

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

2 3 Abstract

4
5 Forest-grassland mosaics are widespread features at the interface between tree- and grass-
6 dominated ecosystems. However, the importance of habitat heterogeneity in these mosaics is
7 not fully appreciated, and the contribution of individual woody and herbaceous habitats to the
8 overall conservation value of the mosaic is unclear. We distinguished six main habitats in the
9 forest-grassland mosaics of the Kiskunság Sand Ridge (Hungary) and compared the species
10 composition, species richness, Shannon diversity, naturalness, selected structural features,
11 environmental variables, and the number of protected, endemic, red-listed and specialist
12 species of the plant communities. Each habitat had species that were absent or rare elsewhere.
13 Grasslands had the highest conservation importance in most respects. North-facing forest
14 edges had the highest species richness, while south-facing edges were primarily important for
15 tree recruitment. Among the forest habitats, small forest patches were the most valuable,
16 while large and medium forest patches had the lowest conservation importance. We showed
17 that the current single-habitat focus of both research and conservation in the studied forest-
18 grassland mosaics is not justified. Instead, an integrated view of the entire mosaic is
19 necessary. Management practices and restoration projects should promote habitat
20 heterogeneity, e.g., by assisting tree and shrub establishment and survival in grasslands. The
21 legislative background should recognize the existence of fine-scale forest-grassland mosaics,
22 which are neither grasslands nor forests, but a mixture.

23
24 **Keywords:** Complexity, Conservation management, Forest edge, Forest patches, Forest-
25 steppe, Landscape heterogeneity

26 27 1. Introduction

28
29 The intensification of land-use practices and the resulting habitat homogenization pose
30 major challenges for current conservation (Ernst et al., 2017; Foley et al., 2005; Rembold et
31 al., 2017; Stoate et al., 2001). Likewise, land abandonment often leads to homogenization
32 (Bergmeier et al., 2010; Plieninger et al., 2015; Ernst et al. 2017). Generally, heterogeneous
33 areas are expected to contain more niches and, consequently, more species than homogeneous
34 areas (Bazzaz, 1975; Chesson, 2000; Tilman, 1982). In fact, spatial heterogeneity seems
35 necessary for the maintenance of biodiversity, ecosystem services, and endangered species
36 (Armengot et al., 2012; Dorresteyn *et al.*, 2015; Valkó et al., 2012). Thus, from a
37 conservation perspective, the presence of various habitat patches in close proximity is
38 considered beneficial (Jakobsson and Lindborg, 2015; Tölgyesi et al., 2017).

39 Habitat heterogeneity and its conservation implications are relatively well studied in
40 agricultural and agroforestry landscapes (e.g., Bennett et al., 2006; Benton et al., 2003;
41 Jakobsson and Lindborg, 2015; Lee and Martin, 2017; Manning et al., 2006; Moreno et al.,
42 2017; Plieninger et al., 2015; Stoate et al., 2001; Tscharrntke et al., 2005). Unfortunately, the
43 importance of habitat heterogeneity for conservation has received less attention in natural
44 mosaics at the interfaces of tree- and grass-dominated biomes (cf. Tews et al., 2004).

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

50 Forest-grassland mosaics represent high conservation significance (Erdős et al., 2018;
51 Prevedello et al., 2018). However, in Eastern Europe, most of these mosaics have been
52 transformed to croplands or non-native tree plantations, while the remaining fragments are
53 threatened by different forms of homogenization (Wesche et al., 2016). In some regions, the
54 spontaneous or human-induced spread of woody species may result in the disappearance of
55 grassland habitats. At the same time, woody habitats are diminishing in other regions due to
56 the combined effects of climate change, sinking groundwater level, and fire (Molnár, 1998;
57 Wesche et al., 2016).

