

39 sandy forest-grassland ecosystems should be prioritized for protection and that scattered
40 trees or groups of trees of native species should be established in extensive treeless
41 grasslands.

42

43 *Key-words:* air humidity, air temperature, climate change, drought, forest edges, forest-
44 steppes, grasslands, vapor pressure deficit (VPD).

45

1. Introduction

Globally, increasing temperature has been observed during the last few decades, and this trend is expected to continue in the 21st century (IPCC, 2018), potentially having severe consequences on the structure, composition, and function of plant communities (Suggitt *et al.*, 2011; Bellard *et al.*, 2012; Hofmeister *et al.*, 2019; Aalto *et al.*, 2022). This tendency is seriously threatening biodiversity as it may result in species and habitat loss (Kappelle *et al.*, 1999; Araújo *et al.*, 2011; Bellard *et al.*, 2012; Erdős *et al.*, 2018a). Climate change has been reported to have a major effect on vegetation dynamics globally (Bakkenes *et al.*, 2002; Walther *et al.*, 2002; Krishnaswamy *et al.*, 2014; Zhan *et al.*, 2022). Although responses of plant communities to climate change are hard to predict, ecosystems that are fragmented either by natural processes or artificially-induced factors could be especially sensitive (Kertész and Mika, 1999; Bartha *et al.*, 2008; Travis *et al.*, 2003; Erdős *et al.*, 2018b).

In the northern hemisphere, the most noticeable naturally fragmented ecosystems are forest-steppes, composed of woody and herbaceous patches (Erdős *et al.*, 2018b). It is reasonable to assume that increasing temperature and decreasing precipitation considerably inhibit the growth of woody vegetation in these ecosystems (Erdős *et al.*, 2022). A drying tendency has been observed, and is expected to become more serious in the future, in the Carpathian Basin, particularly in the Kiskunság (central Hungary) (Bartholy *et al.*, 2007; 2014; Blanka *et al.*, 2013), where forest-steppe forms the natural vegetation. The global drying tendency is additionally exacerbated by regional processes. For example, afforestation (especially with non-native evergreen trees) and the spontaneous spread of invasive species are further reducing water level in the Kiskunság (Tölgyesi *et al.*, 2020). Indeed, the groundwater level is currently declining in the whole area (Bíró *et al.*, 2007; Szabó *et al.*, 2022) resulting in the increasing mortality rate of mature oak trees in forest patches (Molnár, 2003; Molnár *et al.*, 2012).

Microclimate can be defined as the climate condition near the ground level at a small scale, ranging from centimeters to several hundred meters (Davies-Colley *et al.*, 2000; Zellweger *et al.*, 2019; De Frenne *et al.*, 2021). It is likely to regulate plant survival, growth, distribution, and interaction (Arnone *et al.*, 2008; Dingman *et al.*, 2013; De Frenne *et al.*, 2021; Meeussen *et al.*, 2021) and has a significant impact on ecosystem processes such as vegetation dynamics and nutrient cycles (Davies-Colley *et al.*, 2000; Riutta *et al.*, 2012; Schmidt *et al.*, 2019). Air temperature and relative air humidity are the most important microclimate components, which have a profound impact on vegetation under extreme environmental conditions (Sih *et al.*, 2000; Erdős *et al.*, 2014, 2018a; De Frenne *et al.*, 2021). In addition, vapor pressure deficit (VPD), obtained from air temperature and humidity, has a noteworthy influence on how much water is necessary for plants to grow optimally (Şahin *et al.*, 2013; Süle *et al.*, 2020). The relationship between water and plant is extremely sensitive to environmental extremes (e.g., drought events or heat waves), resulting in an increase of VPD that hastens faster plant transpiration into the atmosphere (Reyer *et al.*, 2013). Hence, VPD is considered an important limiting factor for plant

91 survival, growth, and regeneration with ongoing climate change (*Breshears et al.*,
92 2013; *Will et al.*, 2013; *Williams et al.*, 2013).

93 It is well known that vegetation has a significant effect on the climate
94 conditions near the surface (*Geiger et al.*, 2009). Previous works have indicated that
95 microclimatic differences among various habitat types may become more
96 pronounced under climate change, and that canopy cover plays an important role in
97 buffering harsh environmental conditions (*Suggitt et al.*, 2011; *Ashcroft and Gollan*,
98 2012; *Hardwick et al.*, 2015). According to *De Frenne et al.* (2013), microclimate,
99 rather than macroclimate, may be a better predictor of how well canopy cover
100 mitigates extreme temperature. This is especially relevant in ecosystems where tree-
101 dominated and grass-dominated habitats coexist under the same macroclimatic
102 condition. Although microclimate measurements in anthropogenically fragmented
103 ecosystems have received considerable scientific attention (*Chen et al.*, 1993, 1995;
104 *Pohlman et al.*, 2009; *Wright et al.*, 2010; *Luskin and Potts*, 2011; *Magnago et al.*,
105 2015; *Schmidt et al.*, 2019), knowledge of microclimate variables in naturally
106 fragmented vegetation types (e.g., forest-steppes) have received less attention in
107 previous studies (but see *Erdős et al.*, 2014; *Süle et al.*, 2020).

108 Forest-steppes are structured by the co-occurrence of differently sized forest
109 and grassland patches of various types, connected by an intricate network of
110 differently exposed edges (*Erdős et al.*, 2018b). As a result of varying vegetation
111 cover among the habitats in forest-steppes, microclimate can vary significantly even
112 over short distances (*Erdős et al.*, 2023). Vegetation-environment relations have
113 been intensively studied recently, with special emphasis on soil moisture, air
114 humidity, and air temperature patterns (e.g., *Bátori et al.*, 2014; *Erdős et al.*, 2014,
115 2018a; *Tölgyesi et al.*, 2018). However, earlier investigations measured
116 microclimate parameters for only a very short period (typically 24 hours on a
117 selected summer day) in forest-steppes (*Erdős et al.*, 2014, 2018a; *Tölgyesi et al.*,
118 2018; *Milošević et al.*, 2020). These short-term measurements may not be able to
119 capture the most critical microclimatic conditions. To gain more informative
120 microclimate background data, repeated measurements are needed throughout the
121 vegetation period, from spring to autumn. Furthermore, earlier studies did not take
122 into account the full variety of forest-grassland mosaics: some works disregarded
123 the edge habitat (e.g., *Tölgyesi et al.* 2018; *Milošević et al.* 2020), while others
124 restricted their attention to small forest patches and a single type of grassland (e.g.,
125 *Erdős et al.* 2014; *Süle et al.* 2020). Thus, measuring microclimate in a broader
126 spectrum of near-natural forest-steppe habitats is necessary to fill the above
127 knowledge gap.

128 The aim of this study was to describe the microclimate conditions of multiple
129 habitat types throughout the vegetation period, in a sandy forest-steppe ecosystem.
130 Our specific questions were the following: (1) How do air temperature and humidity
131 differ among the studied habitats during the growing season from April to October?
132 (2) Which habitats are more stressed to vegetation growth in terms of vapor pressure
133 deficit?
134

135 **2. Materials and methods**

136

137 2.1. Study area

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139 The study was conducted in the Kiskunság Sand Ridge, a large plain between the
140 Danube and Tisza rivers in central Hungary. For the study, an area near Fülöpháza
141 (N 46° 51'; E 19° 25'), located in the center of the Sand Ridge, has been chosen (*Fig.*
142 *1*). This area is part of the Kiskunság National Park. The climate is subcontinental
143 with a sub-Mediterranean influence, the mean annual temperature and precipitation
144 are 10.5 °C and 530 mm, respectively (*Dövényi*, 2010). The study site is made up of
145 calcareous sand dunes that are covered by humus-poor sandy soils with low water
146 retention capacity; however, humous sandy soils with slightly better moisture supply
147 are found in forest patches (*Várallyay*, 1993).

