



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

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ABSTRACT

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

1. Introduction

Tree plantations are often viewed as a solution to the increasing

demand for timber and fuelwood and as an opportunity to counteract anthropogenic carbon emission (Cubbage et al., 2010; Paquette and Messier, 2010; Bastin et al., 2019; Tölgyesi et al., 2022). These

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

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

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

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

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

listed species and naturalness status?

2. Materials and methods

2.1. Study area

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

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

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

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

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

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

2.2. Field sampling

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

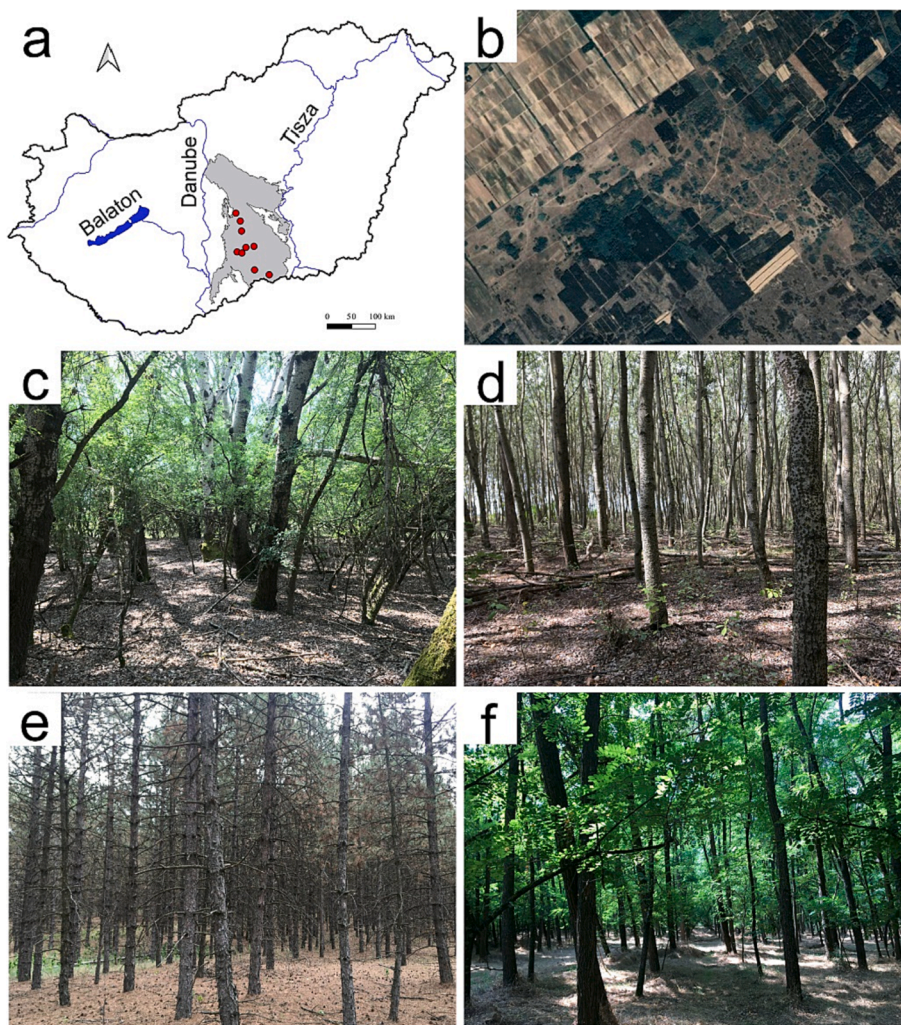


Fig. 1. (A) The nine study sites (indicated by red dots) in the Kiskunság Sand Ridge (gray area), Hungary; (B) satellite photo of a typical landscape in the Kiskunság, with protected near-natural poplar forest patches (in the center and towards the south), surrounded by tree plantations and agricultural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

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

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

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

association names are used according to Borhidi et al. (2012).

2.3. Data analyses

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

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

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

To quantify functional diversity (FD), we chose Rao's quadratic

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

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

distance (Kembel et al., 2010).