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

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

78

79 **2. Material and methods**

80

81 **2.1. Study area**

82 The study was conducted in the Kiskunság Sand Ridge, which is a lowland area
83 between the Danube and Tisza rivers in Hungary. Three study sites were selected:
84 Tatárszentgyörgy (N 47°02', E 19°22'), Fülöpháza (N 46°52', E 19°25'), and Bócsa (N
85 46°41', E 19°27') (Fig. 1a). All three sites are part of the Natura 2000 network of protected
86 areas, and the Fülöpháza and Bócsa sites belong to the Kiskunság National Park. The mean
87 annual temperature is 10.3-10.5 °C, and the mean annual precipitation is 520-550 mm
88 (Tölgyesi et al., 2016). The study sites are characterized by stabilized calcareous sand dunes
89 and interdune depressions that are covered by humus-poor sandy soils with low water
90 retention capacities (Várallyay, 1993).

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

99 Patches of the juniper-poplar forest (*Junipero-Populetum albae*, Natura 2000 category:
100 91N0, Pannonic inland sand dune thicket) are scattered in the grassland. The canopy layer has
101 a cover of 40-60% and is co-dominated by 10-15 m tall *Populus alba* and *P. × canescens*
102 individuals. The shrub layer cover varies between 5 and 80% with heights of 1-5 m, and is
103 composed of *Berberis vulgaris*, *Crataegus monogyna*, *Juniperus communis*, and *Ligustrum*
104 *vulgare*. The most common species in the herb layer include *Anthriscus cerefolium*,
105 *Asparagus officinalis*, *Carex liparicarpos*, *Cynoglossum officinale*, *Poa angustifolia*, and tree
106 and shrub seedlings. Some xeric species, such as *Eryngium campestre*, *Festuca rupicola*, and
107 *Potentilla arenaria*, are mainly found under canopy gaps. The sizes of the forest patches
108 range from a few individual trees (approx. 50 m²) to a few hectares, although patches larger
109 than 1 ha are rare.

110 The study sites were extensively grazed till the end of the 19th century. In the 20th
111 century, the Fülöpháza and the Bócsa sites were used for military exercises, which stopped in
112 1974 (Biró et al., 2013; Kertész et al., 2017). Currently the level of anthropogenic
113 disturbances is very low (strictly regulated tourism and research). There is strong evidence
114 that the mosaic character is a result of climatic features and soil characteristics, and the
115 grassland component persists even without grazing or other forms of disturbances
116 (Bodrogközy, 1982; Erdős et al., 2015; Fekete, 1992). Both the position and the extent of the
117 studied habitat patches are relatively stable at a decadal time-scale: grassland-to-forest or
118 forest-to-grassland transitions are rare and occur very slowly (Erdős et al., 2015; Fekete,
119 1992).

120

121 **2.2. Sampling design**

122 Based on previous research (Erdős et al., 2015), six habitat types were distinguished in
123 the present study: large forest patches (> 0.5 ha), medium forest patches (0.2-0.4 ha), small
124 forest patches (< 0.1 ha), north-facing forest edges, south-facing forest edges, and grasslands.
125 Patches were selected randomly for the study. Plots within the individual patches were placed
126 so as to ensure representativeness and avoid degraded areas such as road or path margins and
127 plantations. Edge plots were established in more or less straight peripheral zones of forest
128 patches > 0.2 ha outward from the outermost tree trunks but still under the canopy. We
129 sampled a total of 90 permanent plots (3 sites × 6 habitats × 5 replicates). Plot size was 25 m²
130 (2 m × 12.5 m at edges, 5 m × 5 m elsewhere). The sizes and shapes of the plots were
131 determined according to the local circumstances: the size was small enough to sample even
132 the smallest forest patches but large enough for a standard coenological relevé, whereas the
133 elongated form of the edge plots ensured that they did not extend into the forest or grassland
134 interiors.

