

Beyond the forest-grassland dichotomy: the gradient-like organization of habitats in forest-steppes

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18 **Abstract**

19 Featuring a transitional zone between closed forests and treeless steppes, forest-steppes cover vast
20 areas and have outstanding conservation importance. The components of this mosaic ecosystem can
21 conveniently be classified into two basic types, forests and grasslands. However, this dichotomic
22 classification may not fit reality as habitat organization can be much more complex. In this study, our
23 aim was to find out if the main habitat types can be grouped into two distinct habitat categories
24 (which would support the dichotomic description), or a different paradigm better fits this complex
25 ecosystem. We selected six main habitats of sandy forest-steppes, and, using 176 relevés, we
26 compared their vegetation based on species composition (NMDS ordination, number of common
27 species of the studied habitats), relative ecological indicator values (mean indicators for temperature,
28 soil moisture, and light availability), and functional species groups (life-form categories, geoelement
29 types, and phytosociological preference groups). According to the species composition, we found a
30 well-defined gradient, with the following habitat order: large forest patches – medium forest patches
31 – small forest patches – north-facing edges – south-facing edges – grasslands. A considerable number
32 of species were shared among all habitats, while the number of species restricted to certain habitat
33 types was also numerous, especially for north-facing edges. The total (i.e., pooled) number of species
34 peaked near the middle of the gradient, in north-facing edges. The relative ecological indicator values
35 and functional species groups showed mostly gradual changes from the large forest patches to the

36 grasslands. Our results indicate that the widely used dichotomic categorization of forest-steppe
37 habitats into forest and grassland patches is too simplistic, potentially resulting in a considerable loss
38 of information. We suggest that forest-steppe vegetation better fits the gradient-based paradigm of
39 landscape structure, which is able to reflect continuous variations.

40 **1 Introduction**

41 Ecosystems where tree-dominated and grass-dominated patches form a mosaic (e.g., savannas, wood
42 pastures and forest-steppes) cover a substantial proportion of Earth's terrestrial surface (House et al.,
43 2003), and their dynamics (e.g. Innes et al., 2013), biodiversity patterns (e.g. Erdős et al., 2018a, b),
44 and conservation importance (e.g. Bergmeier et al., 2010; Prevedello et al., 2018) are in the focus of
45 ecological studies. The components of such systems can conveniently be classified into two basic
46 types, forests and grasslands, which differ substantially in several biotic (e.g., species composition
47 and leaf area) and abiotic (e.g., solar radiation and soil moisture) parameters (Breshears, 2006). The
48 presence of structurally dissimilar patches increases spatial heterogeneity and contributes to the
49 maintenance of species diversity, ecosystem services, and ecological stability (Manning et al., 2009;
50 Santana et al., 2017; Tölgyesi et al., 2018).

51 Forest-steppes form the contact zone between closed-canopy temperate forests and treeless steppes
52 and provide a textbook example of forest-grassland mosaics (Erdős et al., 2018a). In these areas,
53 alternating forest and grassland patches are an inherent feature of the ecosystem (Erdős et al., 2014;
54 Hais et al., 2016; Bátori et al., 2018; Lashchinskiy et al., 2017). It has been highlighted that such
55 complex ecosystems cannot be understood by simply studying the forest and grassland components
56 independently (House et al., 2003; Erdős et al., 2018b). Instead, a holistic approach with an
57 integrated view of the whole mosaic is needed, as these components are ecologically interrelated in
58 several ways. For example, some animal species need both components for their full life cycles,
59 while some plant species may switch preferences between the components in years with different
60 weather patterns (Bartha et al., 2008; Luza et al., 2014).

61 Forests and grasslands have distinct environmental, structural and compositional characteristics, and
62 the interactions of these characteristics result in the emergence of specific edge communities (Erdős
63 et al., 2013, 2014). Edges are major habitats for tree recruitment; thus, they play an important role in
64 forest-steppe dynamics (Erdős et al., 2015). These findings support the notion that, in addition to
65 forest and grassland components, forest edges should also be recognized as important habitats in
66 these mosaic ecosystems.

67 It is well known that treeless areas exert a considerable influence on the microclimatic parameters of
68 the peripheral areas of forests, which may affect the whole area of small forest patches (Schmidt et
69 al., 2017). Thus, it can be assumed that different-sized forest patches differ considerably regarding
70 both structure and species composition.

71 As edges are transitional habitats between the forest and the grassland components, and small forest
72 patches may in some characteristics be transitional between larger forest patches and grasslands, we
73 hypothesize that the habitats of forest-steppe mosaics can be arranged along a gradient. However, this
74 phenomenon in forest-steppes has so far received little scientific attention (Erdős et al., 2018b).

