IDŐJÁRÁS

Strong differences in microclimate among the habitats of a forest-steppe ecosystem

Ho Vu Khanh[1,2,*], **Gabriella Süle** [3], **Bence Kovács** [3], and **László Erdős** [3,4]

[1]*Doctoral School of Environmental Sciences, University of Szeged*
6720 Szeged, Rerrich Béla tér 1, Hungary

[2]*Faculty of Natural Resources-Environment, Kien Giang University*
Kien Giang, Vietnam

[3]*Institute of Ecology and Botany, HUN-REN Centre for Ecological Research*
2163 Vácrátót, Alkotmány u. 2-4., Hungary

[4]*HUN-REN-UD Functional and Restoration Ecology Research Group*
4032 Debrecen, Egyetem sqr. 1., Hungary

*Corresponding author E-mail: hvkhanh@vnkgu.edu.vn

(Manuscript received in final form June 23, 2023)

Abstract— Microclimate has a substantial impact on plant composition, survival, and growth, as well as ecosystem processes. Although microclimatic conditions in anthropogenically fragmented ecosystems have received considerable scientific attention, they are understudied in naturally fragmented ecosystems, including forest-steppes. In addition, earlier investigations in these mosaics only measured microclimate parameters for a very short period (i.e., 24 hours on a single summer day). In the present study, the long-term microclimatic conditions were described in multiple habitat types, both woody and non-woody, in a sandy forest-steppe ecosystem in the Kiskunság, central Hungary. The aim of this study was to answer (1) how air humidity and temperature conditions differ among the studied habitats during the growing season and (2) which habitats are more stressed to vegetation growth regarding vapor pressure deficit (VPD). Wireless sensors recording air temperature and humidity values were used to monitor microclimatic parameters. VPD values were calculated based on the obtained air temperature and humidity, and two thresholds at 1.2 and 3.0 kPa were defined. To compare mean air temperature and humidity variables, as well as above-threshold VPD rate among habitat types, general linear models were used. Our results indicated that open grasslands were the warmest and driest habitats. Among woody habitats, south-facing edges had the harshest microclimatic conditions. The current work also found that small forest patches and larger

forest patches had similar air temperature and humidity variables. Regarding VPD, open grasslands were the most stressed for vegetation growth from May to October. During the summer season, forest patches had a small moderating effect at the limiting threshold of 1.2 kPa VPD, but a stronger moderating effect at the 3.0 kPa threshold. With ongoing climate change, this role of forest patches is expected to become increasingly important in forest-steppes. Therefore, it is suggested that the remaining near-natural forest stands in sandy forest-grassland ecosystems should be prioritized for protection, and that scattered trees or groups of trees of native species should be established in extensive treeless grasslands.

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

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

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

Forest-steppes are structured by the co-occurrence of differently sized forest and grassland patches of various types, connected by an intricate network of differently exposed edges (*Erdős et al.,* 2018b). As a result of varying vegetation cover among the habitats in forest-steppes, microclimate can vary significantly even over short distances (*Erdős et al.,* 2023). Vegetation-environment relations have been intensively studied recently, with special emphasis on soil moisture, air humidity, and air temperature patterns (e.g., *Bátori et al.,* 2014; *Erdős et al.,* 2014, 2018a; *Tölgyesi et al.,* 2018). However, earlier investigations measured microclimate parameters for only a very short period (typically 24 hours on a selected summer

day) in forest-steppes (*Erdős et al.,* 2014, 2018a; *Tölgyesi et al.,* 2018; *Milošević et al.,* 2020). These short-term measurements may not be able to capture the most critical microclimatic conditions. To gain more informative microclimate background data, repeated measurements are needed throughout the vegetation period, from spring to autumn. Furthermore, earlier studies did not take into account the full variety of forest-grassland mosaics: some works disregarded the edge habitat (e.g., *Tölgyesi et al.* 2018; *Milošević et al.* 2020), while others restricted their attention to small forest patches and a single type of grassland (e.g., *Erdős et al.* 2014; *Süle et al.* 2020). Thus, measuring microclimate in a broader spectrum of near-natural forest-steppe habitats is necessary to fill the above knowledge gap.

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

2. Materials and methods

2.1. Study area

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

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

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

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

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

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

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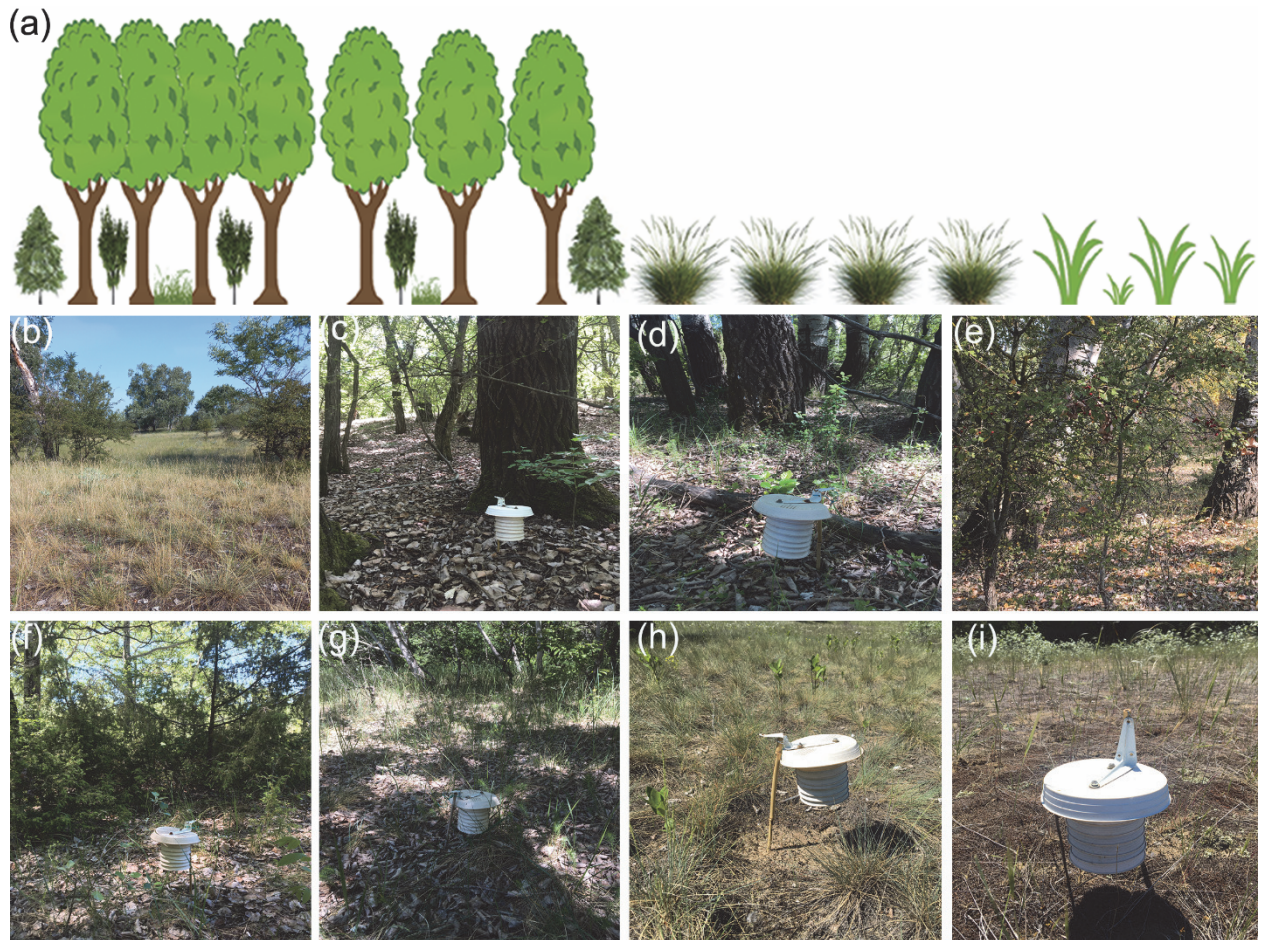
Fig. 2. (a) The model of forest-steppes, and (b) a mosaic of forests and grasslands at the Fülöpháza area. The following seven habitat types were included in this study: (c) large forest patch, (d) medium forest patch, (e) small forest patch, (f) north-facing forest edge, (g) south-facing forest edge,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

2.2. Data collection

Microclimate measurements were carried out in the seven habitat types described above (i.e., large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, open perennial grasslands, and open annual grasslands). Three replicates for each habitat type were used. The air temperature (ºC) and relative air humidity (%) were measured once every month in all seven habitats from April to October 2022. They were measured synchronously 20 cm above the ground surface in the center of each habitat for 24 hours (i.e., a day per month) using MCC USB-502 data loggers (Measurement Computing Corporation, Norton, MA, USA). The resolution of the sensors was

set to once every minute; therefore, each sensor yielded 1440 temperature and 1440 humidity data records per day. The loggers were placed in naturally ventilated radiation shields in order to avoid direct solar radiation. The sampling occasions were selected under clear weather conditions, but the weather was cloudy during the second daytime periods of July and was rainy during the first couple of hours during September.