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

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

141 As potential environmental drivers of vegetation in the different habitats, microclimate
142 variables and soil moisture content were measured in 30 plots (6 habitats × 5 replicates) at the
143 Fülöpháza site. Among the three study sites, Fülöpháza lies in the middle, in an almost equal
144 distance from the other two sites. Air temperature (°C) and relative air humidity (%) were
145 measured synchronously for 24 hours at 25 cm above the ground surface in the centre of each
146 plot using MCC USB-502 data loggers (Measurement Computing Corp). Microclimate
147 loggers were housed in naturally ventilated radiation shields to avoid direct solar radiation,

148 and the logging interval was set to 1 min. Measurements occurred from 3 to 4 August under
149 clear weather conditions. Soil moisture values were measured in the upper 20 cm layer on 26
150 July using a FieldScout TDR300 Soil Moisture Meter (Spectrum Technologies Inc). Five
151 measurements were carried out for each plot, which were then averaged.

152

153 **2.3. Data analyses**

154 To assess the compositional relations of the six habitat types, we performed a non-
155 metric multidimensional scaling (NMDS) using Bray-Curtis distance on the square root
156 transformed cover scores. We conducted the analysis with one to six axes and found that
157 using three or more axes caused only slight and linear decreases of the stress factors compared
158 with the two-dimensional solution, so we decided to use only two axes. The analysis was
159 performed in R 3.4.3 (R Core Team, 2017) using the ‘metaMDS’ function of the *vegan*
160 package (Oksanen et al., 2016).

161 To identify the species that prefer one specific habitat type and are absent or rare in
162 other habitats, we performed a diagnostic species analysis. The phi coefficient was applied as
163 an indicator of the fidelity of a species to certain habitats (Chytrý et al., 2002). The phi
164 coefficient varies between -1 and +1; higher values reflect higher diagnostic values. In this
165 study, species with phi values > 0.200 were considered. Significant ($P < 0.01$) diagnostic
166 species were identified by applying Fisher’s exact test. Analyses were performed with JUICE
167 7.0.45 (Tichý, 2002).

168 Species richness and Shannon diversity were computed for each plot, and the per plot
169 number of species with special conservation relevance was also enumerated, which included
170 all protected, endemic, red-listed and specialist species and was based on Borhidi (1995),
171 Király (2007), and the Database of Hungarian Natural Values (www.termesztvedelem.hu).
172 As a numeric descriptor of habitat naturalness, we used the relative naturalness indicator
173 values of Borhidi (1995), defined for the Hungarian flora. Naturalness indicator values are
174 defined along an ordinal scale and reflect the observed tolerances of species against habitat
175 degradation. Species that tend to be related to natural habitats have higher values, while
176 species that are more frequent in degraded sites have lower values. Despite some criticism,
177 bio-indication in general and naturalness indicators in particular have solid theoretical bases
178 and obvious practical advantages (Diekmann, 2003). Earlier analyses have shown that mean
179 naturalness values are able to indicate habitat naturalness/degradation (Erdős et al., 2017;
180 Sengl et al., 2016, 2017). Here, we calculated the unweighted mean value for each plot, as it is
181 more efficient in site indication than cover-weighted approaches (Tölgyesi et al., 2014).

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

194 The size-class distribution of the trees was studied using 5 cm diameter classes. The
195 distributions were compared with the Kolmogorov-Smirnov test. Stand characteristics, such
196 as the mean and maximum DBH and number of trees per ha, were calculated for both native

197 and adventive species. The nativeness or adventiveness of the tree species was defined
198 according to Király (2009), as shown in Table A1.

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

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

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

220

221 3. Results

222

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

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

238 Habitat type had significant effects on species richness ($\chi^2 = 70.62$, $P < 0.001$),
239 Shannon diversity ($\chi^2 = 12.31$, $P = 0.031$), the number of species with special conservation
240 relevance ($\chi^2 = 129.16$, $P < 0.001$), and the mean naturalness value ($\chi^2 = 70.84$, $P < 0.001$).
241 Considering the pairwise comparisons (Table A3), north-facing edges had the highest species
242 richness followed by south-facing edges (Fig. 3a). Species richness was lowest in large and
243 medium forest patches, while grasslands and small forest patches had intermediate species
244 richness. There were no significant differences among the Shannon diversities of the different
245 habitats, although north-facing edges and south-facing edges seemed to have somewhat

246 higher Shannon diversity values than large, medium, and small forest patches (Fig. 3b). These
247 differences were significant in only the uncorrected set of P values. The number of species
248 with special conservation relevance showed a gradually increasing trend from the large forest
249 patches towards the grasslands (Fig. 3c). A similar pattern was detected for the mean
250 naturalness values (Fig. 3d).