75 In this study, we evaluated six habitat types of sandy forest-steppes: large forest patches, medium
76 forest patches, small forest patches, north-facing forest edges, south-facing forest edges, and
77 grasslands. Our question was whether, based on species composition, functional species groups, and

78 ecological indicator values, these six habitat types can be grouped into two distinct habitat categories
79 (which would support the dichotomic description), or a different paradigm better fits this complex
80 system.

81 **2 Materials and Methods**

82 **2.1 Study area**

83 We performed our study in the Kiskunság Sand Ridge (Central Hungary), near the westernmost
84 extensions of the Eurasian forest-steppe belt. We selected six study sites where forest-grassland
85 mosaics have been preserved in near-natural conditions: Csévharaszt (N 47°17', E 19°24'),
86 Tatárszentgyörgy (N 47°02', E 19°22'), Fülöpháza (N 46°52', E 19°25'), Bócsa (N 46°41', E
87 19°27'), Tázlár (N 46°30', E 19°30'), and Négyestelep (N 46°17', E 19°35'). Each site is
88 characterized by stabilized calcareous sand dunes of aeolian origin. The elevations of the sites vary
89 between 105 and 140 m asl. The mean annual temperature is 10.0-10.7 °C, and the mean annual
90 precipitation is 520-580 mm (Dövényi, 2010). Soils are humus-poor sandy soils with low water
91 retention capacities (Várallyay, 1993).

92 The natural vegetation of the study sites represents a mosaic of forest and grassland patches. The
93 grassland component of the vegetation mosaic is mainly formed by open perennial sand grasslands
94 that are dominated by *Festuca vaginata*, *Stipa borysthena*, and *S. capillata*. Other common species
95 include *Alkanna tinctoria*, *Dianthus serotinus*, *Euphorbia seguieriana*, *Fumana procumbens*,
96 *Koeleria glauca*, and *Potentilla arenaria*. The forest component is represented by differently sized
97 patches of juniper-poplar stands. The canopy layer is 15-20 m high and is co-dominated by *Populus*
98 *alba* and *P. × canescens*. The canopy is open, and its cover typically varies between 40 and 70%.
99 The height of the shrub layer is 1-3 m, and its cover usually ranges from 20 to 80%. The most
100 common shrubs are *Crataegus monogyna*, *Juniperus communis*, *Ligustrum vulgare*, and *Rhamnus*
101 *cathartica*. The herb layer is sparse (10-40%) and is composed of species such as *Anthriscus*
102 *cerefolium*, *Carex flacca*, *C. liparicarpos*, *Pimpinella saxifraga*, *Polygonatum odoratum*, and
103 *Stellaria media*, as well as numerous tree and shrub seedlings. The edges are rather narrow, usually
104 with extensive cover of shrubs (mainly *Crataegus monogyna* and *Juniperus communis*) and herbs
105 (e.g., *Calamagrostis epigeios*, *Poa angustifolia*, *Teucrium chamaedrys*). The names of the plant
106 species are according to Király (2009).

107 All study sites are under legal protection. Their current mosaic patterns are a result of the semiarid
108 climate complemented by the extreme soil conditions. Evidence indicates that the spatial arrangement
109 of the forest and grassland patches is stable, and the existence of the grassland component does not
110 depend on grazing, fire, or other forms of disturbances (Fekete, 1992; Erdős et al., 2015). Due to the
111 legal protection, anthropogenic disturbances in the study sites are minimal (a low level of non-
112 destructive research and strictly regulated tourism). Natural disturbances include the effects of
113 grazers and browsers (*Capreolus capreolus*, *Cervus elaphus*, *Dama dama*, and *Lepus europaeus*) as
114 well as the activity of burrowing animals (*Meles meles*, *Talpa europaea*, and *Vulpes vulpes*), but their
115 influence on the forest-grassland balance is presumably negligible. During the last decades, wildfire
116 occurred in only one of the study sites but areas affected by the fire event were not sampled during
117 our study.

118 **2.2 Vegetation sampling**

119 Within each site, we distinguished six habitat types: large forest patches (> 0.5 ha), medium forest
120 patches (0.2-0.4 ha), small forest patches (< 0.1 ha), north-facing forest edges, south-facing forest
121 edges, and grasslands. Within each habitat, 25-m² plots were established. This size is small enough
122 to sample even the smallest forest patches but large enough for a standard coenological relevé. The
123 plot shape was 5 m × 5 m in the forest patches and grasslands, while we used 2 m × 12.5 m plots at
124 the edges to ensure that the plots did not extend into forest or grassland interiors. Previous studies
125 suggested that plot shape does not have distorting effects on the results at this scale (Keeley and
126 Fotheringham, 2005; Bátori et al., 2018). An edge was defined as the zone outside of the outermost
127 tree trunks but still under the canopy. For edge plots, only forest patches > 0.2 ha were taken into
128 consideration.