2.3. Data analysis

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

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

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

In this study, the exceedance rate was analyzed, which is the percentage of VPD values above an appropriate threshold (1.2 or 3.0 kPa) over a 24-hour period. This approach can help us better understand the microclimatic conditions that affect vegetation growth (*Süle et al.,* 2020). The limiting threshold for the stress effect was set at 1.2 kPa, as suggested by many previous studies (*Novick et al.,* 2016; *Shamshiri et al.,* 2018; *Süle et al.,* 2020), whereas 3 kPa threshold had a stronger inhibitory effect on plant growth and photosynthesis (*Shirke* and *Pathre,* 2004; *Shibuya et al.,* 2018; *Süle et al.,* 2020). A VPD duration curve (DC) was constructed using 1440 VPD values that were averaged over three replicates collected over the period of 24 hours for each habitat per month. This method is similar to the flow duration curve in hydrology and is thoroughly described by *Süle et al.* (2020). In addition, the DC for each replicate was also calculated. Based on this DC, the exceedance rate was calculated per replicate, which was then used for statistical analysis.

The variables related to mean daily air temperature, mean daytime air temperature, mean nighttime air temperature, mean daily relative air humidity (MDAH), mean daytime relative air humidity, and mean nighttime relative air

humidity, as well as exceedance rate were analyzed using general linear models. The fixed factor was the habitat. The "glm" function in R version 4.1.2 was used to build the models with Gaussian family (*R Core Team*, 2021). The assumptions of the models were checked by visual assessment of diagnostic plots. The general linear models were then tested using analysis of variance (ANOVA) with the "Anova" function in the car package (*Fox* and *Weisberg*, 2019). If the model had a significant proportion of variability, all pairwise comparisons of the fixed factor levels were performed using the "emmeans" function in the emmeans package in R (*Lenth,* 2022). The p-values were adjusted with the false discovery rate (FDR) method.

3. Results

3.1. Air temperature patterns

The general 24-hour patterns of air temperature were somewhat similar in all habitats in each month, with a peak around or slightly after noon and a bottom during nighttime (*Fig. 3*). The temperature did not differ largely among habitats in April (*Fig. 3a*), whereas there were larger differences between open grasslands and forests during 24 hours for the other months (*Fig. 3b-g*). A distinct tendency between differently oriented edges was found. South-facing edges had similar patterns to the grasslands during the daytime, but they were closer to the forests at nighttime. North-facing edges resembled forests during the whole day. A similar pattern was observed for the seven-month average (*Fig. 3h*). Temperatures among habitats did not vary largely in the last couple of hours of the July measurement, when the weather was cloudy (*Fig. 3d*), while they fluctuated considerably in the first few hours of the September measurement, when the weather was rainy (*Fig. 3f*).
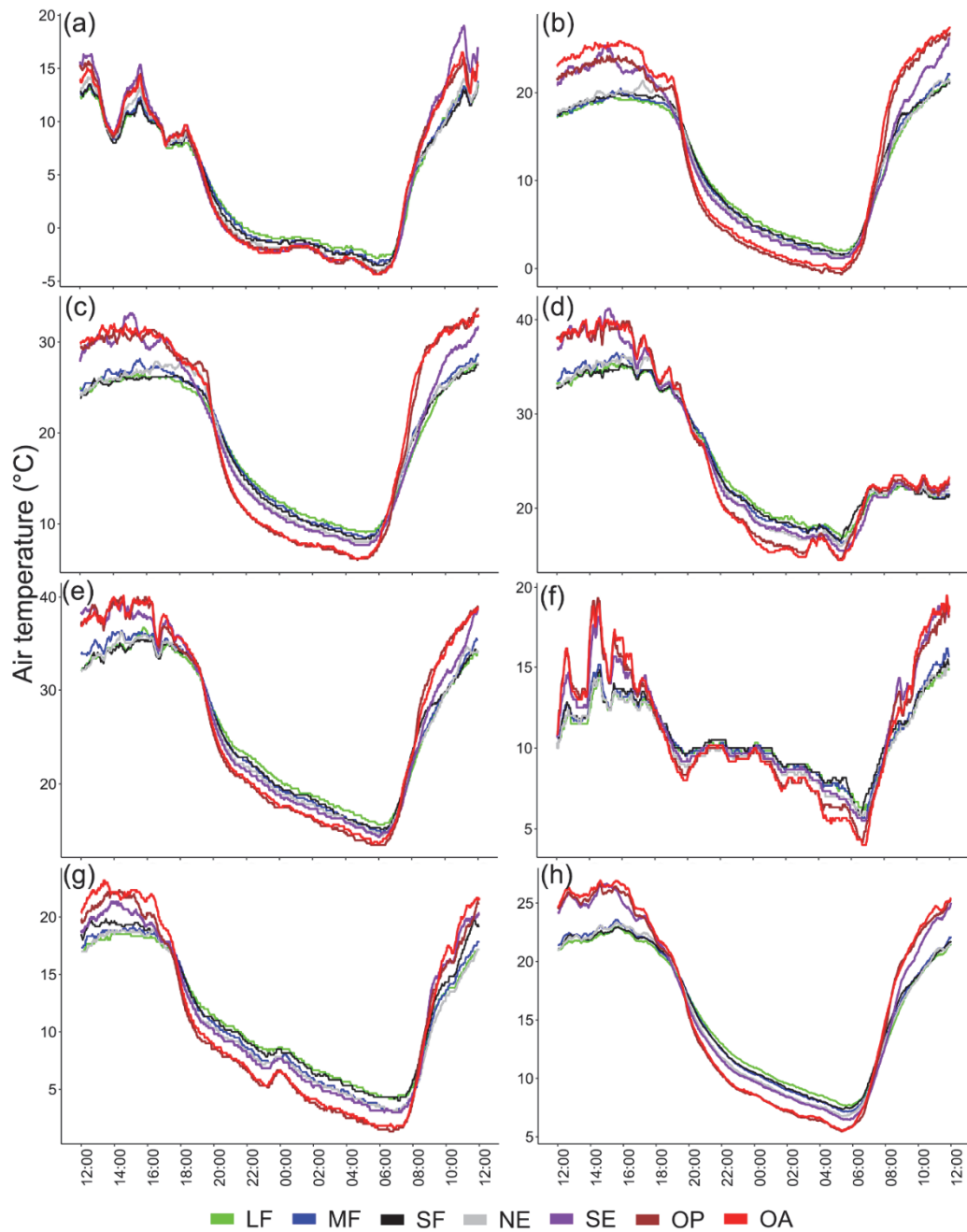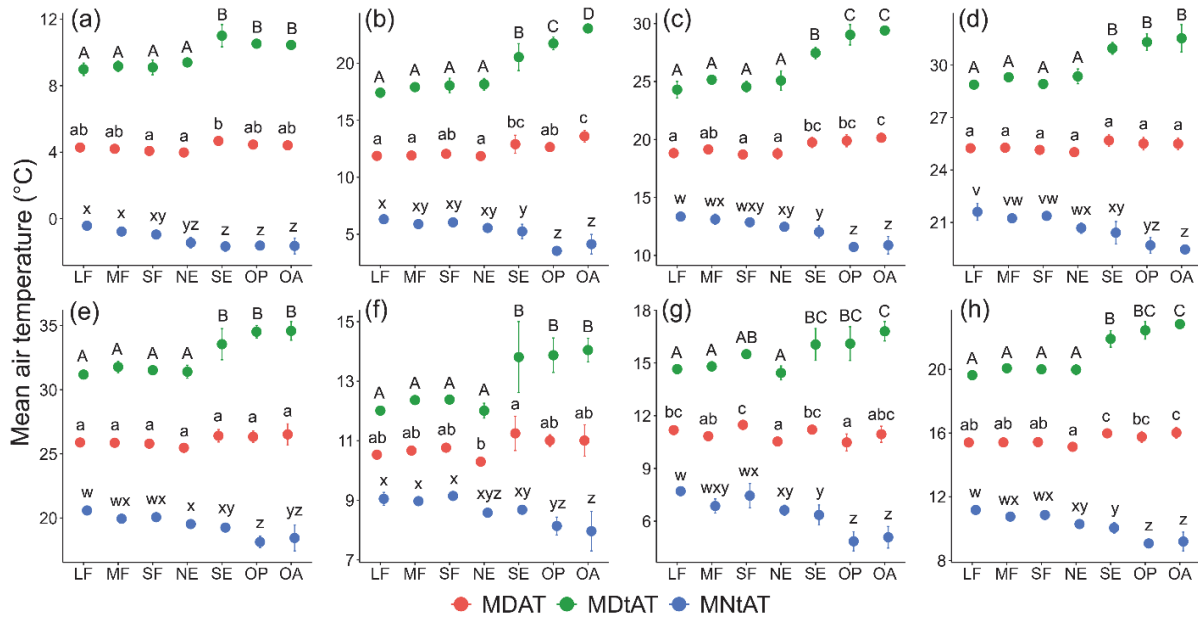
Fig. 3. Air temperature values for the various habitat types over a 24-hour period. The values for each minute are averaged over three replicates. The air temperature values were measured for the following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; OP: open perennial grasslands; OA: open annual grasslands.