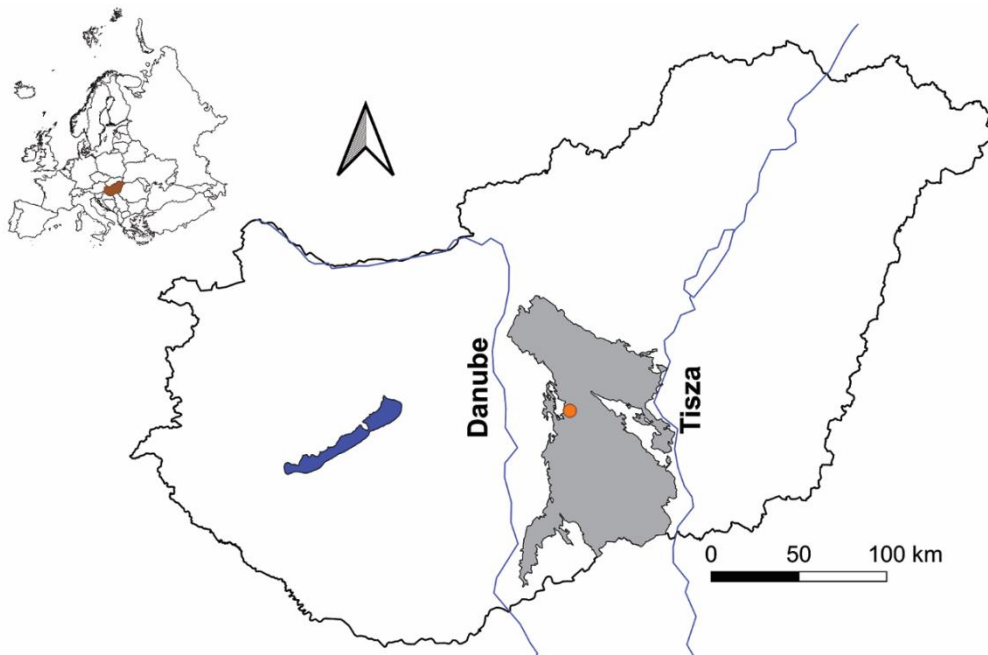
148 The natural vegetation of the area is a mosaic of forest and grassland patches
149 (*Fig. 2a, b*). Forests are naturally fragmented, resulting in a variety of forest patches
150 ranging in size from a few dozen square meters to ca. one hectare. Three differently
151 sized forest groups were defined in this study: large forest patches (> 0.5 ha), medium
152 forest patches (0.2–0.4 ha), and small forest patches (< 0.1 ha) (*Fig. 2c-e*). Forest
153 stands (*Junipero-Populetum albae*) have a canopy cover of approximately 50-70%
154 and are dominated by *Populus alba* trees, with a height of 10-15 m. The shrub layer,
155 with covers of 5-80% and heights of 1-5 m, is structured by *Berberis vulgaris*,
156 *Crataegus monogyna*, *Ligustrum vulgare*, and *Rhamnus catharticus*. The herb layer
157 is typically composed of *Asparagus officinalis*, *Calamagrostis epigeios*, *Carex*
158 *liparicarpos*, *Euphorbia cyparissias*, and *Poa angustifolia*.

159 Edge is defined as the zone out of the outmost trunks of trees, below the canopy
160 layer. The edges are commonly covered by shrubs (mainly *Crataegus monogyna*,
161 *Juniperus communis*, and *Ligustrum vulgare*) and herbaceous species (primarily
162 *Calamagrostis epigeios*, *Cynoglossum officinale*, *Festuca vaginata*, and *Poa*
163 *angustifolia*). In this study, only north- and south-facing edges were considered (*Fig.*
164 *2f, g*) as they are expected to have significantly different environmental conditions
165 (*Stoutjesdijk and Barkman*, 1992; *Ries et al.*, 2004; *Heithecker and Halpern*, 2007).

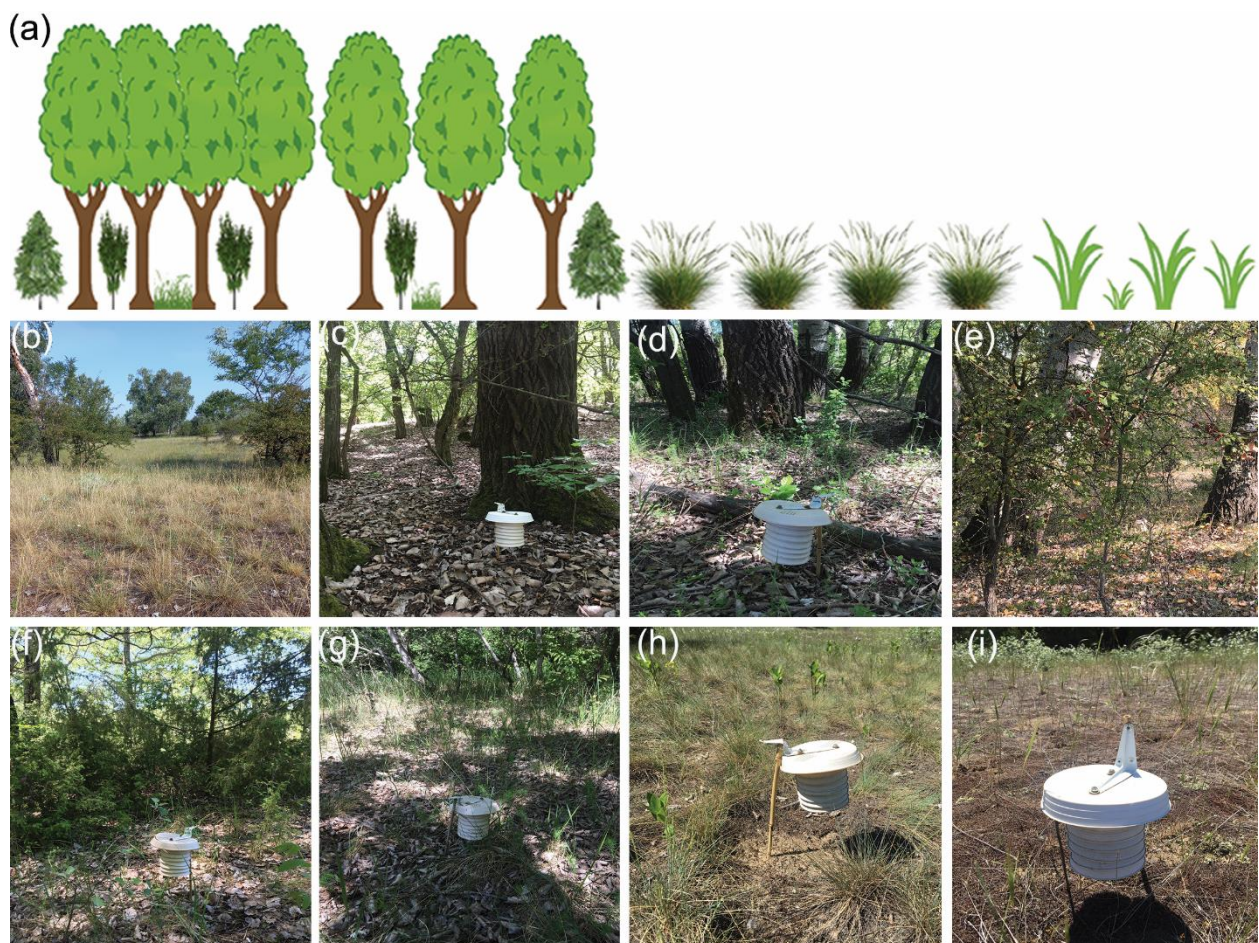
166 The most conspicuous grassland in the study area is open perennial grassland
167 (*Festucetum vaginatae*), with a total vascular plant cover of ca. 50–70% (*Fig. 2h*).
168 *Festuca vaginata*, *Stipa borysthena*, and *S. capillata* are dominant species in this
169 grassland type. Other common species include *Alkanna tinctoria*, *Arenaria*
170 *serpyllifolia*, *Centaurea arenaria*, and *Holosteum umbellatum*.

171 Open annual grasslands (*Secali sylvestris-Brometum tectorum*) are co-
172 dominated by *Bromus tectorum* and *Secale sylvestre*, having a cover of
173 approximately 20-50% (*Fig. 2i*). Other typical species occurring in this grassland
174 include *Bromus squarrosus*, *Poa bulbosa*, *Polygonum arenarium*, *Syrenia cana*, and
175 *Tragus racemosus*. Detailed information about the vegetation of forests, edges, and
176 grasslands in the Kiskunság Sand Ridge is provided in the previous study of *Erdős*
177 *et al.* (2023).

178 The names of vascular plant taxa are according to *Király* (2009), while plant
179 community names follow *Borhidi et al.* (2012).