129 We sampled a total of 176 plots: 27 plots in large forest patches, 29 plots in medium forest patches,
130 and 30 plots each in small forest patches, north-facing edges, south-facing edges, and grasslands.
131 Within each plot, the percentage cover of all vascular plant species of each vegetation layer was
132 estimated visually in April and July 2016. For each species, the largest cover value was used for
133 subsequent data analyses. Percentage cover values for all species recorded in the 176 study plots are
134 given in Supplementary Data A1.
135

136 **2.3 Data analyses**

137 We performed Non-metric Multidimensional Scaling (NMDS) to two dimensions, a robust
138 unconstrained ordination method widely applied in community ecology (Minchin, 1987), based on
139 the presence-absence data of the species, using the Sørensen–Dice index. For the analysis, the 'vegan'
140 R package (Oksanen et al., 2018) was used. Several (minimum 500, maximum 5000) NMDSs were
141 run from random starts to facilitate convergence to a non-local optimum. The result was visualized
142 using centering, half-change scaling and rotation to the axes of Principal Components Analysis
143 (PCA), hence the variance of the points is maximized on the first dimension.

144 To visualize the overlaps of the six studied habitats and assess their distinctness, we applied the
145 technique of Lex et al. (2014). This method shows the number of species restricted to certain habitat
146 types (i.e., habitat distinctness) as well as the number of species present in two or more habitats (i.e.,
147 habitat overlaps). Calculations were performed in MS Excel, and the graphs were prepared with
148 Adobe Photoshop 7.0.

149 We calculated the mean ecological indicator values for temperature, soil moisture, and light
150 availability for each plot. We used the indicator values of Borhidi (1995), which are based on the
151 values of Ellenberg (1992) but extended for the Carpathian Basin. As proven by numerous field
152 measurements, ecological indicator values are able to provide reliable estimates of site conditions
153 (e.g., Schaffers and Sýkora, 2000; Dzwonko, 2001; Tölgyesi et al., 2014). Although the use of mean
154 indicator values is often criticized, it has been shown that they perform well and have a solid
155 theoretical basis (ter Braak and Gremmen, 1987; Diekmann, 2003). Ecological indicator values
156 provide important information as they integrate fluctuating values over time (rather than providing
157 data for a very short period) and reflect site conditions in relation to species' requirements (rather
158 than the mere absolute values of environmental parameters) (Zonneveld, 1983; Bartha, 2002;
159 Diekmann, 2003).

160 Linear mixed effects models were used to test for the effects of habitat type on the mean indicator
161 values of temperature, soil moisture and light availability. We used site as a random effect in the
162 analyses. The statistical tests were implemented using the nlme R package (Pinheiro et al., 2013).

163 The fulfillment of the normality and homoscedasticity assumptions of the models were checked by
164 visual assessments of diagnostic plots. As model residuals showed heterogeneity of variances, we
165 used a variance structure that allowed for different residual spreads for each level of explanatory
166 variable according to Zuur et al. (2009). Tukey's HSD tests were implemented for post hoc pairwise
167 comparisons of the habitat categories using the multcomp R package (Hothorn et al., 2008).

168 Species were classified into life-form categories, geoelement types, and phytosociological preference
169 groups. The categorizations were based on Horváth et al. (1995) and Borhidi (1995). Geoelement
170 types reflect the global distribution of species, while phytosociological preference groups describe
171 the regional preferences of species to certain plant communities. For phytosociological preferences,
172 only the native species were considered, as non-natives tend to have indefinite preferences. The
173 frequency distributions were calculated for all three categorizations for each habitat and were
174 compared using Pearson's chi-squared test.

175 All statistical analyses were performed in the R statistical environment ver. 2.15.2 (R Development
176 Core Team, 2010).

177 **3 Results**

178 In the 176 plots, a total of 232 vascular plant species were found. The NMDS converged after 2267
179 tries and 90 iterations, achieving a stress value of 0.1784. The ordination revealed that the habitats
180 were aligned in the ordination space following the sequence large forest patches – medium forest
181 patches – small forest patches – north-facing edges – south-facing edges – grasslands (Figure 1). The
182 species turnover was mostly gradual. Although the grassland habitat formed a relatively distinct
183 group, its species composition showed some overlap with that of the south-facing edges.