The mean daily air temperatures were very similar among the habitats in most measured months, but the daytime and nighttime values were significantly different among the habitats in each month (*Fig. 4a-g*). The diurnal range values were remarkably large in all habitats, but the largest values were observed in open

perennial and open annual grasslands. The mean daytime air temperature was the highest in south-facing edges and open grasslands, while the mean nighttime air temperature was the lowest in the open grasslands. For the seven-month averaged values, there was an increasing trend of daytime air temperatures along the vegetation gradient, while the opposite trend was seen for the nighttime air temperatures (*Fig. 4h*).

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

3.2. Relative air humidity patterns

The 24-hour patterns of relative air humidity showed the opposite trend compared to air temperature (*Fig. 5*). In April, the values of relative air humidity measured at the same time were quite similar among habitats, although south-facing edges seemed to have somewhat lower relative air humidity than the other habitats at nighttime (*Fig. 5a*). From May to October, the driest habitats were south-facing edges, open perennial grasslands, and open annual grasslands during the daytime (*Fig. 5b-g*). However, open perennial grasslands (and sometimes north-facing edges) were the most humid during the nighttime. This pattern repeated itself for

10

the seven-month mean (*Fig. 5h*). The values of air humidity remained high during the second daytime period of July (*Fig. 5d*), whereas humidity fluctuated significantly in the first couple of hours of April and September (*Fig. 5a, f*).
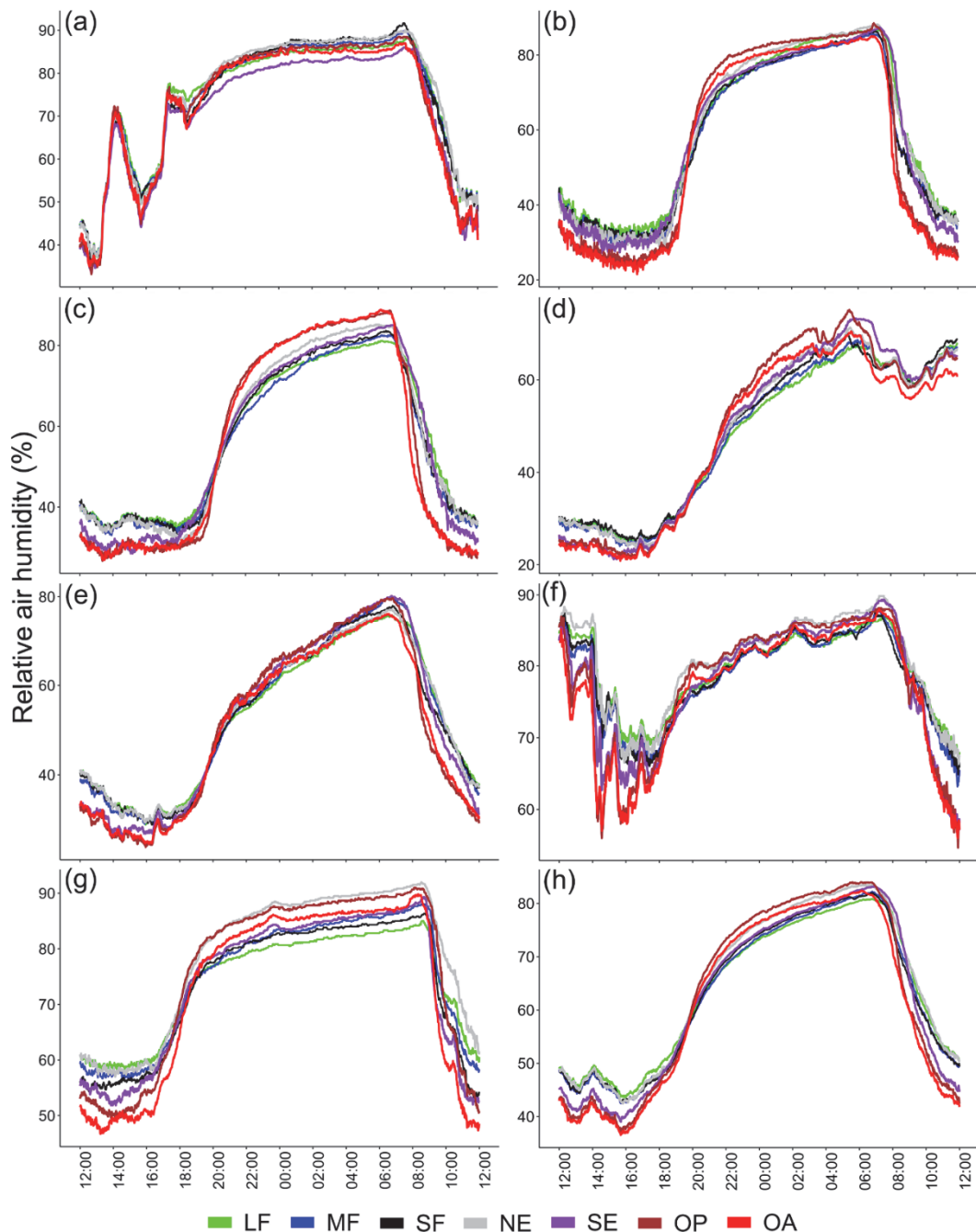

Fig. 5. Relative air humidity values for the various habitat types over a 24-hour period. The values for each minute are averaged over three replicates. The relative air humidity values were measured for the following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October,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

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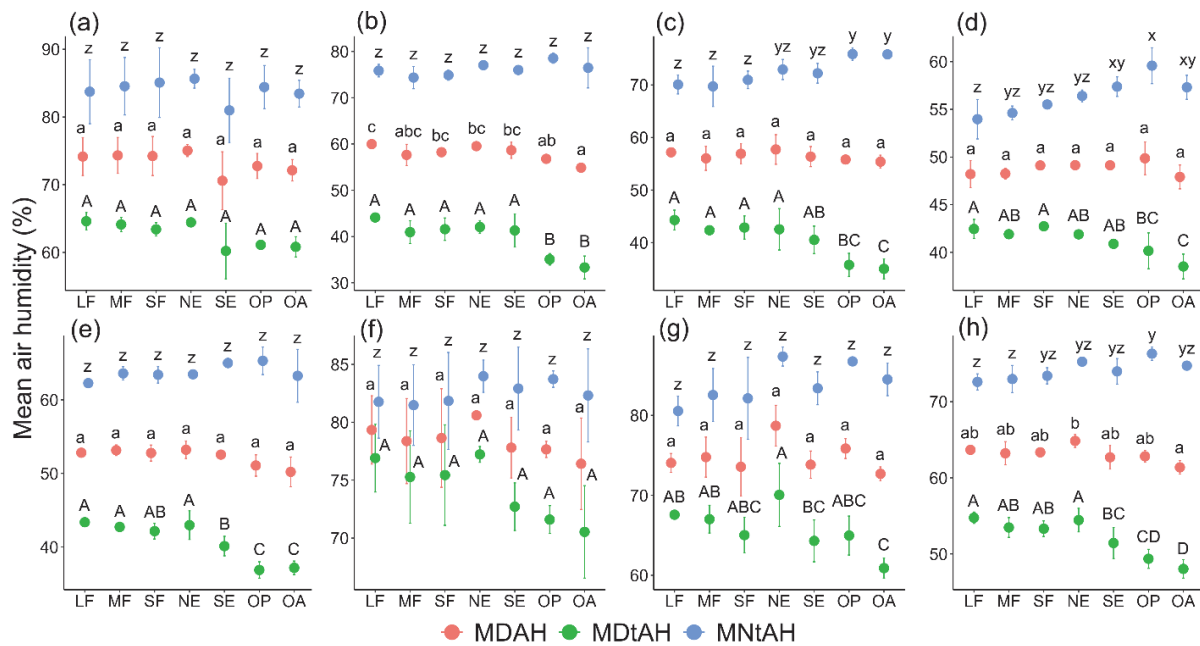

Fig. 6. Mean daily, daytime, and nighttime air humidity values of the habitat types (mean ± standard deviation). The values are averaged over three replicates (large dots). The mean air humidity values were measured for the following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September,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

