



Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics

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ABSTRACT

Forest-grassland mosaics are widespread features at the interface between tree- and grass-dominated ecosystems. However, the importance of habitat heterogeneity in these mosaics is not fully appreciated, and the contribution of individual woody and herbaceous habitats to the overall conservation value of the mosaic is unclear. We distinguished six main habitats in the forest-grassland mosaics of the Kiskunság Sand Ridge (Hungary) and compared the species composition, species richness, Shannon diversity, naturalness, selected structural features, environmental variables, and the number of protected, endemic, red-listed and specialist species of the plant communities. Each habitat had species that were absent or rare elsewhere. Grasslands had the highest conservation importance in most respects. North-facing forest edges had the highest species richness, while south-facing edges were primarily important for tree recruitment. Among the forest habitats, small forest patches were the most valuable, while large and medium forest patches had the lowest conservation importance. We showed that the current single-habitat focus of both research and conservation in the studied forest-grassland mosaics is not justified. Instead, an integrated view of the entire mosaic is necessary. Management practices and restoration projects should promote habitat heterogeneity, e.g., by assisting tree and shrub establishment and survival in grasslands. The legislative background should recognize the existence of fine-scale forest-grassland mosaics, which are neither grasslands nor forests, but a mixture.

1. Introduction

The intensification of land-use practices and the resulting habitat homogenization pose major challenges for current conservation (Ernst et al., 2017; Foley et al., 2005; Rembold et al., 2017; Stoate et al., 2001). Likewise, land abandonment often leads to homogenization (Bergmeier et al., 2010; Plieninger et al., 2015; Ernst et al., 2017). Generally, heterogeneous areas are expected to contain more niches and, consequently, more species than homogeneous areas (Bazzaz, 1975; Chesson, 2000; Tilman, 1982). In fact, spatial heterogeneity seems necessary for the maintenance of biodiversity, ecosystem services, and endangered species (Armengot et al., 2012; Dorresteyn et al., 2015; Valkó et al., 2012). Thus, from a conservation perspective, the presence of various habitat patches in close proximity is considered beneficial (Jakobsson and Lindborg, 2015; Tölgyesi et al., 2017).

Habitat heterogeneity and its conservation implications are relatively well studied in agricultural and agroforestry landscapes (e.g., Bennett et al., 2006; Benton et al., 2003; Jakobsson and Lindborg, 2015;

Lee and Martin, 2017; Manning et al., 2006; Moreno et al., 2017; Plieninger et al., 2015; Stoate et al., 2001; Tscharrntke et al., 2005). Unfortunately, the importance of habitat heterogeneity for conservation has received less attention in natural mosaics at the interfaces of tree- and grass-dominated biomes (cf. Tews et al., 2004).

Forest-grassland mosaics typically consist of numerous types of forest and grassland patches of various sizes, as well as intervening edge communities, with strongly different physiognomies and environmental conditions (Breshears, 2006; Schultz, 2005). In such mosaics, appropriate conservation actions and adequate management strategies require an integrated view of the complex ecosystem (Luza et al., 2014).

Forest-grassland mosaics represent high conservation significance (Erdős et al., 2018; Prevedello et al., 2018). However, in Eastern Europe, most of these mosaics have been transformed to croplands or non-native tree plantations, while the remaining fragments are threatened by different forms of homogenization (Wesche et al., 2016). In some regions, the spontaneous or human-induced spread of woody species may result in the disappearance of grassland habitats. At the

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same time, woody habitats are diminishing in other regions due to the combined effects of climate change, sinking groundwater level, and fire (Molnár, 1998; Wesche et al., 2016).

The conservation importance of habitat heterogeneity in the natural forest-grassland mosaics of Eastern Europe is, as yet, not fully appreciated. Ecological studies have typically focused on either the grassland or the forest component separately, disregarding the mosaic character (Erdős et al., 2015). The same bias exists in conservation practice. For example, restoration efforts usually aim to reconstruct only one of the components (e.g., Filatova and Zolotukhin, 2002; Halassy et al., 2016; Szitár et al., 2016; Török et al., 2014). Projects that intend to restore entire mosaic complexes (i.e., both woody and herbaceous components) are scarce (Török et al., 2017). While grazing and mowing are traditional and effective tools in both restoration and conservation management, changes in land-use in the form of either intensification (e.g., overgrazing, mechanized mowing) or abandonment may reduce heterogeneity and may thus have a detrimental effect on these complex systems (Bergmeier et al., 2010; Öllerer, 2014; Tölgyesi et al., 2017).

In this study, our aim was to explore the contribution of individual woody and herbaceous habitats to the overall conservation value of the entire mosaic. Our questions were the following: (1) If we aim to protect the entire species pool of the mosaic, is it sufficient to conserve one or a few keystone habitats, or is it necessary to conserve all of them? (2) What is the importance of individual habitats in terms of conservation-related characteristics (species richness, diversity, the number of species with special conservation relevance, naturalness, tree size-classes and recruitment, adventives)? (3) How does environmental heterogeneity support the observed vegetation pattern?

