

RESEARCH ARTICLE

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

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Abstract

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

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

KEYWORDS

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

1 | INTRODUCTION

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

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

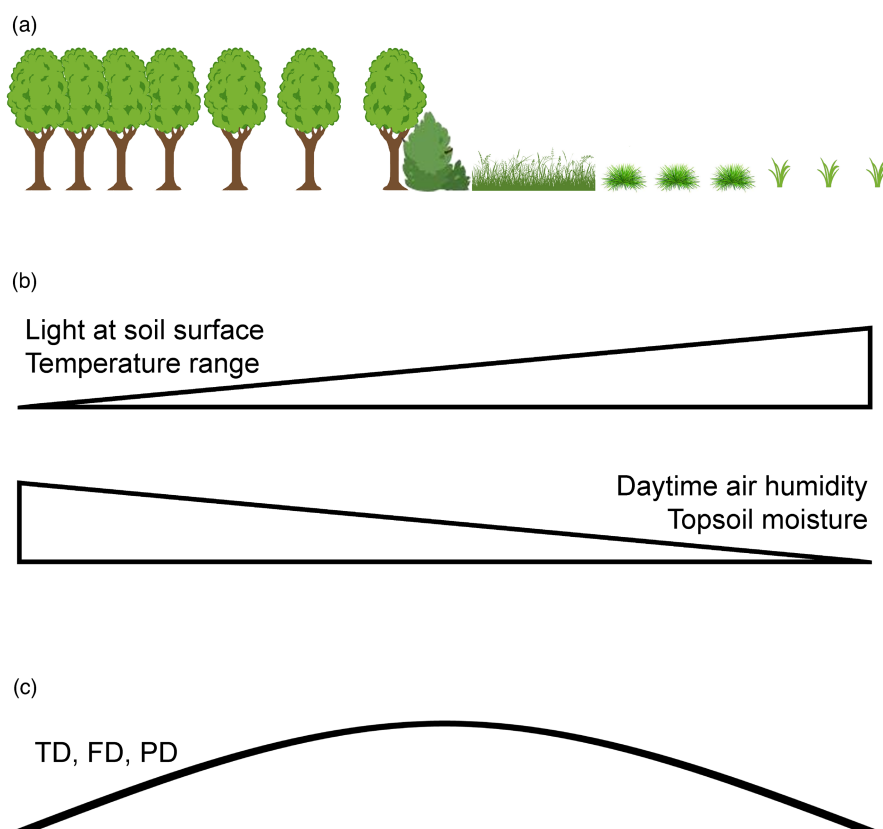


FIGURE 1 (a) Gradient of vegetation cover, ranging from closed-canopy forests to sparse grasslands, (b) environmental gradients caused by the vegetation gradient, (c) assumed pattern of taxonomic, functional and phylogenetic diversity (TD, FD and PD, respectively) along the vegetation cover gradient.

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

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

In the present study, our aim was to examine how species composition as well as taxonomic, functional and phylogenetic diversity vary in multiple habitat types, both woody and non-woody, in a

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

2 | MATERIALS AND METHODS

2.1 | Study area

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

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



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

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

In the present study, the forest edge was defined as the peripheral zone of each forest patch reaching out of the outermost tree trunks (diameter at breast height > 10 cm), but still below the canopy. The edges in the studied ecosystem are relatively narrow and are usually densely covered by shrubs (primarily *Crataegus monogyna* and *Juniperus communis*) and herbs (e.g. *Calamagrostis epigeios*, *Carex liparicarpus*, *Poa angustifolia* and *Teucrium chamaedrys*). Differently oriented edges tend to have different environmental parameters,

and, consequently, may show differences in vegetation characteristics (e.g. Erdős, Kröel-Dulay, et al., 2018; Wicklein et al., 2012). As north- and south-facing edges are expected to show the greatest differences (Harper et al., 2005; Ries et al., 2004), they were included in the study (Figure 2e–f).