184 A considerable number of species were shared among all habitats (Figure 2). Woody habitats (i.e.,
185 forest patches plus forest edges) were strongly related, as shown by the high number of common
186 species. The number of species restricted to single habitat types was also numerous, especially for
187 north-facing edges, although grasslands, small forest patches and south-facing edges also had
188 considerable numbers of species that did not occur elsewhere.

189 The total (i.e., pooled) number of species was the highest in north-facing edges (Figure 2), followed
190 by south-facing edges and small forest patches. Medium forest patches had fewer species, while large
191 forest patches and grasslands had the lowest total number of species.

192 Habitat type significantly influenced the mean ecological indicator values for temperature ($F_{5,165} =$
193 92.55 , $P < 0.001$), soil moisture ($F_{5,165} = 157.325$, $P < 0.001$), and light availability ($F_{5,165} =$
194 226.47 , $P < 0.001$). The mean ecological indicators for temperature showed that large and medium
195 forest patches had the lowest, while grasslands had the highest values (Figure 3a). Small forest
196 patches, north-facing forest edges and south-facing forest edges were intermediate, but their values
197 were similar to those of the large and medium forest patches. The mean ecological indicators for soil
198 moisture showed a continuously decreasing trend from the large and medium forest patches to the
199 grassland, which had the lowest values (Figure 3b). Regarding the mean ecological indicators for
200 light availability, there was a well-defined, gradually increasing trend from the large forest patches
201 towards grasslands (Figure 3c).

202 Pearson's chi-squared test showed that the frequency distributions of the life-form categories,
203 geoelement types, and phytosociological preference groups in the six habitat types were different
204 ($\chi^2 = 635.2$, $df = 30$, $P < 0.001$; $\chi^2 = 339.2$, $df = 25$, $P < 0.001$; $\chi^2 =$

205 587.8, $df = 25$, $P < 0.001$, respectively). There was a continuous change in the life-form categories
206 from the large forest patches towards the grasslands (Figure 4a). Large and medium forest patches
207 did not differ significantly from each other, nor did small forest patches from north-facing edges. The
208 proportions of shrubs and trees decreased towards the grasslands. Therophytes were most frequent in
209 grasslands, while hemicryptophytes reached the maximum value in north-facing edges.

210 The large forest patches were dominated by European and Eurasian species, the proportion of which
211 became progressively smaller towards the grasslands (Figure 4b). In contrast, the proportion of
212 continental species showed a reverse pattern. Other geoelements generally had a subordinate role.
213 The grasslands contained the highest number of endemics and the lowest number of adventives.

214 The proportion of forest-related species showed a decreasing trend from the large forest patches
215 towards the grasslands (Figure 4c). Species related to grasslands showed an opposite trend.
216 Indifferent species (i.e., species with preferences towards multiple plant communities) played an
217 important role in all studied habitats, but their proportion was the highest in medium forest patches.

218 **4 Discussion**

219 The components of forest-grassland mosaic ecosystems are conveniently classified into two basic
220 categories: forest and grassland. The categorization is based on the dominant life-forms, but it
221 correlates with numerous other characteristics, both biotic and abiotic (e.g. Breshears, 2006; Innes et
222 al., 2013; Luza et al., 2014). While this categorization may be acceptable for some purposes, recent
223 evidence has suggested that forest-steppes should not be regarded as simple two-phase systems
224 (Erdős et al., 2018b).

225 Our study revealed a clear gradient regarding the studied characteristics. There was a mostly gradual
226 species turnover from large forest patches to grasslands and gradual changes regarding ecological
227 indicator values and functional species groups. Edges proved to be transitional between the forests
228 and the grasslands, with south-facing edges being more similar to grasslands. Small forest patches
229 represented a transition between medium forest patches and edges. Total species number peaked near
230 the middle of the gradient, i.e., in north-facing edges.

