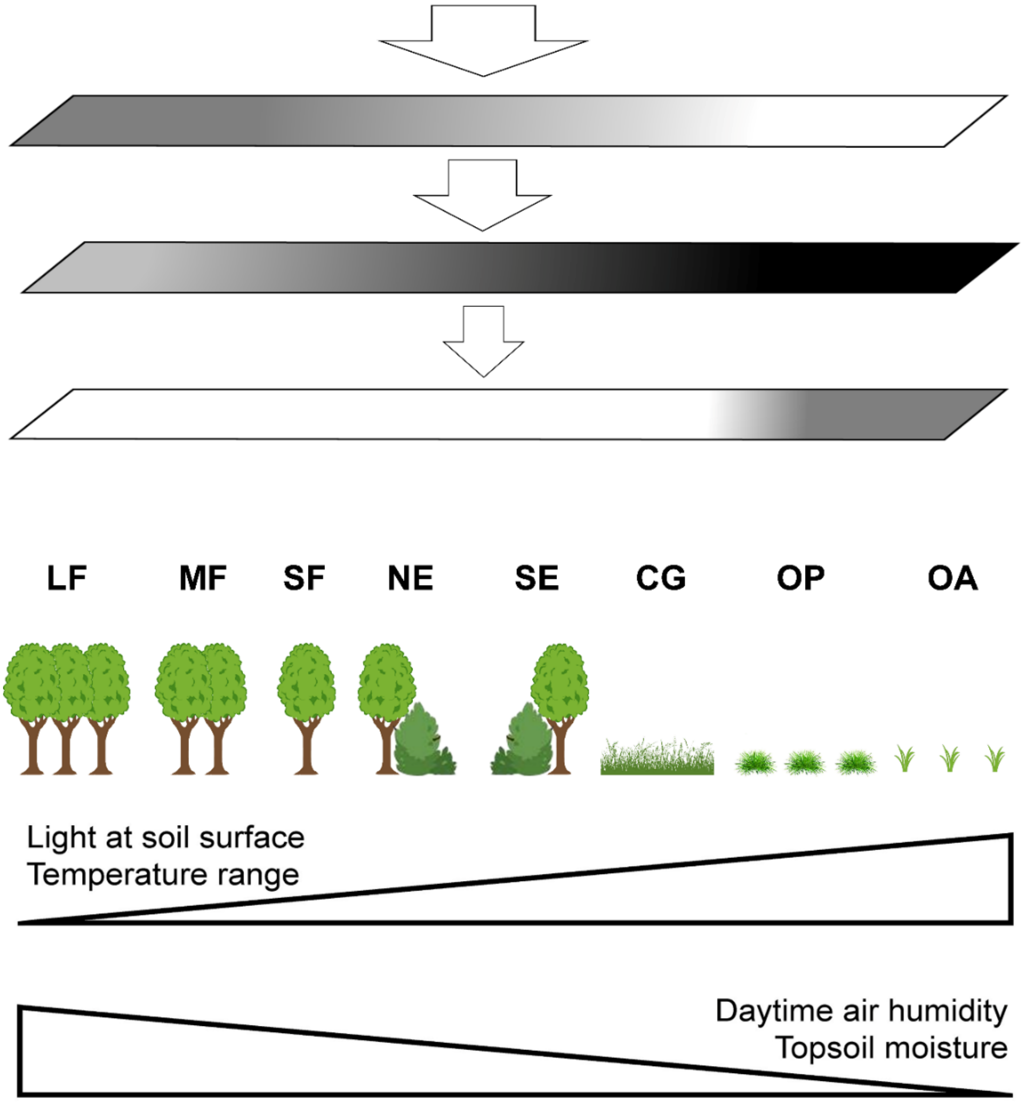

Figure 30. Assembly in the eight studied habitat types of the forest-grassland mosaics in the Kiskunság Sand Ridge. The three components of the filter proposed by Grime and Pierce (2012) are shown as separate filters to increase clarity, but their order should not be interpreted as a hierarchy. Darker colors indicate dominating role of a filter. C: competition, S: stress, D: disturbance. 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

Similarly to Catorci et al. (2011) and Han et al. (2021), we found that 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), or studies that contain a longer section of the disturbance gradient (e.g., Pierce et al., 2007) could provide additional information on assembly rules.

6.3. Study 3: microclimate in the habitats of a forest-steppe ecosystem

6.3.1. Microclimate differences among the habitats

Our first study revealed a gradient in species composition from large forest patches through smaller-sized forest patches and edges to grasslands (Fig. 12). The compositional differences among the habitats were thought to be associated with differences in microclimate. The current study demonstrated that forests indeed have a strongly different microclimate than grasslands (compared to grasslands, forests are cooler during the daytime and warmer during the nighttime, and more humid during the daytime). In this study, especially for temperature, south-facing edges tended to be more similar to grasslands, while north-facing edges tended to be more similar to forests.

The present work confirmed that the harshest conditions were found at the end of the compositional gradient during the growing season. Open grasslands were the hottest and driest at daytime, but the coolest at nighttime, resulting in the largest diurnal range in these habitats. This result is in line with the previous study of Erdős et al. (2014c), who measured the microclimate of forest-grassland mosaics in central Hungary for a short period (only 24 hours on a single summer day). Similar results have been reported from grasslands of other biogeographical regions (Davies-Colley et al., 2000; Wright et al., 2010; Peng et al., 2012; Bogyó et al., 2015).

The importance of forests in reducing environmental extremes under semi-arid conditions of the Kiskunság Sand Ridge was shown in the present study. It is reasonable to assume that the revealed microclimatic patterns are caused by the different vegetation, most notably the differences in vegetation cover, especially canopy cover (Chen et al., 1995). Trees play an essential role in driving the below-canopy microclimate: they reduce temperature variation under the canopy, as they absorb and reflect the solar radiation, they have a cooling effect near the soil surface during the daytime, and release longwave radiation during the nighttime (Magnago et al., 2015; Greiser et al., 2018; Aalto et al., 2022). De Frenne et al. (2019) found that forest patches were 4.1 ºC cooler than open-habitat patches on a global scale. Similarly, canopy sites have been shown to have significantly lower maximum temperatures than non-canopy ones under sunny conditions, differences being ca. 5.2 ºC in Africa (Aalto et al., 2022), and ca. 3.0-5.1 ºC in Europe (Morecroft et al., 1998; von Arx et al., 2012; 2013; Milošević et al., 2020). On the other hand, minimum temperatures in forest patches are on average 1ºC higher than in open-field conditions at night (De Frenne et al., 2021).

