



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

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ABSTRACT

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

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

1. Introduction

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

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

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

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

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

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

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

2. Material and methods

2.1. Study sites

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

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

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

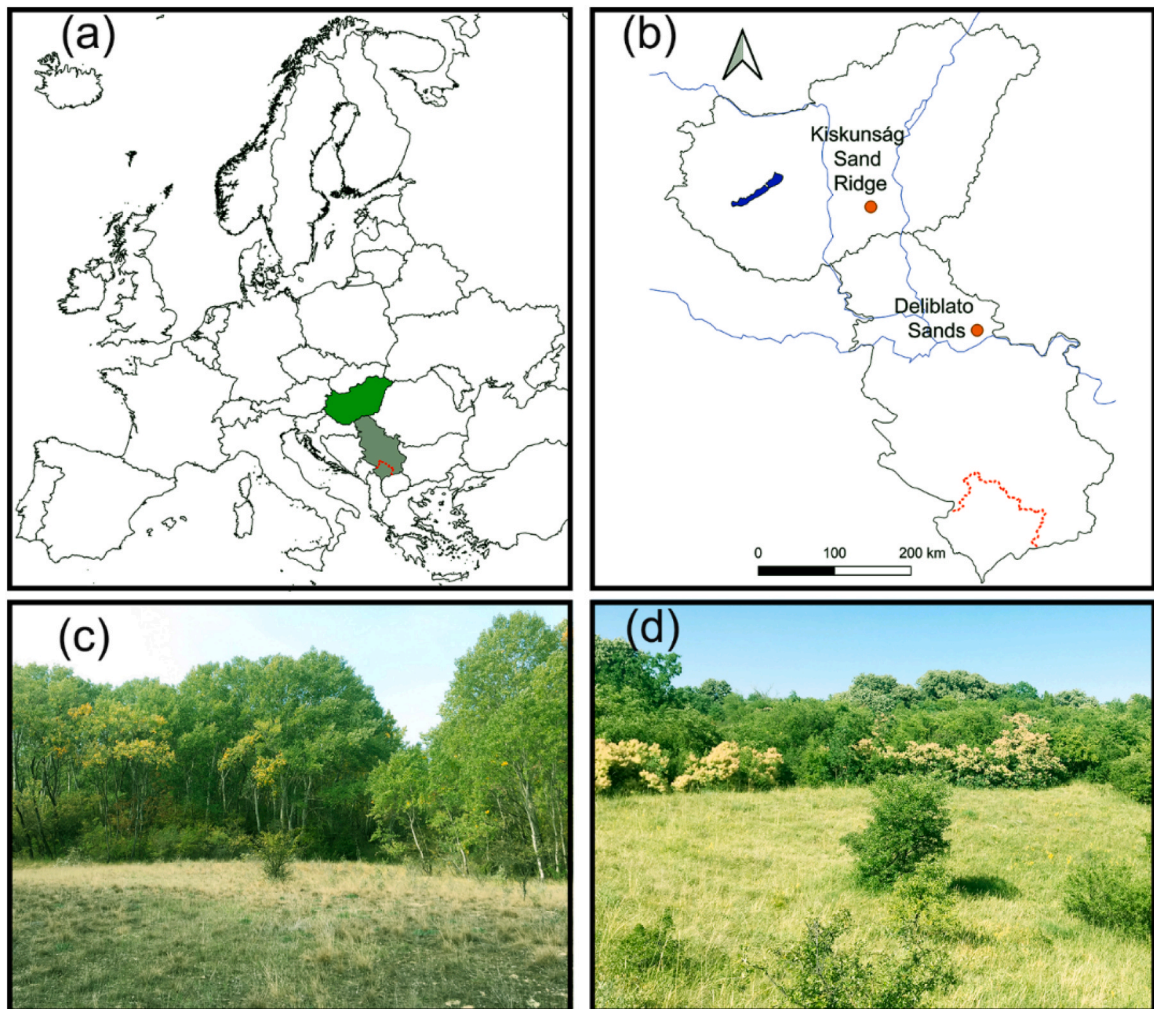


Fig. 1. Location of Hungary (green) and Serbia (gray) in Europe (a). Location of the study sites (orange dots) in Hungary and Serbia (b). Forest–grassland mosaics in the Kiskunság Sand Ridge (c) and the Deliblato Sands (d).

two study sites is approximately 220 km.