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

The VPD values calculated over 24 hours for each month and the seven-month average were quite high around noon but quite low during the nighttime (*Fig. 7a-h*). During the daytime, the VPD values of the woody habitats (i.e., forests and edges) were consistently lower than those of open grasslands, with the exception of April. Interestingly, the south-facing edges had higher VPD values than other woody

habitats and had a similar trend to grasslands, while north-facing edges seemed similar to forest interiors. The VPD values were extremely high in the summer season (from June to August), especially in July and August. There were no large differences among habitats at nighttime. A prominent effect of rain and cloudy sky on air temperature and relative air humidity was observed in July and September, which also affected the 24-hour patterns of VPD (*Fig. 7d, f*).
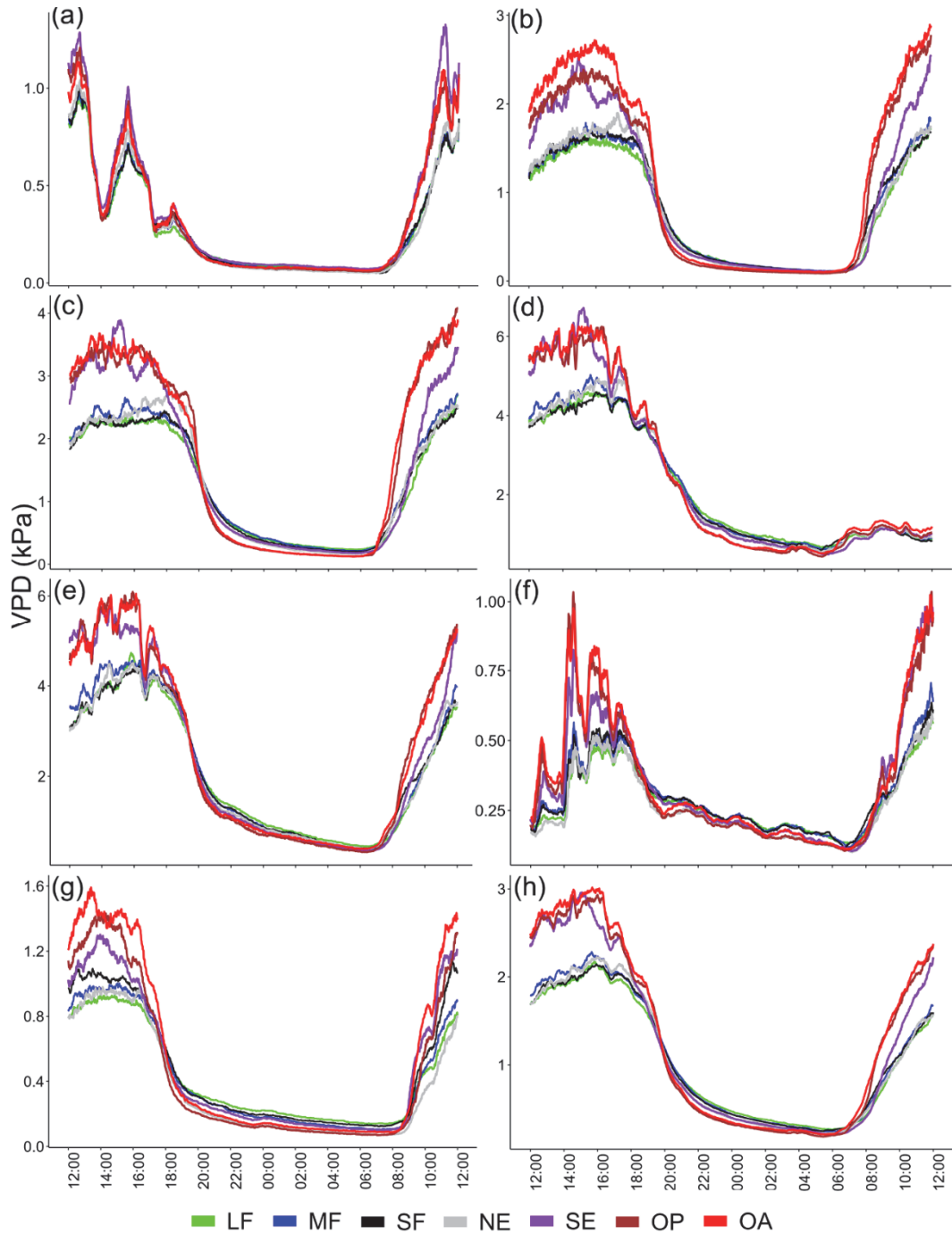

Fig. 7. VPD values for the various habitat types over a 24-hour period. The values for each minute are averaged over three replicates. The VPD values were measured for the following months: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. Habitat type abbreviations are according to the caption of *Fig. 3*.

13

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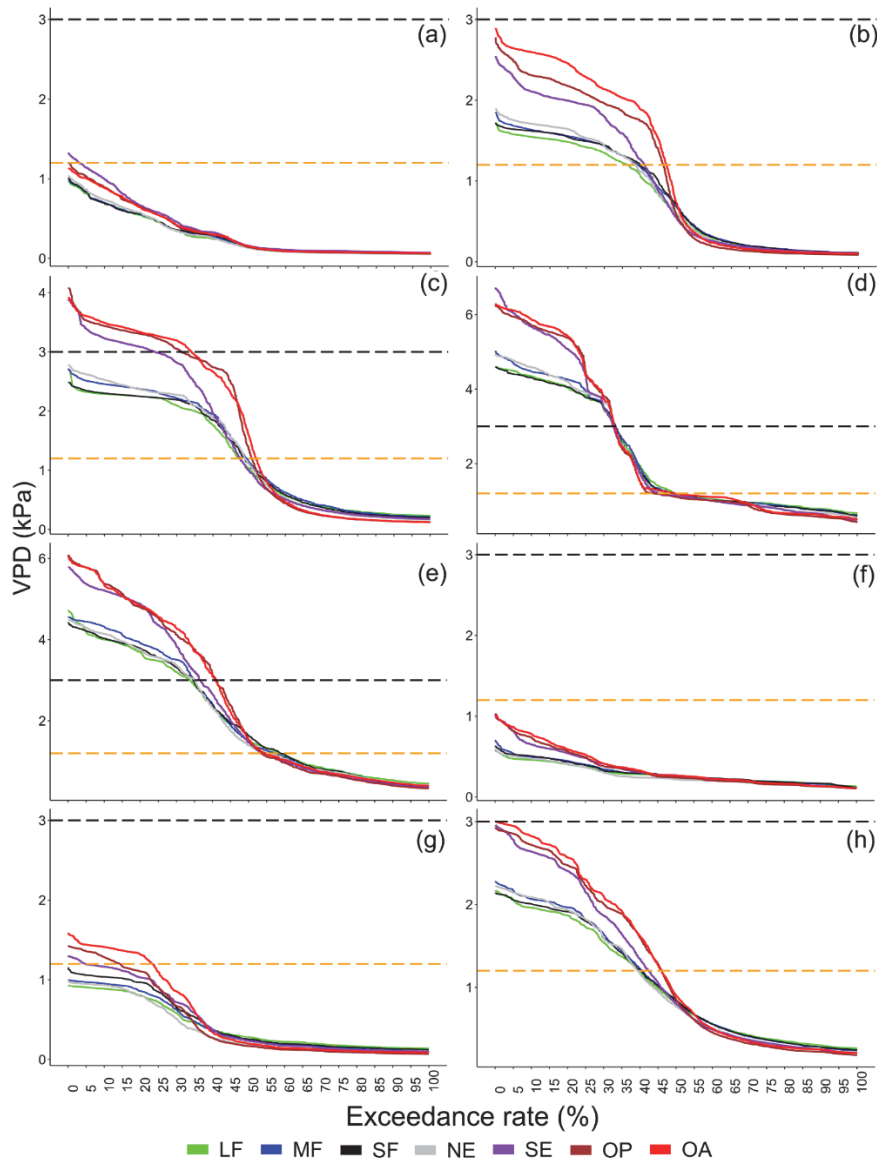
Fig. 8. VPD duration curves for habitat types from a 24-hour measurement period each month: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, (g) October, and (h) seven-month average. The VPD values for each minute are averaged over three replicates. The orange dashed line indicates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