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 181 *Fig. 1.* The location of the Fülöpháza area (orange dot) in the Kiskunság Sand Ridge (grey), central
 182 Hungary.
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184
 185 *Fig. 2.* (a) The model of forest-steppes, and (b) a mosaic of forests and grasslands at the Fülöpháza
 186 area. The following seven habitat types were included in this study: (c) large forest patch, (d)
 187 medium forest patch, (e) small forest patch, (f) north-facing forest edge, (g) south-facing forest edge,
 188 (h) open perennial grassland, and (i) open annual grassland.
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190 2.2. Data collection

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192 Microclimate measurements were carried out in the seven habitat types described
193 above (i.e., large forest patches, medium forest patches, small forest patches, north-
194 facing forest edges, south-facing forest edges, open perennial grasslands, and open
195 annual grasslands). Three replicates for each habitat type were used. The air
196 temperature (°C) and relative air humidity (%) were measured once every month in
197 all seven habitats from April to October 2022. They were measured synchronously
198 20 cm above the ground surface in the center of each habitat for 24 hours (i.e., a day
199 per month) using MCC USB-502 data loggers (Measurement Computing
200 Corporation, Norton, MA, USA). The resolution of the sensors was set to once every
201 minute; therefore, each sensor yielded 1440 temperature and 1440 humidity data
202 records per day. The loggers were placed in naturally ventilated radiation shields in
203 order to avoid direct solar radiation. The sampling occasions were selected under
204 clear weather conditions, but the weather was cloudy during the second daytime
205 periods of July and was rainy during the first couple of hours during September.
206

207 2.3. Data analysis

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209 The following variables were computed from the obtained microclimate data: mean
210 daily air temperature (MDAT), mean daytime air temperature (MDtAT), mean
211 nighttime air temperature (MNtAT), mean daily relative air humidity (MDAH), mean
212 daytime relative air humidity (MDtAH), and mean nighttime relative air humidity
213 (MNtAH). Daytime was defined as the interval from 7:01 a.m. to 7:00 p.m., while
214 nighttime was the interval from 7:01 p.m. to 7:00 a.m. (see *Bátori et al.*, 2014; *Erdős*
215 *et al.*, 2014, 2018a). These variables were calculated for each replicate.

216 Vapor pressure deficit was selected as the meaningful limiting factor for plant
217 growth and productivity (*McDowell et al.*, 2008; *Yuan et al.*, 2019; *Süle et al.*, 2020).
218 Vascular plants may be stressed if VPD values exceed a certain threshold (*Novick et*
219 *al.*, 2016; *Shamshiri et al.*, 2018; *Süle et al.*, 2020). This factor (VPD, Pa) was
220 calculated from the air temperature (t , °C) and relative air humidity (H , %) according
221 to *Bolton* (1980):

$$222 \text{VPD} = (100 - H) \times 6.112 \times e^{(17.67 \times t / (t + 234.5))}$$

223
224
225 In this study, the exceedance rate was analyzed, which is the percentage of VPD
226 values above an appropriate threshold (1.2 or 3.0 kPa) over a 24-h period. This
227 approach can help us better understand the microclimatic conditions that affect
228 vegetation growth (*Süle et al.*, 2020). The limiting threshold for the stress effect was
229 set at 1.2 kPa, as suggested by many previous studies (*Novick et al.*, 2016; *Shamshiri*
230 *et al.*, 2018; *Süle et al.*, 2020), whereas 3 kPa threshold had a stronger inhibitory
231 effect on plant growth and photosynthesis (*Shirke and Pathre*, 2004; *Shibuya et al.*,
232 2018; *Süle et al.*, 2020). A VPD duration curve (DC) was constructed using 1440
233 VPD values that were averaged over three replicates collected over the period of 24
234 hours for each habitat per month. This method is similar to the flow duration curve in

235 hydrology and is thoroughly described by *Süle et al.* (2020). In addition, the DC for
236 each replicate was also calculated. Based on this DC, the exceedance rate was
237 calculated per replicate, which was then used for statistical analysis.

238 The variables related to mean daily air temperature, mean daytime air
239 temperature, mean nighttime air temperature, mean daily relative air humidity
240 (MDAH), mean daytime relative air humidity, and mean nighttime relative air
241 humidity, as well as exceedance rate were analyzed using general linear models. The
242 fixed factor was the habitat. The “glm” function in R version 4.1.2 was used to build
243 the models with Gaussian family (*R Core Team*, 2021). The assumptions of the
244 models were checked by visual assessment of diagnostic plots. The general linear
245 models were then tested using analysis of variance (ANOVA) with the “Anova”
246 function in the car package (*Fox and Weisberg*, 2019). If the model had a significant
247 proportion of variability, all pairwise comparisons of the fixed factor levels were
248 performed using the “emmeans” function in the emmeans package in R (*Lenth*,
249 2022). The p-values were adjusted with the false discovery rate (FDR) method.

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251

3. Results

252 *3.1. Air temperature patterns*

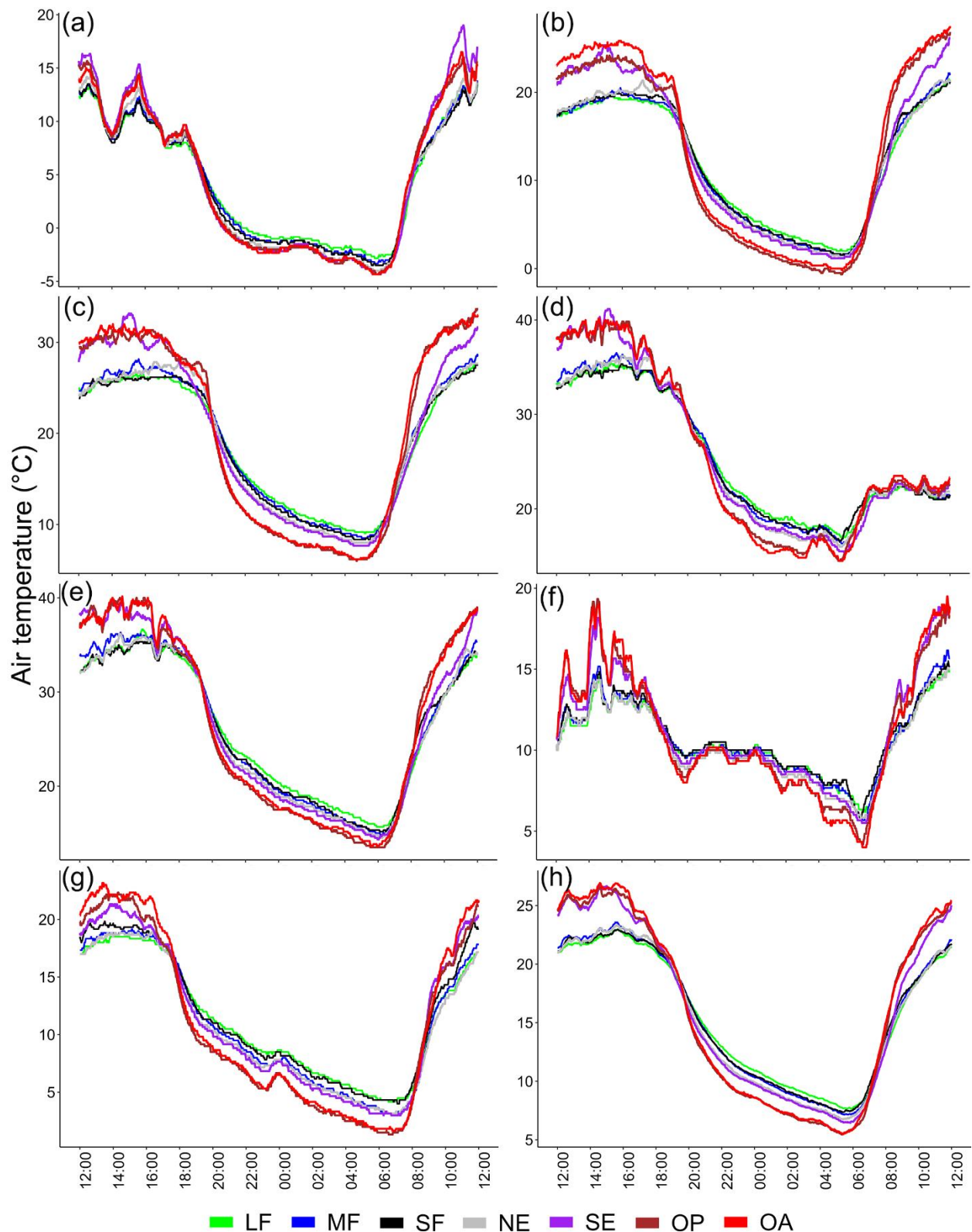
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254 The general 24-hour patterns of air temperature were somewhat similar in all habitats
255 in each month, with a peak around or slightly after noon and a bottom during
256 nighttime (*Fig. 3*). The temperature did not differ largely among habitats in April
257 (*Fig. 3a*), whereas there were larger differences between open grasslands and forests
258 during 24 hours for the other months (*Fig. 3b-g*). A distinct tendency between
259 differently oriented edges was found. South-facing edges had similar patterns to the
260 grasslands during the daytime, but they were closer to the forests at nighttime. North-
261 facing edges resembled forests during the whole day. A similar pattern was observed
262 for the seven-month average (*Fig. 3h*). Temperatures among habitats did not vary
263 largely in the last couple of hours of the July measurement, when the weather was
264 cloudy (*Fig. 3d*), while they fluctuated considerably in the first few hours of the
265 September measurement, when the weather was rainy (*Fig. 3f*).