2.2. Field sampling

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

2.3. Data analysis

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

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

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

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

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

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

Before data analysis, we used the Shapiro–Wilk normality test and the Bartlett test to determine deviations from normality and

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

3. Results

3.1. Species composition and diagnostic species

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

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

3.2. Taxonomic diversity

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

3.3. Functional diversity

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

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

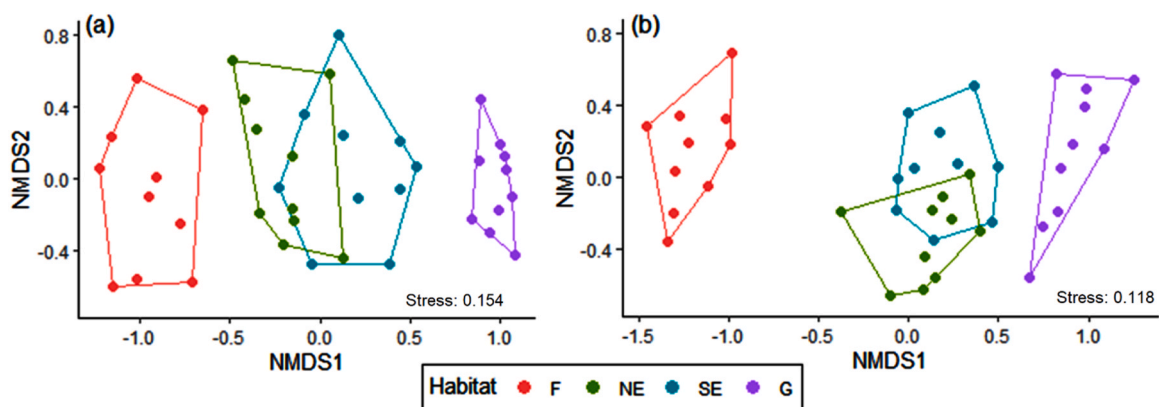


Fig. 2. NMDS ordination diagram of the plots of the Kiskunság (a) and the Deliblato (b) based on the square root-transformed percentage cover data. F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland.