231 In concordance with the mean ecological indicator values calculated in our study, earlier studies have
232 also shown that forest interiors have lower temperature, and higher soil moisture than the
233 neighboring treeless areas (Davies-Colley et al., 2000; Mosquera et al., 2014; Schmidt et al., 2017),
234 whereas edges are generally intermediate regarding the above parameters (Kapos, 1989; Gehlhausen
235 et al., 2000; Mosquera et al., 2014; Schmidt et al., 2017). In addition, we found that the indicator
236 values of north-facing edges resembled those of the forest patches, which is in line with the findings
237 of Matlack (1993). In contrast, the indicator values of south-facing edges were the most similar to
238 those of the grasslands. Ries et al. (2004) predicted that south-facing edges should deviate from
239 forest interiors more than north-facing ones, due to the larger exposure to sunlight. Thus it seems
240 likely that the studied habitats represent a continuous gradient of environmental factors, ranging from
241 the largest forest patches to the open grasslands. This may have extremely important consequences.
242 Forest-steppes have very high species richness (Zlotin, 2002; Erdős et al., 2018a) and habitat
243 heterogeneity has been suggested as an important driver of this high species diversity (Tölgyesi et al.,
244 2018; Erdős et al., 2018b). Our results reinforce and complement these findings, emphasizing that a
245 large number of species can find appropriate habitats somewhere along the gradient, provided that the
246 full range of heterogeneity is preserved in the mosaic.

247 For most of the studied characteristics, small forest patches were similar to north-facing edges. This
248 result indicates that small forest patches are edge-like habitats; that is, they are too small to have a
249 core area. It has been shown that the microclimate of the outer areas of forest patches is strongly
250 influenced by a width of dozens of meters (Ries et al., 2004; Hennenberg et al., 2008; Dodonov et al.,
251 2013; Schmidt et al., 2017).

252 As shown by the geoelement spectra, the sandy forests in our study region are dominated by
253 European and Eurasian species, while the sandy grasslands are richer in continental species. This
254 phenomenon can be explained by biogeographic causes. Deciduous forests extend as a wide belt from
255 Western Europe to Inner Asia (Walter and Breckle, 1989; Schultz, 2005). In contrast, natural
256 grasslands occur from eastern Europe to the Far East, while most Central and Western European
257 grasslands are secondary and depend on human activities such as grazing and mowing. The
258 grasslands in the Carpathian Basin may be understood as the westernmost extensions of the
259 continental grasslands.

260 The sequence of habitats revealed in this study may be termed a coenocline (Whittaker, 1967, 1975).
261 The existence of a quite continuous gradient of the studied habitats suggests that the dichotomic
262 categorization of forest-steppe habitats into forest and grassland patches is a serious and misleading
263 oversimplification, as it is a poor representation of the real heterogeneity of the forest-steppe
264 ecosystem. We believe that forest-steppe patterns better fit the gradient-based paradigm of landscape
265 structure (Cushman et al., 2005; McGarigal and Cushman, 2005), which, rather than using
266 dichotomic categorizations, is able to reflect more continuous variations. More specifically, by using
267 the forest vs. grassland categories, all forest patches (irrespective of their sizes), and the edges are
268 classified into the forest category, disregarding the variability among them, which results in a loss of
269 information (Cushman et al., 2005). Thus, looking beyond the forest-grassland dichotomy seems
270 necessary for a better and more correct understanding of forest-steppe ecosystems. Our study
271 indicates that the gradient-based paradigm may prove useful in other forest-grassland mosaic
272 ecosystems such as savannas, wood pastures, or prairie-forest ecotones. Similarly, the gradient-based
273 approach can be of importance in forest ecosystems suffering from heavy anthropogenic
274 fragmentation.

275 Regarding the vegetation gradient revealed in this study, the question emerges as to what the drivers
276 of this gradient are. In the sand dune areas of the Kiskunság region, background factors such as
277 groundwater depth, soil moisture content, and microclimatic parameters strongly depend on terrain
278 features (e.g., Bátori et al., 2014; Tölgyesi et al., 2014). However, both our field experience and
279 earlier research (e.g., Halupa, 1967; Bölöni et al., 2011) show that patches of poplar forests can be
280 found in various topographical positions: on sand dune tops and ridges, on windward and leeward
281 dune slopes, and in dune slacks, even though these positions differ strongly in terms of abiotic
282 parameters. In other words, there is no apparent relation between the presence of differently sized
283 forest patches and current environmental parameters. The probable explanation for this is twofold.
284 First, the horizontal roots of *Populus alba* may extend up to 40 m or more (Magyar, 1961; Halupa,
285 1967; Szodfridt, 1969). Thus, trees situated in a hostile environment (such as a dry dune ridge) are
286 able to reach soils with a higher humus content and better moisture supply (for example, in a dune
287 slack). Second, forest patches sometimes depend on one or more humus layers buried under the sand
288 (Szodfridt, 1969; Halupa, 1967; Bodrogekőzy, 1982; Molnár, 2003). These buried layers originate
289 from earlier vegetation periods, as the wind has re-deposited the sand dunes several times during the
290 Holocene (Molnár, 2009; Molnár et al., 2012). In summary, the current pattern of differently sized
291 forest patches may reflect an earlier sand dune topography and associated environmental parameters.