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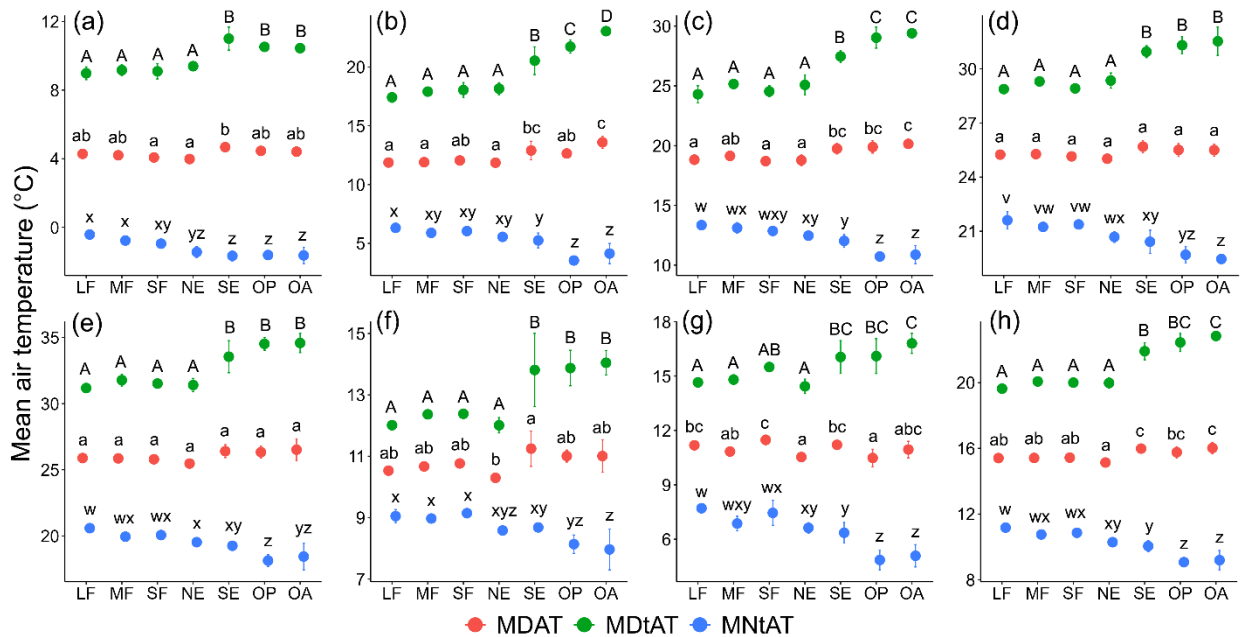


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271 *Fig. 3.* Air temperature values for the various habitat types over a 24-hour period. The values for
 272 each minute are averaged over three replicates. The air temperature values were measured for the
 273 following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October,
 274 and (h) seven-month average. LF: large forest patches; MF: medium forest patches; SF: small forest
 275 patches; NE: north-facing forest edges; SE: south-facing forest edges; OP: open perennial
 276 grasslands; OA: open annual grasslands.

277

278 The mean daily air temperatures were very similar among the habitats in most
 279 measured months, but the daytime and nighttime values were significantly different
 280 among the habitats in each month (*Fig. 4a-g*). The diurnal range values were
 281 remarkably large in all habitats, but the largest values were observed in open perennial
 282 and open annual grasslands. The mean daytime air temperature was the highest in
 283 south-facing edges and open grasslands, while the mean nighttime air temperature
 284 was the lowest in the open grasslands. For the seven-month averaged values, there
 285 was an increasing trend of daytime air temperatures along the vegetation gradient,
 286 while the opposite trend was seen for the nighttime air temperatures (*Fig. 4h*).
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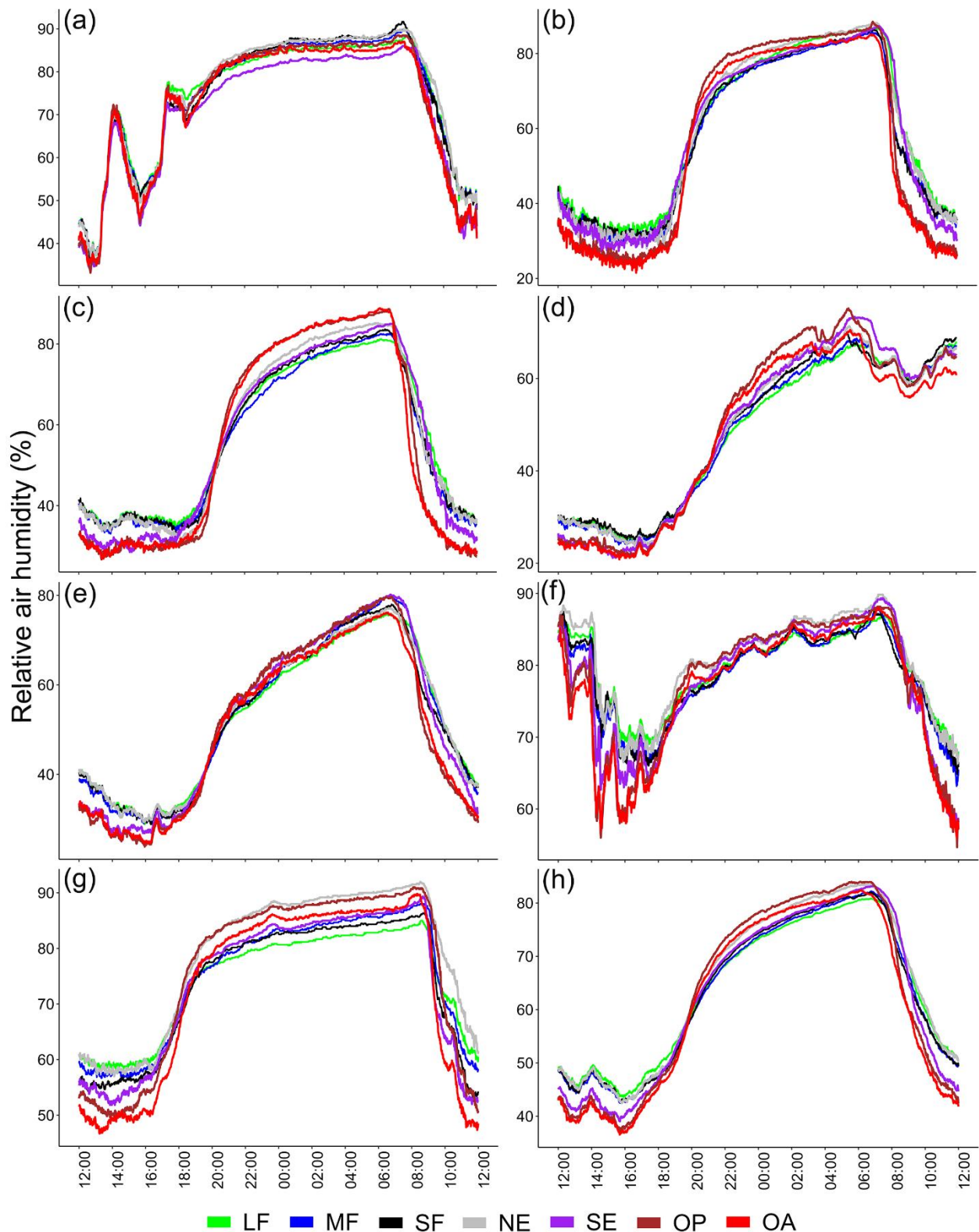