14

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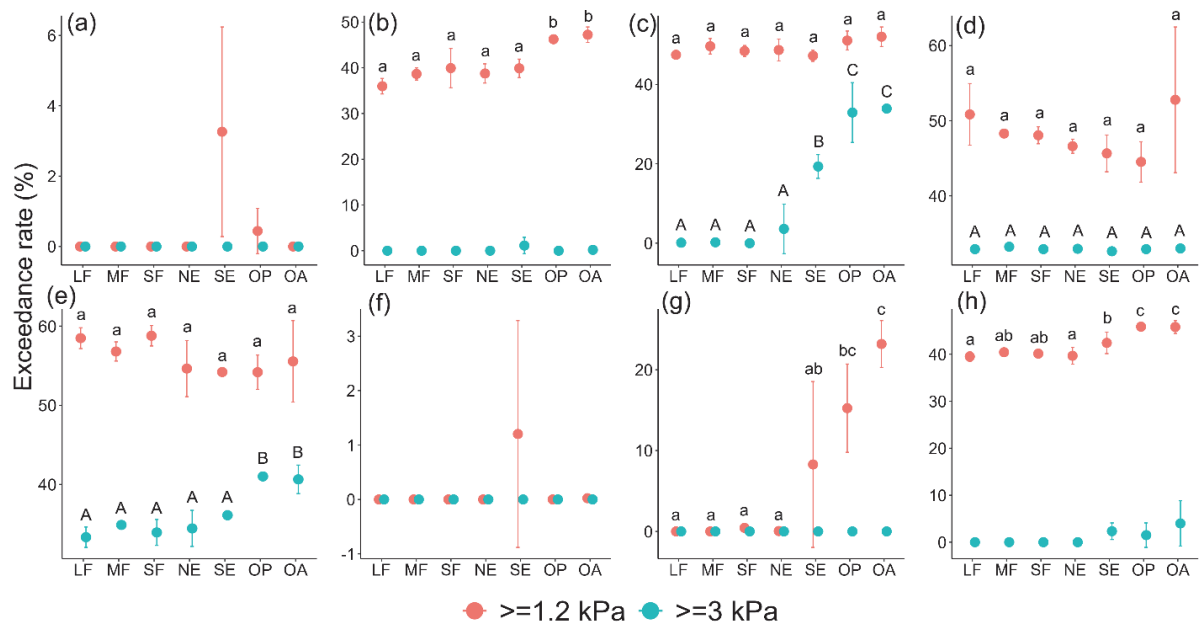
Fig. 9. Exceedance rate (%) for VPD values above 1.2 kPa and above 3.0 kPa (mean ± standard deviation). The values are averaged over three replicates (large dots). Habitat type abbreviations are according to the caption of *Fig. 3*. Different letters indicate significant differences among habitats. Exceedance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

4. Discussion

4.1. Microclimate differences among the habitats

An earlier study revealed a gradient in species composition from large forest patches through smaller-sized forest patches and edges to grasslands (*Erdős et al.,* 2023). The compositional differences among the habitats were thought to be associated with differences in microclimate. The current study demonstrated that forests indeed have a strongly different microclimate than grasslands (compared to grasslands, forests are cooler during the daytime and warmer during the nighttime, and more humid during the daytime). Similar findings were reported by *von Arx et al.* (2012). In this study, especially for temperature, south-facing edges tended to be more similar to grasslands, while north-facing edges tended to be more similar to forests.

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

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

Woody habitats (forests and edges) were more humid than open grasslands at daytime, and daytime air humidity, therefore, exhibited patterns opposite to that of the air temperature. Similar results were reported, among others, from the western United States (*Ma et al.,* 2010), Switzerland (*von Arx et al.,* 2012),

Hungary (*Tölgyesi et al.,* 2020), and the United Kingdom (*Morecroft et al.,* 1998). In the current study, there was no statistically significant difference in nighttime air humidity among the studied habitat types, which is similar to that reported from poplar, black locust, and pine forests as compared to adjacent grasslands (*Tölgyesi et al.,* 2020). Indeed, the significant differences in microclimate variables among habitat types occurred only between May and October, when the foliage of the dominant tree (*Populus alba*) reappears with a high canopy cover of about 50–70%, while microclimate was almost similar among habitats in April, because the foliage has not yet appeared at that time (*Caudullo* and *de Rigo,* 2016). Therefore, canopy cover may be considered the most central factor in creating strong microclimatic differences during daytime (*Godefroid et al.,* 2006).

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

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

that south-facing edges have lower tree density and/or canopy closure than north-facing edges (*Hofmeister et al.,* 2019).

4.2. VPD, an important limiting factor affecting plant growth

Although vapor pressure deficit is inferred from air temperature and relative air humidity, it is regarded as an important environmental factor affecting the photosynthetic process, since it provides information about how water loss influences the stomatal openness or closure, which is related to CO_2 uptake (*Stewart* and *Dwyer,* 1983; *Young* and *Mitchell,* 1994; *Bunce,* 1997; *Novick et al.,* 2016; *Shamshiri et al.,* 2018). The present results indicated that the VPD values were high during daytime and low during nighttime, showing that high transpiration rate and water stress occur during daytime, when the plants carry out photosynthesis (*Jackson* and *Volk,* 1970).

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

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

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

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

When considering the limiting threshold of 1.2 kPa only, the role of forest patches may be ignored in the extremely dry period, from June to August, as the exceedance rate was similar among habitats. However, a stronger moderating effect of the forests was clearly observed when choosing 3.0 kPa as the threshold value for the exceedance rate, which is in line with *Süle et al.* (2020). Therefore, the present study highlights the central role of forest patches in buffering vapor pressure deficit under severe conditions (*Davis et al., 2019*).

4.3.   Implications for conservation and management

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

Here it is important to point out that protecting the near-natural forest patches is very different from afforestation. Indeed, plantations, especially non-native plantations, cannot substitute near-natural forests, as they have serious negative effects on diversity and other ecosystem properties. For example, compared to near-natural forests, *Robinia* plantations had lower native species richness, functional and phylogenetic diversity, as well as naturalness (*Ho et al., 2023*), while *Pinus* plantations compromise soil humus content (*Tölgyesi et al., 2020*)

and are also associated with high fire risk (*Cseresnyés et al.,* 2011). Furthermore, creating large forest stands in sandy drylands may have negative effects on regional underground water balance (*Tölgyesi et al.,* 2020). Tree-planting attempts on ancient or near-natural grasslands are also frowned upon by proponents of open ecosystems, because they risk destroying species, habitats, and ecosystem functioning (*Feurdean et al.,* 2018). Afforestation efforts should therefore be minimized in forest-grassland ecosystems, but planting scattered trees of native species in the open grassland matrix is highly advised and is even regarded as the new standard in increasing higher biodiversity and ecosystem services in Europe (*Manning et al.,* 2009; *Tölgyesi et al.,* 2023).

References

Aalto, I.J., Maeda, E.E., Heiskanen, J., Aalto, E.K., and *Pellikka, P.K.E.,* 2022: Strong influence of trees outside forest in regulating microclimate of intensively modified Afromontane landscapes. *Biogeosciences 19*, 4227–4247. https://doi.org/10.5194/bg-19-4227-2022

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., and *Thuiller, W.,* 2011: Climate change threatens European conservation areas. *Ecol. Lett. 14*, 484–492. https://doi.org/10.1111/j.1461-0248.2011.01610.x

Arnone, J.A., Verburg, P.S.J., Johnson, D.W., Larsen, J.D., Jasoni, R.L., Lucchesi, A.J., Batts, C.M., Von Nagy, C., Coulombe, W.G., Schorran, D.E., Buck, P.E., Braswell, B.H., Coleman, J.S., Sherry, R.A., Wallace, L.L., Luo, Y., and *Schimel, D.S.,* 2008: Prolonged suppression of ecosystem carbon dioxide uptake after an anomalously warm year. *Nature 455*, 383–386. https://doi.org/10.1038/nature07296

Ashcroft, M.B., and *Gollan, J.R.,* 2012: Fine-resolution (25 m) topoclimatic grids of near- surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 × 300 km) and diverse region. *Int. J. Climatol. 32*, 2134–2148. https://doi.org/10.1002/joc.2428

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R., and *Latour, J.B.,* 2002: Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Glob. Change Biol. 8*, 390–407. https://doi.org/10.1046/j.1354-1013.2001.00467.x

Bartha, S., Campetella, G., Ruprecht, E., Kun, A., Házi, J., Horváth, A., Virágh, K., and *Molnár, Z.,* 2008: Will interannual variability in sand grassland communities increase with climate change? *Community Ecol. 9*, 13–21. https://doi.org/10.1556/ComEc.9.2008.S.4

Bartholy, J., Pongrácz, R., and *Gelybó, GY.,* 2007: Regional climate change expected in Hungary for 2071–2100. *App. Ecol. Environ. Res. 5,* 1–17. https://doi.org/10.15666/aeer/0501_001017

Bartholy, J., Pongrácz, R., and *Pieczka, I.,* 2014: How the climate will change in this century? *Hungarian Geogr. Bull. 63*, 55–67. https://doi.org/10.15201/hungeobull.63.1.5

Bátori, Z., Lengyel, A., Maróti, M., Körmöczi, L., Tölgyesi, Cs., Bíró, A., Tóth, M., Kincses, Z., Cseh, V., and *Erdős, L.,* 2014: Microclimate-vegetation relationships in natural habitat islands: species preservation and conservation perspectives. *Időjárás 118*, 257–281.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., and *Courchamp, F.,* 2012: Impacts of climate change on the future biodiversity. *Ecol. Lett. 15*, 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bennie, J., Huntley, B., Wiltshire, A., Hill, M.O., and *Baxter, R.,* 2008: Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecol. Model. 216*, 47–59. https://doi.org/10.1016/j.ecolmodel.2008.04.010

Biró, M., Révész, A., Molnár, Z., and *Horváth, F.*, 2007: Regional habitat pattern of the Danube-Tisza Interfluve in Hungary, I: The landscape structure and habitat pattern; the fen and alkali vegetation. *Acta Bot. Hung. 49*, 267–303. https://doi.org/10.1556/ABot.49.2007.3-4.4

Blanka, V., Mezosi, G., and *Meyer, B.,* 2013: Projected changes in the drought hazard in Hungary due to climate change. *Időjárás 117*, 219–237.