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

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

277

278 4. Discussion

279

280 4.1. Compositional differences among habitats

281 The composition of the studied habitats formed a gradient from large forest patches to
282 grasslands. However, species turnover was not continuous, and two well-defined groups
283 emerged. The first group contained the grassland habitat, which had the most distinct species
284 composition and the highest number of diagnostic species, suggesting that the grassland
285 species pool is poorly represented in other habitats. The second group consisted of all other
286 (woody) habitats with partly overlapping species compositions and fewer diagnostic species.
287 This most basic distinction (woody vs. herbaceous habitats) defines the minimum
288 conservation requirement in the studied ecosystem: To represent a considerable proportion of
289 the species pool of the landscape, it is necessary to preserve both the grassland and at least
290 some of the woody habitats.

291 Given its relatively large variation, the woody habitat group may be further subdivided
292 into edge-like habitats (small forest patches, north-facing edges, and south-facing edges) and
293 forests with core areas (large forest patches and medium forest patches). To achieve a higher
294 landscape-level diversity, it is recommended to conserve at least some edge-like habitats and

295 some forest patches with core areas. However, our results emphasize that all six habitats have
296 their typical species composition and species that are significantly concentrated within each of
297 them. Thus, all habitats deserve special consideration in conservation policy and practice if
298 we aim to protect the highest possible proportion of the species pool.

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

305

306 **4.2. Conservation-related characteristics of the habitats**

307 One of our most important findings was that the six habitats in the studied ecosystem
308 had strongly different conservation-related characteristics. Grasslands had the highest per plot
309 number of species with special conservation relevance (protected, endemic, red-listed, and
310 specialist species). Similarly, in a mosaic of oak forests and xeric grasslands, Molnár (1998)
311 found that grasslands contained more specialist species than either forest interiors or forest
312 edges. Our results show that the grassland habitat had the highest naturalness. In addition,
313 adventive tree seedlings were completely absent from grasslands, which is in good agreement
314 with earlier studies that indicated low invasibility of undisturbed sand grasslands in the region
315 (Bagi, 2008; Csecserits et al., 2016; Szigetvári, 2002). The conservation importance of the
316 grassland habitat is probably further enhanced by other taxa that were not analysed in this
317 study. For example, sandy grasslands are rich in mosses and lichens, including the endemic
318 species *Cladonia magyarica* (Borhidi et al., 2012).

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

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

337 Small forest patches had significantly higher species richness, more species of special
338 conservation interest, and higher naturalness than large and medium forest patches. The
339 differences in stand characteristics were less pronounced, although the number of large trees
340 (DBH > 50 cm) in small forests was low compared to the numbers in medium and large forest
341 patches. Medium and large forest patches had low species richness, only a few species of
342 special conservation relevance, and low naturalness values. In addition, large and medium
343 forest patches hosted the largest proportions of adventive trees; thus, these forests should be

344 regarded as potential invasion hot-spots. Csecserits et al. (2016) identified the following
345 habitats as invasion hot-spots in our study region: tree plantations, agricultural habitats, old-
346 fields, and oak forests. Pándi et al. (2014) concluded that abandoned farms are invasion
347 centres. From these sources, adventive species with good dispersal abilities can easily reach
348 all six habitat types evaluated in this study, but they probably have the best establishment
349 chances in relatively humid and cool habitats such as medium and large forest patches.