Grasslands in the study area are classified into closed perennial grasslands, open perennial grasslands and open annual grasslands. The closed perennial grassland (*Astragalo austriacae-Festucetum rupicolae*; Figure 2g) has a relatively high vegetation cover (usually $>80\%$). The typical dominant species include *Festuca rupicola*, *Stipa*

borysthénica, *S. capillata* and *Calamagrostis epigeios*. The species *Galium verum*, *Poa angustifolia*, *Potentilla arenaria* and *Teucrium chamaedrys* are also common.

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

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

2.2 | Data collection

Each of the eight habitats was sampled using 25-m² plots (5 m × 5 m plots for forest interiors and grasslands and 2 m × 12.5 m plots for forest edges in order to rule out their extension into the interiors of forests or grasslands), following the design of earlier studies (Erdős et al., 2019, 2020; Erdős, Kröel-Dulay, et al., 2018). This plot size was large enough to prepare standard phytocoenological relevés and small enough to examine the smallest forest patches and narrow edges. Edge plots were established in more or less straight peripheral zones of forest patches larger than 0.2 ha. The total number of plots was 494 (60 plots in large forest patches, 64 plots in medium forest patches, 60 plots in open annual grasslands, 50 plots in closed perennial grasslands and 65 plots in each of the other habitat types; Table S1). The slightly unbalanced sampling effort was explained by the fact that some habitat types were rare at some sites. The percentage cover of all vascular plant species in each plot was visually estimated in spring (April–May) and summer (July–August), and the largest recorded cover value was used for data analyses. All vegetation layers (canopy, shrub and herb layer) were estimated and included in all analyses.

2.3 | Trait data

Nine plant functional traits were used in this study: start of the flowering, flowering duration, specific leaf area (SLA), mean plant

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

2.4 | Phylogenetic tree

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

2.5 | Data analyses

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

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

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

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

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

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

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

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

3 | RESULTS

3.1 | Vegetation gradient

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

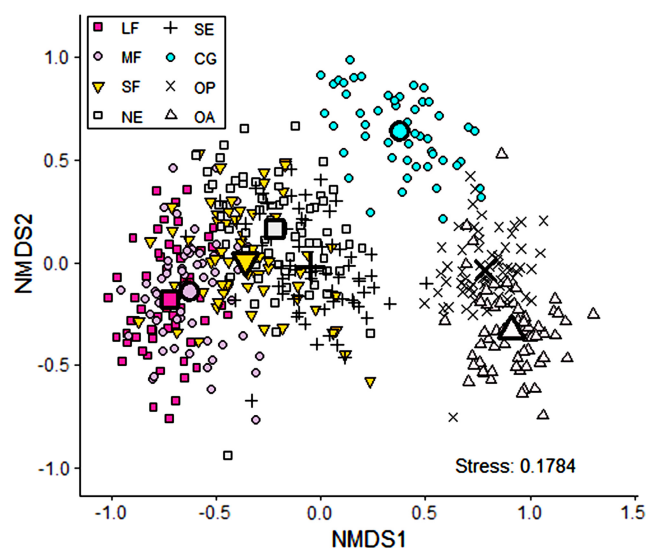


FIGURE 3 Habitat types along the forest-grassland gradient have high turnover in species composition. Forest, edge and grassland types are placed in accordance with their position along the vegetation openness gradient in the ordination diagram. The NMDS ordination was prepared using square-root transformed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

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

3.2 | Taxonomic diversity and edge species

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

The list of diagnostic species related to the eight habitats is presented in Table S5. Several species were diagnostic for two or more habitats (the number of shared diagnostic species was especially high among woody habitats and among grassland habitats). Here, we only consider those species that were diagnostic for a single habitat type. Large, medium and small forest patches had 8, 3 and 0 diagnostic species, respectively. The number of

diagnostic species was 16 for north-facing edges and 4 for south-facing edges. There were 15, 5 and 11 significant diagnostic species in closed grasslands, open perennial grasslands and open annual grasslands, respectively.