Woody habitats (forests and edges) were more humid than open grasslands at daytime, and daytime air humidity, therefore, exhibited patterns opposite to that of the air temperature. Similar results were reported, among others, from the western United States (Ma et al., 2010), Switzerland (von Arx et al., 2012), Hungary (Tölgyesi et al., 2020), and the United Kingdom

(Morecroft et al., 1998). In the current study, there was no statistically significant difference in nighttime air humidity among the studied habitat types, which is similar to that reported from poplar, black locust, and pine forests as compared to adjacent grasslands (Tölgyesi et al., 2020). Indeed, the significant differences in microclimate variables among habitat types occurred only between May and October, when the foliage of the dominant tree (*Populus alba*) reappears with a high canopy cover of ca. 50-70%, while microclimate was almost similar among habitats in April because the foliage has not yet appeared at that time (Caudullo and de Rigo, 2016). Therefore, canopy cover may be considered the most central factor in creating strong microclimatic differences during daytime (Godefroid et al., 2006).

In the study area, small forest patches characterized by open canopy are usually expected to be warmer and drier than larger forest patches, but the present study found that temperature and humidity values did not differ significantly between differently sized forest patches. Several studies generally state that small forests are largely affected by edge influence and are, in practice, very similar to edges, whereas only larger forest patches with core areas are buffered from environmental harshness (Hofmeister et al., 2019; Erdős et al., 2020). In the present study, the importance of maintaining tree cover (even in small forest patches or groves) in regulating the microclimate condition under semi-arid conditions was highlighted, which may also be applied in grassland management. Aalto et al. (2022) stated that trees outside forests (e.g., trees on farmlands, trees in cities, or small tree groups not defined as forests) have the potential in reducing climate change and regulating local and regional temperatures. Although forest fragmentation may reduce the forest's ability to mitigate climate change (Ewers and Banks-Leite, 2013), small forest patches can still regulate the environmental extremes (Mildrexler et al., 2011; Milošević et al., 2020), which is in good agreement with the present results. One possible explanation is that the tree/shrub canopy in all forest patches of this study is primarily composed of broadleaved trees and shrubs with a high canopy cover, creating shade and effectively reducing solar radiation reaching the ground. Microclimate conditions, therefore, were largely similar among differently sized forest patches.

One of the most interesting findings was that the mean daytime temperature of south-facing edges was very close to grasslands, while their nighttime values bear a resemblance to forests. This implied that the canopy of south-facing edges was better at retaining warmth during the night compared to resisting heat during the day. On the other hand, microclimate conditions of north-facing edges were similar to the forest interiors both daytime and nighttime. Similar results for the large temperature differences between north-facing and south-facing edges were reported in oak-chestnut forests and in Douglas-fir forests in the United States (Matlack et al., 1993; Chen et al., 1993). A potential reason for this phenomenon is that southern forest edges tend to receive more direct sunlight and solar radiation in daytime compared to north-facing edges (Stoutjesdijk and Barkman, 1992; Heithecker and Halpern, 2007; Bennie et al., 2008).

6.3.2. VPD, an important limiting factor affecting plant growth

Although vapor pressure deficit is inferred from air temperature and relative air humidity, it is regarded as an important environmental factor affecting the photosynthetic process, since it provides information about how water loss influences the stomatal openness or closure, which is related to CO_2 uptake (Stewart and Dwyer, 1983; Young and Mitchell, 1994; Bunce, 1997;

Novick et al., 2016; Shamshiri et al., 2018). The present results indicated that the VPD values were high during daytime and low during nighttime, showing that high transpiration rate and water stress occur during daytime, when the plants carry out photosynthesis (Jackson and Volk, 1970).

During the growing season, high VPD values were revealed in the summer months (between June and August), due to the high temperature in this season. For example, a temperature rising from 30 to 33°C increased VPD from 1.75 to 2.54 kPa (Will et al., 2013). Increased VPD is likely to exacerbate physiological stress on vegetation, leading to increased water loss or decreased carbon uptake, which influences the survival and growth of plant species (Van Heerwaarden and Teuling, 2014; McDowell et al., 2008). Yuan et al. (2019) reported increased VPD being part of the drivers of a decrease in global-scale plant growth, particularly an increase in drought-related forest mortality. A study in western US forests showed that high VPD significantly decreases Douglas fir growth (Restaino et al., 2016). Another study in the forest–grassland ecotone in the US also highlighted that increased VPD hastened greater transpiration and faster mortality of tree seedlings (Will et al., 2013).

The present results showed that the VPD values were significantly lower within woody habitats than in the open grasslands at daytime, indicating that grasslands were the most stressed for plant growth and productivity. These results are in good agreement with an earlier study in central Hungary, which concluded that the VPD values of small groves were lower than those of open areas (Süle et al., 2020). According to a study conducted in the northwestern United States (Davis et al., 2019), the forest canopy can buffer vapor pressure deficit: VPD was found to be 1.1 kPa lower in habitats with canopy than in those without canopy. Similarly, the long-term mean moderating capacity of the forest canopy for VPD in Switzerland was reported to be up to 0.52 kPa (von Arx et al., 2013).

This study indicated that south-facing edges had higher VPD values than north-facing ones during daytime, despite the fact that both are transition zones. This may be explained by the heat-reflective properties of the sunny side (Süle et al., 2020). Together with air temperature and humidity, it is highlighted that south-facing edges have more unfavorable environmental conditions in comparison to north-facing edges, which may result in reduced diversity (Erdős et al., 2013b; 2018b).

Instead of extreme values (e.g., maximum and minimum values) that occur in a short period, the duration curve can help us to better understand the spatio-temporal VPD pattern (Süle et al., 2020). In terms of the 1.2 kPa stress limiting threshold, exceedance rates of over 30% were observed in all habitats from May to August, indicating that each habitat type is strongly stressed during this period. In autumn, the studied habitats did not differ significantly from each other due to the cloudy and rainy weather conditions in September, but the exceedance rate was the highest in open grasslands in October, from 15.2 to 23.2%. Several studies have reported that for both temperature and VPD, differences between woody and non-woody habitats were larger on sunny days than on cloudy days (Chen et al., 1993; Davies-Colley et al., 2000). As there is little heating of soil and air on cloudy days (Urban et al., 2012), the difference between woody and non-woody habitats was small or non-existent in September.

When considering the limiting threshold of 1.2 kPa only, the role of forest patches may be ignored in the extremely dry period, from June to August, as the exceedance rate was similar among habitats. However, a stronger moderating effect of the forests was clearly observed when choosing 3.0 kPa as the threshold value for the exceedance rate, which is in line with Süle et al. (2020). Therefore, the present study highlights the central role of forest patches in buffering vapor pressure deficit under severe conditions.

6.4. Study 4: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity of near-natural forests and tree plantations

6.4.1. Species composition

The NMDS analysis found that each habitat type had its own species assemblage, although some overlaps do exist (Fig. 24). 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 shrub and weed control during the initial five years, etc.) may be directly responsible for the 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 4). 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 disturbed grasslands or arable fields. 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 disturbed grasslands/arable fields that complete their whole life cycle during spring (e.g., *Lamium amplexicaule*, *Secale sylvestre*, *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., 2013b), 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.

6.4.2. 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. 25a). 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., spontaneously appearing 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. 25b) 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. In addition, *Populus alba* had the highest cover of non-native species (Fig. S7b), indicating a high level of alien invasion.