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

358

359 **4.3. Environmental heterogeneity**

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

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

375

376 **4.4. Conclusions and implications for conservation policy and practice**

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

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

390 Inappropriate legislation is a possible explanation why the complexity of forest-
391 grassland mosaics has been neglected in both research and management in Eastern Europe
392 (Babai et al., 2015; Hartel et al., 2013; Korotchenko and Peregrym, 2012; Tölgyesi et al.,

393 2017; Varga et al., 2016). From a legal perspective, an area may be treated as either forest or
394 grassland, but not as a mosaic of both. These two categories (i.e., forest and grassland) do not
395 match reality in Eastern Europe, where the natural vegetation of large areas is actually a
396 mosaic of woody and herbaceous patches.

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

400

401 **Statement of competing interests**

402 The authors have no competing interests to declare.

403

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411

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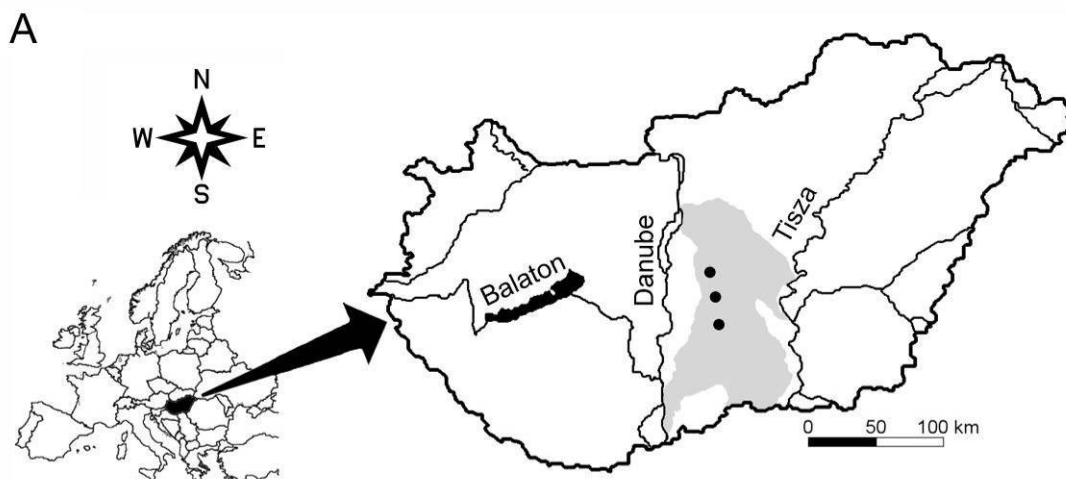
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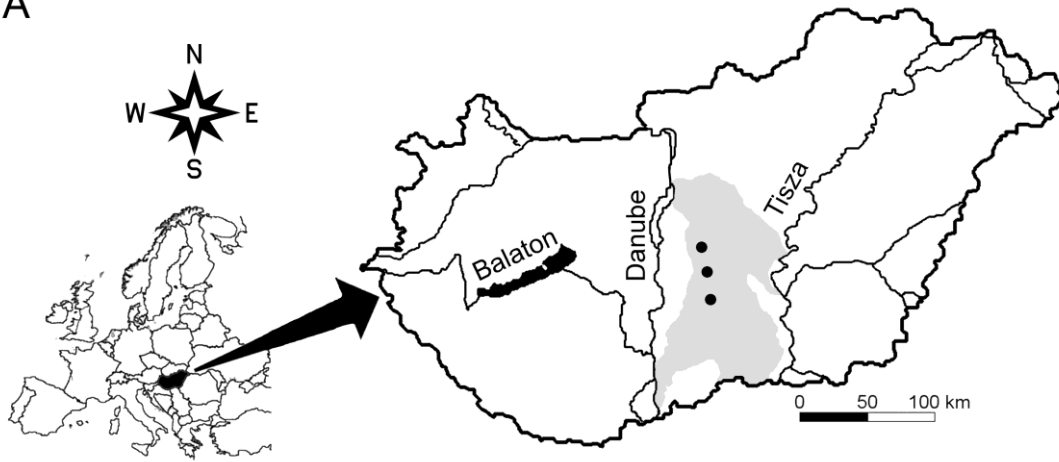
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624 **Fig. 1. (a)** Locations of the Kiskunság Sand Ridge (grey) between the Danube and Tisza
625 rivers in Hungary and the three study sites (black dots); from north to south:
626 Tatárszentgyörgy, Fülöpháza, Bócsa. **(b)** Mosaic of woody and herbaceous vegetation at the
627 Fülöpháza site.
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629 (grayscale figure to be published in print)
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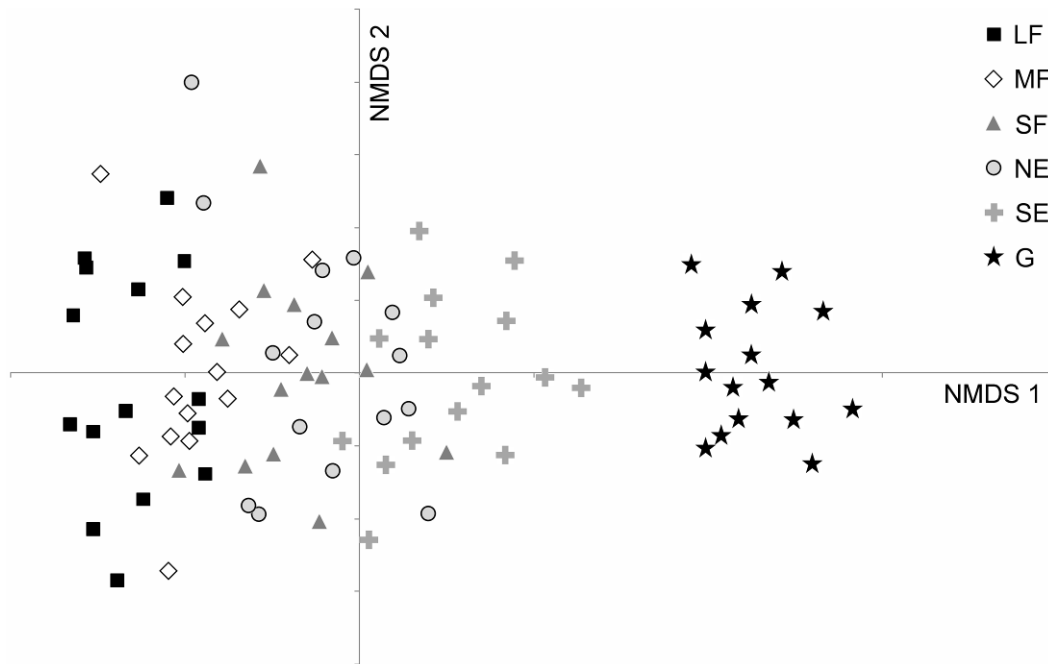
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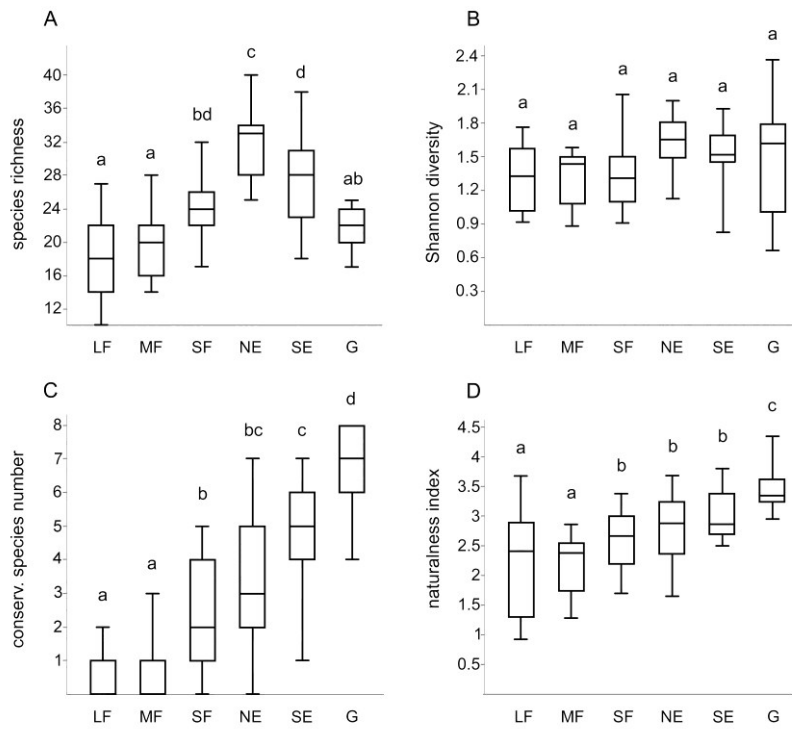