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

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

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

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

3. Results

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

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

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

Habitat type significantly influenced the number of native species

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

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

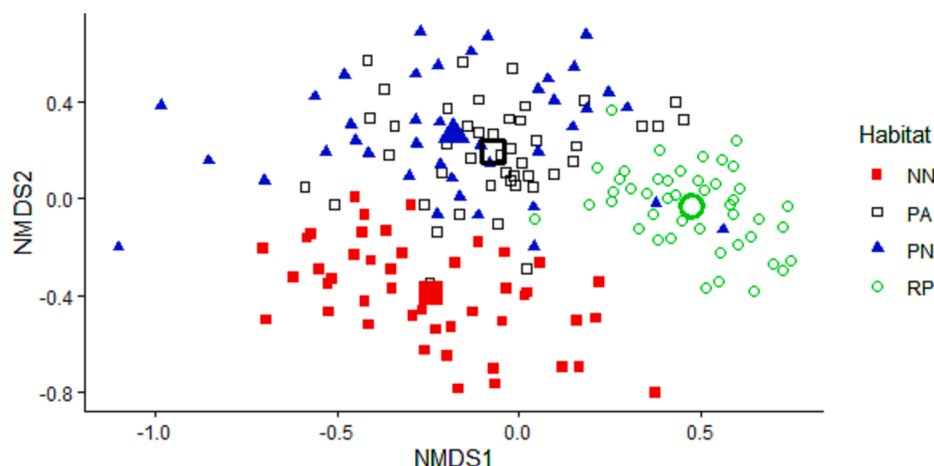


Fig. 2. NMDS ordination scattergram of 175 plots. NN: near-natural poplar forests; PA: plantations of native *Populus alba*; PN: plantations of non-native *Pinus nigra*; RP: plantations of non-native *Robinia pseudoacacia*. Large signs show the centroids for each habitat. Stress = 0.25.

Table 2

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

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

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

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

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

4. Discussion

4.1. Species composition

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

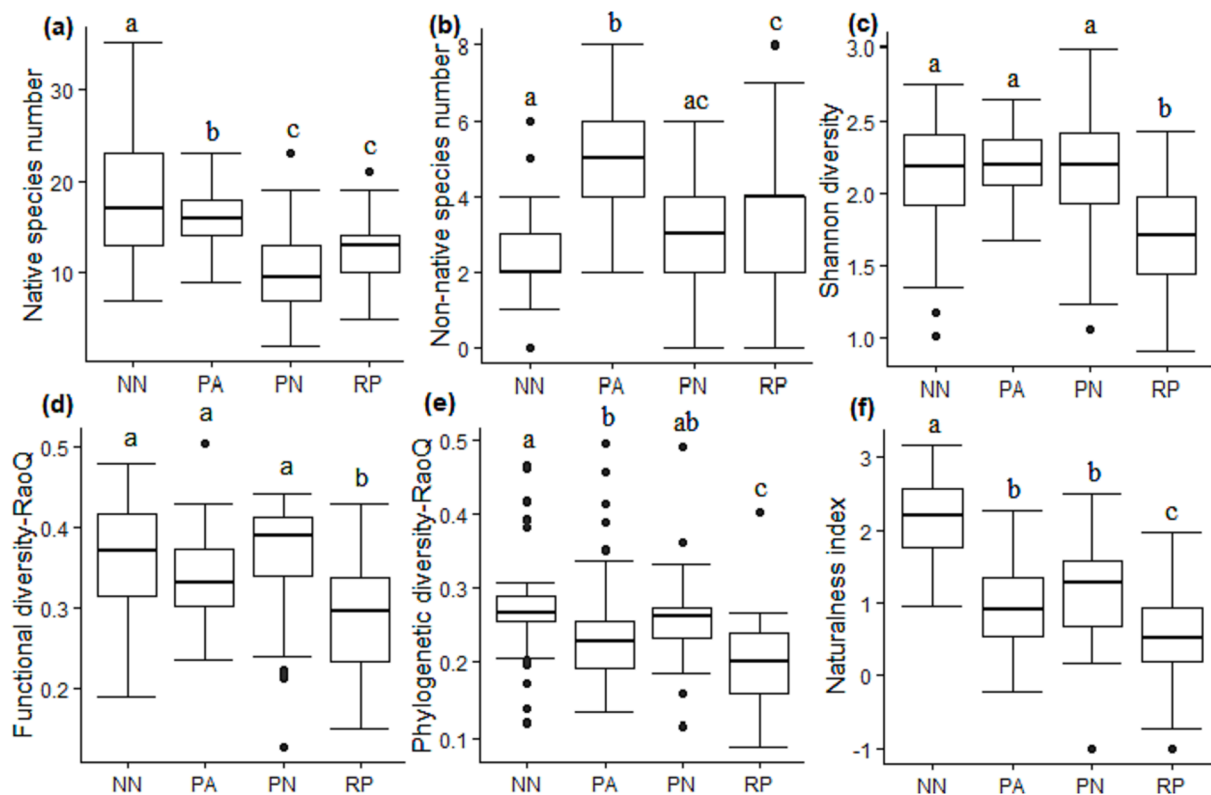


Fig. 3. The number of native species (A), the number of non-native species (B), Shannon diversity (C), functional diversity (D), phylogenetic diversity (E), and the mean naturalness values (F) of the four habitat types. Different letters indicate significant differences ($p < 0.05$). NN: near-natural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