2. Material and methods

2.1. Study area

The study was conducted in the Kiskunság Sand Ridge, which is a lowland area between the Danube and Tisza rivers in Hungary. Three study sites were selected: Tatárszentgyörgy (N 47°02', E 19°22'), Fülöpháza (N 46°52', E 19°25'), and Bócsa (N 46°41', E 19°27') (Fig. 1a). All three sites are part of the Natura 2000 network of protected areas, and the Fülöpháza and Bócsa sites belong to the Kiskunság National Park. The mean annual temperature is 10.3–10.5 °C, and the mean annual precipitation is 520–550 mm (Tölgyesi et al., 2016). The study sites are characterized by stabilized calcareous sand dunes and interdune depressions that are covered by humus-poor sandy soils with low water retention capacities (Várallyay, 1993).

The vegetation is a mosaic of woody and herbaceous components (Fig. 1b). The open perennial sand grassland (*Festucetum vaginatae*, Natura 2000 category: 6260, *Pannonic sand steppes, a habitat of community importance in the European Union) is the most widespread natural herbaceous community of the study sites. The total cover of vascular plants usually varies between 40 and 70%, and the rest of the area is covered by mosses, lichens, or bare sand. The dominant species are *Festuca vaginata*, *Stipa borysthénica*, and *S. capillata*, while *Alkanna tinctoria*, *Dianthus serotinus*, *Euphorbia seguieriana*, *Fumana procumbens*, and *Poa bulbosa* are also common.

Patches of the juniper-poplar forest (*Junipero-Populetum albae*, Natura 2000 category: 91N0, Pannonic inland sand dune thicket) are scattered in the grassland. The canopy layer has a cover of 40–60% and is co-dominated by 10–15 m tall *Populus alba* and *P. × canescens* individuals. The shrub layer cover varies between 5 and 80% with heights of 1–5 m, and is composed of *Berberis vulgaris*, *Crataegus monogyna*, *Juniperus communis*, and *Ligustrum vulgare*. The most common species in the herb layer include *Anthriscus cerefolium*, *Asparagus officinalis*, *Carex liparicarpus*, *Cynoglossum officinale*, *Poa angustifolia*, and tree and shrub seedlings. Some xeric species, such as *Eryngium campestre*, *Festuca rupicola*, and *Potentilla arenaria*, are mainly found under canopy gaps. The sizes of the forest patches range from a few individual trees (approx.

50 m²) to a few hectares, although patches larger than 1 ha are rare.

The study sites were extensively grazed till the end of the 19th century. In the 20th century, the Fülöpháza and the Bócsa sites were used for military exercises, which stopped in 1974 (Biró et al., 2013; Kertész et al., 2017). Currently the level of anthropogenic disturbances is very low (strictly regulated tourism and research). There is strong evidence that the mosaic character is a result of climatic features and soil characteristics, and the grassland component persists even without grazing or other forms of disturbances (Bodroγκözy, 1982; Erdős et al., 2015; Fekete, 1992). Both the position and the extent of the studied habitat patches are relatively stable at a decadal time-scale: grassland-to-forest or forest-to-grassland transitions are rare and occur very slowly (Erdős et al., 2015; Fekete, 1992).

2.2. Sampling design

Based on previous research (Erdős et al., 2015), six habitat types were distinguished in the present study: large forest patches (> 0.5 ha), medium forest patches (0.2–0.4 ha), small forest patches (< 0.1 ha), north-facing forest edges, south-facing forest edges, and grasslands. Patches were selected randomly for the study. Plots within the individual patches were placed so as to ensure representativeness and avoid degraded areas such as road or path margins and plantations. Edge plots were established in more or less straight peripheral zones of forest patches > 0.2 ha outward from the outermost tree trunks but still under the canopy. We sampled a total of 90 permanent plots (3 sites × 6 habitats × 5 replicates). Plot size was 25 m² (2 m × 12.5 m at edges, 5 m × 5 m elsewhere). The sizes and shapes of the plots were determined according to the local circumstances: the size was small enough to sample even the smallest forest patches but large enough for a standard coenological relevé, whereas the elongated form of the edge plots ensured that they did not extend into the forest or grassland interiors.

Within each plot, the percent covers of all vascular plant species in all vegetation layers were visually estimated in April (spring aspect) and July (summer aspect) 2016. Visual estimations were done by the same person in all plots. Of the spring and summer cover values, for each species, the largest value was used for subsequent data analyses.

All individual trees were inventoried in the plots, and the diameter at breast height (DBH) was measured for trees taller than 1.3 m.

As potential environmental drivers of vegetation in the different habitats, microclimate variables and soil moisture content were measured in 30 plots (6 habitats × 5 replicates) at the Fülöpháza site. Among the three study sites, Fülöpháza lies in the middle, in an almost equal distance from the other two sites. Air temperature (°C) and relative air humidity (%) were measured synchronously for 24 h at 25 cm above the ground surface in the centre of each plot using MCC USB-502 data loggers (Measurement Computing Corp). Microclimate loggers were housed in naturally ventilated radiation shields to avoid direct solar radiation, and the logging interval was set to 1 min. Measurements occurred from 3 to 4 August under clear weather conditions. Soil moisture values were measured in the upper 20 cm layer on 26 July using a FieldScout TDR300 Soil Moisture Meter (Spectrum Technologies Inc.). Five measurements were carried out for each plot, which were then averaged.

