Journal of Forest Science, 71, 2025 (1): 23–39 *Original Paper*

https://doi.org/10.17221/59/2024-JFS

High light availability offsets low naturalness regarding diversity but cannot compensate for reduced ecological value: A case study of near-natural forests and tree plantations in Serbia

Khanh Vu Ho[1,2,3], *Mirjana Ćuk*[4,5], *Andraž Čarni*[6,7,8], *Dragana Vukov*[4],
Miloš Ilić[4], *László Erdős*[9,10]*

[1]*Faculty of Natural Resources-Environment, Kien Giang University, Kien Giang, Vietnam*
[2]*Doctoral School of Environmental Sciences, University of Szeged, Szeged, Hungary*
[3]*Lendület Seed Ecology Research Group, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Vácrátót, Hungary*
[4]*Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Novi Sad, Serbia*
[5]*Department of Botany and Zoology, Faculty of Science, Masaryk University in Brno, Brno, Czech Republic*
[6]*Institute of Biology, Research Centre of the Slovenian Academy of Sciences and Arts, Ljubljana, Slovenia*
[7]*Macedonian Academy of Sciences and Arts, Skopje, Republic of North Macedonia*
[8]*School for Viticulture and Enology, University of Nova Gorica, Nova Gorica, Slovenia*
[9]*Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Vácrátót, Hungary*
[10]*Department of Ecology, University of Debrecen, Debrecen, Hungary*
**Corresponding author: erdos.laszlo@ecolres.hu*

Citation: Ho K.V., Ćuk M., Čarni A., Vukov D., Ilić M., Erdős L. (2025): High light availability offsets low naturalness regarding diversity but cannot compensate for reduced ecological value: A case study of near-natural forests and tree plantations in Serbia. J. For. Sci., 71: 23–39.

Abstract: In Eastern Europe, near-natural forest patches are decreasing and are gradually replaced by non-native plantations. Tree plantations are commonly thought to be simple ecosystems with low conservation value, although this conclusion is mainly based on simple taxonomic diversity indices, which ignore functional and phylogenetic diversity. In this study, our objective was to compare species composition, diagnostic species, taxonomic, functional, and phylogenetic diversity, as well as naturalness status between two near-natural forest types (*Quercus-Tilia* and *Populus alba*) and two common plantation types (non-native *Pinus sylvestris* and non-native *Robinia pseudoacacia*) in the Deliblato Sands, Serbia. Our results showed that the species composition significantly differed in the four habitats. Each habitat had some species that were significantly concentrated in them. Most of the diagnostic species in the *Quercus-Tilia* forests were forest specialist plant species, while those in *Populus alba* forests were species associated with warmer and drier habitats, whereas the plantations hosted diagnostic species with broader ecological tolerances. Native species richness, total species diversity, and functional and phylogenetic diversity were similar in the four studied habitats, which can be explained by the combined effects of light regime and naturalness. We assessed low naturalness (i.e. high degradation) in plantations, which can be expected to reduce diversity. However, higher light availability was probably able to compensate for this effect. Non-native plantations, especially *Robinia pseudoacacia* plantations, were the most degraded and hosted the highest non-native species richness, implying that they are ecologically undesirable. In light of our results, we suggest that near-natural forest stands should be protected and efforts to restore these forests should be given high priority. Furthermore, it is advisable to continue with a forestry strategy that involves replacing non-native plantations with native ones, such as *Tilia tomentosa*, in the Deliblato Sands.

Keywords: degraded habitats; ecological indicators; exotic tree plantations; functional diversity; phylogenetic diversity

---

Supported by the Ministry of Science, Technological Development and Innovation of the Republic of Serbia (grants No. 451-03-66/2024-03/200125 and No. 451-03-65/2024-03/200125), and by the Slovenian Research and Innovation Agency (grant No. ARIS P1-0236).

https://doi.org/10.17221/59/2024-JFS

Tree plantations are expanding worldwide, as they provide economic benefits and may also address imminent environmental challenges such as climate change and the decline of biodiversity (FAO 2022). While the replacement of native plants with plantations generally leads to a decline in local biodiversity, planting trees on degraded, abandoned, or agricultural land can substantially increase opportunities for biodiversity conservation (Chapman, Chapman 1999; Pawson et al. 2013; Tomaz et al. 2013; Tölgyesi et al. 2022). Tree plantations (i.e. intensively managed planted forests) covered approximately 3% of the global forest area, or 131 million ha, in 2020 (FAO 2022). Meanwhile, according to Forest Europe (2020), tree plantations occupy ca. 3.8% of the forested land in Europe, and 52.8% of them are non-native tree plantations.

Despite occupying a relatively minor fraction of the world's landscape, tree plantations belong to the most controversial topics related to forest sustainability and biodiversity conservation (Pawson et al. 2013). Plantations are recognised as 'biological deserts' (Stephens, Wagner 2007). For example, tree plantations have a low conservation value (Šibíková et al. 2019; Ho et al. 2023a) and they are known as hotspots of plant invasion in the landscape (Csecserits et al. 2016). In addition, they may have negative impacts on ecosystem services (e.g. reduced shelter and food supply for fauna, loss of local and regional water balance) (Santos et al. 2017; Tölgyesi et al. 2020; Ho et al. 2023a). The unfavourable view of tree plantations is at times justified, but it should not be applied to all plantations. A growing body of evidence shows that plantations provide many ecosystem services (e.g. carbon sequestration, phytoremediation, as well as soil and water stabilisation) (Albert et al. 2021; Hynes et al. 2021; Xi et al. 2021), can provide habitats for protected, endemic, and red-listed plant species (Bremer, Farley 2010; Horák et al. 2019), and may increase the connectivity of landscape mosaics for conservation efforts (Kanninen 2010).

Understory vegetation is crucial for biodiversity conservation, as it harbours over 80% of the plant species found within a forest community (Gilliam 2007). Also, it plays an important role in ecological functions or processes (Landuyt et al. 2019). For instance, understory plants provide habitat (e.g. hiding and nesting place) and foraging material for many species (Gilliam 2007; Beason et al. 2020). However, understory vegetation is strongly impacted by the composition and structure of the overstory, leading to differences in abiotic conditions such as temperature, light, pH, and nutrients on the soil surface among various canopy types (Slabejová et al. 2019; Mikulová et al. 2019). It is therefore necessary to assess the influence of dominant tree species on the structure and composition of understory species, as the resulting knowledge may contribute to better management practice to enhance biodiversity as well as the plantation ecological functions and services. Many studies show that monoculture plantations have fewer understory species than near-natural forests (Brockerhoff et al. 2008; Sobuj, Rahman 2011; Calviño-Cancela et al. 2012; Rédei et al. 2020). This pattern, however, may not hold true under all circumstances. Slabejová et al. (2019), for example, found that black locust plantations had higher understory species richness than oak-hornbeam forests and did not differ in the understory species number compared to floodplain forests and oak forests.

Apart from taxonomic diversity, functional diversity (i.e. the variability in functional traits among organisms) and phylogenetic diversity (i.e. the diversity in evolutionary lineages within a community) represent additional facets of biodiversity. These dimensions provide valuable insights into ecosystem processes, productivity, dynamics, stability, and the provisioning of ecosystem services (Scherer-Lorenzen 2008; Cadotte et al. 2011; Flynn et al. 2011). Although high taxonomic diversity is sometimes associated with high functional and phylogenetic diversity in plants (Cadotte et al. 2009; Selvi et al. 2016) and several other taxa (Jacoboski et al. 2016; Junggebauer et al. 2021), the situation is not so simple in most cases (Doxa et al. 2020; Erdős et al. 2023; Ho et al. 2023b).

In the Pannonian biogeographical region, the area of natural/near-natural forests is declining partly because they are replaced with plantations of *Pinus nigra*, *P. sylvestris*, *Robinia pseudoacacia*, and different *Populus* species (Molnár et al. 2012). However, the knowledge how abiotic conditions, species composition, conservation value, and various aspects of biodiversity (taxonomic, functional, and phylogenetic diversity) differ between near-natural forests and different types of tree plantations is still extremely limited. In this study, we aimed to reveal how the above characteristics vary between near-natural forests and three common types of plantations (native deciduous, non-native evergreen, and non-native deciduous) in the southern part of the Pannonian region. The following questions were asked: (*i*) How do abiotic parameters differ between the near-natural forests and different plantations, as indicated by ecological indicator values? (*ii*) Does the species composition of near-natural forests differ from plantations? (*iii*) Does taxonomic, functional, and phylogenetic diversity of near-natural forests differ from that of plantations? (*iv*) How does the naturalness of the near-natural forest stands and the plantation types differ?

MATERIAL AND METHODS

Study area. The Deliblato Sands, the largest sand-covered region in Serbia, is located in southern Banat between the Danube River and the southwestern slopes of the Carpathian Mountains (Figure 1A). Its area is approximately 340 km^2, with a length of around 35 km and a width of 11 km (Kadović et al. 2016). It has a moderate continental climate, with a mean annual temperature of 12.5 °C and precipitation of 664 mm (Ćuk et al. 2023). This region is made up of aeolian sand dunes, featuring sandy soils poor in humus and possessing limited water retention capacity (Sipos et al. 2022).