288
 289 *Fig. 4.* Mean daily, daytime, and nighttime air temperature values of the habitat types (mean \pm
 290 standard deviation). The values are averaged over three replicates (large dots). The mean air
 291 temperature values were measured for the following months: (a) April, (b) May, (c) June, (d) July,
 292 (e) August, (f) September, (g) October, and (h) seven-month average. Habitat type abbreviations
 293 are according to the caption of *Fig. 3*. Different letters indicate significant differences among
 294 habitats. MDAT: mean daily air temperature; MDtAT: mean daytime air temperature; MNtAT:
 295 mean nighttime air temperature.
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297 3.2. Relative air humidity patterns

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 299 The 24-hour patterns of relative air humidity showed the opposite trend compared to
 300 air temperature (*Fig. 5*). In April, the values of relative air humidity measured at the
 301 same time were quite similar among habitats, although south-facing edges seemed to
 302 have somewhat lower relative air humidity than the other habitats at nighttime (*Fig.*
 303 *5a*). From May to October, the driest habitats were south-facing edges, open perennial
 304 grasslands, and open annual grasslands during the daytime (*Fig. 5b-g*). However,
 305 open perennial grasslands (and sometimes north-facing edges) were the most humid
 306 during the nighttime. This pattern repeated itself for the seven-month mean (*Fig. 5h*).
 307 The values of air humidity remained high during the second daytime period of July

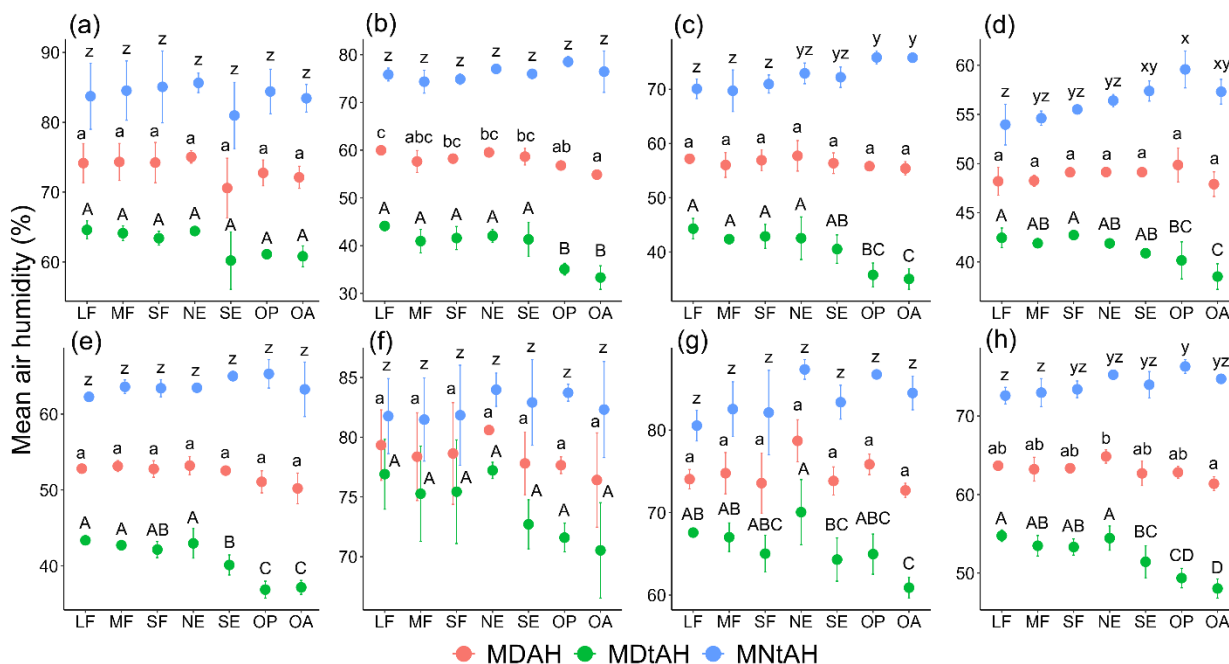
308 (Fig. 5d), whereas humidity fluctuated significantly in the first couple hours of April
 309 and September (Fig. 5a, f).
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311
 312 *Fig. 5.* Relative air humidity values for the various habitat types over a 24-hour period. The values for
 313 each minute are averaged over three replicates. The relative air humidity values were measured for the
 314 following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and
 315 (h) seven-month average. Habitat type abbreviations are according to the caption of *Fig. 3*.
 316

317 The present study showed that, with the exception of May, mean daily air
 318 humidity did not differ significantly among habitats (*Fig. 6*). A similar pattern was
 319 also revealed for the mean nighttime air humidity values, but a peak was shown at
 320 open perennial grasslands in June and July (*Fig. 6c, d*). Regarding mean daytime air
 321 humidity, open grasslands were the driest habitats in most months, followed by south-
 322 facing edges (*Fig. 6a-g*). For the seven-month averaged values, both open grassland
 323 types had the lowest daytime air humidity, while open perennial grasslands had the
 324 highest air humidity at night (*Fig. 6h*). Rain generated a very similar but more
 325 pronounced jittering in the air humidity data as in the air temperature.

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327

328 *Fig. 6.* Mean daily, daytime, and nighttime air humidity values of the habitat types (mean \pm
 329 standard deviation). The values are averaged over three replicates (large dots). The mean air
 330 humidity values were measured for the following months: (a) April, (b) May, (c) June, (d) July,
 331 (e) August, (f) September, (g) October, and (h) seven-month average. Habitat type abbreviations
 332 are according to the caption of *Fig. 3*. Different letters indicate significant differences among
 333 habitats. MDAH: mean daily air humidity; MDtAH: mean daytime air humidity; MNtAH: mean
 334 nighttime air humidity.

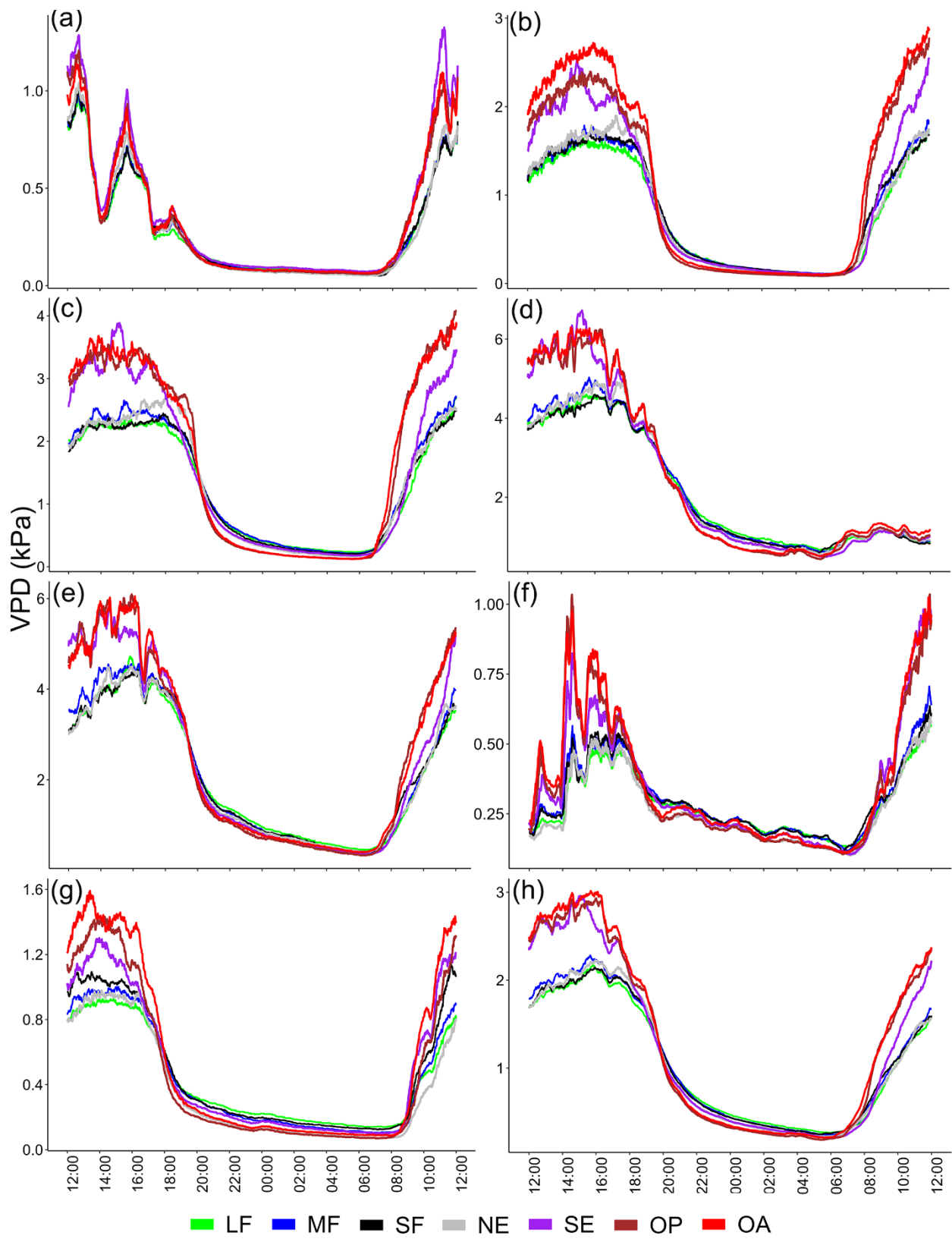
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336 3.3. The patterns of vapor pressure deficit (VPD)