3.3 | Functional diversity

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

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

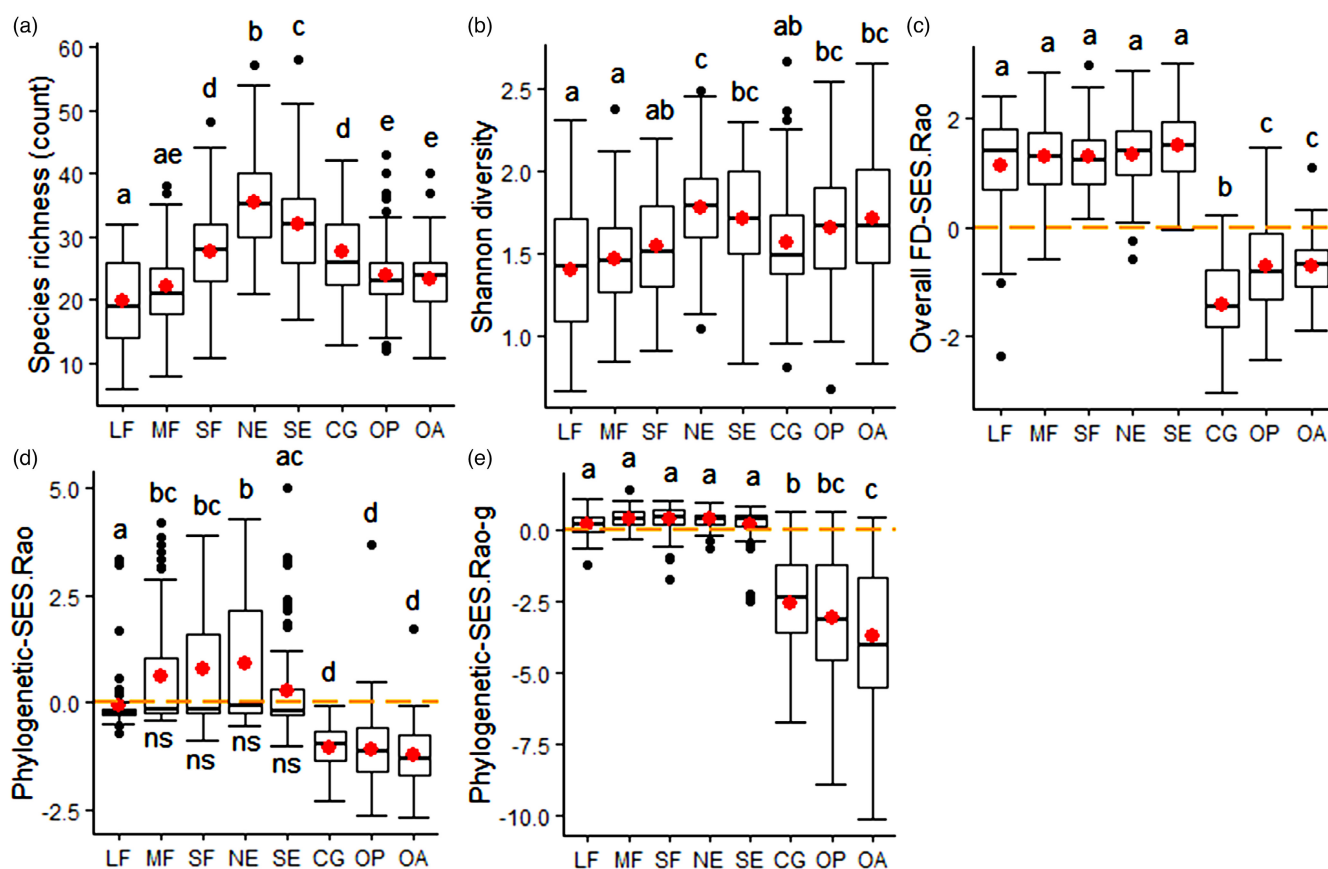


FIGURE 4 Differences in diversity measures between habitat types. Diversity measures include species richness (a), Shannon diversity (b), standardised effect size of Rao's quadratic entropy (SES.RaoQ) for functional diversity based on all traits (c), SES.RaoQ for phylogenetic diversity (d) and SES.RaoQ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