The natural vegetation of the study area is a forest-steppe, i.e. a mosaic of *Quercus-Tilia* forests and grasslands in a large part of the area, and a mosaic of *Populus* and *Quercus* forests and grasslands in the southernmost parts, near the Danube River (Parabućski 1980; Butorac, Panjković 2013). *Quercus-Tilia* forest stands (*Querco-Tilietum tomentosae)* are co-dominated by 15–25 m tall *Tilia tomentosa* and *Quercus robur* individuals, with a canopy cover of 60–100% (Figure 1B). The shrub layer, with a cover of 30–90% and a height of 1–5 m, is primarily composed of *Cornus sanguinea*, *Ligustrum vulgare*, *Lonicera xylosteum*, and *Rhamnus cathartica*. The herb layer is mainly characterised by *Alliaria petiolata*, *Corydalis solida*, *Veronica hederifolia*, and *Viola suavis*.

Populus alba forests in this area usually have a canopy cover of 30–70% (Figure 1C). The shrub layer, with a cover of 30–70%, is characterised by *Juniperus communis, Ligustrum vulgare, Berberis vulgaris,* and *Prunus mahaleb*. The herb layer is typically composed of *Brachypodium sylvaticum*, *Carex liparocarpos*, *Festuca rupicola*, and *Poa angustifolia*. This forest type is highly fragmented, and the size of individual forest patches is quite small.

We classified the remnants of *Quercus-Tilia* forests and white poplar (*Populus alba)* forests as near-natural forests because they occur naturally in legally protected areas, are dominated by native species, and show no visible signs of recent human intervention. Historically, the near-natural forest area has shrunk dramatically. Currently, *Quercus-Tilia* forests are mostly concentrated in the central part of the Deliblato special nature reserve, while *Populus alba* forests occur only in the south-eastern part of the reserve (Ćuk et al. 2023).

Afforestation efforts in the Deliblato Sands began in 1818 and are still going on (Ćuk et al. 2023). Consequently, the landscape of this area is now characterised by extensive tree plantations, primarily composed of the non-native deciduous black locust (*Robinia pseudoacacia*) and the non-native evergreen Scots pine (*Pinus sylvestris*) mixed with Austrian pine (*Pinus nigra*) (Ćuk et al. 2023).

Pinus sylvestris plantations commonly feature canopy covers ranging between 30% and 80% (Figure 1D). The shrub layer has a cover of 10–80%, with some common species such as *Celtis australis*, *Crataegus monogyna*, *Ligustrum vulgare*, and *Lonicera xylosteum*. The most common species in the herb layer include *Brachypodium sylvaticum*, *Geum urbanum*, *Erigeron annuus*, and *Teucrium chamaedrys*. The first *Pinus* plantations in the Deliblato Sands were established during the 19th century, but large areas were planted only after World War Two, and the majority of the *Pinus* stands originate from the 1970s.

Robinia pseudoacacia plantations typically exhibit an overall canopy coverage ranging approximately from 60% to 90% (Figure 1E). The shrub layer, with a cover of 40–80%, includes species such as *Berberis vulgaris*, *Cornus sanguinea*, *Crataegus monogyna*, and *Ligustrum vulgare*. The dominant species in the herb layer is *Bromus sterilis*. Other common species are *Alliaria petiolata*, *Chelidonium majus*, *Geum urbanum*, and *Polygonatum biflorum*. *Robinia* was introduced into the Deliblato Sands in the 19th century, and the large-scale application of the species gained momentum in the 20th century.

Currently, neither *Pinus* nor *Robinia* plantations are managed, except for the removal of the trees when they reach an appropriate age.

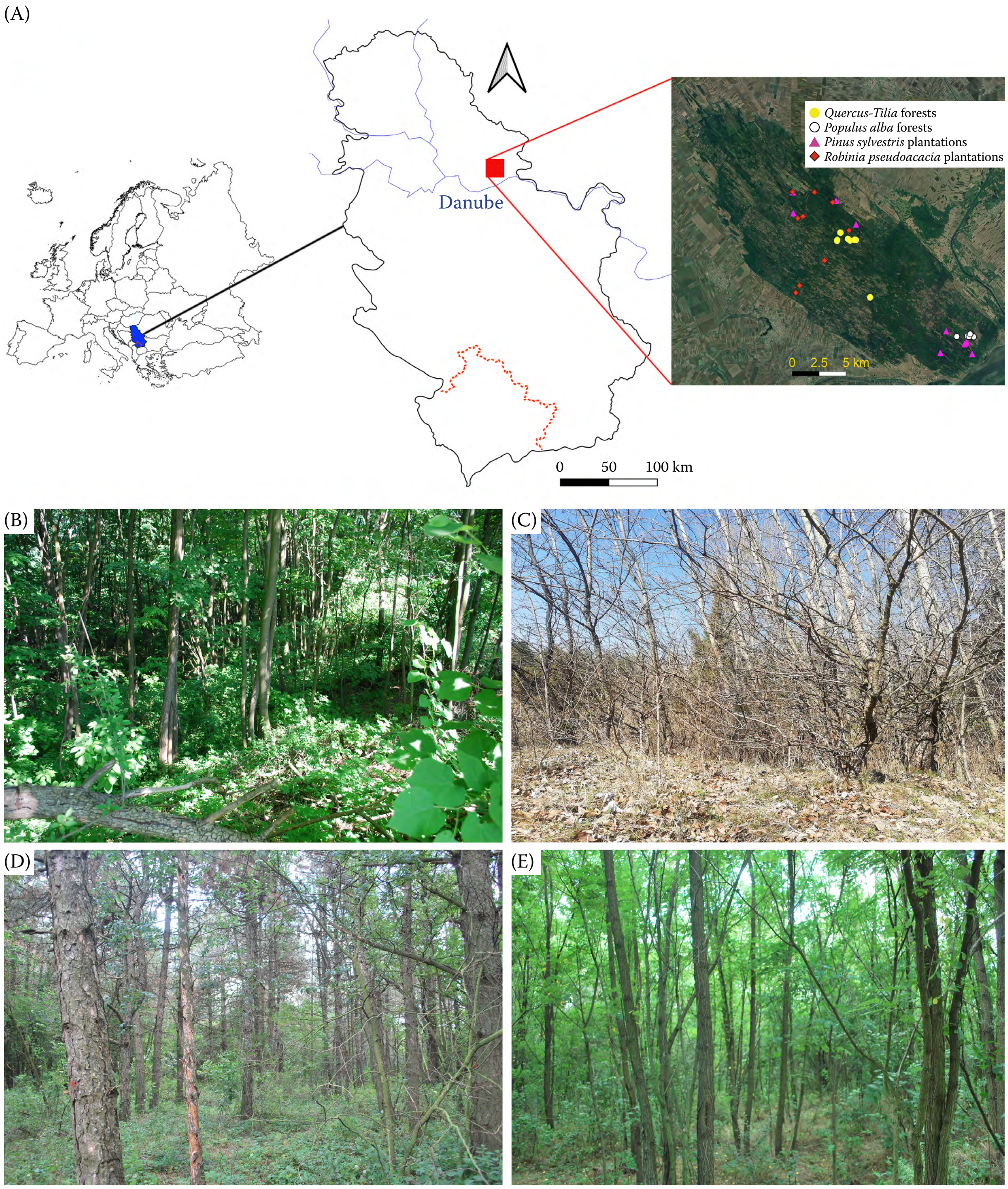

Figure 1. (A) Location of Serbia (blue) in Europe and the Deliblato Sands in Serbia (red square), (B) *Quercus-Tilia* forests, (C) *Populus alba* forests, (D) *Pinus sylvestris* plantations, (E) *Robinia pseudoacacia* plantations

Plant species nomenclature is based on the Plant List (2013), while plant association names follow Ćuk (2019).

Sampling design. We sampled four habitats: *Quercus-Tilia* forests, *Populus alba* forests, plantations of the non-native evergreen *Pinus sylvestris*, and plantations of the non-native deciduous *Robinia pseudoacacia*. Mature *Quercus-Tilia* and *Populus alba* forests and even-aged tree plantations with a diameter at breast height (*DBH*) exceeding 10 cm were selected to sample vegetation.

We used 10 m × 10 m plots for the identification of all vascular plant species, visually estimating their cover according to the Braun-Blanquet cover-abundance scale. Ten study plots were established randomly in each of the four habitats (40 plots in total). We classified vegetation into three layers: canopy layer (trees exceeding 5 m in height), shrub layer (woody plants with a height less than 5 m), and herb layer (herbaceous and small woody plants – such as tree seedlings, saplings, shrubs, and woody vines – measuring less than 0.5 m in height). However, only the shrub and herb layers were included in the analyses in this study. Two unidentified taxa (*Ornithogalum* sp. and *Prunus* sp.), neither of which appeared in > 1 of the 40 plots, were excluded from the functional and phylogenetic diversity, as well as naturalness and ecological indicator value analyses.

Data analysis. For those analyses that required cover data, the Braun-Blanquet scores were transformed to cover values according to Tüxen and Ellenberg (1937) (Table 1).

To reveal the differences in species composition across the four habitats, non-metric multidimensional scaling (NMDS) was performed using the Bray-Curtis dissimilarity on the square-root transformed cover percentages. As overlaps were detected in the ordination space, we applied permutational multivariate analysis of variance (PERMANOVA) with 999 permutations to confirm compositional distinctness between the habitats. The NMDS was conducted with the 'metaMDS' function, and the PERMANOVA analysis was carried out using the 'adonis2' function, both of which are available in the vegan package of R (Version 4.3.2; Oksanen et al. 2022; R Core Team 2023). If the PERMANOVA test showed a significant difference with a p-value lower than 0.05, the pairwise comparisons were employed using the 'pairwise.adonis' function in the funfuns package and *P*-values were manually adjusted by the false discovery rate (FDR) method (Trachsel 2022).