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338 The VPD values calculated over 24-hours for each month and the seven-month
 339 average were quite high around noon but quite low during the nighttime (*Fig. 7a-h*).
 340 During the daytime, the VPD values of the woody habitats (i.e., forests and edges)
 341 were consistently lower than those of open grasslands, with the exception of April.
 342 Interestingly, the south-facing edges had higher VPD values than other woody
 343 habitats and had a similar trend to grasslands, while north-facing edges seemed
 344 similar to forest interiors. The VPD values were extremely high in the summer
 345 season (from June to August), especially in July and August. There were no large
 346 differences among habitats at nighttime. A prominent effect of rain and cloudy sky

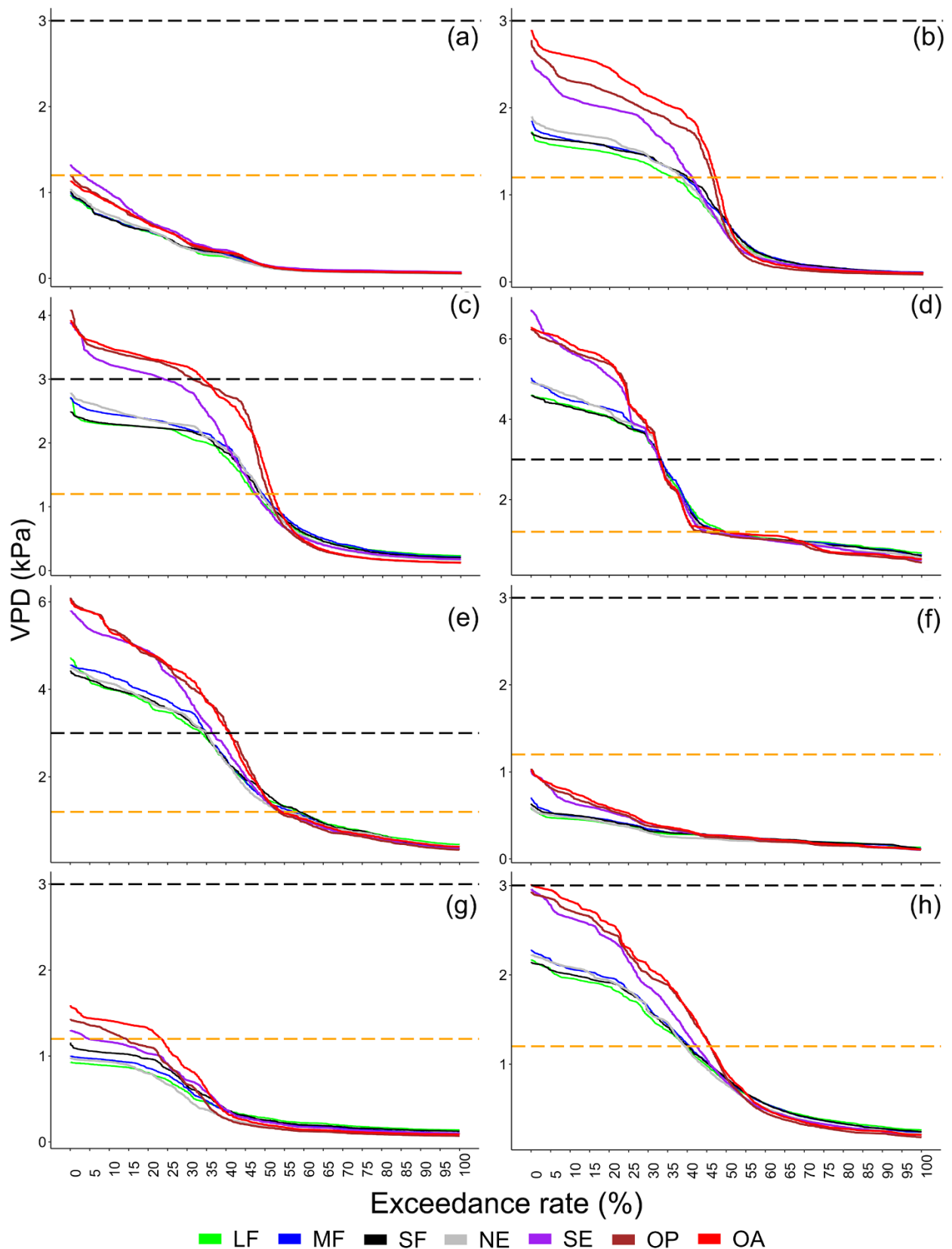
347 on air temperature and relative air humidity was observed in July and September,
 348 which also affected the 24h patterns of VPD (*Fig. 7d, f*).
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350
 351 *Fig. 7.* VPD values for the various habitat types over a 24-hour period. The values for each minute
 352 are averaged over three replicates. The VPD values were measured for the following months: (a)
 353 April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month
 354 average. Habitat type abbreviations are according to the caption of Figure 3.

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Based on the VPD duration curves (*Fig. 8*), it was found that VPD values exceeded the 1.2 kPa stress threshold for all habitats from May to August. In October, south-facing edges and open grasslands had VPD values higher than 1.2 kPa, but with a low exceedance rate from 4.64% to 23.3%. In terms of the 3 kPa threshold, the summer season seemed critical, with open grasslands and south-facing edges having higher exceedance rates than other habitats. For the seven-month average VPD values, the exceedance rate for 1.2 kPa varied between 39.3 and 46.0% in the studied habitats, while the exceedance rate for 3 kPa was less than 1%, with open annual grasslands having the highest value (*Fig. 8h*).