292 Our study has focused on forest habitats, analysing only one grassland type, the open perennial sand
293 grassland, which dominates the study sites. Other herbaceous habitats play a subordinate role in the
294 study sites. It can be assumed that non-forest habitats also form a gradient. For example, *Salix*
295 *rosmarinifolia* subshrub communities occur mainly in dune slacks with favorable water availability
296 (Bodrogekőzy, 1982; Borhidi et al., 2012). Closed sand steppes thrive under semi-dry conditions
297 (Borhidi et al., 2012) and have been shown to be compositionally related to forest edges (Erdős et al.,
298 2013), while open perennial sand grasslands and annual sand grasslands live under the harshest
299 circumstances. Also, there may be considerable differences between the differently sized grasslands,
300 with the smallest grassland patches of natural openings resembling forest edges (Molnár, 1998). The
301 possible gradient-like arrangement of non-forest communities in the studied mosaic ecosystem calls
302 for further studies to understand forest-steppe heterogeneity in the frame of the gradient-based
303 paradigm of landscape structure.

304 **5 Conflict of Interest**

305 The authors declare that the research was conducted in the absence of any commercial or financial
306 relationships that could be construed as a potential conflict of interest.

307 **6 Author Contributions**

308 LE, GK-D, and PT conceived the research idea. LE, GK-D, ZB, CT, PT, and PJK collected the data.
309 KS, ÁB-F, CT, and PJK performed the statistical analyses. LE and PT, with contributions from GK-
310 D, wrote the paper. All authors discussed the results and commented on the manuscript.

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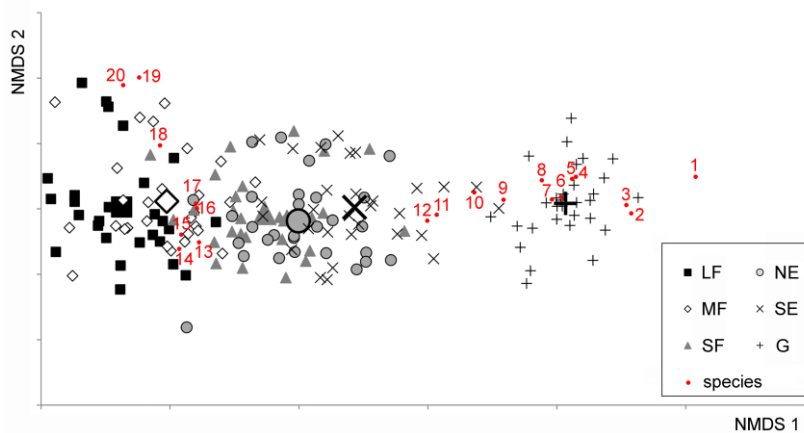
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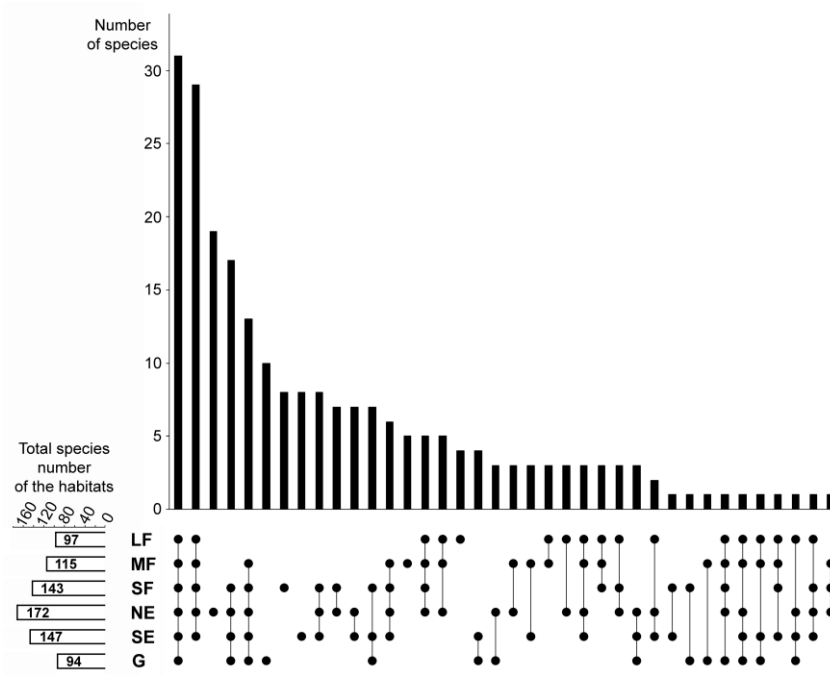
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483 Figures