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

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

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

3.4 | Phylogenetic diversity and phylogenetic signal

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

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

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

4 | DISCUSSION

4.1 | Vegetation gradient

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

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

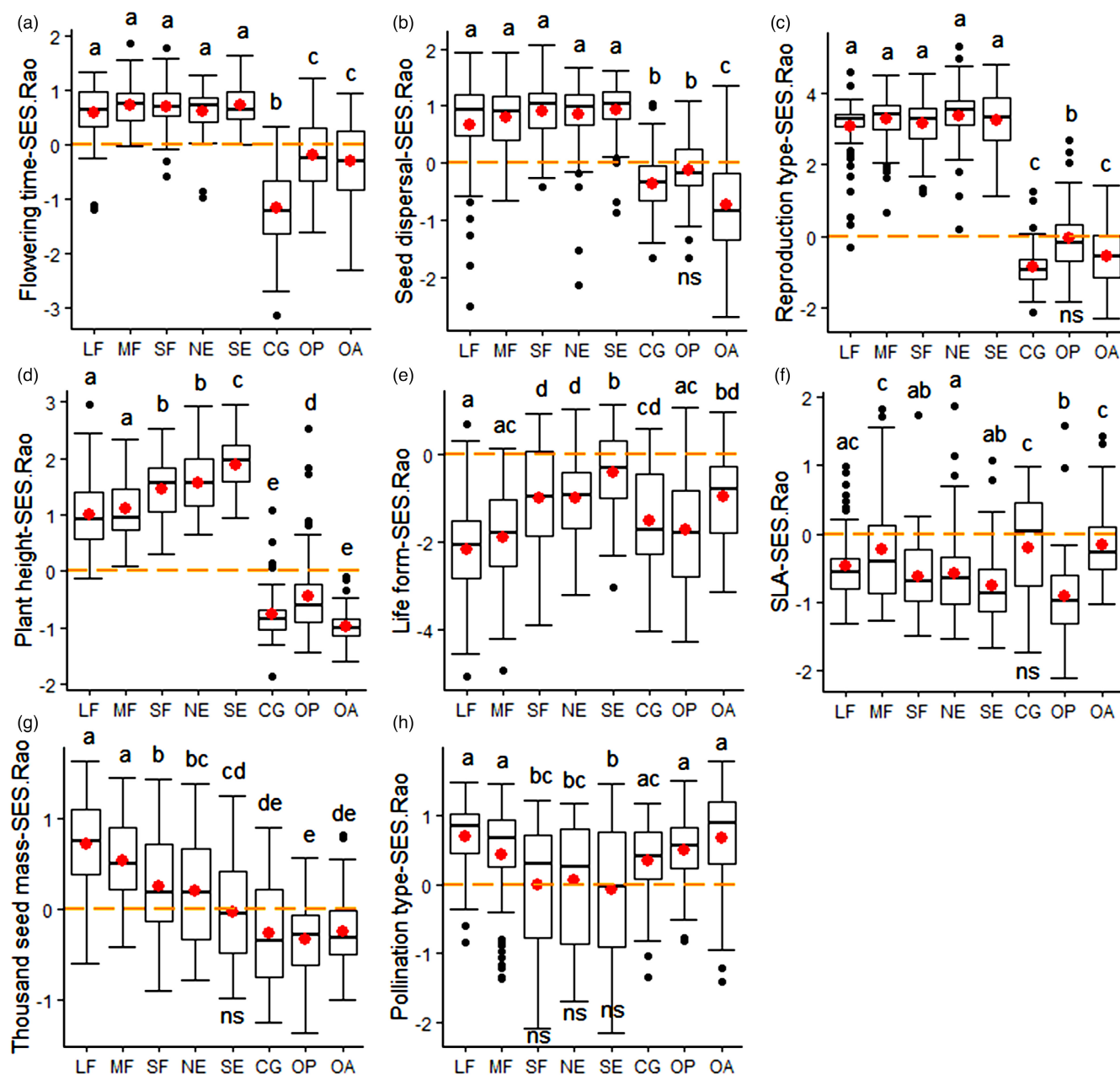


FIGURE 5 Differences in trait-wise functional diversity between habitat types. Traits include flowering time (a), seed dispersal (b), reproduction type (c), plant height (d), life form (e), specific leaf area (f), thousand seed mass (g) and pollination type (h). Habitat type abbreviations are according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