2.3. Data analyses

To assess the compositional relations of the six habitat types, we performed a non-metric multidimensional scaling (NMDS) using Bray-Curtis distance on the square root transformed cover scores. We conducted the analysis with one to six axes and found that using three or more axes caused only slight and linear decreases of the stress factors compared with the two-dimensional solution, so we decided to use only two axes. The analysis was performed in R 3.4.3 (R Core Team, 2017) using the 'metaMDS' function of the *vegan* package (Oksanen et al.,

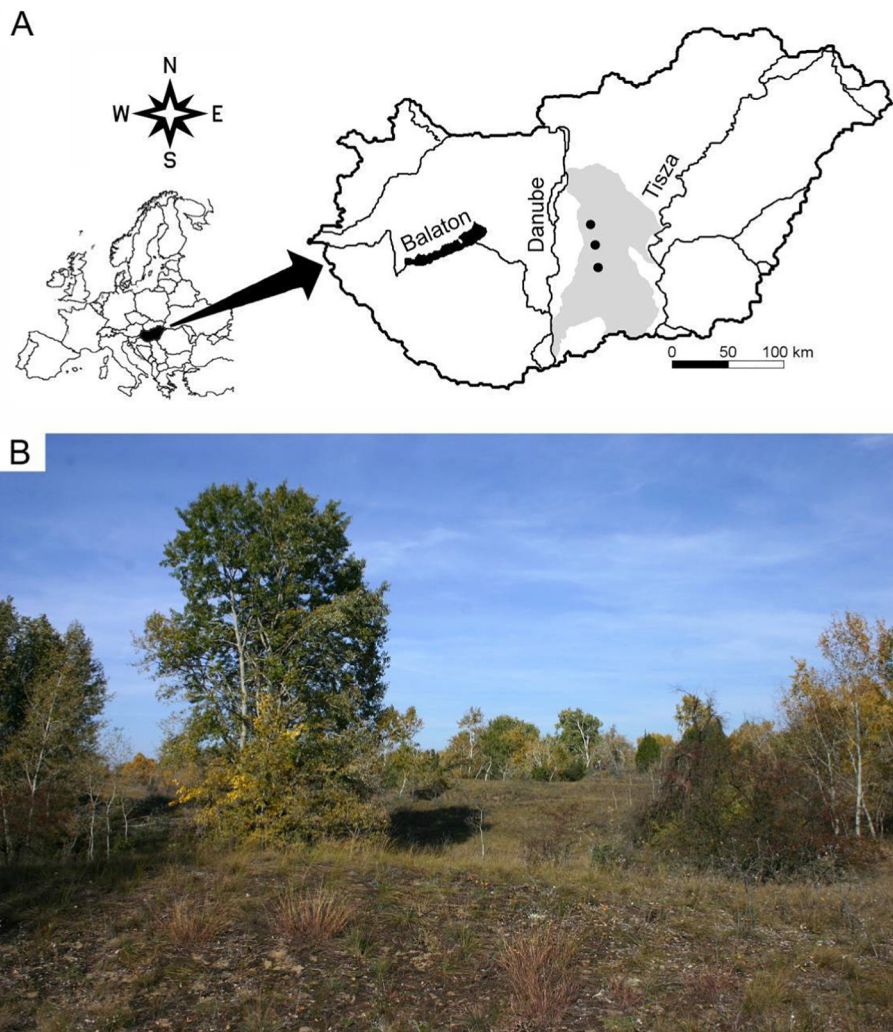


Fig. 1. (a) Locations of the Kiskunság Sand Ridge (grey) between the Danube and Tisza rivers in Hungary and the three study sites (black dots); from north to south: Tatárszentgyörgy, Fülöpháza, Bócsa. (b) Mosaic of woody and herbaceous vegetation at the Fülöpháza site.

2016).

To identify the species that prefer one specific habitat type and are absent or rare in other habitats, we performed a diagnostic species analysis. The phi coefficient was applied as an indicator of the fidelity of a species to certain habitats (Chytrý et al., 2002). The phi coefficient varies between -1 and $+1$; higher values reflect higher diagnostic values. In this study, species with phi values > 0.200 were considered. Significant ($P < 0.01$) diagnostic species were identified by applying Fisher's exact test. Analyses were performed with JUICE 7.0.45 (Tichý, 2002).

Species richness and Shannon diversity were computed for each plot, and the per plot number of species with special conservation relevance was also enumerated, which included all protected, endemic, red-listed and specialist species and was based on Borhidi (1995), Király (2007), and the Database of Hungarian Natural Values (www.termeszetvedelem.hu). As a numeric descriptor of habitat naturalness, we used the relative naturalness indicator values of Borhidi (1995), defined for the Hungarian flora. Naturalness indicator values are defined along an ordinal scale and reflect the observed tolerances of species against habitat degradation. Species that tend to be related to natural habitats have higher values, while species that are more frequent in degraded sites have lower values. Despite some criticism, bio-indication in general and naturalness indicators in particular have solid theoretical bases and obvious practical advantages (Diekmann, 2003). Earlier analyses have shown that mean naturalness values are able to

indicate habitat naturalness/degradation (Erdős et al., 2017; Sengli et al., 2016, 2017). Here, we calculated the unweighted mean value for each plot, as it is more efficient in site indication than cover-weighted approaches (Tölgyesi et al., 2014).