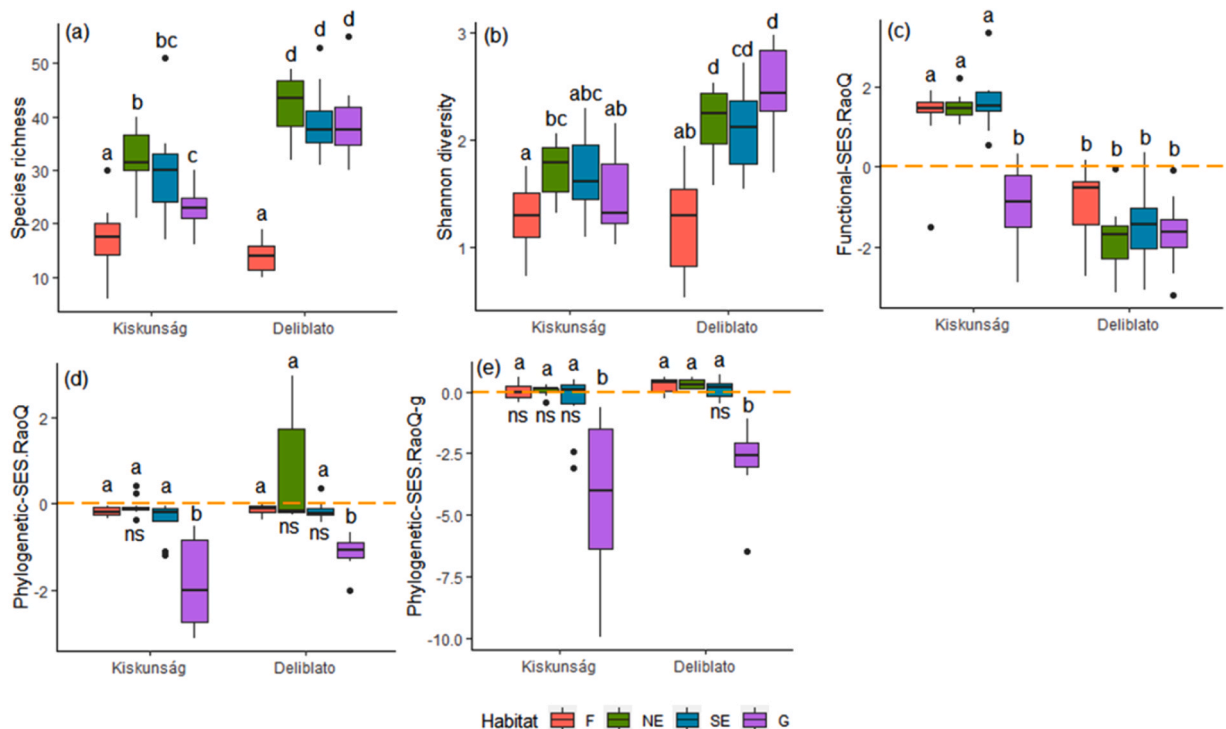


Fig. 3. Species richness (a), Shannon diversity (b), and functional diversity of all traits based on the standardized effect size of Rao's quadratic entropy (SES.RaoQ) (c), phylogenetic diversity of all species (d), phylogenetic diversity of only angiosperm species (e) of the four habitat types in the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