Bogyó, D., Magura, T., Nagy, D. D., and *Tóthmérész, B.,* 2015: Distribution of millipedes (*Myriapoda, diplopoda*) along a forest interior – Forest edge – Grassland habitat complex. *ZooKeys, 510*, 181–195. https://doi.org/10.3897/zookeys.510.8657

Bolton, D., 1980: The computation of equivalent potential temperature. *Mon. Weather Rev. 108*, 1046–1053. https://doi.org/10.1175/1520-0493(1980)108<1046:TCOEPT>2.0.CO;2

Borhidi, A., Kevey, B., and *Lendvai, G.,* 2012: Plant communities of Hungary. Academic Press, Budapest.

Breshears, D.D., Adams, H.D., Eamus, D., McDowell, N.G., Law, D.J., Will, R.E., Williams, A.P. and *Zou, C.B.,* 2013: The critical amplifying role of increasing atmospheric moisture demand on tree mortality and associated regional die-off. *Front. Plant Sci.* 4, 266. https://doi.org/10.3389/fpls.2013.00266

Breshears, D.D., Nyhan, J.W., Heil, C.E., and *Wilcox, B.P.,* 1998: Effects of Woody Plants on Microclimate in a Semiarid Woodland: Soil Temperature and Evaporation in Canopy and Intercanopy Patches. *Int. J. Plant Sci.* 159, 1010–1017. https://doi.org/10.1086/314083

Bunce, J.A., 1997: Does transpiration control stomatal responses to water vapour pressure deficit? *Plant Cell. Environ. 20*, 131–135. https://doi.org/10.1046/j.1365-3040.1997.d01-3.x

Caudullo, G., and *de Rigo, D.,* 2016: Populus alba in Europe: distribution, habitat, usage and threats. In: (Eds. *San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A.*), European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg, e010368+

Chen, J., Franklin, J. F., and *Spies, T. A.*, 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agric. For. Meteorol. 63*, 219–237. https://doi.org/10.1016/0168-1923(93)90061-L

Chen, J., Franklin, J. F., and *Spies, T. A.*, 1995: Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecol. Appl. 5*, 74–86. https://doi.org/10.2307/1942053

Cseresnyés, I., Szécsy, O., and *Csontos, P.,* 2011: Fire risk in Austrian pine (*Pinus nigra*) plantations under various temperature and wind conditions. *Acta Bot. Croat. 70*, 157–166. https://doi.org/10.2478/v10184-010-0022-5

Davies-Colley, R.J., Payne, G. W., and *van Elswijk, M.,* 2000: Microclimate gradients across a forest edge. *N. Z. J. Ecol.* 24, 111–121.

Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E., and *Abatzoglou, J. T.*, 2019: Microclimatic buffering in forests of the future: the role of local water balance. *Ecography 42*, 1–11. https://doi.org/10.1111/ecog.03836

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M.B., Christiansen, D.M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D.H., Koelemeijer, I.A., Lembrechts, J.J., Marrec, R., Meeussen, C., Ogée, J., Tyystjärvi, V., Vangansbeke, P., and *Hylander, K.,* 2021: Forest microclimates and climate change: Importance, drivers and future research agenda. *Glob. Chang Biol. 27*, 2279–2297, https://doi.org/10.1111/gcb.15569

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. A., Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petrik, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G-R., White, P.S, Woods, K.D., Wulf, M., Graae, B.J., and *Verheyen, K.,* 2013: Microclimate moderates plant responses to macroclimate warming. *P. Natl. Acad. Sci. 110*, 18561–18565. https://doi.org./10.1073/pnas.1311190110

De Frenne, P., Zellweger, F., Rodriguez-Sanchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K. and *Lenoir, J.,* 2019: Global buffering of temperatures under forest canopies. *Nat. Ecol. Evol. 3*, 744–749. https://doi.org/10.1038/s41559-019-0842-1

Dingman, J.R., Sweet, L.C., McCullough, I., Davis, F.W., Flint, A., Franklin, J., and *Flint, L.E.,* 2013: Cross-scale modeling of surface temperature and tree seedling establishment in mountain landscapes. *Ecol. Process. 2*, 1–15. https://doi.org/10.1186/2192-1709-2-30

Dövényi, Z., 2010: *Magyarország kistájainak katasztere.* MTA FKI, Budapest.

Erdős, L., Ambarlı, D., Anenkhonov, O.A., Bátori, Z., Cserhalmi, D., Kiss, M., Kröel-Dulay, G., Liu, H., Magnes, M., Molnár, Z., Naqinezhad, A., Semenishchenkov, Y.A., Tölgyesi, C., and *Török, P.,* 2018b: The edge of two worlds: A new review and synthesis on Eurasian forest-steppes. *Appl. Veg. Sci. 21*, 345–362. https://doi.org/10.1111/avsc.12382

Erdős, L., Gallé, R., Körmöczi, L., and *Bátori, Z.,* 2013: Species composition and diversity of natural forest edges: Edge responses and local edge species. *Community Ecol. 14*, 48–58. https://doi.org/10.1556/ComEc.14.2013.1.6

Erdős, L., Ho, K. V., Bátori, Z., Kröel-Dulay, G., Ónodi, G., Tölgyesi, C., Török, P., and *Lengyel, A.,* 2023: Taxonomic, functional and phylogenetic diversity peaks do not coincide along a compositional gradient in forest-grassland mosaics. *J. Ecol. 111*, 182–197. https://doi.org/10.1111/1365-2745.14025

Erdős, L., Kröel-Dulay, G., Bátori, Z., Kovács, B., Németh, C., Kiss, P. J., and *Tölgyesi, C.,* 2018a: Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics. *Biol. Conserv. 226*, 72–80. https://doi.org/10.1016/j.biocon.2018.07.029

Erdős, L., Tölgyesi, Cs., Horzse, M., Tolnay, D., Hurton, A., Schulcz, N., Körmöczi, L., Lengyel, A., and *Bátori, Z.,* 2014: Habitat complexity of the Pannonian forest-steppe zone and its nature conservation implications. *Ecol. Complex. 17*, 107–118. https://doi.org/10.1016/j.ecocom.2013.11.004

Erdős, L., Török, P., Szitár, K., Bátori, Z., Tölgyesi, C., Kiss, P. J., Bede-Fazekas, Á., and *Kröel-Dulay, G.,* 2020: Beyond the forest-grassland dichotomy: the gradient-like organization of habitats in forest-steppes. *Front. Plant Sci. 11,* 236. https://doi.org/10.3389/fpls.2020.00236

Erdős, L., Török, P., Veldman, J. W., Bátori, Z., Bede-Fazekas, Á., Magnes, M., Kröel-Dulay, G., and *Tölgyesi, C.,* 2022: How climate, topography, soils, herbivores, and fire control forest–grassland coexistence in the Eurasian forest-steppe. *Biol. Rev. 97,* 2195–2208. https://doi.org/10.1111/brv.12889

Ewers, R.M. and *Banks-Leite, C.,* 2013: Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests. *PLoS One 8,* e58093, https://doi.org/10.1371/journal.pone.0058093

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S.M., and *Hickler, T.,* 2018: Biodiversity-rich European grasslands: ancient, forgotten ecosystems. *Biol. Conserv. 228*, 224–232. https://doi.org/10.1016/j.biocon.2018.09.022

Foit, J., Kašák, J., and *Nevoral, J.,* 2016: Habitat requirements of the endangered longhorn beetle *Aegosoma scabricorne* (Coleoptera: Cerambycidae): a possible umbrella species for saproxylic beetles in European lowland forests. *J. Insect Conserv. 20*, 837–844. https://doi.org/10.1007/s10841-016-9915-5

Fox, J., and *Weisberg, S.,* 2019: An {R} Companion to Applied Regression, Third Edition. Thousand Oaks CA: Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Geiger, R., Aron, R.H. and *Todhunter, P.,* 2009: The Climate Near the Ground. Rowman & Littlefield.