The species richness, Shannon diversity, number of species with special conservation relevance, and naturalness values were analysed in the R environment with linear mixed-effects models. Site was included as the random factor and habitat was the fixed factor. We used a Poisson error term for the count data (species richness and the number of species with special conservation relevance) and assumed a Gaussian distribution for the continuous variables (Shannon diversity and mean naturalness value). We used the 'glmer' function of the *lme4* package (Bates et al., 2015) for the former situation, and the 'lme' function of the *nlme* package (Pinheiro et al., 2016) for the latter one. The full models were tested for significance with analysis of variance, and if the model explained a significant proportion of the variability, we considered pairwise comparisons of the levels of the fixed factor. To account for multiple comparisons, we adjusted the resulting P values with the false discovery rate (FDR) method.

The size-class distribution of the trees was studied using 5 cm diameter classes. The distributions were compared with the Kolmogorov-Smirnov test. Stand characteristics, such as the mean and maximum DBH and number of trees per ha, were calculated for both native and adventive species. The nativeness or adventiveness of the tree species was defined according to Király (2009), as shown in Table A1.

Using the collected microclimate data, we calculated the following variables: mean daily air temperature, mean daytime air temperature, mean nighttime air temperature, mean daily relative air humidity, mean daytime relative air humidity, and mean nighttime relative air humidity. Daytime was defined here as the interval from 7:01 a.m. to 7:00 p.m., while nighttime was the interval from 7:01 p.m. to 7:00 a.m.

To assess the relationships between environmental variables and vegetation pattern, we conducted a distance-based redundancy analysis (dbRDA) in the R environment using the ‘capscale’ function of the *vegan* package (Oksanen et al., 2016). The ordination was performed using Bray-Curtis distance on the square root transformed species cover scores. For a preliminary dbRDA model, we included seven environmental variables (all six microclimatic variables mentioned above, and soil moisture) and calculated the variance inflation factor (VIF) of each variable to check for multicollinearity. We then removed the variable with the highest VIF and recreated the model. We continued this step-by-step refinement until every VIF was less than five. Finally, we retained only daily mean temperature, nighttime mean temperature, daily mean relative humidity, and mean soil moisture. To find the best model using any of these four explanatory variables, we used the forward selection method (‘ordstep’ function). We tested the final dbRDA model and the effect of each explanatory variable for significance with analysis of variance using 1000 permutations each.

The plant species names follow Király (2009), while the plant community names are according to Borhidi et al. (2012).

3. Results

We found a total of 182 plant species in the 90 plots. The NMDS ordination indicated a well-defined gradient in the following sequence: large forest patches – medium forest patches – small forest patches and north-facing edges – south-facing edges – grasslands (Fig. 2). Most groups overlapped considerably (especially small forest patches and north-facing edges), but grasslands were distinct from the other habitats.

The significant ($P < 0.01$) diagnostic species of the six habitats are shown in Table A2. Large forest patches had seven diagnostic species, mostly native shrubs (e.g., *Cornus sanguinea*, *Prunus spinosa*). Two native shrubs (*Crataegus monogyna*, *Berberis vulgaris*) were identified as diagnostic species for medium forest patches. Seven species were significantly associated with small forest patches, most of which were herbs (e.g., *Solanum dulcamara*, *Eryngium campestre*). North-facing edges had ten diagnostic species (e.g., *Carlina vulgaris*, *Polygala comosa*). South-facing edges also had ten diagnostic species (e.g., *Koeleria glauca*, *Poa bulbosa*), of which they shared four species with the grassland

habitat. Twenty species were associated with grasslands (e.g., *Alkanna tinctoria*, *Fumana procumbens*).

Habitat type had significant effects on species richness ($\chi^2 = 70.62$, $P < 0.001$), Shannon diversity ($\chi^2 = 12.31$, $P = 0.031$), the number of species with special conservation relevance ($\chi^2 = 129.16$, $P < 0.001$), and the mean naturalness value ($\chi^2 = 70.84$, $P < 0.001$). Considering the pairwise comparisons (Table A3), north-facing edges had the highest species richness followed by south-facing edges (Fig. 3a). Species richness was lowest in large and medium forest patches, while grasslands and small forest patches had intermediate species richness. There were no significant differences among the Shannon diversities of the different habitats, although north-facing edges and south-facing edges seemed to have somewhat higher Shannon diversity values than large, medium, and small forest patches (Fig. 3b). These differences were significant in only the uncorrected set of P values. The number of species with special conservation relevance showed a gradually increasing trend from the large forest patches towards the grasslands (Fig. 3c). A similar pattern was detected for the mean naturalness values (Fig. 3d).