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

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

3.4. Phylogenetic diversity

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

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

4. Discussion

4.1. Species composition and diagnostic species

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

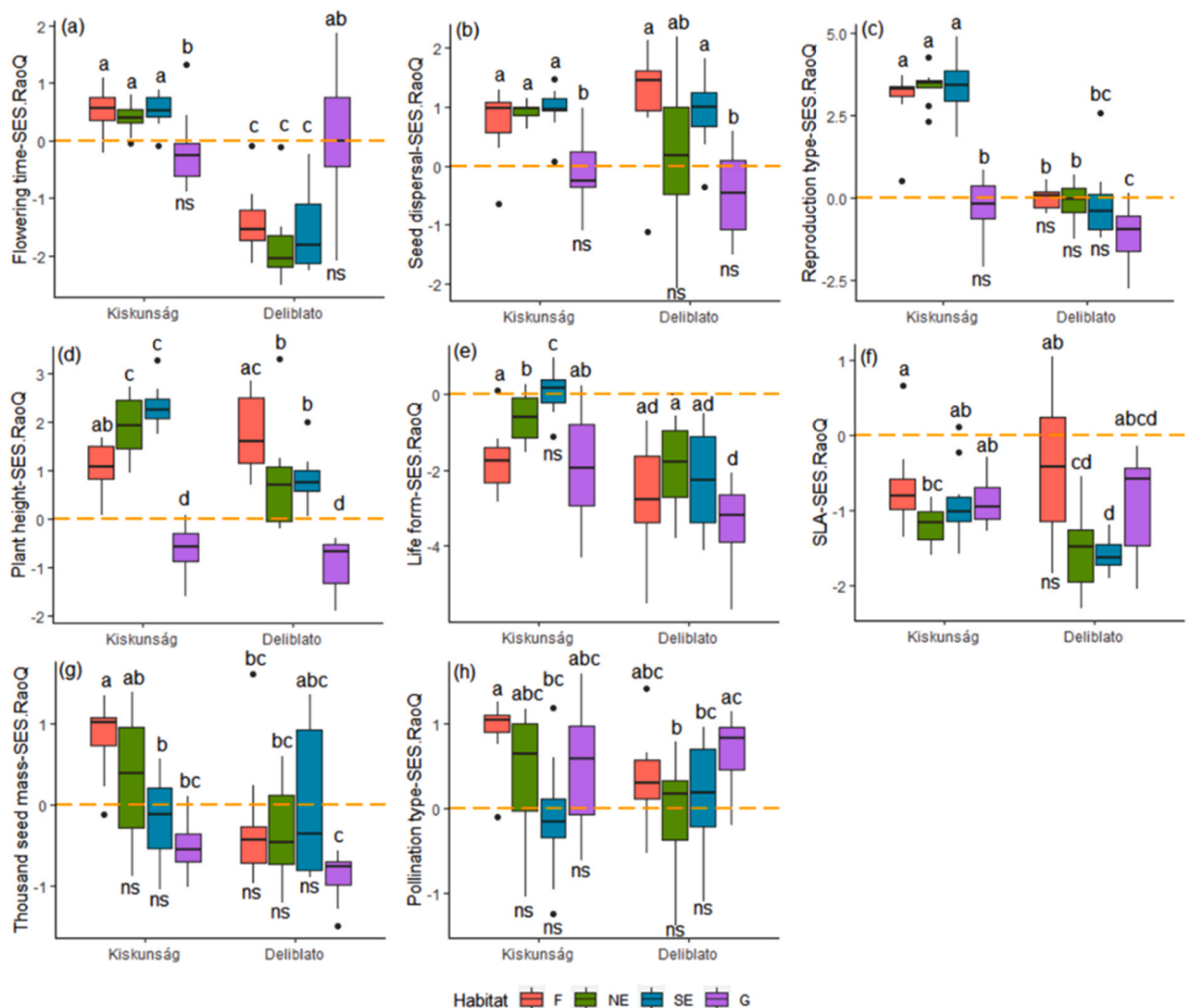


Fig. 4. Functional diversity of single traits. Flowering time (a), seed dispersal (b), reproduction type (c), life form (d), plant height (e), specific leaf area (f), thousand seed mass (g), and pollination type (h). F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland. Habitats not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

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

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

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

forest edge communities.

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

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

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

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

4.2. Taxonomic diversity

Forest interiors had the lowest species richness and Shannon diversity in both sites (Fig. 3a, b). Earlier studies in the region (Erdős et al., 2018b, 2023) and in Kazakh forest-steppes (Bátori et al., 2018) have reported similar results; therefore, this seems to be a general phenomenon at the scale of the study (25 m²).

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

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

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

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

4.3. Functional diversity

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

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

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

Lastly, there was higher variability in flowering time in the woody habitats of the Kiskunság than in those of the Deliblato. Particularly, in the Deliblato, the most dominant species started flowering in early summer (May or June), and the flowering duration was only two months. In contrast, these traits were more diverse in the Kiskunság, resulting in higher functional diversity for flowering time (Fig. 4a).

4.4. Phylogenetic diversity

Phylogenetic diversity peaked at the north-facing edges in the Deliblato, although this habitat did not differ significantly from the other woody habitats (Fig. 3d). However, if only angiosperm species were included in the analysis of phylogenetic diversity, the peak disappeared (Fig. 3e). This effect was likely caused by *Juniperus communis*, which is a common gymnosperm species at the north-facing edges of Deliblato but was not common at the north-facing edges of the study site in the Kiskunság, where no similar peak appeared. Other non-angiosperm species were rare; therefore, they had little influence on phylogenetic diversity.

The general pattern of phylogenetic diversity was similar in the Kiskunság and the Deliblato, i.e., forests and edges had higher phylogenetic diversity than grasslands. This result is in good agreement with previous findings reported from a Brazilian savanna ecosystem (Gastauer et al., 2017). Procheş et al. (2006), Lososová et al. (2015) and Gerhold et al. (2018) argued that phylogenetic diversity is determined by evolutionary history: evolutionarily old habitats are expected to possess higher phylogenetic diversity than evolutionarily young habitats. Our results seem to confirm this view, as woody habitats have a much longer history in the region (dating back to the Mesozoic) than grassland habitats (dating back only to the late Tertiary) (Lososová et al., 2015).