Godefroid, S., Rucquoij, S., and *Koedam, N.,* 2006: Spatial variability of summer microclimates and plant species response along transects within clearcuts in a beech forest. *Plant Ecol. 185,* 107–121. https://doi.org/10.1007/s11258-005-9088-x

Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., and *Hylander, K.,* 2018: Monthly microclimate models in a managed boreal forest landscape. *Agric For Meteorol. 250–251*, 147–158. https://doi.org/10.1016/j.agrformet.2017.12.252

Hardwick, S. R., Toumi, R., Pfeifer, M., Turner, E. C., Nilus, R., and *Ewers, R. M.,* 2015: The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agric For Meteorol. 201*, 187–195. https://doi.org/10.1016/j.agrformet.2014.11.010

Heithecker, T.D., and *Halpern, C.B.,* 2007: Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. *For. Ecol. Manag. 248*, 163–173. https://doi.org/10.1016/j.foreco.2007.05.003

Ho, K.V., Kröel-Dulay, G., Tölgyesi, C., Bátori, Z., Tanács, E., Kertész, M., Török, P., and Erdős, L., 2023: Non-native tree plantations are weak substitutes for near-natural forests regarding plant diversity and ecological value. *For. Ecol. Manag. 531*. 120789. https://doi.org/10.1016/j.foreco.2023.120789

Hofmeister, J., Hošek, J., Brabec, M., Střalková, R., Mýlová, P., Bouda, M., Pettit, J. L., Rydval, M., and Svoboda, M., 2019: Microclimate edge effect in small fragments of temperate forests in the context of climate change. *For. Ecol. Manag. 448*, 48–56. https://doi.org/10.1016/j.foreco.2019.05.069

IPCC., 2018: *Summary for Policymakers*. In: (eds. Masson-Delmotte, V., Zhai, P., Pörtner, H.O., Roberts, D., Skea, J., Shukla, P.R., Pirani, A., Moufouma-Okia, W., Péan, C., Pidcock, R., Connors, S., Matthews, J.B.R., Chen, Y., Zhou, X., Gomis, M.I., Lonnoy, E., Maycock, T., Tignor, M., and Waterfield, T.,), Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. Cambridge University Press, Cambridge, UK and New York, NY, USA, 3–24. https://doi.org/10.1017/9781009157940.001

Jackson, W.A., and Volk, R.J., 1970: Photorespiration. *Annu. Rev. Plant Physio. 21*, 385–432. https://doi.org/10.1146/annurev.pp.21.060170.002125

Kappelle, M., Van Vuuren, M. M. I., and Baas, P., 1999: Effects of climate change on biodiversity: A review and identification of key research issues. *Biodivers. Conserv. 8*, 1383–1397. https://doi.org/10.1023/A:1008934324223

Kertész, A., and Mika, J., 1999: Aridification, climate change is South-eastern Europe. *Phys. Chem. Earth Pt. A. 24*, 913–920. https://doi.org/10.1016/S1464-1895(99)00135-0

Király G., 2009: Új magyar füvészkönyv. Aggtelek National Park.

Krishnaswamy, J., John, R., and Joseph, S., 2014: Consistent response of vegetation dynamics to recent climate change in tropical mountain regions. *Glob. Change Biol. 20*, 203–215. https://doi.org/10.1111/gcb.12362

Lenth, R. V., 2022: *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.7.5. https://CRAN.R-project.org/package=emmeans

Luskin, M. S., and Potts, M. D., 2011: Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic Appl. Ecol. 12*, 540–551. https://doi.org/10.1016/j.baae.2011.06.004

Ma, S.Y., Concilio, A., Oakley, B., North, M. and Chen, J.Q., 2010: Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. *For. Ecol. Manag. 259*, 904–915. https://doi.org/10.1016/j.foreco.2009.11.030

Magnago, L.F.S., Rocha, M.F., Meyer, L., Martins, S.V., and Meira-Neto, J.A.A., 2015: Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodivers. Conserv. 24*, 2305–2318. https://doi.org/10.1007/s10531-015-0961-1

Manning, A.D., Gibbons, P., and Lindenmayer, D.B., 2009: Scattered trees: a complementary strategy for facilitating adaptive responses to climate change in modified landscapes? *J. Appl. Ecol. 46*, 915–919. https://doi.org/10.1111/j.1365-2664.2009.01657.x

Matlack, G.R., 1993: Microenvironment variation within and among deciduous forest edge sites in the eastern United State. *Biol. Conserv. 66*, 185–194. https://doi.org/10.1016/0006-3207(93)90004-K

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., and Yepez, E. A., 2008: Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytol. 178*, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Meeussen, C., Govaert, S., Vanneste, T., Bollmann, K., Brunet, J., Calders, K., Cousins, S.A.O., De Pauw, K., Diekmann, M., Gasperini, C., Hedwall, P.O., Hylander, K., Iacopetti, G., Lenoir, J., Lindmo, S., Orczewska, A., Ponette, Q., Plue, J., Sanczuk, P., Selvi, F., Spicher, F., Verbeeck, H., Zellweger, F., Verheyen, K., Vangansbeke, P., and De Frenne, P., 2021: Microclimatic edge-to-interior gradients of European deciduous forests. *Agric For Meteorol. 311*. 108699. https://doi.org/10.1016/j.agrformet.2021.108699

Mildrexler, D. J., Zhao, M., and Running, S. W., 2011: A global comparison between station air temperatures and MODIS land surface temperatures reveals the cooling role of forests. *J. Geophys. Res. 116*, G03025. https://doi.org/10.1029/2010JG001486

Milošević, D.D., Dunjić, J., and *Stojanović, V.,* 2020: Investigating Micrometeorological Differences between Saline Steppe, Forest-steppe and Forest Environments in Northern Serbia during a Clear and Sunny Autumn Day. *Geogr. Pannonica 24*, 176–186. https://doi.org/10.5937/gp24-25885

Molnár, Z., 2003: A Kiskunság száraz homoki növényzete. Természetbúvár Alapítvány Kiadó, Budapest (in Hungarian).

Molnár, Z., Biró, M., Bartha, S., and *Fekete, G.,* 2012: *Past trends, present state and future prospects of Hungarian forest-steppes.* In: (Eds. *Werger, M.J.A.* and *van Staalduinen, M.A.*), Eurasian Steppes. Springer, Berlin, 209–252. https://doi.org/10.1007/978-94-007-3886-7_7

Morecroft, M.D., Taylor, M.E. and *Oliver, H.R.*, 1998: Air and soil microclimates of deciduous woodland compared to an open site. *Agric. For. Meteorol. 90*, 141–156. https://doi.org/10.1016/S0168-1923(97)00070-1

Novick, K.A., Ficklin, D.L., Stoy, P.C., Williams, C.A., Bohrer, G., Oishi, A.C., Papuga, S. A., Blanken, P.D., Noormets, A., Sulman, B.N., Scott, R.L., Wang, L., and *Phillips, R.P.,* 2016: The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nat. Clim. Chang. 6*, 1023–1027. https://doi.org/10.1038/nclimate3114

Ónodi, G., Botta-Dukát, Z., Winkler, D., and *Rédei, T.,* 2021: Endangered lowland oak forest steppe remnants keep unique bird species richness in Central Hungary. *J. For. Res. 33*, 343–355. https://doi.org/https://doi.org/10.1007/s11676-021-01317-9

Peng, J., Dong, W., Yuan, W., and *Zhang, Y.,* 2012: Responses of grassland and forest to temperature and precipitation changes in Northeast China. *Adv. Atmos. Sci. 29*, 1063–1077. https://doi.org/10.1007/s00376-012-1172-2

Pohlman, C. L., Turton, S. M., and *Goosem, M.*, 2009: Temporal variation in microclimatic edge effects near powerlines, highways and streams in Australian tropical rainforest. *Agric. For. Meteorol. 149*, 84–95. https://doi.org/10.1016/j.agrformet.2008.07.003

R Core Team., 2021: R: a language and environment for statistical computing. https://cran.r-project.org/bin/windows/base/

Restaino, C. M., Peterson, D. L., and *Littell, J.,* 2016: Increased water deficit decreases Douglas fir growth throughout western US forests. *Proc. Natl Acad. Sci. USA* 113, 9557–9562. https://doi.org/10.1073/pnas.1602384113

Reyer, C.P.O., Leuzinger, S., Rammig, A., Wolf, A., Bartholomeus, R.P., Bonfante, A., de Lorenzi, F., Dury, M., Gloning, P., Abou Jaoudé, R., Klein, T., Kuster, T.M., Martins, M., Niedrist, G., Riccardi, M., Wohlfahrt, G., de Angelis, P., de Dato, G., François, L., ... and *Pereira, M.*, 2013: A plant's perspective of extremes: Terrestrial plant responses to changing climatic variability. *Glob. Change Biol. 19*, 75–89. https://doi.org/10.1111/gcb.12023

Ries, L., Fletcher, Jr., Battin, J., and *Sisk, T.D.,* 2004: Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained. *Annu. Rev. Ecol. Evol. Syst. 35*, 491–522. https://doi.org/10.1146/annurev.ecolsys.35.112202.130148