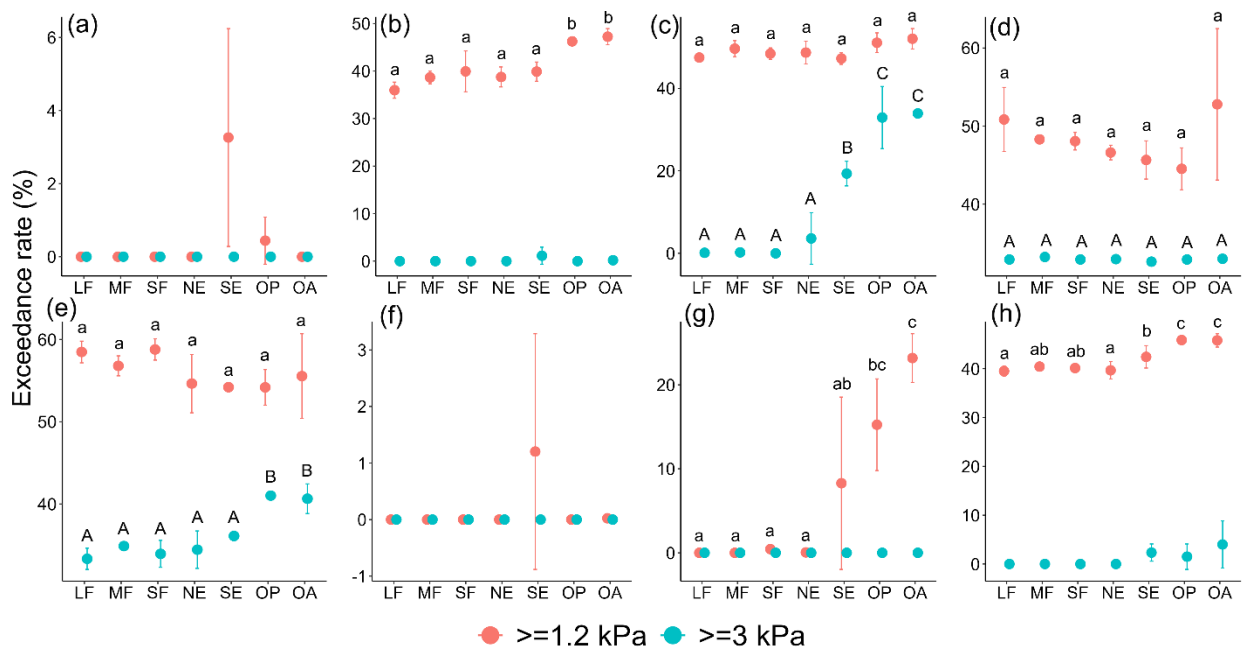


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367 *Fig. 8.* VPD duration curves for habitat types from a 24-hour measurement period each month: (a)
 368 April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month
 369 average. The VPD values for each minute are averaged over three replicates. The orange dashed
 370 line indicates the 1.2 kPa physiological threshold; the black dashed line indicates the 3.0 kPa
 371 threshold, above which the exceedance rates significantly diversified. Habitat type abbreviations
 372 are according to the caption of *Fig. 3*.

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Exceedance rate was significantly different among habitats from May to October, except for July and September (Fig. 9). The study revealed that the exceedance rate was very low in April and September (Fig. 9a, f). In May, the most stressed habitats were open grasslands at a 1.2 kPa physiological threshold (Fig. 9b). For June, open grasslands were the most stressed, followed by south-facing edges at a 3 kPa limiting threshold (Fig. 9c). Interestingly, all habitats were very stressed and were thus not significantly different among habitats in July at both limiting thresholds (Fig. 9d), while open grasslands were the harshest habitats in August at the 3 kPa threshold and in October at 1.2 kPa threshold, respectively (Fig. 9e, g). Regarding the averaged values for seven months, open grasslands were the most stressed to plant growth, followed by south-facing edges only at the 1.2 kPa threshold (Fig. 9h).



387

388 *Fig. 9.* Exceedance rate (%) for VPD values above 1.2 kPa and above 3.0 kPa (mean \pm standard
 389 deviation). The values are averaged over three replicates (large dots). Habitat type abbreviations
 390 are according to the caption of *Fig. 3*. Different letters indicate significant differences among
 391 habitats. Exceedance rate for each month: (a) April, (b) May, (c) June, (d) July, (e) August, (f)
 392 September, (g) October, and (h) seven-month average. Due to the 5% lower mean exceedance rate
 393 and data with many zeros, statistical analysis was not applied for the exceedance rate above 1.2
 394 kPa in April and September, and it was not used for the exceedance rate above 3 kPa in April,
 395 May, September, October, and seven-month average.

396

397

4. Discussion

4.1. Microclimate differences among the habitats

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399
 400 An earlier study revealed a gradient in species composition from large forest patches
 401 through smaller-sized forest patches and edges to grasslands (Erdős *et al.*, 2023).
 402 The compositional differences among the habitats were thought to be associated with
 403 differences in microclimate. The current study demonstrated that forests indeed have

404 a strongly different microclimate than grasslands (compared to grasslands, forests
405 are cooler during the daytime and warmer during the nighttime, and more humid
406 during the daytime). Similar findings were reported by *von Arx et al.* (2012). In this
407 study, especially for temperature, south-facing edges tended to be more similar to
408 grasslands, while north-facing edges tended to be more similar to forests.

409 The present work confirmed that the harshest conditions were found at the end
410 of the vegetation gradient during the growing season (*Fig. 2a*). Open grasslands were
411 the hottest and driest at daytime, but the coolest at nighttime, resulting in the largest
412 diurnal range in these habitats. This result is in line with the previous study of *Erdős*
413 *et al.* (2014), who measured the microclimate of forest-grassland mosaics in central
414 Hungary for a short period (only 24 hours on a single summer day). Similar results
415 have been reported from grasslands of other biogeographical regions (*Davies-Colley*
416 *et al.*, 2000; *Wright et al.*, 2010; *Peng et al.*, 2012; *Bogyó et al.*, 2015).

417 The importance of forests in reducing environmental extremes under semi-arid
418 conditions of the Kiskunság Sand Ridge was shown in the present study. It is
419 reasonable to assume that the revealed microclimatic patterns are caused by the
420 different vegetation, most notably the differences in vegetation cover, especially
421 canopy cover (*Chen et al.*, 1995). Trees play an essential role in driving the below-
422 canopy microclimate: they reduce temperature variation under the canopy, as they
423 absorb and reflect the solar radiation, they have a cooling effect near the soil surface
424 during the daytime, and release longwave radiation during the nighttime (*Magnago et*
425 *al.*, 2015; *Greiser et al.*, 2018; *Aalto et al.*, 2022). *De Frenne et al.* (2019) found that
426 forest patches were 4.1 °C cooler than open-habitat patches on a global scale.
427 Similarly, canopy sites have been shown to have significantly lower maximum
428 temperatures than non-canopy ones under sunny conditions, differences being ca.
429 5.2 °C in Africa (*Aalto et al.*, 2022), and ca. 3.0-5.1 °C in Europe (*Morecroft et al.*,
430 1998; *von Arx et al.*, 2012; 2013; *Milošević et al.*, 2020). On the other hand,
431 minimum temperatures in forest patches are on average 1°C higher than in open-
432 field conditions at night (*De Frenne et al.*, 2021).

433 Woody habitats (forests and edges) were more humid than open grasslands at
434 daytime, and daytime air humidity, therefore, exhibited patterns opposite to that of
435 the air temperature. Similar results were reported, among others, from the western
436 United States (*Ma et al.*, 2010), Switzerland (*von Arx et al.*, 2012), Hungary
437 (*Tölgyesi et al.*, 2020), and the United Kingdom (*Morecroft et al.*, 1998). In the
438 current study, there was no statistically significant difference in nighttime air
439 humidity among the studied habitat types, which is similar to that reported from
440 poplar, black locust, and pine forests as compared to adjacent grasslands (*Tölgyesi*
441 *et al.*, 2020). Indeed, the significant differences in microclimate variables among
442 habitat types occurred only between May and October, when the foliage of the
443 dominant tree (*Populus alba*) reappears with a high canopy cover of ca. 50-70%,
444 while microclimate was almost similar among habitats in April because the foliage
445 has not yet appeared at that time (*Caudullo and de Rigo*, 2016). Therefore, canopy
446 cover may be considered the most central factor in creating strong microclimatic
447 differences during daytime (*Godefroid et al.*, 2006).

448 Small forest patches are usually expected to be warmer and drier than larger
449 forest patches, but the present study found that temperature and humidity values did
450 not differ significantly between differently sized forest patches. Several studies
451 generally state that small forests are largely affected by edge influence and are, in
452 practice, very similar to edges, whereas only larger forest patches with core areas
453 are buffered from environmental harshness (*Hofmeister et al.*, 2019; *Erdős et al.*,
454 2020; 2023). In the present study, the importance of maintaining tree cover (even in
455 small forest patches or groves) in regulating the microclimate condition under semi-
456 arid conditions was highlighted. *Aalto et al.* (2022) stated that trees outside forests
457 (e.g., trees on farmlands, trees in cities, or small tree groups not defined as forests)
458 have the potential in reducing climate change and regulating local and regional
459 temperatures. Although forest fragmentation may reduce the forest's ability to
460 mitigate climate change (*Ewers and Banks-Leite*, 2013), small forest patches can still
461 regulate the environmental extremes (*Mildrexler et al.*, 2011; *Milošević et al.*, 2020),
462 which is in good agreement with the present results. One possible explanation is that
463 the tree/shrub canopy in all forest patches of this study is primarily composed of
464 broadleaved trees and shrubs with a high canopy cover, creating shade and
465 effectively reducing solar radiation reaching the ground. Microclimate conditions,
466 therefore, were largely similar among differently sized forest patches.