Table 1. Braun-Blanquet cover-abundance scores are converted into percentage cover values

Braun-Blanquet value	Cover value (%)
r/+	0.1
1	2.5
2	15.0
3	37.5
4	62.5
5	87.5

To identify the species that prefer one specific habitat and are absent or rare in the others, we computed phi-coefficients as fidelity indicators for the species of each habitat (Chytrý et al. 2002). We considered a species diagnostic for a particular habitat when its phi value was larger than 0.2. Fisher's exact test ($P < 0.05$) was applied to reveal significant diagnostic species. The analysis was done using JUICE (Version 7.1.30, 2020). In addition, we also added to each species its coenological preference according to Borhidi (1995).

In this study, the total species diversity per plot (evaluated using the Shannon diversity index) was computed by means of the 'diversity' function of the R vegan package (Oksanen et al. 2022), while the number of native and non-native species was also counted for each plot.

To calculate functional diversity (*FD*) in each plot, we used Rao's quadratic entropy (*RaoQ*) as it is a robust measure of functional diversity (Botta-Dukát 2005; Ricotta 2005). The overall functional diversity per plot was calculated by combining nine functional 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 S1 in the Electronic Supplementary Material (ESM)]. *SLA*, mean plant height, and thousand seed mass were included due to their significant ecological relevance (Westoby 1998), whereas the other traits reflect essential ecosystem functions (see Weiher et al. 1999). As the quantitative traits were less normally distributed, logarithmic transformation was applied to flowering duration, *SLA*, plant height, and thousand seed mass prior to *FD* analysis to improve normality. We used the 'gawdis' function of the gawdis package in R to compute species dissimilarity because of its ability to address the challenge of unbalanced contributions from multiple traits and even traits encoded with fuzzy coding (de Bello et al. 2021a).

We also used Rao's quadratic entropy to reveal phylogenetic diversity (*PD*), allowing us to compare phylogenetic and functional diversity within the same conceptual and mathematical framework (Jucker et al. 2013; Swenson 2014; de Bello et al. 2021b). We used the 'phylo.maker' function of the V.PhyloMaker2 package in R (Version 4.3.2) to construct the phylogeny of 167 species found in our study from a 365 198-species mega-tree under scenario 3, in which undetermined species were assigned to their closest relatives (Jin, Qian 2022). The final phylogenetic tree is shown in Figure S1 in the ESM. After that, the 'cophenetic' function of the picante package in R was employed to calculate the matrix of phylogenetic distances (Kembel et al. 2010). Finally, the 'rao.diversity' function of the SYNCSA package was applied in order to compute *RaoQ* for both functional and phylogenetic diversity (Debastiani, Pillar 2012).

To account for the potential impact of species richness on *RaoQ* and to assess whether habitats demonstrated functional and phylogenetic over- or underdispersion, the standardised effect size of *RaoQ* (*SES.RaoQ*) was calculated using the equation: (observed *RaoQ* value –mean expected *RaoQ* values)/standard deviation of expected *RaoQ* values (de Bello et al. 2021b). The species labels in the trait matrix were permuted through 999 randomisations to generate null models for functional indices, following the R code provided by de Bello et al. (2021b). Meanwhile, null models for phylogenetic indices were created by rearranging the species names in the phylogeny, using the R code outlined in Swenson (2014). Positive *SES* values indicate overdispersion or divergence, implying that the species are more distant than expected by chance. In contrast, negative *SES* values indicate underdispersion or clustering, which implies that the species are closer than expected by chance. The statistical significance of observed *SES* values compared to null expectation *SES* values was determined using the two-sided Wilcoxon signed-rank test (Bernard-Verdier et al. 2012; Nooten et al. 2021).

In this study, abiotic parameters [temperature, soil moisture, soil nutrients, soil reaction (pH), and light intensity] were determined using species ecological indicator values derived from the presence/absence data for each plot. The ecological indicator values were extracted from Borhidi (1995). Despite the frequent criticism of using the mean indicator values, they appear to perform well in ecological analyses and have a robust theoretical foundation (Persson 1981; Ter Braak, Gremmen 1987; Diekmann 2003). A wide range of earlier studies showed that the ecological indicator values can provide reliable estimates of abiotic variables (Dzwonko 2001; Fanelli et al. 2007; Szymura et al. 2014; Scherrer, Guisan 2019).

We used the naturalness indicator values of Borhidi (1995) to determine the degree of naturalness in the habitats (i.e. their position along the natural degradation continuum). The approach is similar to the ecological indicator values and has been increasingly applied in the Pannonian region (Erdős et al. 2017, 2018, 2022; Ho et al. 2023a). It relies on the varying tolerances of different plant species to degradation, with some species favouring natural or near-natural habitats and others exhibiting tolerance towards, or even benefitting from degradation (Erdős et al. 2022). Species associated with natural habitats are assigned high scores, while those affiliated with degraded areas receive low scores. The unweighted mean naturalness value was computed for each plot.

The number of non-native and native species, total species diversity (Shannon diversity), functional and phylogenetic diversity, as well as mean ecological indicator and naturalness values were tested for normal distribution and variance homogeneity using the Shapiro-Wilk normality test and the Bartlett test. We compared functional diversity, the mean ecological indicator values for soil reaction (pH), and the mean naturalness index between different habitats by one-way ANOVA and subsequent Tukey's HSD post hoc test. Regarding the other indices, since the assumptions of analysis of variance were not met, we used the non-parametric Kruskal-Wallis test to determine the significant differences between four habitat types using the 'kruskal.test' function in R. If this test revealed a significant proportion of variability, pairwise comparisons between habitat types were conducted, with *P*-values adjusted using the false discovery rate (FDR) method via the 'pairwise.wilcox.test' function. A significance level of 0.05 was chosen, and *P*-values equal to or lower than this value were considered statistically significant.

RESULTS

According to the NMDS ordination, *Quercus-Tilia* forests, *Populus* forests, and *Robinia* plantations constituted three well-distinguishable groups (Figure 2). Although they had some overlaps with *Pinus* plantations, the PERMANOVA test showed a significant difference between the habitats ($F = 4.547$, $P < 0.001$, $R^2 = 0.275$). Significant habitat differences were detected in all pairwise comparisons ($P < 0.05$) (Table S2 in the ESM).

https://doi.org/10.17221/59/2024-JFS

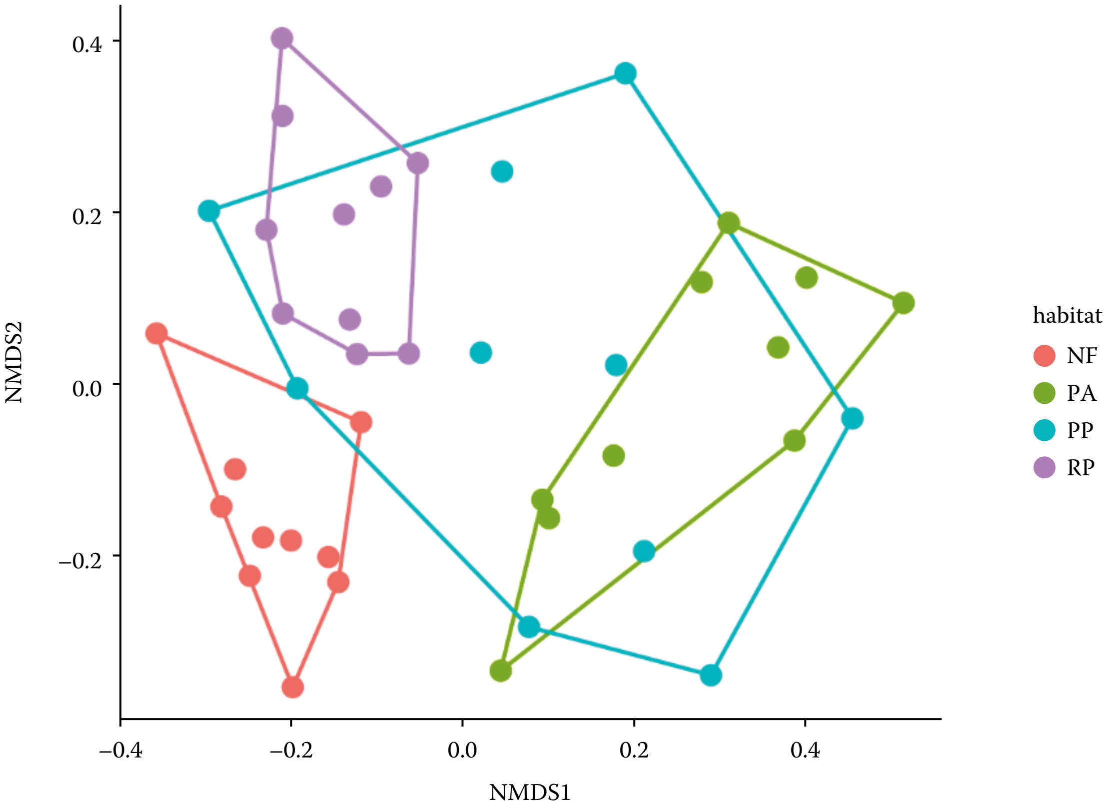

Figure 2. NMDS ordination scattergram of 40 plots

NMDS – non-metric multidimensional scaling; NF – *Quercus-Tilia* forests; PA – *Populus alba* forests; PP – *Pinus sylvestris* plantations; RP – *Robinia pseudoacacia* plantations; stress = 0.224

The habitat type did not have a significant effect on the mean ecological indicator values for temperature ($\chi^2 = 0.638$, $P = 0.888$), but it considerably influenced those for soil moisture ($\chi^2 = 11.1$, $P = 0.011$), soil nutrients ($\chi^2 = 20.9$, $P < 0.001$), pH ($F = 3.785$, $P = 0.019$), and light availability ($\chi^2 = 27.5$, $P < 0.001$) (Figure 3). According to the pairwise comparisons (Figure 3; Table S3 in the ESM), the mean ecological indicator values for soil moisture were the highest in *Quercus-Tilia* forests and *Robinia* plantations, and the lowest in *Populus* forests (Figure 3B). The plantations of *Pinus sylvestris* showed intermediate values. Regarding the soil nutrient content, *Robinia* plantations had the highest ecological indicator values, although they did not differ significantly from *Quercus-Tilia* forests (Figure 3C). The *Populus alba* fragments had the lowest mean ecological indicator values for soil nutrients but they were not notably different from *Pinus* plantations. The mean ecological values for soil reaction (pH) showed that *Populus alba* forests had the highest, while *Robinia* plantations had the lowest values (Figure 3D). Although *Quercus-Tilia* forests and *Pinus* plantations showed intermediate values, the box plot revealed a somewhat low soil pH value for *Pinus* plantations. By removing the single outlier from the *Pinus sylvestris* plantation, this habitat exhibited significantly lower mean ecological indicator values for pH than all other habitats (Figure S2 in the ESM). The mean ecological indicator values for light availability were the highest in *Populus* forests, and the lowest in *Quercus-Tilia* forests, while they were intermediate in *Pinus* and *Robinia* plantations (Figure 3E).