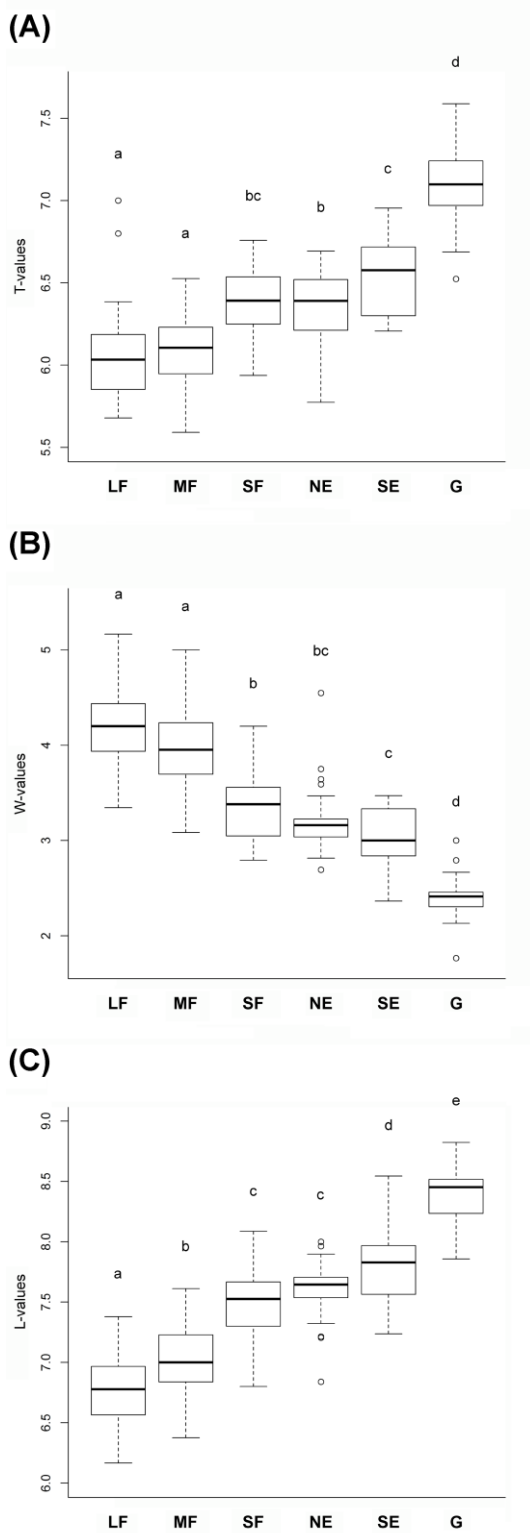
484

- 485 **Figure 1.** NMDS ordination scatterplot of the 176 plots. Only the top 20 species, according to the
486 correlation to the ordination space (i.e., square root of the goodness of fit), are displayed. LF: large
487 forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE:
488 south-facing edges, G: grasslands. The centroids for each habitat are drawn with larger signs. Species
489 are as follows: 1: *Kochia laniflora*, 2: *Erophila verna*, 3: *Alkanna tinctoria*, 4: *Crepis rheoadifolia*, 5:
490 *Polygonum arenarium*, 6: *Holosteum umbellatum*, 7: *Poa bulbosa*, 8: *Syrenia cana*, 9: *Arenaria*
491 *serpyllifolia*, 10: *Euphorbia seguieriana*, 11: *Stipa borysthenica* + *capillata*, 12: *Festuca vaginata*,
492 13: *Ligustrum vulgare*, 14: *Berberis vulgaris*, 15: *Rhamnus catharticus*, 16: *Celtis occidentalis*, 17:
493 *Crataegus monogyna*, 18: *Bromus sterilis*, 19: *Stellaria media*, 20: *Anthriscus cerefolium*.