467 One of the most interesting findings was that the mean daytime temperature of
468 south-facing edges was very close to grasslands, while their nighttime values bear a
469 resemblance to forests. This implied that the canopy of south-facing edges showed
470 more resistance to cooling during nighttime than to heating during daytime. On the
471 other hand, microclimate conditions of north-facing edges were similar to the forest
472 interiors both daytime and nighttime. Similar results for the large temperature
473 differences between north-facing and south-facing edges were reported in oak-
474 chestnut forests and in Douglas-fir forests in the United States (*Matlack et al.*, 1993;
475 *Chen et al.*, 1993). A potential reason for this phenomenon is that southern forest
476 edges tend to receive more direct sunlight and solar radiation in daytime compared
477 to north-facing edges (*Stoutjesdijk and Barkman*, 1992; *Heithecker and Halpern*,
478 2007; *Bennie et al.*, 2008). Another possibility is that south-facing edges have lower
479 tree density and/or canopy closure than north-facing edges (*Hofmeister et al.*, 2019).

480

481 *4.2. VPD, an important limiting factor affecting plant growth*

482

483 Although vapor pressure deficit is inferred from air temperature and relative air
484 humidity, it is regarded as an important environmental factor affecting the
485 photosynthetic process, since it provides information about how water loss
486 influences the stomatal openness or closure, which is related to CO₂ uptake (*Stewart*
487 *and Dwyer*, 1983; *Young and Mitchell*, 1994; *Bunce*, 1997; *Novick et al.*, 2016;
488 *Shamshiri et al.*, 2018). The present results indicated that the VPD values were high
489 during daytime and low during nighttime, showing that high transpiration rate and
490 water stress occur during daytime, when the plants carry out photosynthesis
491 (*Jackson and Volk*, 1970).

492 During the growing season, high VPD values were revealed in the summer
493 months (between June and August), due to the high temperature in this season. For
494 example, a temperature rising from 30 to 33°C increased VPD from 1.75 to 2.54 kPa
495 (Will *et al.*, 2013). Increased VPD is likely to exacerbate physiological stress on
496 vegetation, leading to increased water loss or decreased carbon uptake, which
497 influences the survival and growth of plant species (Van Heerwaarden and Teuling,
498 2014; McDowell *et al.*, 2008). Yuan *et al.* (2019) reported increased VPD being part
499 of the drivers of a decrease in global-scale plant growth, particularly an increase in
500 drought-related forest mortality. A study in western US forests showed that high
501 VPD significantly decreases Douglas fir growth (Restaino *et al.*, 2016). Another
502 study in the forest–grassland ecotone in the US also highlighted that increased VPD
503 hastened greater transpiration and faster mortality of tree seedlings (Will *et al.*,
504 2013).

505 The present results showed that the VPD values were significantly lower within
506 woody habitats than in the open grasslands at daytime, indicating that grasslands
507 were the most stressed for plant growth and productivity. These results are in good
508 agreement with an earlier study in central Hungary, which concluded that the VPD
509 values of small groves were lower than those of open areas (Süle *et al.*, 2020).
510 According to a study conducted in the northwestern United States (Davis *et al.*,
511 2019), the forest canopy can buffer vapor pressure deficit: VPD was found to be 1.1
512 kPa lower in habitats with canopy than in those without canopy. Similarly, the long-
513 term mean moderating capacity of the forest canopy for VPD in Switzerland was
514 reported to be up to 0.52 kPa (von Arx *et al.*, 2013).

515 This study indicated that south-facing edges had higher VPD values than north-
516 facing ones during daytime, despite the fact that both are transition zones. This may
517 be explained by the heat-reflective properties of the sunny side (Süle *et al.*, 2020).
518 Together with air temperature and humidity, it is highlighted that south-facing edges
519 have more unfavorable environmental conditions in comparison to north-facing
520 edges, which may result in reduced diversity (Erdős *et al.*, 2013; 2018a; 2023).

521 Instead of extreme values (e.g., maximum and minimum values) that occur in
522 a short period, the duration curve can help us to better understand the spatio-temporal
523 VPD pattern (Süle *et al.*, 2020). In terms of the 1.2 kPa stress limiting threshold,
524 exceedance rates of over 30% were observed in all habitats from May to August,
525 indicating that each habitat type is strongly stressed during this period. In autumn,
526 the studied habitats did not differ significantly from each other due to the cloudy and
527 rainy weather conditions in September, but the exceedance rate was the highest in
528 open grasslands in October, from 15.2 to 23.2%. Several studies have reported that
529 for both temperature and VPD, differences between woody and non-woody habitats
530 were larger on sunny days than on cloudy days (Chen *et al.*, 1993; Davies-Colley *et al.*,
531 2000). As there is little heating of soil and air on cloudy days (Urban *et al.*,
532 2012), the difference between woody and non-woody habitats was small or non-
533 existent in September.

534 When considering the limiting threshold of 1.2 kPa only, the role of forest
535 patches may be ignored in the extremely dry period, from June to August, as the
536 exceedance rate was similar among habitats. However, a stronger moderating effect

537 of the forests was clearly observed when choosing 3.0 kPa as the threshold value for
538 the exceedance rate, which is in line with *Süle et al.* (2020). Therefore, the present
539 study highlights the central role of forest patches in buffering vapor pressure deficit
540 under severe conditions (*Davis et al.*, 2019).

541

542 4.3. Implications for conservation and management

543

544 It is well known that forests have a buffering function to regulate climate extremes
545 (*Breshears et al.*, 1998; *von Arx et al.*, 2013; *Davis et al.*, 2019). The current study
546 highlighted that even the smallest forest patches (<0.1 ha) had an important function
547 in mitigating macroclimatic harshness. Therefore, woody habitats may become
548 refuges for plant species that require cooler temperature and/or higher humidity.
549 With ongoing climate change, the role of forest patches, groves, or even scattered
550 trees is expected to become increasingly important (*Manning et al.*, 2009; *Erdős et*
551 *al.*, 2018a; *Süle et al.*, 2020). In addition, forest patches in forest-grassland mosaics
552 host a specific flora and fauna and also have considerable carbon sequestration
553 capacity (*Foit et al.*, 2016; *Erdős et al.*, 2018b; *Ónodi et al.*, 2021; *Süle et al.*, 2021;
554 *Tölgyesi et al.*, 2022). Thus, the remaining near-natural poplar stands should be
555 protected throughout the study region, as well as in other forest-grassland ecosystems
556 of the world.

557 Here it is important to point out that protecting the near-natural forest patches
558 is very different from afforestation. Indeed, plantations, especially non-native
559 plantations, cannot substitute near-natural forests, as they have serious negative
560 effects on diversity and other ecosystem properties. For example, compared to near-
561 natural forests, *Robinia* plantations had lower native species richness, functional and
562 phylogenetic diversity, as well as naturalness (*Ho et al.*, 2023), while *Pinus*
563 plantations compromise soil humus content (*Tölgyesi et al.*, 2020) and are also
564 associated with high fire risk (*Cseresnyés et al.*, 2011). Furthermore, creating large
565 forest stands in sandy drylands may have negative effects on regional underground
566 water balance (*Tölgyesi et al.*, 2020). Tree-planting attempts on ancient or near-
567 natural grasslands are also frowned upon by proponents of open ecosystems because
568 they risk destroying species, habitats, and ecosystem functioning (*Feurdean et al.*,
569 2018). Afforestation efforts should therefore be minimized in forest-grassland
570 ecosystems, but planting scattered trees of native species in the open grassland
571 matrix is highly advised and is even regarded as the new standard in increasing
572 higher biodiversity and ecosystem services in Europe (*Manning et al.*, 2009;
573 *Tölgyesi et al.*, 2023).

574

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