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

4.2 | Taxonomic diversity and edge-species

The hypothesis that taxonomic diversity would show a hump-backed curve along the gradient was partly supported by our results. Species richness peaked at the middle of the gradient and gradually

decreased towards both ends (Figure 4a). This result was in good accordance with earlier observations in natural or semi-natural forest edges (e.g. Bátori et al., 2018; Erdős et al., 2019; Molnár, 1998; Pinder & Rosso, 1998) as well as with the edge effect theory (e.g. Odum, 1971; Risser, 1995). This theory assumes that edges are more species-rich than habitat interiors are, as they contain species from both adjacent habitats as well as their own species (edge-species). Our results confirmed the existence of edge-species: we were able to identify species that preferred either north-facing or south-facing

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

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

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

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

Compared to species richness, Shannon diversity showed a slightly different pattern (Figure 4b). While Shannon diversity, similar to species richness, was high at the edges (at the middle of the gradient), it was also high in the open grassland habitats. It is possible that environmental harshness (low soil moisture, temperature extremes and low soil humus content; Borhidi et al., 2012) prevents vascular plant species from reaching high cover values, resulting in

greater species evenness, which leads to higher Shannon diversity. Similarly, Bernard-Verdier et al. (2012) found that species evenness increased with decreasing soil depth, which was due to the fact that the species that reached high cover values on deep soils could not become dominant under harsher conditions. In addition to the harsh environment, disturbance may also support great species evenness by preventing a few competitive species from reaching high cover values (Cardinale et al., 2000; Svensson et al., 2012). Compared to any other habitat in the studied ecosystem, open annual grasslands are more affected by disturbances (trampling of grazers and browsers, extreme droughts and moving sand; Borhidi et al., 2012). This may effectively limit their species richness, but at the same time, it can ensure high Shannon diversity.

Results from other woody-herbaceous ecosystems are in line with our findings only partly. For example, Mogashoa et al. (2021) studied a gradient of woody plant cover in a semi-arid African savanna and found that the Shannon diversity of grasses was the highest at medium woody cover, while tree diversity was

the lowest at this point. In an Australian woodland, Price and Morgan (2008) found that species richness was the highest at the shrubless end of the gradient, with a second peak appearing at medium shrub cover.

4.3 | Functional diversity

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

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

It is worth emphasising that large forest patches proved to be functionally diverse habitats in our study, even though they had the lowest species richness values. This reinforces the view that species richness is not necessarily informative of functional diversity (e.g. De Pauw et al., 2021; Díaz & Cabido, 2001; Purschke et al., 2013). In forests, the average size of individual plants is larger than that in grasslands, which may imply that fewer individuals are sampled in a plot, possibly resulting in lower species richness (Luczaj & Sadowska, 1997). At the same time, it is possible

that large plants tend to exclude other plants with similar traits in their proximity, while they can coexist with plants possessing different traits because of their lower niche overlap, indicating the importance of competition towards the less harsh end of the gradient (cf. Weiher & Keddy, 1995). This may have resulted in a higher functional diversity at the sampling scale used in the present study.

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

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

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

4.4 | Phylogenetic diversity and phylogenetic signal

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

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

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

We found weak but significant phylogenetic signal for the majority of traits (Table 2), suggesting that these traits are phylogenetically conserved. The results of previous studies investigating the relationship between ecological similarity and phylogenetic relatedness vary considerably (Losos, 2008). For example, Prinzing et al. (2001) detected phylogenetic signal for ecophysiological traits among Central European vascular plant species. Chazdon et al. (2003)

found phylogenetic signal for reproductive traits and growth form in Neotropical woody taxa. In contrast, examining a North American subalpine plant community, CaraDonna and Inouye (2015) detected significant phylogenetic signal for only a subset of the studied flowering traits. Silvertown et al. (2006) found no phylogenetic signal for plant niches in English meadow communities. Thus, the presence of phylogenetic signal for traits revealed in our study should not be considered a general phenomenon, as the relation between functional traits and phylogeny may vary among habitats, taxa and traits.

5 | CONCLUSIONS

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

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

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

AUTHOR CONTRIBUTIONS

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

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

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

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

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