The list of diagnostic species associated with the four habitats is shown in Table 2. *Quercus-Tilia* forests had 11 diagnostic species, most of which were typical species of mesic and dry forests (e.g. *Clematis vitalba*, *Corydalis solida*, and *Polygonatum odoratum*). *Populus* forests contained 16 diagnostic species, most of which were typical species of dry forests and dry grasslands, and some were indifferent species (e.g. *Carex liparocarpos*, *Gagea pratensis*, and *Juniperus communis*). *Pinus* plantations had only 4 diagnostic species, two of which were indifferent (*Brachypodium sylvaticum* and *Taraxacum*

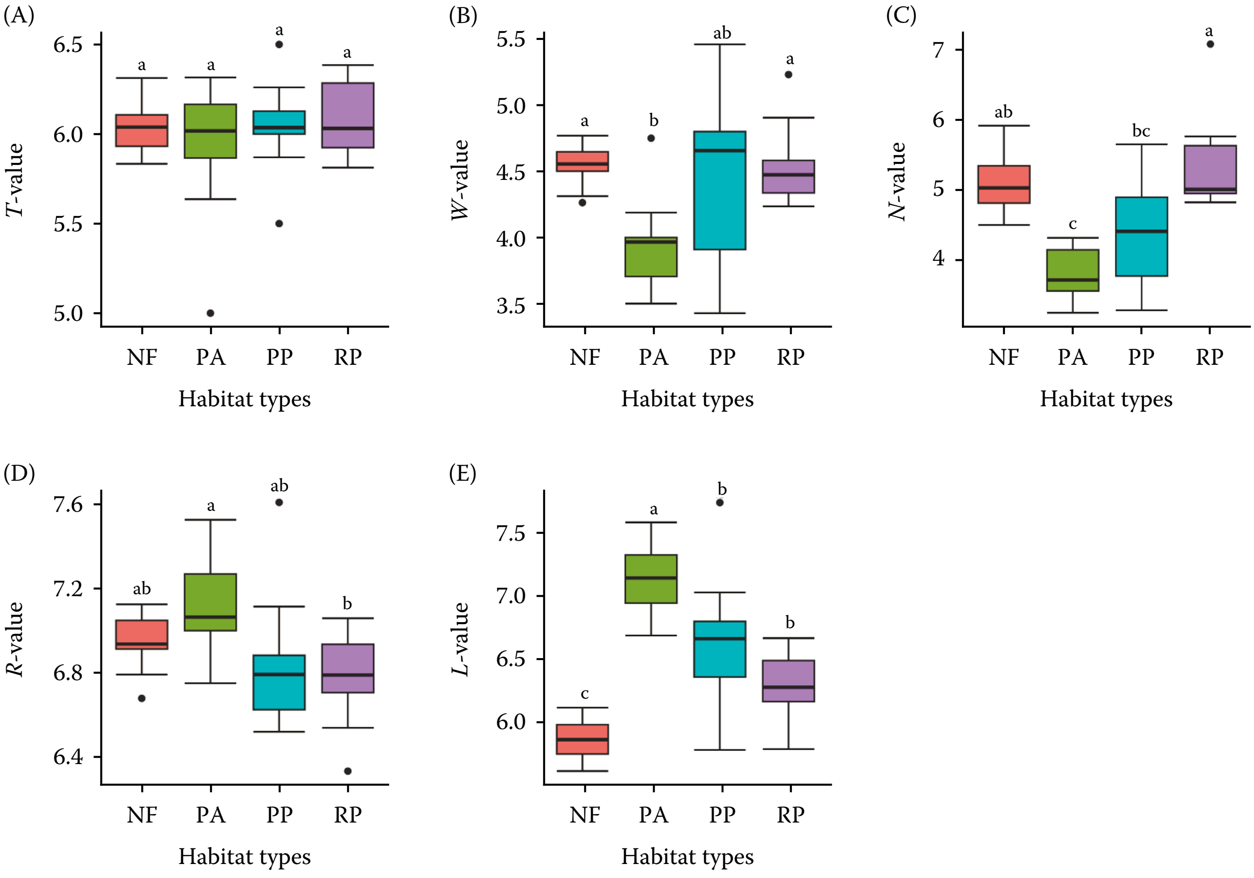

Figure 3. Mean ecological indicator values for (A) temperature, (B) soil moisture, (C) soil nutrient, (D) soil reaction (pH), and (E) light availability for the studied habitats

a–c – significant differences ($P < 0.05$); NF – *Quercus-Tilia* forests; PA – *Populus alba* forests; PP – *Pinus sylvestris* plantations; RP – *Robinia pseudoacacia* plantations; *T*-value – ecological indicator for temperature; *W*-value – ecological indicator for soil moisture; *N*-value – ecological indicator for soil nutrient content; *R*-value – ecological indicator for soil reaction; *L*-value – ecological indicator for light availability

campylodes) and one was a weed (*Lactuca serriola*). *Robinia* plantations had 13 diagnostic species with various coenological preferences (e.g. *Bromus sterilis*, *Chelidonium majus*, and *Viola hirta).*

The habitat type significantly influenced the number of non-native species ($\chi^2 = 14.5$, $P = 0.002$), but it did not affect the number of native species ($\chi^2 = 0.750$, $P = 0.861$) and total species diversity (Shannon diversity) ($\chi^2 = 7.105$, $P = 0.069$) (Figure 4). Considering the pairwise comparisons (Table S3 in the ESM), the number of non-native species was the lowest in *Populus* forests, although it did not significantly differ from that of the *Quercus-Tilia* forests. The number of non-native species of *Quercus-Tilia* forests was significantly lower than that of the *Robinia* plantations ($P = 0.033$) and marginally lower than that of the *Pinus* plantations ($P = 0.063$).

Although the habitat type had no significant effect on phylogenetic diversity ($\chi^2 = 5.527$, $P = 0.137$) and functional diversity ($F = 1.894$, $P = 0.148$), phylogenetic and functional diversity appeared to be somewhat higher in *Populus alba* forests than in the other habitats (Figure 4D, E). *Quercus-Tilia* forests were phylogenetically and functionally underdispersed, while *Populus* forests were not significantly different from the null model expectation (Table S4 in the ESM). Non-native tree plantations showed functional underdispersion, but phylogenetically random patterns (Table S4 in the ESM).

The habitat type significantly affected the naturalness value ($F = 10.3$, $P < 0.001$). The mean naturalness value was the highest in *Quercus-Tilia* forests, the lowest in *Robinia pseudoacacia* plantations, and intermediate in the other two habitats (Figure 4F; Table S3 in the ESM).

https://doi.org/10.17221/59/2024-JFS

Table 2. Significant diagnostic species of the four habitats with phi coefficients > 0.200, and their coenological preferences

Species	NF	PA	PP	RP	Coenological preferences
Alliaria petiolate	31.8*	–	–	31.8*	indifferent
Clematis vitalba	36.3*	–	–	–	mesic forests
Corydalis solida	73.9***	–	–	–	mesic forests
Euonymus europaeus	39.9*	–	–	–	mesic forests
Fritillaria montana	50.5*	–	–	–	dry forests
Lonicera xylosteum	60.3***	–	–	–	mesic forests
Polygonatum odoratum	47.5**	–	–	–	dry forests
Tilia tomentosa	41.6*	–	–	–	mesic forests
Veronica hederifolia	41.6*	–	–	–	weed communities
Viburnum lantana	64.1***	–	–	–	dry forests
Viola suavis	64.1***	–	–	–	dry forests
Carex hirta	–	47.5**	–	–	indifferent
Carex liparocarpos	–	57.9***	–	–	dry grasslands
Equisetum ramosissimum	–	50.5*	–	–	dry grasslands
Eryngium campestre	–	47.5**	–	–	indifferent
Euphorbia cyparissias	–	36.2*	–	–	indifferent
Festuca rupicola	–	64.1***	–	–	dry grasslands
Gagea pratensis	–	59.0**	–	–	dry forests
Juniperus communis	–	36.2*	–	–	indifferent
Lamium purpureum	–	37.9*	–	–	weed communities
Poa angustifolia	–	73.9***	–	–	indifferent
Populus alba	–	47.5**	–	–	dry forests
Prunus mahaleb	–	39.9*	–	–	dry forests
Seseli annuum	–	37.9*	–	–	dry grasslands
Taraxacum erythrospermum	–	48.1**	–	–	dry grasslands
Tragopogon orientalis	–	50.5*	–	–	indifferent
Vicia sativa ssp. *nigra*	–	66.7***	–	–	indifferent
Brachypodium sylvaticum	–	–	31.8*	–	indifferent
Celtis australis	–	–	35.6*	35.6*	dry forests
Lactuca serriola	–	–	37.9*	–	weed communities
Taraxacum campylodes	–	–	50.5*	–	indifferent
Ailanthus altissima	–	–	–	50.5*	indifferent
Alyssum tortuosum	–	–	–	50.5*	dry grasslands
Bromus sterilis	–	–	–	63.2***	indifferent
Chelidonium majus	–	–	–	63.2***	weed communities
Cornus sanguinea	–	–	–	33.0*	indifferent
Crataegus monogyna	–	–	–	38.6**	scrubs
Geum urbanum	–	–	–	34.8*	scrubs
Glechoma hederacea	–	–	–	59.0**	indifferent
Poa pratensis	–	–	–	50.5*	mesic grasslands
Polygonatum biflorum	–	–	–	41.6*	mesic forests
Robinia pseudoacacia	–	–	–	45.6**	indifferent
Viola hirta	–	–	–	47.5**	mesic forests