Recruitment of native trees (mainly *Populus alba* and *P. × canadensis*, to a much lesser degree *Quercus robur*) seemed to occur in mainly the south-facing edges and to a lesser degree in the north-facing edges and grasslands (Fig. 4, Table 1). In contrast, the recruitment of adventive trees (e.g., *Ailanthus altissima*, *Celtis occidentalis*, *Padus serotina*, and *Robinia pseudoacacia*) was concentrated in the forest interiors of all patch sizes and north-facing edges, while it was rare in the south-facing edges and completely absent in grasslands. The numbers of larger native trees (DBH > 5 cm) were almost equal in large, medium, and small forest patches, while adventive trees with DBH > 5 cm were present in only large forest patches. Large native trees (DBH > 50 cm) were present in mainly large and medium forest patches and to a lesser degree in small forest patches. Adventive tree species were not able to develop to large sizes in any of the studied habitats. According to the Kolmogorov-Smirnov tests (Table 2), the six habitats formed two groups: large, medium, and small forest patches were similar to one another, but differed significantly from the other three habitats (north-facing edges, south-facing edges, and grasslands).

The results of the environmental measurements are shown in Table A4. The best dbRDA model contained all four explanatory variables that were retained (daily mean temperature, nighttime mean temperature, daily mean relative humidity, and soil moisture), and it was significant ($R^2 = 0.276$, $F = 3.76$, $P < 0.001$). Although three of the variables were retained during variable selection, they had nonsignificant effects (nighttime mean temperature: $F = 1.28$, $P = 0.214$, daily mean humidity: $F = 0.98$, $P = 0.394$, and soil moisture: $F = 1.67$, $P = 0.099$), and only daily mean temperature had a significant effect ($F = 2.81$, $P = 0.019$). The dbRDA biplot (Fig. 5) indicated that woody (forest and edge) and non-woody (grassland) habitats were separated according to daily mean temperature, with higher values pointing towards the grassland. Interestingly, soil moisture, although having only a marginally significant effect, explained the distribution of the woody habitat types in the ordination space.

4. Discussion

4.1. Compositional differences among habitats

The composition of the studied habitats formed a gradient from large forest patches to grasslands. However, species turnover was not continuous, and two well-defined groups emerged. The first group contained the grassland habitat, which had the most distinct species composition and the highest number of diagnostic species, suggesting that the grassland species pool is poorly represented in other habitats. The second group consisted of all other (woody) habitats with partly overlapping species compositions and fewer diagnostic species. This most basic distinction (woody vs. herbaceous habitats) defines the

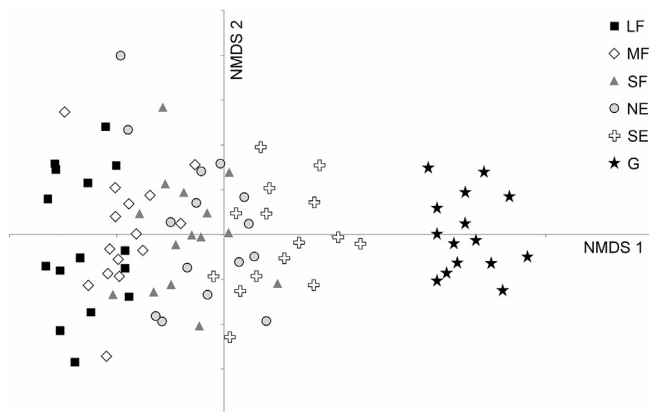


Fig. 2. NMDS ordination scattergram of the 90 relevés. Stress factor: 0.149; $R^2_{\text{NMDS2}} = 0.820$, $R^2_{\text{NMDS1}} = 0.035$. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