Some previous studies suggested that low species richness is usually accompanied by low functional and phylogenetic diversity in both plant (Cadotte et al., 2009; Jucker et al., 2013; Selvi et al., 2016) and animal communities (Jacoboski et al., 2016; Martello, 2018; Junggebauer et al., 2021). However, in line with Bernard-Verdier et al. (2013), Bässler et al. (2016), and Doxa et al. (2020), our results emphasize that species richness is not always predictive of functional or phylogenetic diversity.

4.5. Limitations of the current study

When evaluating the results of the present work, some considerable limitations of the study have to be taken into account. To ensure comparability, we selected two study sites in relative proximity, but this entails that one has to be careful when drawing general conclusions from this study. This is especially true for functional and phylogenetic diversity, where similar studies along interior-edge-exterior gradients are extremely rare.

Although the two study sites are located in the same biogeographical region and are very similar in terms of climate, soil, vegetation, landscape pattern, and land-use history, there are undoubtable differences between them, which could have influenced the results. For example, the Kiskunság is in the center of the Carpathian Basin, while the Deliblato is near its southern periphery. This small biogeographical difference means that the two sites were differently available to immigrant steppe species during the Holocene through a southeastern and a northwestern corridor (Magyari et al., 2010). In addition, the climate is slightly different, with somewhat

higher mean annual temperature and mean annual precipitation at the Deliblato site. Also, there are minor differences in altitude (110–130 m asl for the Kiskunság site and 140–160 m for the Deliblato site). Finally, the species composition and the structure of the vegetation also shows differences. For example, forest patches are typically larger and both the forest canopy and the grassland have larger total cover values in the Deliblato than in the Kiskunság.

5. Conclusions and future directions

Our results showed that forest edges in the study systems had rather distinct species composition and their own set of diagnostic species that avoid habitat interiors. This lends support to the view that forest edge should be considered a community in its own right, rather than a simple mix of the two neighboring communities.

While species richness and Shannon diversity were found to be highest at edges in the Kiskunság, this was not the case in the Deliblato, indicating that the edge effect hypothesis is not a general rule. There is a need for more studies, especially in natural and near-natural ecosystems to discern at which scales and under what circumstances (e.g., soil, edge structure, characteristics of the adjacent vegetation units, etc.) the edge effect hypothesis can be confirmed.

The multi-trait functional diversity was significantly higher in woody habitats (forest patches and edges) than in grasslands in the Kiskunság, while it was similar among the four habitat types in the Deliblato. This clearly contradicts the stress-dominance hypothesis and emphasizes that functional diversity depends on several factors such as canopy openness and the traits of the dominant species. We conclude that it is too early to draw general conclusions on functional diversity patterns across edges.

We found that phylogenetic diversity was higher in woody habitats than in grasslands, which may be explained by the younger evolutionary age of grasslands. Our study showed that taxonomic diversity is not always indicative of functional and phylogenetic diversity.

Our study should be understood as a tentative step to better understand multiple aspects of diversity across edges in near-natural ecosystems. We would like to stress that future works on diversity patterns should include the analysis of functional and phylogenetic diversity.

Ethics statement

Permission to carry out fieldworks in the protected areas was granted by the Pest County Government Office, Department of Environmental Protection, Nature Conservation, and Waste Management, Hungary (permit no. PE/KTFO/1615/2021) and the Ministry of Environmental Protection, Republic of Serbia (permit no. 353-01-1266/2022-04).

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CRediT authorship contribution statement

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Khanh Vu Ho, Mirjana Ćuk, Tijana Šikuljak, Zoltán Bátori, Csaba Tölgyesi, Attila Fűrész, Péter Török, Alida Anna Hábczyus, Anna Hegyesi, Z. Ladin Coşgun and László Erdős. The first draft of the manuscript was written by Khanh Vu Ho and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Declaration of Competing Interest

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

Data Availability

The datasets generated and analyzed during the current study are available in the Zenodo repository, <https://zenodo.org/record/7675504#.ZCNEoPbMKUk>.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02625](https://doi.org/10.1016/j.gecco.2023.e02625).

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