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; NF – *Quercus-Tilia* forests; PA – *Populus alba* forests; PP – *Pinus sylvestris* plantations; RP – *Robinia pseudoacacia* plantations

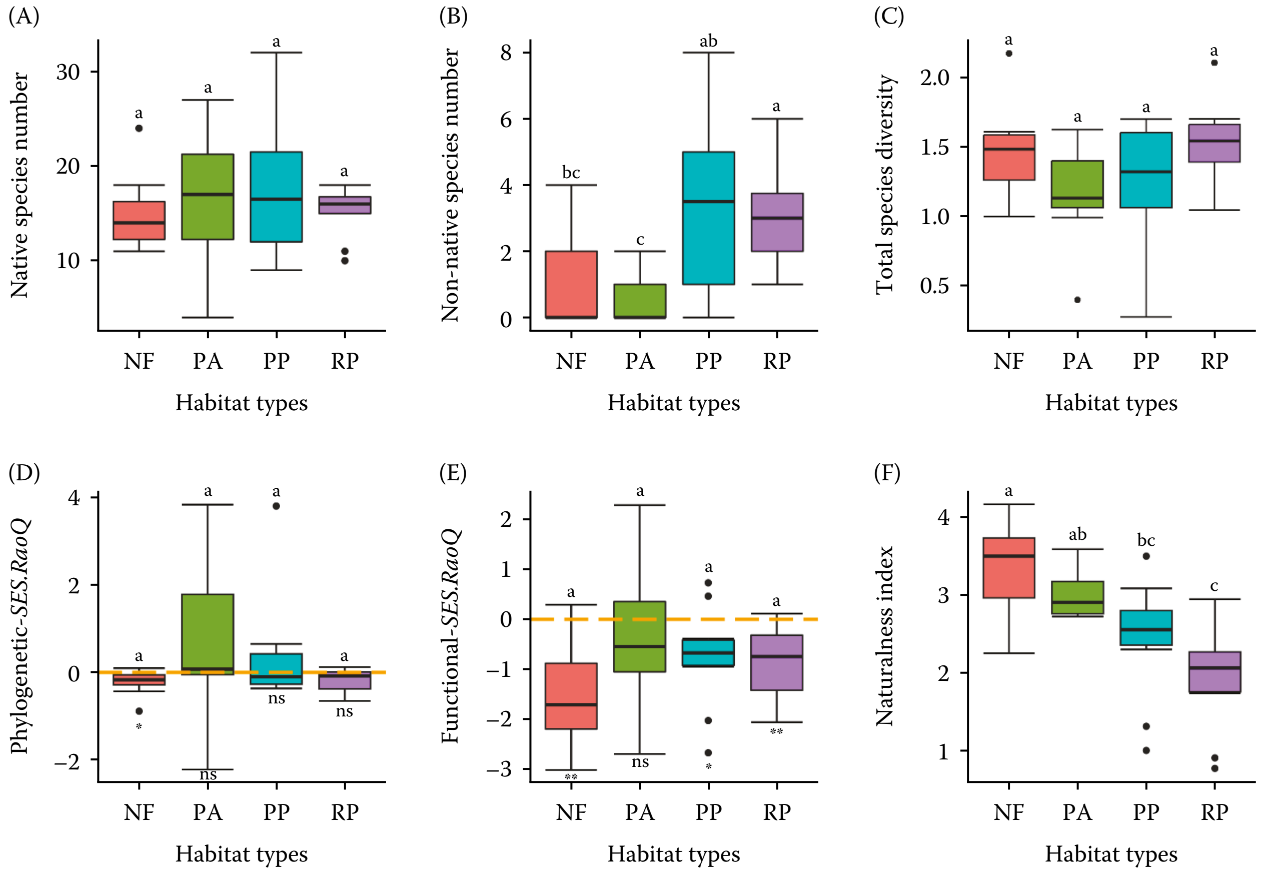

Figure 4. (A) Native species richness, (B) non-native species richness, (C) total species diversity evaluated by the Shannon diversity index, (D) phylogenetic diversity, (E) functional diversity, and (F) the mean naturalness values of the four habitat types

a–c – significant differences ($P < 0.05$); NF – *Quercus-Tilia* forests; PA – *Populus alba* forests; PP – *Pinus sylvestris* plantations; RP – *Robinia pseudoacacia* plantations; *RaoQ* – Rao's quadratic entropy; *SES.RaoQ* – standardised effect size of Rao's quadratic entropy; ns – non-significant differences between observed *SES.RaoQ* values and the null model expectation (two-sided Wilcoxon signed rank test); negative *SES* (standardised effect size) values indicate trait underdispersion, positive values indicate trait overdispersion

DISCUSSION

Abiotic conditions and species composition. Our results indicated that most of the abiotic parameters differed markedly between various habitats, which may partly be explained by the effects dominant tree species exerted on their environment. For example, canopy openness seems to influence both light availability and soil moisture. Particularly, small *Populus alba* forest fragments, with the most open canopy (Table S5 in the ESM), experienced the highest light availability but the lowest soil moisture levels. In contrast, *Quercus-Tilia* forests, with their dense canopy, had low light conditions and high soil moisture levels. *Robinia* plantations, with their nitrogen-fixing ability, showed increased soil nitrogen levels (Slabejová et al. 2019; Nicolescu et al. 2020), which was also confirmed by our results. *Pinus* plantations have a thick litter layer that decomposes slowly and increases soil acidity (Kováč et al. 2005; Lindroos et al. 2011; Mikulová et al. 2019). The phenomenon seems to be true in our study when one outlier value was excluded from the analysis. Although most abiotic variables were largely different between the various habitat types, temperature was similar in the four habitats. One potential explanation is that the ecological indicator values for temperature reflect the latitudinal and altitudinal distribution of the species (Borhidi 1995), which means that these values indicate coarse-scale distribution. Thus, indicator values for temperature are effec-

https://doi.org/10.17221/59/2024-JFS

tive at finer scales only when there is a large difference between the habitats, which was not probably the case in our study. Another possible explanation for the lack of significant differences in temperature values may be that even open-canopied forests are able to maintain the relatively cold temperature, as shown by Ho et al. (2024).

The NMDS results revealed that the species composition showed significant differences between the four habitats, although some overlaps were observed between *Pinus* plantations and the other habitats (Figure 2). The differences in composition may partly be driven by dominant tree species, as they shape abiotic conditions (Figure 3). Apart from the dominant tree species, forestry practices may also lead to compositional distinctness between native forests and tree plantations: mechanical site preparation causes significant soil disturbance and topsoil removal and leads to a scarcity of propagules and a reduced colonisation capacity for forest-related species, while understory plants are removed through weeding operations (Onyekwelu, Olabiwonnu 2016; Rédei et al. 2020). Although plantations are not currently managed actively, the legacy from earlier management may still influence the present species composition. Our results confirmed that tree plantations cannot replace the species composition of native forests, which is in line with other studies in the Pannonian region (Slabejová et al. 2019; Ho et al. 2023a) and Western Europe (Calviño-Cancela et al. 2012). The third possible reason underlying compositional differences is provided by the differences in primary abiotic environmental factors (i.e. not evoked by the vegetation itself). The soil type is the same in all habitat types included in this study, but minor differences in selected soil parameters may be possible. Unfortunately, no measurements were carried out in this respect during our works. Almost all plots were prepared on flat or nearly flat surfaces, but there were slight differences regarding the elevation range of the four habitats (*Quercus-Tilia* forests: 140–170 m; *Populus* forests: 40–90 m; *Pinus* plantations: 70–175 m; *Robinia* plantations: 150–175 m). Although we think these differences could have only a very limited influence on species composition, these effects cannot be ruled out completely and detailed environmental studies should be done in future.

The analyses of diagnostic species indicated that all habitats had their own species that were rare or absent elsewhere (Table 2). Most diagnostic species in the *Quercus-Tilia* forests were forest specialists, while plantations hosted diagnostic species with broader ecological tolerances. This indicates that forestry activities create disturbances that are not suitable for the survival of forest-related species. In addition, low light conditions and high soil moisture of *Quercus-Tilia* forest favoured mesic forest species (e.g. *Clematis vitalba, Corydalis solida*, *Lonicera xylosteum*, and *Viola suavis*). In our study, *Fritillaria montana* was restricted to *Quercus-Tilia* forests and it did not occur in any of the plantations. This species is legally protected and relatively rare in Serbia (Tomović et al. 2007). In addition, the populations of *Fritillaria montana* in the Deliblato Sands have some special morphological characteristics compared to other populations; thus, they may represent a unique genetic value.