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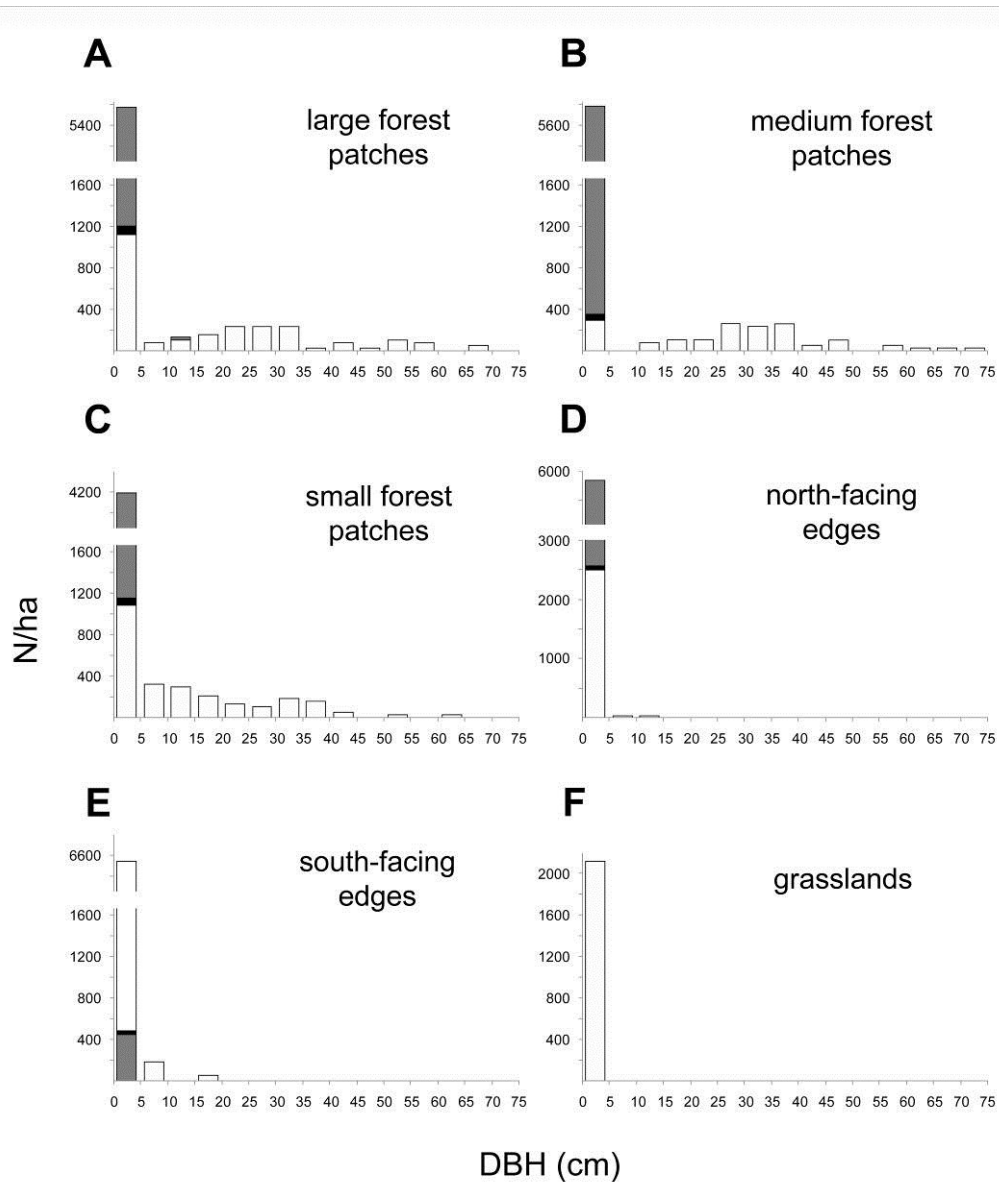