Compared to the richness of native and non-native species, Shannon diversity showed a slightly different pattern (Fig. 25c). 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 (Fig. S7), 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. This is the primary factor behind the high cover of native species in *Robinia pseudoacacia* plantations.

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. 25d). 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. 25a), while functional diversity remained the same (Fig. 25d). 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. 25e). 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.

Our study indicated that near-natural forests had the highest cover and number of native species, with an outstanding contribution of both shrub and herb layers, resulting in a complex vertically stratified structure. In contrast, the low plant species richness and cover of *Pinus* as well as the low plant number of *Robinia* plantations (accompanied by the dominance of a few plant species in *Robinia* plantations) created a simplified composition, structure and function. The differences in species composition, cover and number 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. Indeed, a wide range of studies showed that 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; Ónodi et al., 2021), 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).

6.4.3. Ecological value of the studied habitats

The fact that plantations had significantly lower naturalness status than near-natural forests (Fig. 25f) 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. 26). 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).

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 7). 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., 2008b). 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 7). 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 and could threaten nature reserves if they spread into them.

Some other studies performed in the region also found that monoculture tree plantations are ecologically weak substitutes for near-natural forests (Table 7). Ónodi et al. (2021) 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 7. 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. (2021)
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.

6.5. Study 5: Forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity.

6.5.1. 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. 27a, b). Similar results were reported from Kazakh sandy forest-steppes (Bátori et al., 2018), Croatian rocky forest-steppes (Erdős et al., 2019c), 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). Therefore, species composition of edges that was not characteristic of any of the habitat interiors seems to be a general pattern in the sandy forest-steppes of the Carpathian Basin.

We found that species composition differed significantly between the differently oriented edges (Table S10), 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 (see results of Study 3).

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., 2014c; Bátori et al., 2018) and other natural or semi-natural forest-grassland mosaics (Hennenberg et al., 2005; Erdős et al., 2019c). 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 5 and 6) 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., 2013b, 2014c, 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 in 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. There are species associated with edges in our region, but they occur and are connected to grassland habitats in other regions. Therefore, for certain species, when using a broader categorization, they are sensitive to edges (Ries and Sisk, 2010). According to Ries et al. (2004) and Ries and Sisik (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. 27, Tables 5 and 6). 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*).

6.5.2. Taxonomic diversity

Forest interiors had the lowest species richness and Shannon diversity in both sites (Fig. 28a, b). Earlier studies in the region (Erdős et al., 2018b) 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. An additional possible explanation is that there was very intensive forest use (grazing, coppicing) in the Kiskunság. Consequently, hardly any real forest species survived, resulting in only a few shade-tolerant plant species at every scale (regional, local).

In the Kiskunság, edges (especially north-facing ones) had the highest species richness and Shannon diversity (Fig. 28a, 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., 2014c), Croatia (Erdős et al., 2019c), 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. 28a, 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. 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. 27), 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. 28a, 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 S4). 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). 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).

6.5.3. 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. 28c). 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., 2014c, 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. 28c). 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 S4). 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. 29d, e). Different seed masses may be adaptive for plants with different heights, resulting in high functional diversity for this trait (Fig. 29g).

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 (Kühn et al., 2004). 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. 29c). When *Populus alba* was removed from the data, the functional diversity for reproduction type was reduced drastically in the Kiskunság woody habitats (Fig. S8). 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 (e.g., *Cornus sanguinea, Cotinus coggygria, Polygonatum latifolium, Quercus robur,* and *Tilia tomentosa)*. In contrast, these traits were more diverse in the Kiskunság, resulting in higher functional diversity for flowering time (Fig. 29a). The presence of an open canopy enables the coexistence of species with varying flowering times. *Stellaria media*, for example, exhibits a year-round blooming period, whereas *Carex liparicarpos* has a much shorter flowering duration, spanning only 2 months.

6.5.4. 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. 28d). However, if only angiosperm species were included in the analysis of phylogenetic diversity, the peak disappeared (Fig. 28e). Similar to results in Study 1 and Study 4, 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.

7. Conclusions and implications

7.1. Conclusions

In Hungarian sandy forest-grassland mosaics, 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), which is in line with the edge-effect theory. Shannon diversity was found to be high near the middle and at the open end of the gradient. Functional and phylogenetic diversities were high throughout woody habitats (in forests and at edges), and were significantly lower in grasslands. In the light of results, functional and phylogenetic diversities do not necessarily coincide with taxonomic diversity along vegetation cover gradients. We revealed that all habitat types were dominated by the stress-tolerator strategy, but the most important role of environmental filtering was found in sand grasslands. The importance of the stress-tolerator strategy decreased towards 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 towards the harsh end of the gradient. The compositional and CSR gradients were associated with an environmental harshness gradient. Tree cover played an important role in mitigating microclimate harshness, while the harshest conditions were found at the end of the vegetation gradient during the growing season. The microclimate conditions of south-facing edges were more similar to grasslands, while those of north-facing edges were more similar to forests.

Near-natural forests found in sandy forest-grassland mosaics had significantly different species compositions from native and non-native tree platantions in the Kiskunság region. Near-natural forests had the highest number of diagnostic species, most of which 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. 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. 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.

When studying forest edges in two distant sandy forest-steppes in Pannonian region (one in the Kiskunság and another in the Deliblato), we confirmed that forest edges had rather distinct species composition and their own set of diagnostic species that avoid 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 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 forests and edges was higher than that of grasslands both in the Kiskunság and the Deliblato, which probably reflects the different evolutionary age of the habitats.

7.2. Implications for conservation and practice

Due to inadequate legislation, research and practical nature conservation usually consider an area either a closed forest or an open grassland, but do not recognize the entire forest-grassland mosaic (e.g., Török et al., 2014, Dieler et al., 2017, Ónodi et al., 2021, Reis et al., 2021). In light of our results, we suggest that an integrated view of the coexisting states is required for effective conservation of forest-steppe ecosystems. In other words, it is crucial to maintain habitat heterogeneity in sandy forest-steppe ecosystem by protecting all habitats.

Unfortunately, forest patches in sandy forest-steppes are usually degraded or completely eliminated by human activity. This may threaten the existence of edges which rely on sufficiently sized forest patches. In adition, it is well known that forests have a buffering function to regulate climate extremes (Breshears et al., 1998; von Arx et al., 2013; Davis et al., 2019). The current study highlighted that even the smallest forest patches (<0.1 ha) had an important function in mitigating macroclimatic harshness. Therefore, woody habitats may become refuges for plant species and all other creatures that require cooler temperature and/or higher humidity. With ongoing climate change, the role of forest patches, groves, or even scattered trees is expected to become increasingly important (Manning et al., 2009; Erdős et al., 2018b; Süle et al., 2020). Moreover, forest patches in forest-grassland mosaics host a specific flora and fauna and also have considerable carbon sequestration capacity (Foit et al., 2016; Erdős et al., 2018a; Ónodi et al., 2021; Süle et al., 2021; Tölgyesi et al., 2022).