Riutta, T., Slade, E.M., Bebber, D.P., Taylor, M.E., Malhi, Y., Riordan, P., Macdonald, D.W., and *Morecroft, M.D.,* 2012: Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. *Soil Biol. Biochem. 49*, 124–131. https://doi.org/10.1016/j.soilbio.2012.02.028

Şahin, M., Yıldız, B.Y., Şenkal, O., and *Peştemalci, V.,* 2013: Estimation of the vapour pressure deficit using NOAA-AVHRR data. *Int. J. Remote Sens. 34*, 2714–2729. https://doi.org/10.1080/01431161.2012.750021

Schmidt, M., Lischeid, G., and *Nendel, C.,* 2019: Microclimate and matter dynamics in transition zones of forest to arable land. *Agric. For. Meteorol. 268*, 1–10. https://doi.org/10.1016/j.agrformet.2019.01.001

Shamshiri, R.R., Jones, J.W., Thorp, K.R., Ahmad, D., Man, H.C., and *Taheri, S.,* 2018: Review of optimum temperature, humidity, and vapour pressure deficit for microclimate evaluation and control in greenhouse cultivation of tomato: A review. *Int. Agrophysics 32*, 287–302. https://doi.org/10.1515/intag-2017-0005

Shibuya, T., Kano, K., Endo, R., and *Kitaya, Y.*, 2018: Effects of the interaction between vapor-pressure deficit and salinity on growth and photosynthesis of Cucumis sativus seedlings under different CO_2 concentrations. *Photosynthetica 56*, 893–900. https://doi.org/10.1007/s11099-017-0746-8

Shirke, P. A., and *Pathre, U. V.*, 2004: Influence of leaf-to-air vapour pressure deficit (VPD) on the biochemistry and physiology of photosynthesis in Prosopis juliflora. *J. Exp. Bot. 55*, 2111–2120. https://doi.org/10.1093/jxb/erh229

Sih, A., Jonsson, B.G., and *Luikart, G.,* 2000: Do edge effects occur over large spatial scale? *Tree 15*, 134–135. https://doi.org/10.1016/S0169-5347(00)01838-3

Stewart, D.W., and *Dwyer, L.M.,* 1983: Stomatal response to plant water deficits. *J. Theor. Biol. 104*, 655–666. https://doi.org/10.1016/0022-5193(83)90253-9

Stoutjesdijk, P., and *Barkman, J.J.,* 1992: *Microclimate, vegetation and fauna.* Opulus, Uppsala.

Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., and Thomas, C.D., 2011: Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos, 120,* 1–8. https://doi.org/10.1111/j.1600-0706.2010.18270.x

Süle, G., Balogh, J., Fóti, S., Gecse, B., and *Körmöczi, L.,* 2020: Fine-scale microclimate pattern in forest-steppe habitat. *Forests 11,* 1–16. https://doi.org/10.3390/f11101078

Süle, G., Fóti, S., Körmöczi, L., Petrás, D., Kardos, L., and *Balogh, J.,* 2021: Co-varying effects of vegetation structure and terrain attributes are responsible for soil respi ration spatial patterns in a sandy forest–steppe transition zone. *Web Ecol. 21,* 95–107. https://doi.org/10.5194/we-21-95-2021

Szabó, A., Gribovszki, Z., Kalicz, P., Szolgay, J., and *Bolla, B.,* 2022: The soil moisture regime and groundwater recharge in aged forests in the Sand Ridge region of Hungary after a decline in the groundwater level: an experimental case study. *J. Hydrol. Hydromech. 70,* 308–320. https://doi.org/10.2478/johh-2022-0019

Tölgyesi C., Valkó O., Deák B., Kelemen A., Bragina T.M., Gallé R., Erdős L., and *Bátori Z.,* 2018: Tree-herb coexistence and community assembly in natural forest-steppe transitions. *Plant Ecol. Divers. 11,* 465–477. https://doi.org/10.1080/17550874.2018.1544674

Tölgyesi, C., Kelemen, A., Bátori, Z., Kiss, R., Hábenczyus, A.A., Havadtői, K., Varga, A., Erdős, L., Frei, K., Tóth, B., and *Török, P.,* 2023: Maintaining scattered trees to boost carbon stock in temperate pastures does not compromise overall pasture quality for the livestock. *Agric. Ecosyst. Environ. 351,* 108477. https://doi.org/10.1016/j.agee.2023.108477

Tölgyesi, C., Török, P., Hábenczyus, A. A., Bátori, Z., Valkó, O., Deák, B., Tóthmérész, B., Erdős, L., and *Kelemen, A.,* 2020: Underground deserts below fertility islands? Woody species desiccate lower soil layers in sandy drylands. *Ecography 43,* 848–859. https://doi.org/10.1111/ecog.04906

Tölgyesi, C., Buisson, E., Hem, A., Temperton, V. M. and *Török, P.,* 2022: Urgent need for updating the slogan of global climate actions from "tree planting" to "restore native vegetation.". *Restor. Ecol. 30,* e13594. https://doi.org/10.1111/rec.13594

Travis, J. M. J., 2003: Climate change and habitat destruction: A deadly anthropogenic cocktail. *Proc. R. Soc. Lond.* B. 270, 467–473. https://doi.org/10.1098/rspb.2002.2246

Urban, O., Klem, K., Ač, A., Havránková, K., Holišová, P., Navrátil, M., Zitová, M., Kozlová, K., Pokorný, R., Šprtová, M., Tomášková, I., Špunda, V., and *Grace, J.,* 2012: Impact of clear and cloudy sky conditions on the vertical distribution of photosynthetic CO_2 uptake within a spruce canopy. *Funct. Ecol. 26,* 46–55. https://doi.org/10.1111/j.1365-2435.2011.01934.x

Van Heerwaarden, C.C., and *Teuling, A.J.,* 2014: Disentangling the response of forest and grassland energy exchange to heatwaves under idealized land-atmosphere coupling. *Biogeosciences, 11,* 6159–6171. https://doi.org/10.5194/bg-11-6159-2014

Várallyay, G., 1993: *Soils in the region between the rivers Danube and Tisza (Hungary).* In (Eds. *Szujkó-Lacza, J.* and *Kováts, D.*), The flora of the Kiskunság National Park I. Hungarian Natural History Museum. 21–42.

von Arx, G., Dobbertin, M. and *Rebetez, M.,* 2012: Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment in Switzerland. *Agric. For. Meteorol. 166–167,* 144–155. https://doi.org/10.1016/j.agrformet.2012.07.018

von Arx, G., Graf Pannatier, E., Thimonier, A., and *Rebetez, M.,* 2013: Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. J. Ecol. 101: 1201–1213. https://doi.org/10.1111/1365-2745.12121

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., and *Bairlein, F.,* 2002: Ecological responses to recent climate change. *Nature 416,* 389–437. https://doi.org/10.1038/416389a

Will, R. E., Wilson, S. M., Zou, C. B., and *Hennessey, T. C.,* 2013: Increased vapor pressure deficit due to higher temperature leads to greater transpiration and faster mortality during drought for tree seedlings common to the forest–grassland ecotone. *New Phytol. 200*, 366–374. https://doi.org/10.1111/nph.12321

Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., Swetnam, T. W., Rauscher, S. A., Seager, R., Grissino-Mayer, H. D., Dean, J. S., Cook, E. R., Gangodagamage, C., Cai, M., and *Mcdowell, N. G.*, 2013: Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change. 3*, 292–297. https://doi.org/10.1038/nclimate1693

Wright, T. E., Kasel, S., Tausz, M., and *Bennett, L. T.*, 2010: Edge microclimate of temperate woodlands as affected by adjoining land use. *Agric. For. Meteorol. 150*, 1138–1146. https://doi.org/10.1016/j.agrformet.2010.04.016

Young, A. and Mitchell, N., 1994: Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biol. Conserv. 67*, 63–72. https://doi.org/10.1016/0006-3207(94)90010-8

Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong, W., Hu, Z., Jain, A. K., Jiang, C., Kato, E., Li, S., Lienert, S., Liu, S., Nabel, J.E.M.S., Qin, Z., Quine, T., ... and *Yang, S.*, 2019: Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Sci. Adv. 5*, 1–13. https://doi.org/10.1126/sciadv.aax1396

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., and *Coomes, D.,* 2019: Advances in Microclimate Ecology Arising from Remote Sensing. *Trends Ecol. Evol. 34*, 327–341. https://doi.org/10.1016/j.tree.2018.12.012

Zhan, C., Liang, C., Zhao, L., Jiang, S., Niu, K., Zhang, Y., and *Cheng, L.*, 2022: Vegetation Dynamics and its Response to Climate Change in the Yellow River Basin, China. *Front. Environ. Sci. 10*, 1–18. https://doi.org/10.3389/fenvs.2022.892747