Due to high light availability and low soil moisture, *Populus* forests hosted diagnostic species associated with warmer and drier habitats, among them many species that are usually considered grassland specialists (e.g. *Carex liparocarpos*, *Equisetum ramosissimum*, *Festuca rupicola*, *Seseli annuum*, and *Taraxacum erythrospermum*).

Pinus plantations had the lowest number of diagnostic species, most of which were indifferent or weed species. The low number of diagnostic species is in line with the result of the NMDS, which indicated large compositional overlaps with the other habitats (Figure 2). The diagnostic species of *Robinia* plantations were quite variable, with species typical of mesic forests, scrubs, mesic or dry grasslands, and even indifferent species. This may be related to certain biological characteristics of *Robinia pseudoacacia*. For example, the leaf expansion of *Robinia pseudoacacia* typically occurs rather late (from the end of April to early May) (Cierjacks et al. 2013), leading to abiotic conditions (light, temperature, and humidity) that are likely similar to grasslands during the spring months. However, once the canopy becomes fully leafy, the abiotic conditions tend to resemble those of forests. In addition, nutrient-demanding diagnostic species such as *Ailanthus altissima*, *Chelidonium majus*, *Geum urbanum*, and *Glechoma hederacea* were present, which is likely related to the nitrogen-fixing capability of *Robinia pseudoacacia*. This may contribute to the ability of *R. pseudoacacia* to create specific plant communities with distinct species compositions (Chytrý 2013).

Naturalness and diversity patterns. Our findings revealed that *Quercus-Tilia* forests had significantly higher naturalness compared to tree plantations, implying that these forests were the least degraded and disturbed, which indicates a high level of ecological integrity. Tree plantations, especially *Robinia* plantations, on the other hand, showed significant degradation and disturbance, highlighting the severity of management practices in these ecosystems, accompanied by the effects of the planted trees themselves. Similar results were found in a Hungarian sandy region (Ho et al. 2023a). Also, low naturalness was reported from *Pinus nigra* plantations compared to neighbouring dry oak forests in southern Hungary and from hybrid *Poplar* plantations compared to adjacent native poplar forests in southwestern Slovakia (Erdős et al. 2017).

The richness of non-native species was high in the two non-native tree plantation types, indicating that non-native tree plantations are ecologically dangerous because they support the spread of non-natives. Csecserits et al. (2016) showed that plantations of both native and non-native trees can become invasion hotspots. Our results complement these findings and emphasise that plantations of non-native tree species may be particularly dangerous from this aspect. Similarly, previous studies in a Hungarian sandy region found that non-native tree plantations had a higher number of non-native species than near-natural forests (Rédei et al. 2020; Ho et al. 2023a). Another study, conducted on a wider scale spanning five nations (Czech Republic, Slovakia, Hungary, Romania, and Ukraine), revealed that *Robinia* plantations exhibited a higher alien species richness than three types of natural forests (floodplain forests, oak forests, and oak-hornbeam forests) (Slabejová et al. 2019). One of the most important findings in our study was that the two near-natural forest types had fewer non-native species than *Pinus* plantations and *Robinia* plantations. This reinforces the conservation perspective of Bremer and Farley (2010) suggesting that forests are more valuable than tree plantations. Several other studies in the Pannonian region also show that near-natural forests have a higher ecological value than plantations, including a higher number of forest specialist plants (Rédei et al. 2020) and a higher diversity of bird species in comparison with both native and non-native tree plantations (Ónodi et al. 2022).

The overwhelming majority of earlier research shows that plantations are typically species-poor compared to forests (Brockerhoff et al. 2008; Sobuj, Rahman 2011; Calviño-Cancela et al. 2012; Rédei et al. 2020; Ho et al. 2023a). Our study, however, contradicted the preceding findings: the number of native species did not differ significantly between near-natural forests and the plantation types. This can be explained in relation to anthropogenic disturbance and the light regime. Forest specialist species are often sensitive to habitat management practices (Brunet et al. 2011; Rédei et al. 2020). Therefore, *Quercus-Tilia* forests without anthropogenic disturbance had favourable conditions for the existence and development of forest specialists. However, these forest stands had low light intensity due to the closed canopy, leading to intense competition between plant species for light. This competition results in the dominance of shade-tolerant species, potentially suppressing light-dependent species. Plantations, on the other hand, were disturbed habitats due to human activity; thus, disturbance-tolerant generalists, weeds, or dry grassland species can colonise and replace forest specialists in plantations (Fried et al. 2010; Rédei et al. 2020). This may lead to a balance of the number of native species in tree plantations and *Quercus-Tilia* forests.

Total species diversity using the Shannon diversity index followed the same pattern as native species richness: no substantial differences between habitats were found. This was contrary to many studies that found lower richness and Shannon diversity in plantations compared to natural/near-natural forest stands (Sobuj, Rahman 2011; Calviño-Cancela et al. 2012; Onyekwelu, Olabiwonnu 2016). However, some other research had outcomes comparable with our results. For instance, Shannon diversity was found to be similar between forests and plantations in southeastern Kyushu, Japan (Ito et al. 2004). Also, *Pinus nigra* plantations and *Populus alba* plantations had similar Shannon diversity compared to near-natural poplar forests in Hungary (Ho et al. 2023a).

Functional and phylogenetic diversity showed no significant differences between the studied habitats (Figure 4). A potential explanation could be linked to canopy openness (= light availability) and naturalness. Our findings indicated that plantations had low naturalness, suggesting a high level of human-induced disturbance. Several previous studies have indicated that disturbances associated with human activities may result in a stronger environmental filter, which tends to shape community assemblages composed of closely related species with a high degree of trait similarity (Helmus et al. 2010; Katovai et al. 2012; Arnan et al. 2018). Consequently, such disturbances contribute to lower levels of phylogenetic and functional diversity in plantations. On the other hand, the studied plantations had relatively open canopies (compared to the near-natural *Quercus-Tilia* forests), which can lead to high functional and phylogenetic diversity (Ho et al. 2023b). In contrast, the studied near-natural *Quercus-Tilia* forests had closed canopies and high naturalness, which eventually resulted in functional and phylogenetic diversity comparable with those of the plantations. Some previous studies also reported that there were no significant differences in functional and phylogenetic diversity between monoculture tree plantations and near-natural forests. For instance, functional and phylogenetic diversity of *Pinus nigra* plantations were similar to those of near-natural poplar forests in Hungary (Ho et al. 2023a). Piwczyński et al. (2016) found similar phylogenetic diversity between *Pinus sylvestris* plantations and natural oak forests in Poland, while Malysz et al. (2019) demonstrated similar functional diversity between native *Araucaria* forests and *Araucaria* and *Pinus* plantations in Brazil.

Functional diversity was high in *Populus alba* forests, although not significantly higher than in the other habitats. This can be explained by the combined effects of light availability and naturalness. *Populus* forests had the highest light availability while naturalness was also relatively high in this type, possibly resulting in high functional diversity. Similarly, phylogenetic diversity seemed to be somewhat high in *Populus alba* forests. The peak, however, vanished when only angiosperm species were included in the analysis of phylogenetic diversity (Figure S3 in the ESM). This outcome was likely attributable to *Juniperus communis*, a common gymnosperm species in *Populus alba* forests.

CONCLUSION

To sum up, dominant tree species seemed to strongly influence various abiotic parameters. Many diversity indices were probably driven by two primary factors: light availability and naturalness. High light availability compensates for low naturalness, resulting in similar native species richness, total species diversity (i.e. Shannon), functional and phylogenetic diversity between *Quercus-Tilia* forests, *Populus alba* forests, *Pinus sylvestris* plantations, and *Robinia pseudoacacia* plantations. However, similar diversity does not necessarily entail a similar ecological value. *Quercus-Tilia* forests possess a unique species composition that plantations cannot replace (e.g. many species of mesic forests, including *Fritillaria montana*, are not found in plantations). In addition, *Quercus-Tilia* forests had low non-native species richness, while non-native plantations hosted significantly more non-natives in their understories, including, among others, the dangerous invasive *Ailanthus altissima*.

The area of *Quercus-Tilia* forest patches and *Populus alba* forest fragments in the Deblilato region is relatively small (ca. 380 ha and 170 ha, respectively), and the former type is restricted to the central part, while the latter type to the southeastern part of the Reserve (Ćuk et al. 2023). From an ecological and conservation point of view, we recommend that the remnants of these near-natural forests should be protected and efforts to restore these forests should be given high priority.

According to Ćuk et al. (2023), nearly 16 812 ha of the Deliblato Sands is covered by tree plantations. Of them, 64% (10 821 ha) are *Robinia* plantations, approximately 27% (4 601 ha) are *Pinus* plantations, while less than 1% are *Populus* plantations (59.26 ha), *Tilia* plantations (37.45 ha), and *Quercus* plantations (0.68 ha). In light of our results, non-native tree plantations have some unfavourable ecological features. Hence, a shift in forestry strategy from non-native to native tree species stands out as a desirable alternative to existing practices and can be expected to improve the preservation of the natural ecosystems of the region. With a negligible area ratio in the region, native tree plantations (e.g. *Tilia tomentosa*) should be expanded to replace non-native tree plantations, which are expected to increase habitat heterogeneity and support higher biodiversity. We found that high light conditions can enhance diversity patterns for plantations; thus, opting for selective thinning instead of clearing up could prove advantageous in tree plantations, maintaining a continuous forest with a sparse canopy.