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). Our results demonstrated that plantations, especially non-native plantations, cannot substitute near-natural forests, as they have serious negative effects on diversity and other ecosystem properties. 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 (Paillet et al., 2010; Rédei el al., 2020). 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). Importantly, our study indicated that forest edges were important in terms of diversity and conservation values; thus, including edges among native tree plantation patches (i.e., embedding open habitat patches into the planned plantation patch-mosaic) could increase habitat heterogeneity and support higher biodiversity (Vasiliev and Greenwood, 2022).

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. Furthermore, creating large forest stands in sandy drylands may have negative effects on regional underground water balance (Tölgyesi et al., 2020). Tree-planting attempts on ancient or near-natural grasslands are also frowned upon by proponents of open ecosystems because they risk destroying species, habitats, and ecosystem functioning (Feurdean et al., 2018). Afforestation efforts should therefore be minimized in forest-grassland ecosystems, but maintaining and planting scattered trees of native species in the open grassland matrix is highly advised and is even regarded as the new standard in increasing higher biodiversity and ecosystem services in Europe (Manning et al., 2009; Tölgyesi et al., 2023). 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 nature conservation priority areas.

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SUMMARY

Forest-steppes are among the most complex non-tropical ecosystems, featuring a mosaic-like arrangement of several different habitats. Although forest-steppes have long been studied by ecologists, only a very few researches have examined multiple forest-steppe habitats, both woody and non-woody, both natural and anthropogenic, at the same time. Accordingly, our knowledge of the importance and conservation implications of habitat heterogeneity in this unique ecosystem is still rather limited. In addition, the patterns of phylogenetic and functional diversities as well as ecological strategies in forest-steppe mosaics are virtually unknown, which may limit the effectiveness of conserving forest-steppes.

Microclimate has a significant effect on vegetation, but the knowledge of microclimate variables in forest-grassland mosaics is still rather limited. Up to now, microclimate parameters were only measured for a very short period (typically 24 hours on a single summer day). Moreover, earlier studies usually did not take into account the full variety of forest-grassland mosaics, especially the knowledge gap on edges. In the Pannonian region, plantations of *Pinus nigra*, *P. sylvestris*, *Robinia pseudoacacia*, and different *Populus* species are widespread in forest-steppe landscapes. 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).

The general aim of this study was to provide information on the habitat heterogeneity of sandy forest-steppes to support the conservation of this ecosystem in the Pannonian region. The specific aims were to find out: (1) how species composition, as well as taxonomic, functional, and phylogenetic diversity, vary in multiple habitat types, both woody and non-woody, as well as edges, in a sandy forest-steppe ecosystem; (2) what the dominant CSR strategies and assembly processes of the communities of sandy forest-steppes are, (3) how the microclimate conditions of multiple habitat types throughout the vegetation period are in a sandy forest-steppe ecosystem; (4) how the species composition, diversity, and ecological value of near-natural forests differ from 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; (5) 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 the Pannonian region.

For the first study, eight main habitats of Hungarian forest-grassland mosaics were investigated, representing along a vegetation gradient, and were compared their species composition as well as their taxonomic, functional, and phylogenetic diversity. Non-metric multidimensional scaling (NMDS) was performed to reveal the species composition. Species richness and Shannon diversity were calculated for each plot. The diagnostic species of each habitat were identified by calculating phi-coefficients as indicators of fidelity. To quantify overall functional diversity (FD) and phylogenetic diversity, plot-level Rao's quadratic entropy (RaoQ) was calculated. To eliminate the effect of species richness on RaoQ, and to determine whether the habitats are functionally and phylogenetically over- or underdispersed, the standardized effect size of RaoQ (SES.RaoQ) was performed. The results demonstrated that there was a compositional gradient, ranging from large forest patches through smaller-sized

forest patches and edges to closed and open grasslands. Each habitat had species that were rare or absent elsewhere. The highest species richness was found at north-facing edges, followed by south-facing edges, gradually decreasing both towards forest patches and grasslands. Thus, this study strongly supports the edge-effect hypothesis. Shannon diversity was high at edges and the end of gradients (i.e., open annual and open perennial grasslands). Contrary to species richness and Shannon diversity, functional diversity was significantly higher in woody habitats (forests and edges) than in grasslands. When studying the functional diversity of individual traits, the functional diversities of flowering time, seed dispersal, reproduction type, plant height, and thousand seed mass were higher in woody habitats than in grassland habitats. For life form and mean plant height, south-facing edges had the highest functional diversity, followed by north-facing edges and small forest patches. Closed perennial grasslands, open annual grasslands, and medium forest patches had the highest functional diversity for SLA, while the functional diversity of pollination type reached its maxima towards the endpoints of the gradient. Phylogenetic diversity tended to show a peak near the middle of the gradient when all species were considered, but this pattern disappeared when non-angiosperms (*Botrychium lunaria, Ephedra distachyia, Equisetum ramosissimum, Juniperus communis, J. virginiana, Pinus nigra,* and *P. sylvestris)* 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 diversity if we are to gain a better understanding of how ecosystems work.

For the second study, eight plant communities of Hungarian forest-steppes were investigated. The trade-off between three key traits related to leaf size and economics was used to calculate Grime's CSR value for each species, based on which the mean value for each vegetation type was determined. 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). Our results showed that CSR values were observed across a variety of habitat types, constituting three main 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 comprised the third group. Although each habitat type was dominated by the stress-tolerator strategy, ecological strategies differed significantly among the habitats. The importance of competition was larger in woody habitats (i.e., forests and edges) than in grasslands, but stress-tolerator strategy decreased towards the less harsh end of the gradient (i.e., from grasslands to forests). Disturbance played the most important role in the open perennial and the open annual grassland communities. We suggest that CSR strategies provide an effective tool for studying plant community assembly rules along environmental gradients.

For the microclimate study, a vegetation gradient of Hungarian forest-grassland mosaics was measured. Wireless sensors recording air temperature and humidity values were used to monitor microclimatic parameters once every month in all seven habitats from April to October 2022. Vapor pressure deficit (VPD) values were calculated based on the obtained air temperature and humidity, and two thresholds at 1.2 and 3.0 kPa were defined. The present work demonstrated that forests indeed have a strongly different microclimate than grasslands. In comparison to grasslands, forests are cooler during the daytime and warmer during the nighttime, and more humid during the daytime. In this study, especially for temperature, south-facing edges tended to be more similar to grasslands, while north-facing edges tended to be more similar to forests. In terms of VPD, open grasslands were the most stressed for vegetation growth from May to October. During the summer season, forest patches had a small moderating effect at the limiting threshold of 1.2 kPa VPD, but a stronger moderating effect at the 3.0 kPa threshold. Interestingly, we found that even small forest patches (less than 0.1 ha in size) have a very important function in mitigating macroclimatic harshness. This study had two main suggestions: (1) the remaining near-natural forest stands in sandy forest-grassland ecosystems should be protected and (2) scattered trees or groups of trees of native species should be encouraged in extensive treeless grasslands (where woody vegetation has been destroyed anthropogenically).