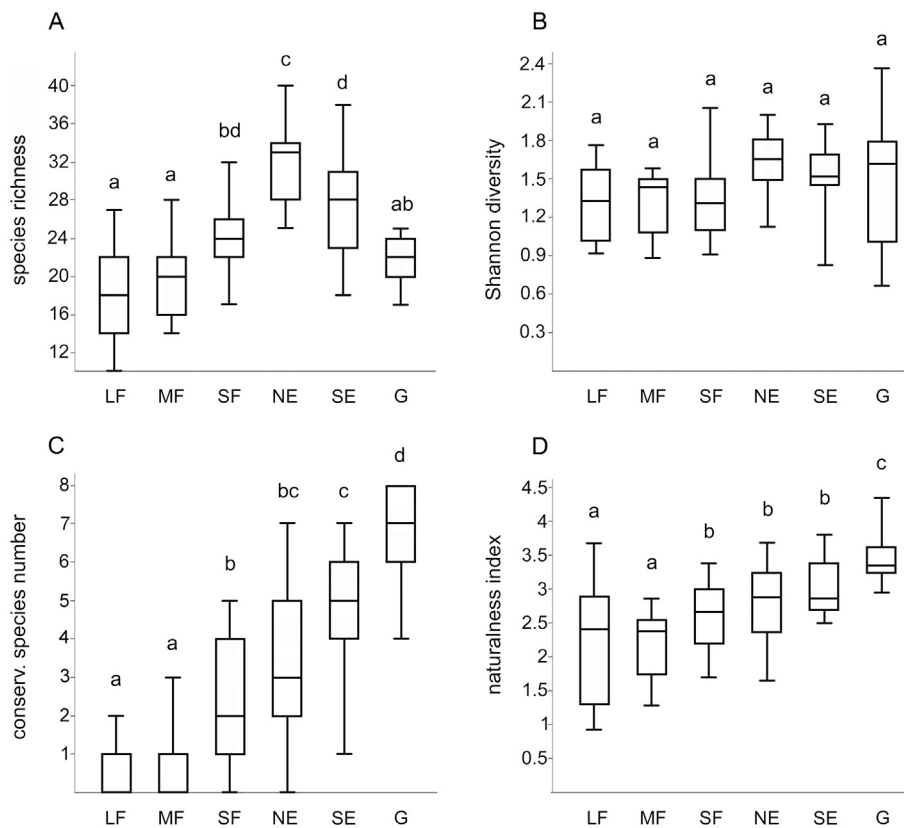


Fig. 3. Species richness (A), Shannon diversity (B), the number of species with special conservation importance (C), and mean naturalness values (D) of the six habitats. Different letters above the boxes indicate significant differences. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

minimum conservation requirement in the studied ecosystem: To represent a considerable proportion of the species pool of the landscape, it is necessary to preserve both the grassland and at least some of the woody habitats.

Given its relatively large variation, the woody habitat group may be further subdivided into edge-like habitats (small forest patches, north-facing edges, and south-facing edges) and forests with core areas (large forest patches and medium forest patches). To achieve a higher landscape-level diversity, it is recommended to conserve at least some edge-like habitats and some forest patches with core areas. However, our results emphasize that all six habitats have their typical species composition and species that are significantly concentrated within each of them. Thus, all habitats deserve special consideration in conservation policy and practice if we aim to protect the highest possible proportion of the species pool.

Until very recently, between-habitat compositional differences have received surprisingly little attention in Eastern European forest-grassland mosaics, where conservation efforts usually focus on only the grassland component (Erdős et al., 2013). In line with the results of Bátori et al. (2018), Kelemen et al. (2017) and Tölgyesi et al. (2017), our study revealed low redundancy between the woody and herbaceous components, which calls for increased efforts to conserve forest habitats in the studied ecosystem.

4.2. Conservation-related characteristics of the habitats

One of our most important findings was that the six habitats in the studied ecosystem had strongly different conservation-related characteristics. Grasslands had the highest per plot number of species with special conservation relevance (protected, endemic, red-listed, and specialist species). Similarly, in a mosaic of oak forests and xeric grasslands, Molnár (1998) found that grasslands contained more specialist species than either forest interiors or forest edges. Our results show that the grassland habitat had the highest naturalness. In

addition, adventive tree seedlings were completely absent from grasslands, which is in good agreement with earlier studies that indicated low invasibility of undisturbed sand grasslands in the region (Bagi, 2008; Csecserits et al., 2016; Szigetvári, 2002). The conservation importance of the grassland habitat is probably further enhanced by other taxa that were not analysed in this study. For example, sandy grasslands are rich in mosses and lichens, including the endemic species *Cladonia magyarica* (Borhidi et al., 2012).

In our study, edges (especially north-facing ones) had the highest species richness, which is in line with the edge-effect theory (Risser, 1995). Similarly, forest edges were proven to be quite species-rich in other natural and near-natural mosaics in Eastern Europe (Erdős et al., 2013; Molnár, 1998), Asia (Bátori et al., 2018), and South America (de Casenave et al., 1995; Pinder and Rosso, 1998). In addition to hosting high fine-scale species richness, edges play an important role in tree recruitment: The number of native tree seedlings and saplings was the highest in south-facing edges, but it was also considerable in north-facing ones. Thus, forest edges may play a crucial role in the dynamics of forest-grassland mosaics (Erdős et al., 2015).

Forest patches of different sizes may be substantially dissimilar in several respects, although most earlier studies have been conducted in anthropogenic mosaics (e.g., Carranza et al., 2012; Gignac and Dale, 2007; Kolb and Diekmann, 2005; Rosati et al., 2010). In the fine-scale natural mosaics of Hungary, forest patches are usually very small (typically up to a few hectares) (Wesche et al., 2016). The small range of forest patch sizes may explain why forest patches of different sizes have received little attention. Interestingly, despite this small variation in size (the lower threshold of the large forest category was only 0.5 ha in our study), considerable differences were found among small forest patches on the one hand, and medium and large forest patches on the other.