Acknowledgement: The authors are thankful to Dolly Tolnay for her help with the trait databases.

REFERENCES

Albert G., Gallegos S.C., Greig K.A., Hanisch M., de la Fuente D.L., Föst S., Maier S.D., Sarathchandra C., Phillips H.R.P., Kambach S. (2021): The conservation value of forests and tree plantations for beetle (Coleoptera) communities: A global meta-analysis. Forest Ecology and Management, 491: 119201.

Arnan X., Arcoverde G.B., Pie M.R., Ribeiro-Neto J.D., Leal I.R. (2018): Increased anthropogenic disturbance and aridity reduce phylogenetic and functional diversity of ant communities in Caatinga dry forest. Science of the Total Environment, 631–632: 429–438.

Beason R.D., Riesch R., Koricheva J. (2020): Tidying up the cluttered understorey: Foraging strategy mediates bat activity responses to invasive rhododendron. Forest Ecology and Management, 475: 118392.

Bernard-Verdier M., Navas M.L., Vellend M., Violle C., Fayolle A., Garnier E. (2012): Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. Journal of Ecology, 100: 1422–1433.

Borhidi A. (1995): Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian Flora. Acta Botanica Hungarica, 39: 97–181.

Botta-Dukát Z. (2005): Rao's quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science, 16: 533–540.

Bremer L.L., Farley K.A. (2010): Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. Biodiversity and Conservation, 19: 3893–3915.

Brockerhoff E.G., Jactel H., Parrotta J.A., Quine C.P., Sayer J. (2008): Plantation forests and biodiversity: Oxymoron or opportunity? Biodiversity and Conservation, 17: 925–951.

Brunet J., Valtinat K., Mayr M.L., Felton A., Lindbladh M., Bruun H.H. (2011): Understory succession in post-agricultural oak forests: Habitat fragmentation affects forest specialists and generalists differently. Forest Ecology and Management, 262: 1863–1871.

Butorac B., Panjković B. (2013): Edicija Vegetacija Vojvodine, Knjiga 1: Peščarska vegetacija u Vojvodini. Novi Sad, Pokrajinski zavod za zaštitu prirode: 159. (in Serbian)

Cadotte M.W., Cavender-Bares J., Tilman D., Oakley T.H. (2009): Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. PloS One, 4: e5695.

Cadotte M.W., Carscadden K., Mirotchnick N. (2011): Beyond species: Functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology, 48: 1079–1087.

Calviño-Cancela M., Rubido-Bará M., van Etten E.J.B. (2012): Do eucalypt plantations provide habitat for native forest biodiversity? Forest Ecology and Management, 270: 153–162.

Chapman C.A., Chapman L.J. (1999): Forest restoration in abandoned agricultural land: A case study from East Africa. Conservation Biology, 13: 1301–1311.

Chytrý M. (2013): Vegetation of the Czech Republic 4. Forest and Scrub Vegetation. Prague, Academia: 551. (in Czech)

Chytrý M., Tichý L., Holt J., Botta-Dukát Z. (2002): Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science, 13: 79–90.

Cierjacks A., Kowarik I., Joshi J., Hempel S., Ristow M., von der Lippe M., Weber E. (2013): Biological flora of the British Isles: *Robinia pseudoacacia*. Journal of Ecology, 101: 1623–1640.

Csecserits A., Botta-Dukát Z., Kröel-Dulay G., Lhotsky B., Ónodi G., Rédei T., Szitár K., Halassy M. (2016): Tree plantations are hot-spots of plant invasion in a landscape with heterogeneous land-use. Agriculture, Ecosystems & Environment, 226: 88–98.

Ćuk M. (2019): Status i vremenska dinamika flore i vegetacije Deliblatske peščare. [Ph.D. Thesis.] Novi Sad, University of Novi Sad. (in Serbian)

Ćuk M., Ponjarac R., Igić D., Ilić M., Oldja M., Vukov D., Čarni A. (2023): Historical overview of the Deliblato Sands afforestation. Šumarski list, 147: 383–392.

de Bello F., Botta-Dukát Z., Lepš J., Fibich P. (2021a): Towards a more balanced combination of multiple traits when computing functional differences between species. Methods in Ecology and Evolution, 12: 443–448.

de Bello F., Carmona C.P., Dias A.T.C., Götzenberger L., Moretti M., Berg M.P. (2021b): Handbook of Trait-Based Ecology: From Theory to R Tools. Cambridge, Cambridge University Press: 295.

Debastiani V.J., Pillar V.D. (2012): SYNCSA – R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. Bioinformatics, 28: 2067–2068.

Diekmann M. (2003): Species indicator values as an important tool in applied plant ecology – A review. Basic and Applied Ecology, 4: 493–506.

Doxa A., Devictor V., Baumel A., Pavon D., Médail F., Leriche A. (2020): Beyond taxonomic diversity: Revealing spatial mismatches in phylogenetic and functional diversity facets in Mediterranean tree communities in southern France. Forest Ecology and Management, 474: 118318.

Dzwonko Z. (2001): Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. Journal of Applied Ecology, 38: 942–951.

Erdős L., Bátori Z., Penksza K., Dénes A., Kevey B., Kevey D., Magnes M., Sengl P., Tölgyesi C. (2017): Can naturalness indicator values reveal habitat degradation? A test of four methodological approaches. Polish Journal of Ecology, 65: 1–13.

Erdős L., Kröel-Dulay G., Bátori Z., Kovács B., Németh C., Kiss P.J., Tölgyesi C. (2018): Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics. Biological Conservation, 226: 72–80.

Erdős L., Bede-Fazekas Á., Bátori Z., Berg C., Kröel-Dulay G., Magnes M., Sengl P., Tölgyesi C., Török P., Zinnen J. (2022): Species-based indicators to assess habitat degradation: Comparing the conceptual, methodological, and ecological relationships between hemeroby and naturalness values. Ecological Indicators, 136: 108707.

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

Fanelli G., Pignatti S., Testi A. (2007): An application case of ecological indicator values (Zeigerwerte) calculated with a simple algorithmic approach. Plant Biosystems – An International Journal Dealing with All Aspects of Plant Biology, 141: 15–21.

FAO (2022): The State of the World's Forests 2022. Forest Pathways for Green Recovery and Building Inclusive, Resilient and Sustainable Economies. Rome, Food and Agriculture Organization of the United Nations: 141.

Flynn D.F.B., Mirotchnick N., Jain M., Palmer M.I., Naeem S. (2011): Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. Ecology, 92: 1573–1581.

Forest Europe (2020): State of Europe's Forests 2020. Bratislava, Ministerial Conference on the Protection of Forests in Europe – Forest Europe: 392.

Fried G., Petit S., Reboud X. (2010): A specialist-generalist classification of the arable flora and its response to changes in agricultural practices. BMC Ecology, 10: 20.

Gilliam F.S. (2007): The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience, 57: 845–858.

Helmus M.R., Keller W.B., Paterson M.J., Yan N.D., Cannon C.H., Rusak J.A. (2010): Communities contain closely related species during ecosystem disturbance. Ecology Letters, 13: 162–174.

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

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

Ho K.V., Süle G., Kovács B., Erdős L. (2024): Strong differences in microclimate among the habitats of a forest-steppe ecosystem. Időjárás, 128: 1–26.

Horák J., Brestovanská T., Mladenović S., Kout J., Bogusch P., Halda J.P., Zasadil P. (2019): Green desert?: Biodiversity patterns in forest plantations. Forest Ecology and Management, 433: 343–348.

Hynes E.F., Whisson D.A., Di Stefano J. (2021): Response of an arboreal species to plantation harvest. Forest Ecology and Management, 490: 119092.

Ito S., Nakayama R., Buckley G.P. (2004): Effects of previous land-use on plant species diversity in semi-natural and plantation forests in a warm-temperate region in southeastern Kyushu, Japan. Forest Ecology and Management, 196: 213–225.

Jacoboski L.I., Debastiani V.J., de Mendonça-Lima A., Hartz S.M. (2016): How do diversity and functional nestedness of bird communities respond to changes in the landscape caused by eucalyptus plantations? Community Ecology, 17: 107–113.

Jin Y., Qian H. (2022): V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. Plant Diversity, 44: 335–339.

Jucker T., Carboni M., Acosta A.T.R. (2013): Going beyond taxonomic diversity: Deconstructing biodiversity patterns reveals the true cost of iceplant invasion. Diversity and Distributions, 19: 1566–1577.

Junggebauer A., Hartke T.R., Ramos D., Schaefer I., Buchori D., Hidayat P., Scheu S., Drescher J. (2021): Changes in diversity and community assembly of jumping spiders (Araneae: Salticidae) after rainforest conversion to rubber and oil palm plantations. PeerJ, 9: e11012.

Kadović R., Bohajar Y.A.M., Perović V., Belanović Simić S., Todosijević M., Tošić S., Anđelić M., Mlađan D., Dovezenski U. (2016): Land sensitivity analysis of degradation using MEDALUS model: Case study of Deliblato Sands, Serbia. Archives of Environmental Protection, 42: 114–124.

Kanninen M. (2010): Plantation forests: Global perspectives. In: Bauhus J., van der Meer P., Kanninen M. (eds): Ecosystem Goods and Services from Plantation Forests. London, Earthscan: 1–15.

Katovai E., Burley A.L., Mayfield M.M. (2012): Understory plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island, Solomon Islands. Biological Conservation, 145: 214–224.