For the fourth study, 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) were investigated in the Kiskunság Sand Ridge, central Hungary. Similar to the first study, non-metric multidimensional scaling (NMDS), diagnostic species, Shannon diversity, plot-level Rao's quadratic entropy were performed. The number of non-native and native species per plot was also counted. To show how many of the species with high conservation importance (protected, endemic, and red-listed plant species) live in particular habitats, a Venn-diagram was created. The unweighted mean naturalness value per plot was calculated using the species present in each plot. This study found that there were significant differences in species composition among the four habitats. Near-natural forest patches had the highest richness of native species and the lowest richness of non-natives. They exhibited both the highest naturalness index and the greatest number of species with special conservation importance. Also, near-natural forests had high functional and phylogenetic diversity. Among the plantations, *Populus alba* plantations were ecologically more valuable than *Pinus* or *Robinia* plantations in most respects, and the latter proved the ecologically least valuable. In the light of results, it is suggested that the remaining near-natural forests of the study region should be prioritized for conservation and restoration. If establishing plantations is unavoidable, the native *Populus alba* should be preferred over the exotic *Pinus* or *Robinia.*

In the last study, 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) were investigated. Non-metric multidimensional scaling (NMDS) was performed, diagnostic species were identified, species richness, Shannon diversity, and SES.RaoQ were calculated, which is similar to the first study. Based on species composition and the existence of edge-related species, edges should be considered separate habitats in sandy forest-grassland mosaics. Although species richness and Shannon diversity were the highest at north-facing edges in the Kiskunság, they did not differ significantly between the grasslands and the edges in the Deliblato, indicating that the edge effect hypothesis is not a general rule and the topic needs further studies. 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. The study found that phylogenetic diversity was higher in woody habitats than in grasslands, which may be explained by the younger evolutionary age of grasslands. This study also indicated that taxonomic diversity is not always indicative of functional and phylogenetic diversity, highlighting the need of considering multiple aspects of diversity in future studies.

To sum up, species composition and CSR strategy gradient were arranged along the environmental harshness gradient. Taxonomic, phylogenetic, and functional diversities, as well as conservation value, had different patterns, peaking in different habitats of sandy forest-steppes in the Pannonian region. Consequently, practical conservation has to focus on multiple habitats of sandy forest-steppes and similar mosaic-like habitats simultaneously. Non-native tree plantations cannot substitute near-natural forests located in sandy forest-steppes regarding diversity and ecological values; therefore, protecting and reconstructing these forest patches are a high-priority.

APPENDIX

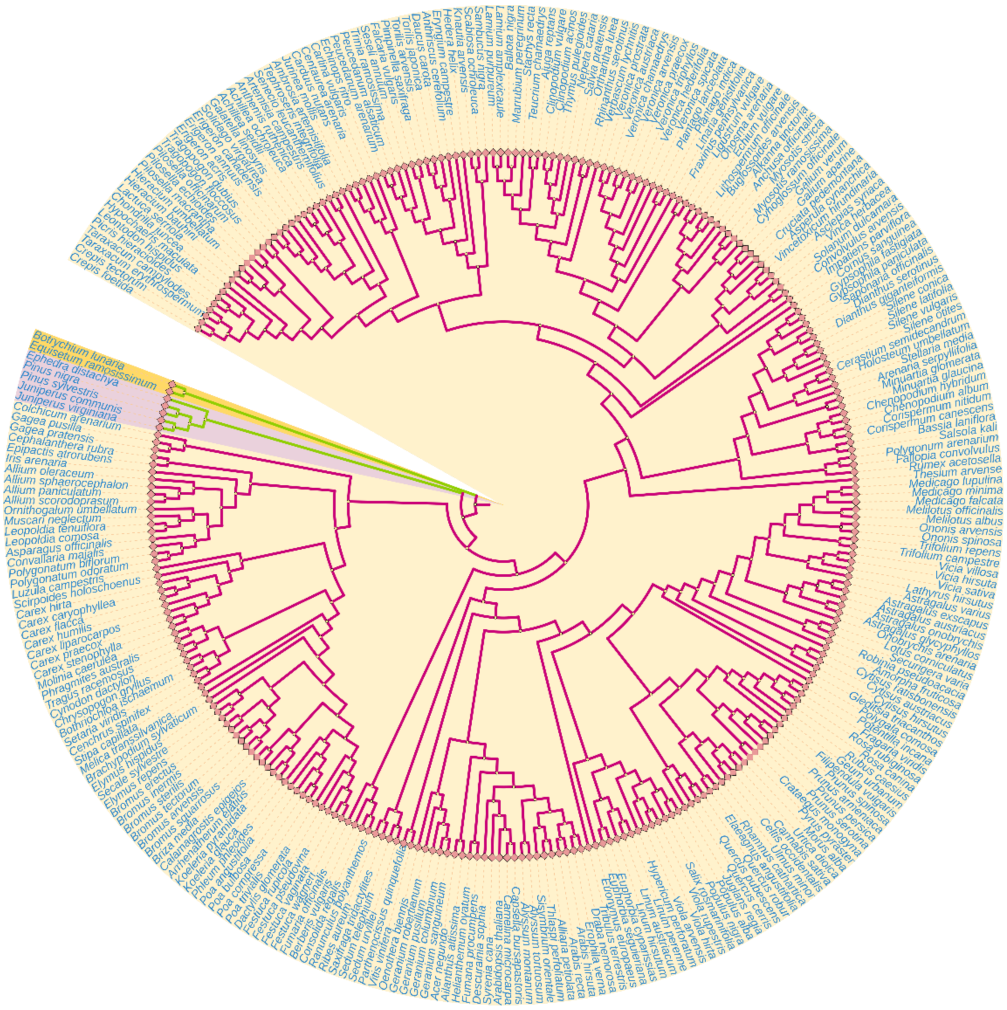

Figure S1. Phylogenetic tree containing 289 species (Study 1: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity in forest-grassland mosaics). The orange zone includes two pteridophyte species, the purple zone includes five gymnosperms species, while the remaining species are angiosperms.