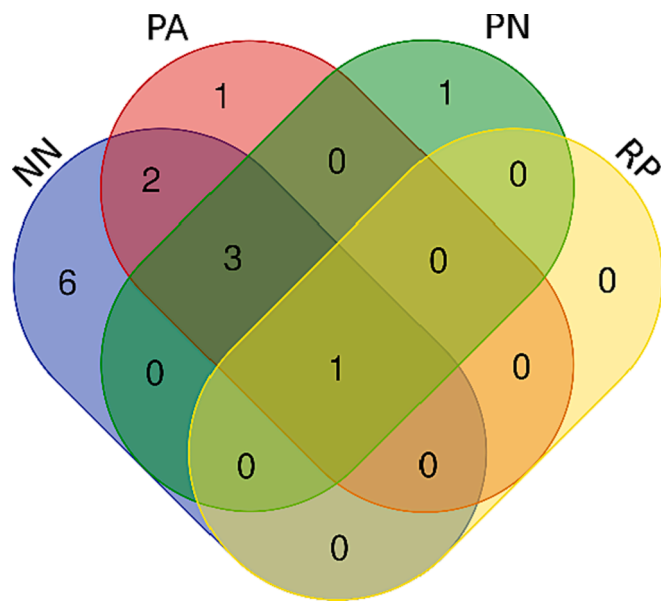


Fig. 4. Venn diagram of species with high conservation importance (protected, endemic, and/or red-listed species) according to their habitat. NN: near-natural poplar forests. PA: plantations of native *Populus alba*; PN: plantations of non-native *Pinus nigra*; RP: plantations of non-native *Robinia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

compositional differences between the near-natural forests (without forestry activity) and the tree plantations (Rédei et al., 2020; Tölgyesi et al., 2020). Second, the different dominant species alter their

environment differently, which may result in compositional differences. For example, *Pinus* plantations tend to have a deep layer of slowly decaying leaf litter, and lower soil pH than near-natural forests or deciduous plantations (Kováč et al., 2005; Kárik and Makineci, 2013; Mikulová et al., 2019), while *Robinia* plantations significantly increase the N-content of the soil (Šibíková et al., 2019; Tölgyesi et al., 2020).

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

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

Although the number of real forest specialist plant species is relatively low almost everywhere in the Kiskunság Sand Ridge (e.g., Erdős et al., 2013), the diagnostic species of the near-natural poplar forests

nevertheless tend to show a higher level of specialization than the three plantation types. For example, *Polygonatum odoratum* and *Thymus pannonicus* are to some degree specialized to xeric forests and dry grasslands, respectively. In contrast, the diagnostic species of the plantations have much wider ecological tolerances.

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

4.2. Diversity patterns

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

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

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

Anthriscus cerefolium) to become dominant.

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

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

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

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

4.3. Ecological value of the studied habitats

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

Our study found that near-natural forests harbored more protected, endemic, and red-listed species than plantations (Fig. 4). This is in good accordance with earlier observations ([Cotter et al., 2017](#); [Šibíková et al., 2019](#); [Singh et al., 2021](#)). An important finding is that plantations of the native *Populus alba* had a better capacity to support protected, endemic, and red-listed species than plantations of non-native species. *Robinia* plantations proved to be especially poor in species of high conservation

value. This is in line with the results of Deák et al. (2016), who found that most specialist species of high conservation importance could not survive under *Robinia* plantations. The probable reason is that the increased N-availability of the soils of *Robinia* plantations favors weedy species of high competitive ability, while it tends to negatively affect more valuable specialist species (Deák et al., 2016).

4.4. Implications for conservation and forestry

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

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

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

Some other studies performed in the region also found that

Table 3

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

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

⁽¹⁾ Mixed oak-poplar forests.

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

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

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

CRediT authorship contribution statement

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

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

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

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