Small forest patches had significantly higher species richness, more species of special conservation interest, and higher naturalness than large and medium forest patches. The differences in stand

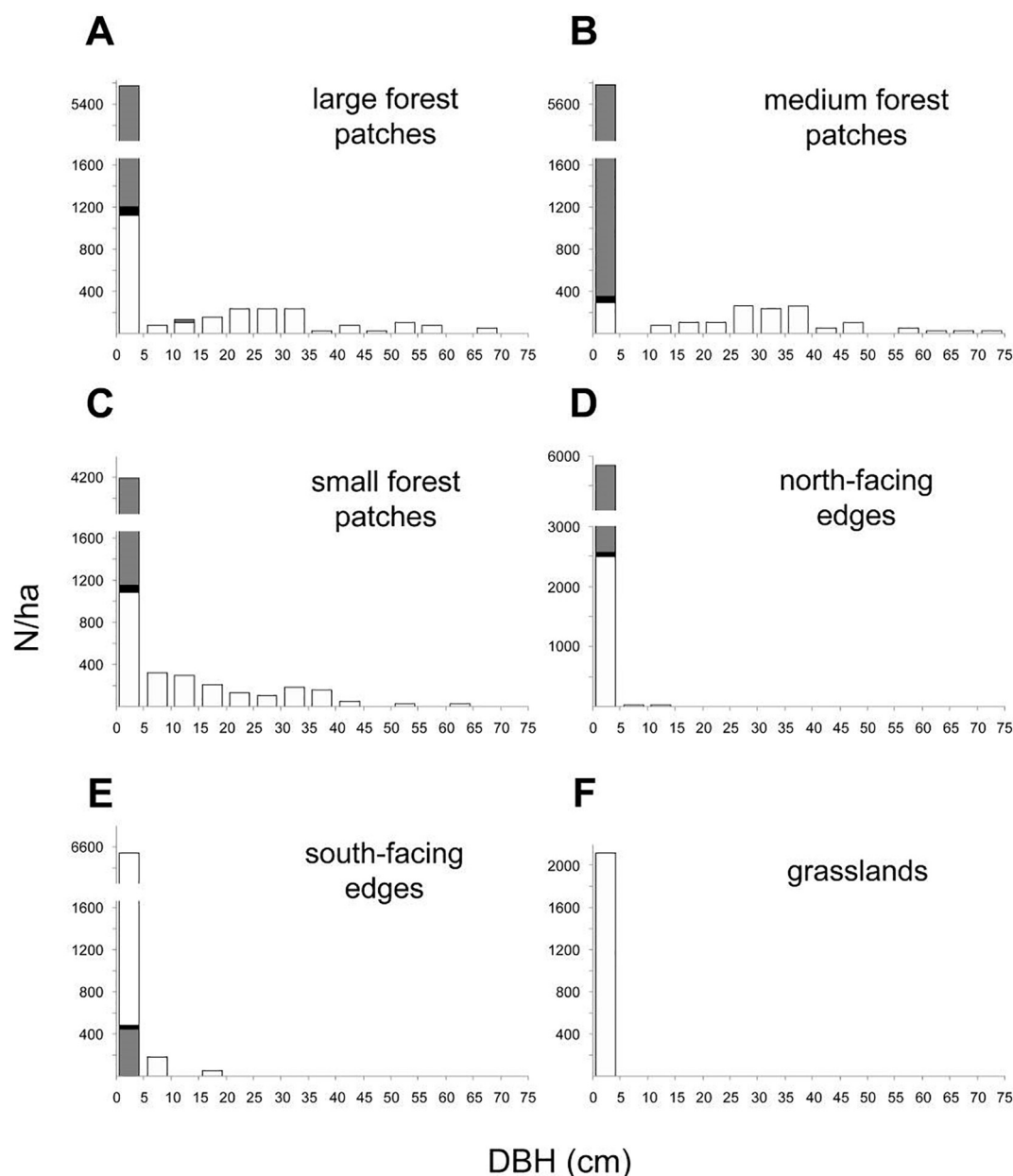


Fig. 4. DBH class distribution of *Populus alba* + *P. × canadensis* (white), other native trees (black), and adventive trees (grey) in large forest patches (A), medium forest patches (B), small forest patches (C), north-facing edges (D), south-facing edges (E), and grasslands (F).

Table 1

Stand characteristics of the six habitats. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

	LF	MF	SF	NE	SE	G
DBH < 5 cm						
N/ha native trees	1200.0	346.7	1146.7	2560.0	6080.0	2106.7
N/ha adventive trees	4373.3	5440.0	3040.0	3280.0	453.3	–
DBH > 5 cm						
N/ha native trees	1440.0	1360.0	1520.0	53.3	240.0	–
N/ha adventive trees	26.7	–	–	–	–	–
mean DBH (cm)	30.3	33.9	22.0	8.3	7.9	–
DBH > 50 cm						
N/ha native trees	240.0	133.3	53.3	–	–	–
N/ha adventive trees	–	–	–	–	–	–
max. DBH (cm)	68.4	70.0	62.7	10.5	16.9	–

Table 2

Results of the Kolmogorov-Smirnov tests for the six habitats regarding DBH class distribution. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

D\P	LF	MF	SF	NE	SE	G
LF		0.994	0.968	< 0.001	0.001	< 0.001
MF	0.13		0.849	< 0.001	0.002	< 0.001
SF	0.13	0.20		0.010	0.013	< 0.001
NE	0.67	0.67	0.53		0.863	0.735
SE	0.67	0.67	0.53	0.13		0.724
G	0.80	0.80	0.67	0.13	0.13	

Significant differences are highlighted in bold.

characteristics were less pronounced, although the number of large trees (DBH > 50 cm) in small forests was low compared to the numbers in medium and large forest patches. Medium and large forest patches had low species richness, only a few species of special