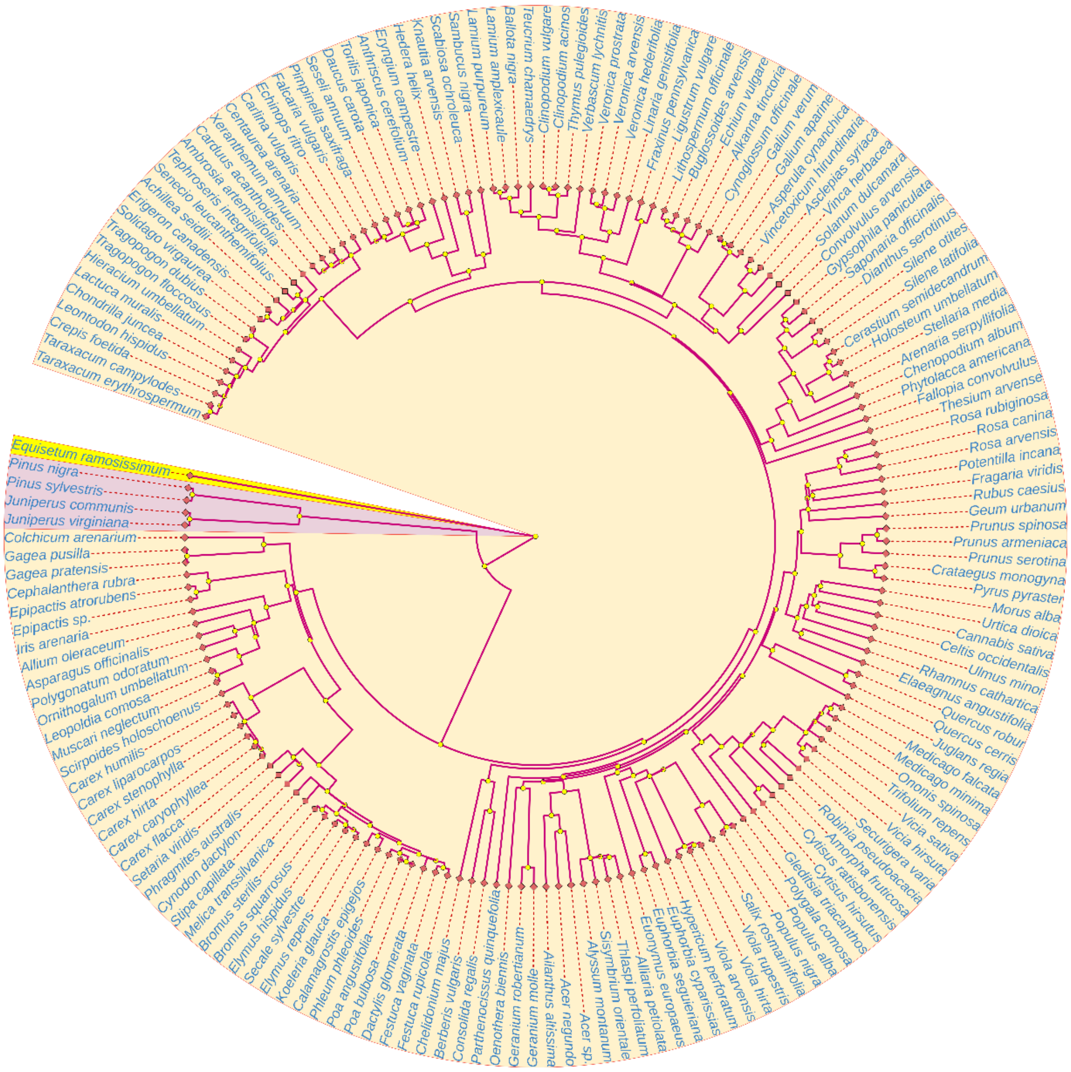

Figure S2. Phylogenetic tree containing 173 species (Study 4: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity of near-natural forest and tree plantations). The yellow zone includes one pteridophyte species, the purple zone includes four gymnosperms species, while the remaining species are angiosperms.

Figure S3. Phylogenetic tree containing 225 species (Study 5: forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity). The purple zone includes one pteridophyte species, the yellow zone includes two gymnosperms species, while the remaining species are angiosperms.

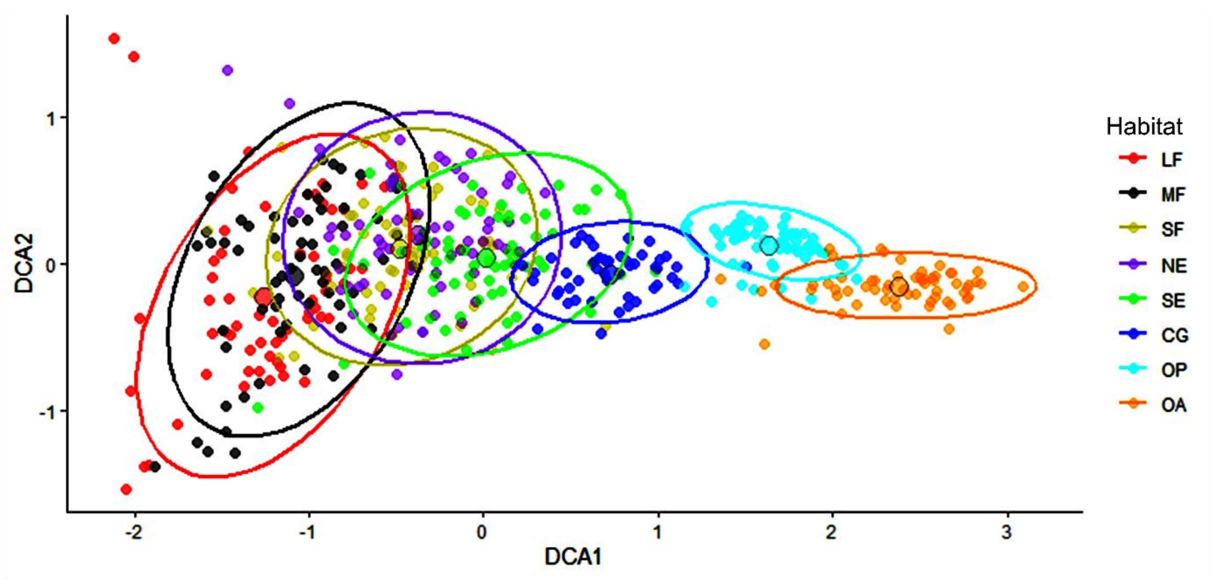

Figure S4. DCA ordination scattergram of the 494 plots (Study 2: plant strategies and community assembly rules in forest-grassland mosaics). Large symbols indicate the centroids for each vegetation type. Ordination ellipses were drawn based on standard deviation of point scores, where the directions of the major axis of the ellipse were defined by the weighted correlation. 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. Eigenvalues were 0.58 and 0.21 for axis 1 and 2, respectively. Gradient length was 5.21 for the first axis.

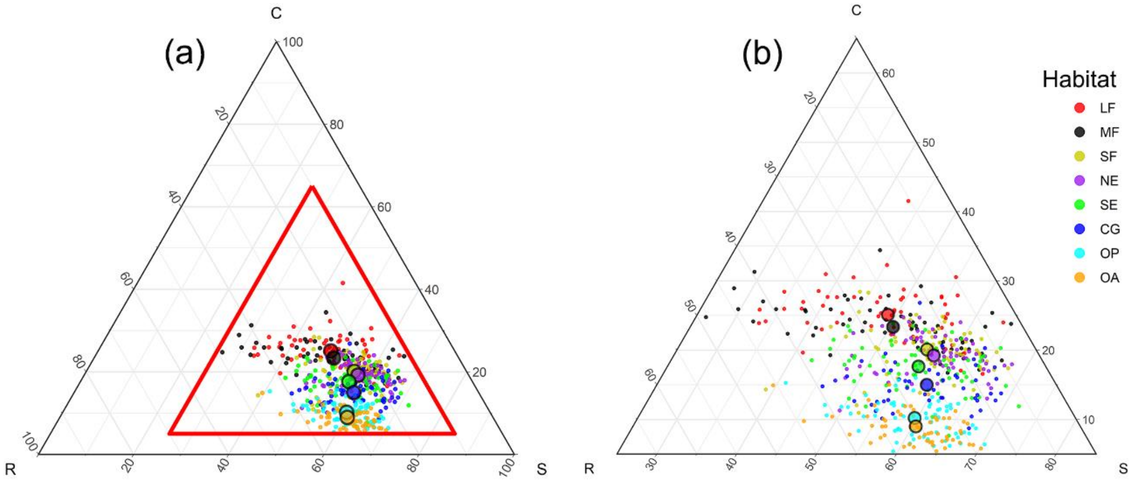

Figure S5. Ternary plots of weighted mean values of CSR strategies with square-root transformed cover scores for the eight vegetation types (Study 2: plant strategies and community assembly rules in forest-grassland mosaics). A red triangle in plot (a) shows the boundaries of plot (b). Larger symbols indicate the mean value for each vegetation type. 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.