Kembel S.W., Cowan P.D., Helmus M.R., Cornwell W.K., Morlon H., Ackerly D.D., Blomberg S.P., Webb C.O. (2010):

Picante: R tools for integrating phylogenies and ecology. Bioinformatics, 26: 1463–1464.

Kováč Ľ., Kostúrová N., Miklisová D. (2005): Comparison of collembolan assemblages (Hexapoda, Collembola) of thermophilous oak woods and *Pinus nigra* plantations in the Slovak Karst (Slovakia). Pedobiologia, 49: 29–40.

Landuyt D., De Lombaerde E., Perring M.P., Hertzog L.R., Ampoorter E., Maes S.L., De Frenne P., Ma S., Proesmans W., Blondeel H., Sercu B.K., Wang B., Wasof S., Verheyen K. (2019): The functional role of temperate forest understorey vegetation in a changing world. Global Change Biology, 25: 3625–3641.

Lindroos A.J., Derome J., Derome K., Smolander A. (2011): The effect of Scots pine, Norway spruce and silver birch on the chemical composition of stand throughfall and upper soil percolation water in northern Finland. Boreal Environment Research, 16: 240–250.

Malysz M., Milesi S.V., Dos Santos A.S., Overbeck G.E. (2019): Functional patterns of tree communities in natural *Araucaria* forests and old monoculture conifer plantations. Acta Botanica Brasilica, 33: 777–785.

Mikulová K., Jarolímek I., Bacigál T., Hegedüšová K., Májeková J., Medvecká J., Slabejová D., Šibík J., Škodová I., Zaliberová M., Šibíková M. (2019): The effect of non-native black pine (*Pinus nigra* J. F. Arnold) plantations on environmental conditions and undergrowth diversity. Forests, 10: 548.

Molnár Z., Biró M., Bartha S., Fekete G. (2012): Past trends, present state and future prospects of Hungarian forest-steppes. In: Werger M.J.A., van Staalduinen M.A. (eds): Eurasian Steppes: Ecological Problems and Livelihoods in a Changing World. Dordrecht, Springer: 209–252.

Nicolescu V.N., Rédei K., Mason W.L., Vor T., Pöetzelsberger E., Bastien J.C., Brus R., Benčať T., Đodan M., Cvjetkovic B., Andrašev S., La Porta N., Lavnyy V., Mandžukovski D., Petkova K., Roženbergar D., Wąsik R., Mohren G.M.J., Monteverdi M.C. et al. (2020): Ecology, growth and management of black locust (*Robinia pseudoacacia* L.), a non-native species integrated into European forests. Journal of Forestry Research, 31: 1081–1101.

Nooten S.S., Lee R.H., Guénard B. (2021): Evaluating the conservation value of sacred forests for ant taxonomic, functional and phylogenetic diversity in highly degraded landscapes. Biological Conservation, 261: 109286.

Oksanen J., Simpson G.L., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Solymos P., Stevens M.H.H., Szoecs E. et al. (2022): vegan: Community Ecology Package. R package version 2.6-2. Available at: https://CRAN.R-project.org/package=vegan

Ónodi G., Botta-Dukát Z., Winkler D., Rédei T. (2022): Endangered lowland oak forest steppe remnants keep unique bird species richness in Central Hungary. Journal of Forestry Research, 33: 343–355.

Onyekwelu J.C., Olabiwonnu A.A. (2016): Can forest plantations harbour biodiversity similar to natural forest ecosystems over time? International Journal of Biodiversity Science, Ecosystem Services & Management, 12: 108–115.

Parabućski S. (1980): Potencijalna vegetacija Deliblatakog peska. In: Marinković P. (ed.): Deliblatski pesak. Novi Sad, Specijalni prirodni rezervat Deliblatski pesak Šumsko industrijski kombinat Pančevo: 312–314. (in Serbian)

Pawson S.M., Brin A., Brockerhoff E.G., Lamb D., Payn T.W., Paquette A., Parrotta J.A. (2013): Plantation forests, climate change and biodiversity. Biodiversity and Conservation, 22: 1203–1227.

Persson S. (1981): Ecological indicator values as an aid in the interpretation of ordination diagrams. Journal of Ecology, 69: 71–84.

Piwczyński M., Puchałka R., Ulrich W. (2016): Influence of tree plantations on the phylogenetic structure of understorey plant communities. Forest Ecology and Management, 376: 231–237.

R Core Team (2023): R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. Available at: https://cran.r-project.org/bin/windows/base/

Rédei T., Csecserits A., Lhotsky B., Barabás S., Kröel-Dulay G., Ónodi G., Botta-Dukát Z. (2020): Plantation forests cannot support the richness of forest specialist plants in the forest-steppe zone. Forest Ecology and Management, 461: 117964.

Ricotta C. (2005): A note on functional diversity measures. Basic and Applied Ecology, 6: 479–486.

Santos F.M., Chaer G.M., Diniz A.R., de Carvalho Balieiro F. (2017): Nutrient cycling over five years of mixed-species plantations of *Eucalyptus* and *Acacia* on a sandy tropical soil. Forest Ecology and Management, 384: 110–121.

Scherer-Lorenzen M. (2008): Functional diversity affects decomposition processes in experimental grasslands. Functional Ecology, 22: 547–555.

Scherrer D., Guisan A. (2019): Ecological indicator values reveal missing predictors of species distributions. Scientific Reports, 9: 3061.

Selvi F., Carrari E., Coppi A. (2016): Impact of pine invasion on the taxonomic and phylogenetic diversity of a relict Mediterranean forest ecosystem. Forest Ecology and Management, 367: 1–11.

Šibíková M., Jarolímek I., Hegedüšová K., Májeková J., Mikulová K., Slabejová D., Škodová I., Zaliberová M., Medvecká J. (2019): Effect of planting alien *Robinia pseudoacacia* trees on homogenization of Central European forest vegetation. Science of the Total Environment, 687: 1164–1175.

Sipos G., Marković S.B., Gavrilov M.B., Balla A., Filyó D., Bartyik T., Mészáros M., Tóth O., van Leeuwen B., Lukić T., Urdea P., Onaca A., Mezősi G., Kiss T. (2022): Late Pleistocene and Holocene aeolian activity in the Deliblato Sands, Serbia. Quaternary Research, 107: 113–124.

Slabejová D., Bacigál T., Hegedüšová K., Májeková J., Medvecká J., Mikulová K., Šibíková M., Škodová I., Zaliberová M., Jarolímek I. (2019): Comparison of the understory vegetation of native forests and adjacent *Robinia pseudoacacia* plantations in the Carpathian-Pannonian region. Forest Ecology and Management, 439: 28–40.

Sobuj N.A., Rahman M. (2011): Comparison of plant diversity of natural forest and plantations of Rema-Kalenga Wildlife Sanctuary of Bangladesh. Journal of Forest and Environmental Science, 27: 127–134.

Stephens S.S., Wagner M.R. (2007): Forest plantations and biodiversity: A fresh perspective. Journal of Forestry, 105: 307–313.

Swenson N.G. (2014): Functional and Phylogenetic Ecology in R. New York, Springer: 212.

Szymura T.H., Szymura M., Macioł A. (2014): Bioindication with Ellenberg's indicator values: A comparison with measured parameters in Central European oak forests. Ecological Indicators, 46: 495–503.

Ter Braak C.J.F., Gremmen N.J.M. (1987): Ecological amplitudes of plant species and the internal consistency of Ellenberg's indicator values for moisture. Vegetatio, 69: 79–87.

The Plant List (2013): The Plant List. Version 1.1. Available at: http://www.theplantlist.org

Tölgyesi C., Török P., Hábenczyus A.A., Bátori Z., Valkó O., Deák B., Tóthmérész B., Erdős L., Kelemen A. (2020): Underground deserts below fertility islands? Woody species desiccate lower soil layers in sandy drylands. Ecography, 43: 848–859.

Tölgyesi C., Buisson E., Helm A., Temperton V.M., Török P. (2022): Urgent need for updating the slogan of global climate actions from 'tree planting' to 'restore native vegetation.'. Restoration Ecology, 30: e13594.

Tomaz C., Alegria C., Monteiro J.M., Teixeira M.C. (2013): Land cover change and afforestation of marginal and abandoned agricultural land: A 10year analysis in a Mediterranean region. Forest Ecology and Management, 308: 40–49.

Tomović G., Vukojičić S., Niketić M., Zlatković B., Stevanović V. (2007): *Fritillaria* (*Liliaceae*) in Serbia: Distribution, habitats and some taxonomic notes. Phytologia Balcanica, 13: 359–370.

Trachsel J. (2022): funfuns: Functions I Use (Title Case). R package version 0.1.2. Available at: https://github.com/Jtrachsel/funfuns/

Tüxen R., Ellenberg H. (1937): Der systematische und der ökologische Gruppenwert: Ein Beitrag zur Begriffsbildung und Methodik der Pflanzensoziologie. Jahresbericht der Naturhistorischen Gesellschaft zu Hannover, 81–87: 171–184. Available at: https://www.zobodat.at/pdf/Jber-Naturhist-Ges-Hannover_81-87_0171-0184.pdf (in German).

Weiher E., van der Werf A., Thompson K., Roderick M., Garnier E., Eriksson O. (1999): Challenging Theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science, 10: 609–620.

Westoby M. (1998): A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil, 199: 213–227.

Xi B., Clothier B., Coleman M., Duan J., Hu W., Li D., Di N., Liu Y., Fu J., Li J., Jia L., Fernández J.E. (2021): Irrigation management in poplar (*Populus* spp.) plantations: A review. Forest Ecology and Management, 494: 119330.

Received: August 18, 2024
Accepted: November 19, 2024