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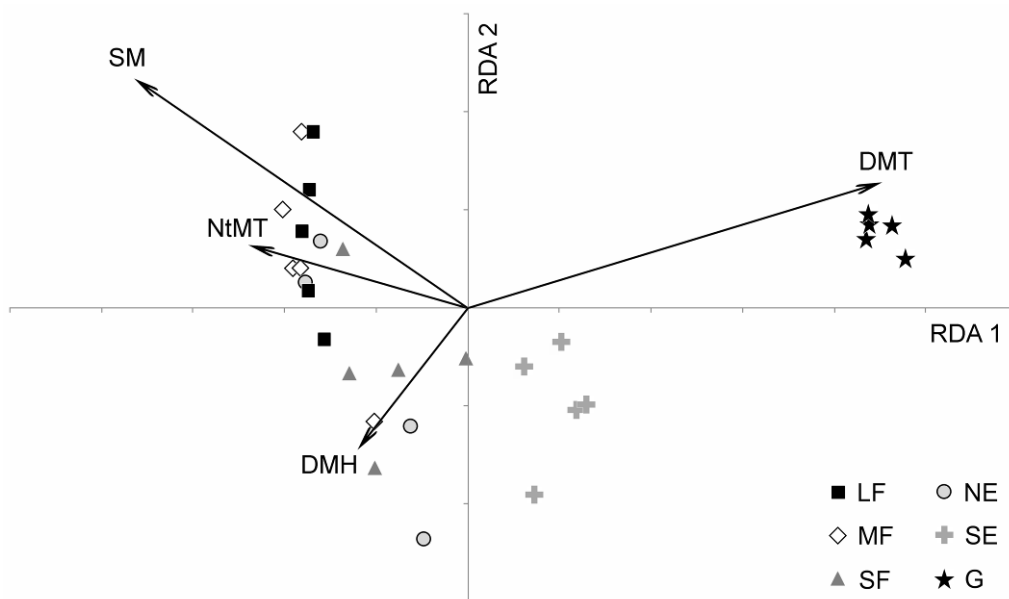
Fig. 2. NMDS ordination scattergram of the 90 relevés. Stress factor: 0.149; $R^2_{\text{NMDS2}} = 0.820$, $R^2_{\text{NMDS1}} = 0.035$. LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.



638
 639 **Fig. 3.** Species richness (A), Shannon diversity (B), the number of species with special
 640 conservation importance (C), and mean naturalness values (D) of the six habitats. Different
 641 letters above the boxes indicate significant differences. LF: large forest patches, MF: medium
 642 forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G:
 643 grasslands.
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645
 646 **Fig. 4.** DBH class distribution of *Populus alba* + *P. × canescens* (white), other native trees
 647 (black), and adventive trees (grey) in large forest patches (A), medium forest patches (B),
 648 small forest patches (C), north-facing edges (D), south-facing edges (E), and grasslands (F).
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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.

658 **Table 1.** Stand characteristics of the six habitats. LF: large forest patches, MF: medium forest
 659 patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G:
 660 grasslands.
 661

	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	-

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664 **Table 2.** Results of the Kolmogorov-Smirnov tests for the six habitats regarding DBH class
 665 distribution. LF: large forest patches, MF: medium forest patches, SF: small forest patches,
 666 NE: north-facing edges, SE: south-facing edges, G: grasslands.
 667

DVP	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	

668