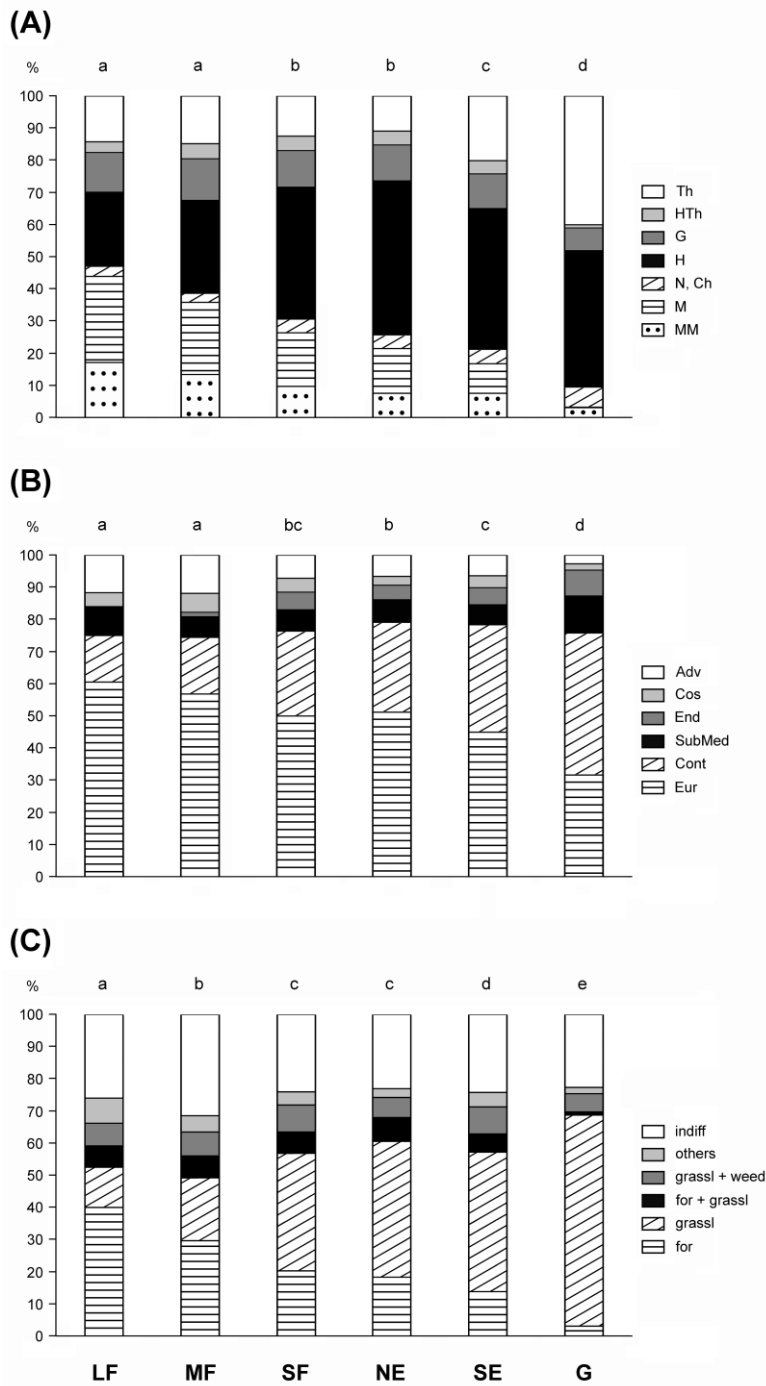
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495 **Figure 2.** Relationships among the studied habitats in terms of species composition overlaps and
 496 distinctness. The upper panel shows the number of those species that were found in the habitats
 497 indicated by the dots in the lower panel. For example, the first column shows that there are 31 species
 498 that were found in all six habitats, whereas the third column shows that there are 19 species which are
 499 restricted to the north-facing grassland habitat. The small panel in the bottom left corner shows the
 500 total (i.e., pooled) number of species in each habitat. LF: large forest patches, MF: medium forest
 501 patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.



502

503 **Figure 3.** Mean ecological indicator values for (A) temperature, (B) soil moisture, and (C) light
504 availability for the studied habitats. The habitats not sharing a letter are significantly different. LF:
505 large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges,
506 SE: south-facing edges, G: grasslands.



507

508 **Figure 4.** Frequency distributions for (A) life-form categories, (B) geoelement types, and (C)
 509 phytosociological preference groups of the six studied habitats. Th: therophytes, HTh:
 510 hemitherophytes, G: geophytes, H: hemicryptophytes, N: nanophanerophytes, Ch: chamaephytes, M:
 511 microphanerophytes, MM: meso- and megaphanerophytes; Adv: adventives, Cos: cosmopolitans,
 512 End: endemics, SubMed: submediterranean species, Cont: continental species, Eur: European and
 513 Eurasian species; indiff: indifferent species, others: species of edges, scrubs, and disturbed
 514 communities, grassl+weed: species related to grasslands and weed communities, for+grassl: species
 515 commonly found in forests and grasslands, grassl: grassland-related species, for: forest-related
 516 species; LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-

517 facing edges, SE: south-facing edges, G: grasslands. The habitats not sharing a letter over the bars are
518 significantly different.