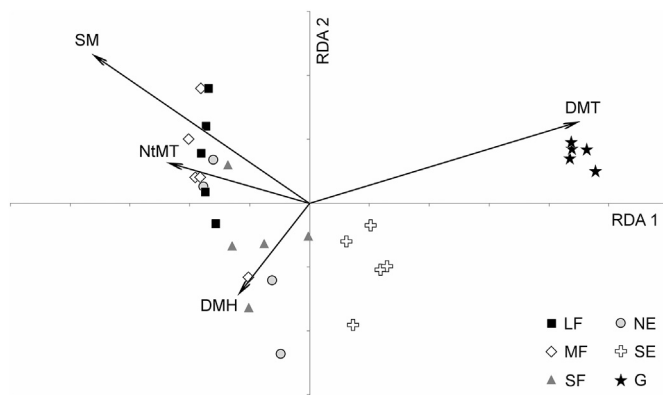


Fig. 5. Biplot of the dbRDA of the six main habitats in Fülöpháza. Constrained inertia: 37.6, unconstrained inertia: 62.4%; eigenvalues of the first and second axes: 2.170 and 0.256, respectively. DMT: daily mean temperature, DMH: daily mean relative humidity, NtMT: nighttime mean temperature, SM: soil moisture; LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

conservation relevance, and low naturalness values. In addition, large and medium forest patches hosted the largest proportions of adventive trees; thus, these forests should be regarded as potential invasion hot-spots. Csecserits et al. (2016) identified the following habitats as invasion hot-spots in our study region: tree plantations, agricultural habitats, old-fields, and oak forests. Pándi et al. (2014) concluded that abandoned farms are invasion centres. From these sources, adventive species with good dispersal abilities can easily reach all six habitat types evaluated in this study, but they probably have the best establishment chances in relatively humid and cool habitats such as medium and large forest patches.

Medium and large forest patches seemed to have relatively low conservation importance. However, they added structural characteristics to the landscape that small forest patches lacked. The noticeable number of native shrubs and large trees (DBH > 50 cm) should be considered important from a conservation perspective. For example, large trees provide habitat for several protected animals, including insects (e.g., *Aegosoma scabricorne* and *Oryctes nasicornis*) and birds (e.g., *Coracias garrulus* and other cavity-nesting birds) (Foit et al., 2016; Gaskó, 2009). It should also be kept in mind that the existence of edges depends on forest patches of sufficient size.

4.3. Environmental heterogeneity

Environmental parameters are expected to differ between woody and herbaceous patches in mosaic ecosystems (e.g., Breshears, 2006; Schmidt et al., 2017). In our study, the daily mean temperature differed significantly between woody and herbaceous habitats, while soil moisture showed conspicuous differences among the different woody habitats. Although the causal relations between vegetation and the environment are complex, it may be assumed that trees modify their environment in a way that has a profound effect on the herb layer (cf. Scholes and Archer, 1997). This moderating effect is expected to be especially strong in harsh environments (Callaway and Walker, 1997) such as the semi-arid Kiskunság Sand Ridge.

Soil moisture and daily mean and daytime mean air humidity were higher in the forest patches than in the grasslands, while the daily mean and daytime mean temperature were lower, and the maxima and minima of both temperature and humidity were less extreme in the forest patches. Thus, conserving woody habitats is important for creating environments that are suitable for mesic plants that would be unable to survive in the dry grassland component of the mosaic. This role of trees and groves is predicted to become increasingly important with ongoing climate change (Manning et al., 2009).

4.4. Conclusions and implications for conservation policy and practice

Our study implies that maintaining habitat heterogeneity through the protection of various habitats is of crucial conservation importance. Some habitats have outstanding species richness, some possess high resistance against invasion, and others are important mainly for tree recruitment or structural reasons. In addition, all habitats have characteristic species compositions with species that are absent or rare elsewhere.

In concordance with the findings of Török et al. (2017) and Weking et al. (2016), our study suggests that it is not sufficient to focus on either the grassland or the forest components in conservation-oriented research and practice. Rather, an integrated view of the entire mosaic is urgently needed. For example, the establishment of native trees should be promoted in areas where they have been reduced through cutting, overgrazing or fire (e.g., by deploying safe sites for seedlings). Management practices should be adapted to support native tree recruitment (e.g., by decreasing grazing pressure). During restoration projects, the reconstruction of forest patches should be of high priority.

Inappropriate legislation is a possible explanation why the complexity of forest-grassland mosaics has been neglected in both research and management in Eastern Europe (Babai et al., 2015; Hartel et al., 2013; Korotchenko and Peregrym, 2012; Tölgyesi et al., 2017; Varga et al., 2016). From a legal perspective, an area may be treated as either forest or grassland, but not as a mosaic of both. These two categories (i.e., forest and grassland) do not match reality in Eastern Europe, where the natural vegetation of large areas is actually a mosaic of woody and herbaceous patches.

Adapting conservation policy and practice to fit the complexity of forest-grassland mosaics may be a difficult task; however, there is no alternative if the natural values of these unique ecosystems are to be conserved.

Statement of competing interests

The authors have no competing interests to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.07.029>.

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