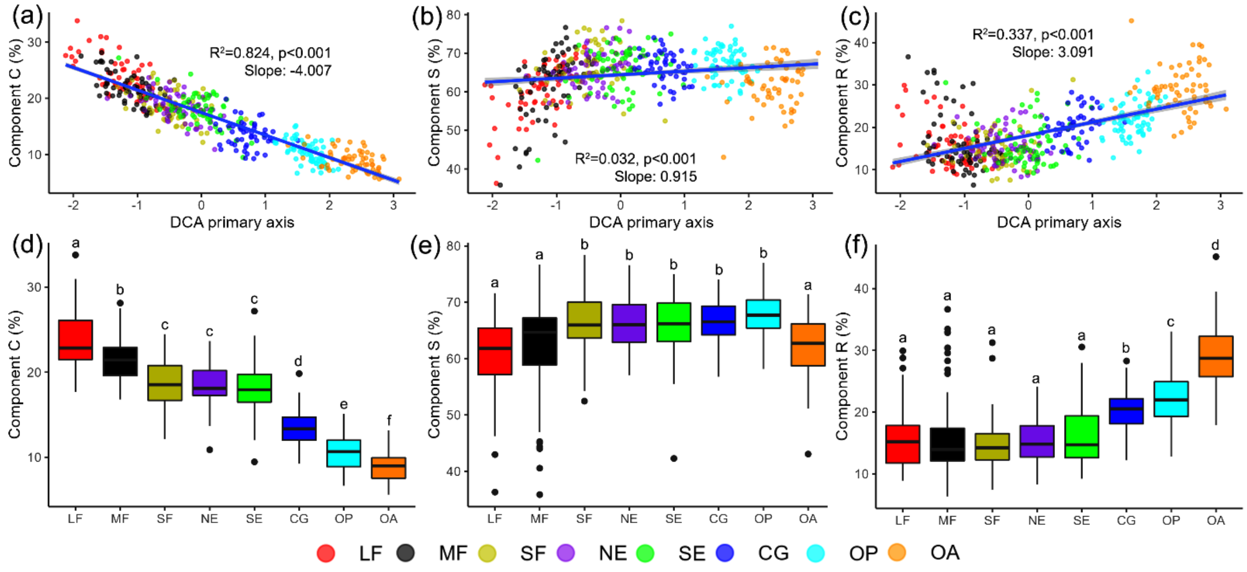

Figure S6. Relationships between plot scores on the primary DCA ordination axis and each weighted strategy component using square-root transformation of cover scores: (a) C; (b) S, and (c) R; p-value and adjusted R-squared were calculated using linear regression; Slope: the slope value of the regression line; blue line is regression line, and grey area around the line represents the 95% confidence interval (Study 2: plant strategies and community assembly rules in forest-grassland mosaics). 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 α = 0.05 significance level. 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.

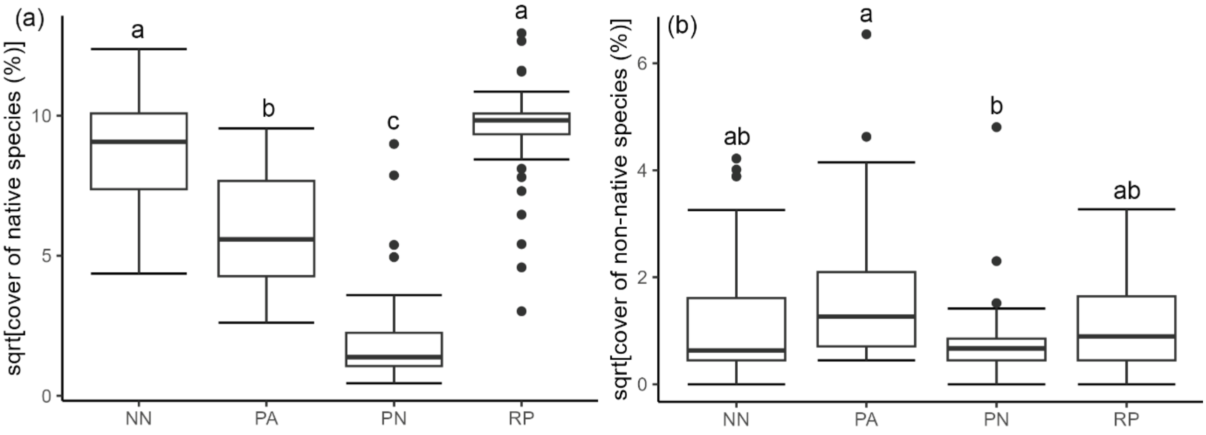

Figure S7. The cover of native species (a) and non-native species (b) of the four habitat types. Different letters indicate significant differences (p<0.05) (Study 4: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity of near-natural forests and tree plantations). 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*. A square-root transformation (sqrt) on the cover values of both native and non-native species was applied to meet the assumptions of the models.

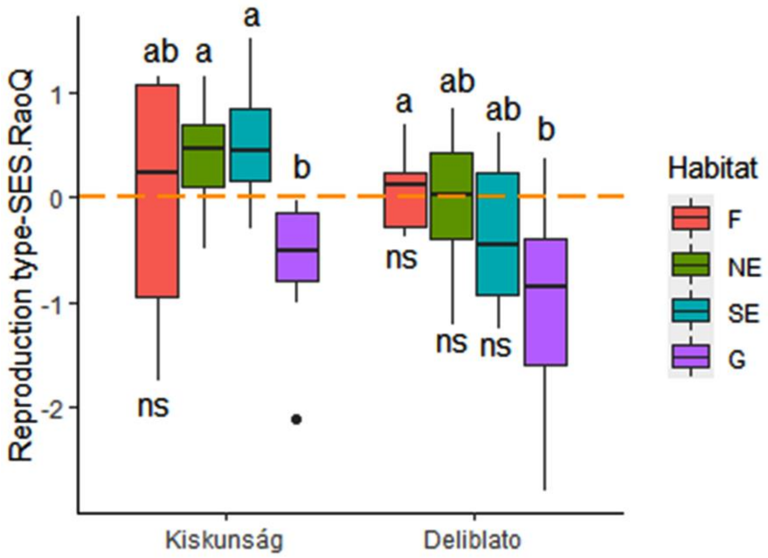

Figure S8. Functional diversity of reproduction type excluding *Populus alba* species (Study 5: forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity). F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland. Habitats not sharing 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. The 13 study sites with coordinates and elevation, and the distribution of relevés across habitats and sites in both Study 1 (species composition, edge-related species, taxonomic, functional, and phylogenetic diversity in forest-grassland mosaics) and Study 2 (plant strategies and community assembly rules in forest-grassland mosaics). 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°47'26"	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. The distribution of plots across habitats and sites (Study 4: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity of near-natural forests and tree plantations). NN: near-natural poplar forests; PA: plantations of native *Populus alba; PN:* plantations of non-native *Pinus nigra*; and RP: plantations of non-native *Robinia pseudoacacia*.

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 S3. Estimated cover values of the canopy, shrub, and herb layers, as well as species richness (mean ± standard error) (Study 4: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity of near-natural forests and tree plantations). 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 S4. Estimated cover values 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 (Study 5: forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity). 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 S5. 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 mass 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 S6: Statistical results of the pairwise comparisons of species composition (Study 1: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity in forest-grassland mosaics). 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.

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 S7. Statistical results between observed SES.RaoQ values and the null model expectation (two-sided Wilcoxon signed rank test) (Study 1: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity in forest-grassland mosaics). 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

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 S7 (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 S7 (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 S8. Statistical results of the pairwise comparisons of species composition (Study 4: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity of near-natural forests and tree plantations). 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 S9. List of species with high conservation importance (i.e., protected, endemic, and/or red-listed species) (Study 4: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity of near-natural forests and tree plantations). NN: near-natural poplar forests; PA: plantations of native *Populus alba; PN:* plantations of non-native *Pinus nigra*; *and RP:* plantations of non-native *Robinia pseudoacacia*. X: species appearing in each habitat. P: Protected spcies, SP: strictly protected species E: endemic species, R: red-listed species

Species	NN	PA	PN	RP	Value
Alkanna tinctoria			X		P
Centaurea arenaria	X	X	X		P
Cephalanthera rubra	X	X			P
Chamaecytisus hirsutus	X				P
Colchicum arenarium	X	X			SP/E/R
Dianthus serotinus	X				P/E/R
Echinops ruthenicus		X			P/R
Epipactis atrorubens	X				P/R
Epipactis sp.	X				P
Festuca vaginata	X	X	X		E/R
Iris arenaria	X				P/E/R
Stipa borysthenica+capillata	X	X	X		P
Tragopogon floccosus	X	X	X	X	P/E/R
Vinca herbacea	X				P

Table S10. Statistical results of the pairwise comparisons of species composition (Study 5: forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity). 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 S11. Statistical results between observed SES.RaoQ values and the null model expectation (two-sided Wilcoxon signed rank test) (Study 5: forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity). 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 S11 (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 S11. (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

LIST OF PUBLICATIONS RELATED TO THE THESIS

MTMT ID: 10080804

1. Erdős, L., **Ho, K. V.,** Bátori, Z., Kröel-Dulay, G., Ónodi, G., Tölgyesi, C., 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. https://doi.org/10.1111/1365-2745.14025. **IF$_{2022}$ = 5.5 (D1)**
2. Erdős, L., **Ho, K. V.,*** Bede-Fazekas, A., Kröel-Dulay, G., Tölgyesi, C., Bátori, Z., & Péter Török, P., 2024. 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. https://doi.org/10.1111/jvs.13228. **IF$_{2022}$ = 2.8 (Q1).**
   ** Erdős, L. and Ho, K. V. contributed equally to this work and are joint first authors*
3. **Ho, K. V.,** Süle, G., Kovács, B., & Erdős, L., 2024. Strong differences in microclimate among the habitats of a forest-steppe ecosystem. Időjárás, 128, 1-26. https://doi.org/10.28974/idojaras.2024.1.1. **IF$_{2022}$ = 0.9 (Q4)**
4. **Ho, K. V.,** Kröel-Dulay, G., Tölgyesi, C., Bátori, Z., Tanács, E., Kertész, M., Török, P., & Erdős, L., 2023. Non-native tree plantations are weak substitutes for near-natural forests regarding plant diversity and ecological value. Forest Ecology and Management, 531, 120789. https://doi.org/10.1016/j.foreco.2023.120789. **IF$_{2022}$ = 3.7 (D1).**
5. **Ho, K. V.,** Ćuk, M., Šikuljak, T., Kröel-Dulay, G., Bátori, Z., Tölgyesi, C., Fűrész, A., Török, P., Hábenczyus, A. A., Hegyesi, A., Coşgun, Z. L., & Erdős, L., 2023. Forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity. Global Ecology and Conservation, 46, e02625. https://doi.org/10.1016/j.gecco.2023.e02625. **IF$_{2022}$ = 4 (Q1).**
6. **Ho, K. V.,** Kröel-Dulay, G., Lengyel, A., Ónodi, G., Bátori, Z., Tölgyesi, C., Török, P., & Erdős, L., 2022. Functional structure reveals distinctions in plant community assembly of forest-grassland mosaics – a study case in hungary. In: Molnár Dániel and Molnár Dóra (Eds), XXV. Tavaszi Szél Konferencia 2022, Absztraktkötet. May 6-8, Pécs, Hungary, p. 169-170.
7. Erdős, L., Török, P., Bátori, Z., Kröel-Dulay, G., **Ho, K. V**., Weldman, J. W., & Tölgyesi, C., 2022. Forest-grassland coexistence in Eurasian forest-steppes. In: Hrivnák R. & Slezák M. (eds), 30th Conference of the European Vegetation Survey: Plant communities in changing environment. Abstract book. May 9–13, 2022, Bratislava (Slovakia) Slovakia, p. 58.
8. **Ho, K.,** Kröel–Dulay, G., Lengyel, A., Ónodi, G., Bátori, Z., Tölgyesi, C., Török, P., & Erdős, L., 2023. Patterns of taxonomic, functional, and phylogenetic diversity in forest–grassland mosaics. In: Zasadil Petr, Ludvíková Vendula & Báldi András (Eds), 6th European Congress of Conservation Biology: Biodiversity crisis in a changing world. Book of abstracts, August 22–26, 2022, Prague, Czech Republic, p. 26.
9. **Ho, K. V.,** Kröel-Dulay, G., Tölgyesi, C., Bátori, Z., Tanács, E, Kertész. M., Török, P., & Erdős, L., 2023. Plantations cannot well substitute for near-natural forests in terms of diversity patterns and ecological value - a case study in Hungary. In: Hajdú Péter, (Eds),

XXVI. Tavaszi Szél Konferencia 2023, Absztrakt kötet, May 5-7, 2023, Miskolc, Hungary, p. 101-102

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