

1 **Effects of various cutting treatments and topographic factors on**
2 **microclimatic conditions in Dinaric fir-beech forests**

3
4 Janez Kermavnar*¹, Mitja Ferlan¹, Aleksander Marinšek^{1,3}, Klemen Eler^{2,1}, Andrej Kobler⁴,
5 Lado Kutnar¹

6
7 ¹Slovenian Forestry Institute, Department of Forest Ecology, Večna pot 2, 1000 Ljubljana,
8 Slovenia

9 ²University of Ljubljana, Biotechnical faculty, Department of Agronomy, Jamnikarjeva ulica
10 101, 1000 Ljubljana, Slovenia

11 ³Higher Vocational College for Forestry and Hunting, Ljubljanska cesta 2, 6230 Postojna,
12 Slovenia

13 ⁴Slovenian Forestry Institute, Department of Forest and Landscape Planning and Monitoring,
14 Večna pot 2, 1000 Ljubljana, Slovenia

15 *Corresponding author: Tel.: +38612007831, e-mail: janez.kermavnar@gozdis.si

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34 **Abstract**

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36 Forest microclimate is strongly affected by local topography and management activities, as
37 these directly alter overstory structure. In the present work we analysed the dependence of
38 observed patterns of spatio-temporal microclimatic variations on topographic, canopy- and
39 management-related factors. A forestry experiment was conducted in managed fir-beech forests
40 in the Dinaric Mountains (Slovenia), which are characterized by rugged karstic terrain with
41 numerous sinkholes. In 2012, cutting treatments representing a range in the intensity of
42 overstory removal were performed: uncut controls (CON), 50% cut of stand growing stock
43 (intermediate management intensity – IMI) and 100% cut (high management intensity – HMI)
44 creating 0.4 ha canopy gaps. Fine-scale variation in aspect and slope and its effects on
45 microclimate was assessed by comparing central, south-facing and north-facing within-
46 sinkhole positions. We measured microclimatic variables (air temperature – T, relative
47 humidity – RH) 0.5 m above the ground over three consecutive post-treatment growing seasons.
48 Microclimatic variables showed an increase (T and vapour pressure deficit – VPD) or decrease
49 (RH) with management intensity. Daily T_{\max} and VPD_{\max} in HMI treatment were up to 5.9 °C
50 (on average 3.5 °C) and up to 1.4 kPa (on average 0.6 kPa) higher than those in CON treatment,
51 respectively, whereas daily RH_{\min} was up to 22.7 (on average 13.0) percentage points lower.
52 Regarding intra-seasonal patterns, microclimatic differences between treatments were largest
53 during the summer. South-facing plots in the HMI treatment overall exhibited the most extreme
54 conditions, i.e. the highest T_{\max} and lowest RH_{\min} . Differences in microclimate between
55 treatments were strongly modulated by canopy cover. The results also suggest that overstory
56 removal increases topography-mediated variation in microclimate, as evidenced by significant
57 differences in T, RH and VPD along the fine-scale topographic gradient within the created
58 canopy gaps.

59 **Key words:** tree cutting; air temperature; relative humidity; vapour pressure deficit; karst
60 topography; canopy cover

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67 **1. Introduction**

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69 Trees and forest stands are known for their marked impact on local (micro)climate (Aussenac,
70 2000; Renaud et al., 2010). Forest ecosystems function as a thermal insulator, meaning that the
71 daytime air temperature is lower, the daily temperature range is smaller and it is warmer during
72 the night compared to forest edges and canopy gaps without tree canopies (Chen et al., 1993;
73 Kovács et al., 2017; De Frenne et al., 2019). Owing to sheltering from direct insolation and
74 increasing evaporative cooling (Thom et al., 2020), forests are often referred to as specific
75 abiotic environments where microclimatic conditions can significantly deviate from the
76 regional macroclimate (Frey et al., 2016; Macek et al., 2019). Decoupling between
77 microclimate and macroclimate has important implications for the forest biota living in these
78 environments (Zellweger et al., 2019). Such buffering effects are directly influenced by
79 silvicultural measures, which primarily alter the structure of forest stands (Zheng et al., 2000;
80 Aussenac, 2000; Ehbrecht et al., 2019). The formation of canopy gaps induces higher levels of
81 direct short-wave solar radiation reaching the forest floor and greater losses of outgoing long-
82 wave radiation from soils. The modulation of the light regime is expected to be the main process
83 through which canopy openings influence forest microclimate (Thom et al., 2020). For
84 example, Abd Latif and Blackburn (2010) demonstrated that the air temperature in gaps was
85 influenced directly by the amount and duration of solar radiation received.

86 Apart from the direct effects of forest management on microclimate, other environmental
87 factors (e.g. local topography, soil characteristics) have been proven to be very important for
88 differences in microclimate at smaller spatial scales, particularly in areas with heterogeneous
89 topographical setups (Grimmond et al., 2000; Frey et al., 2016; Greiser et al., 2018), such as
90 karst landscape. Topographically driven spatial variability of microclimate and soil properties
91 are expected to be the most clearly expressed in mountainous landforms (Cantlon, 1953). Even
92 so, these ecological phenomena also apply to lowland areas (e.g. Sewerniak et al., 2017;
93 Sewerniak and Puchałka, 2020). As such, the effects of tree cutting might interact with these
94 factors, inducing more complicated patterns in microclimatic variables. For instance,
95 differences in aspect position and slope inclination induce changes in incident radiation and soil
96 moisture (Sewerniak et al., 2017), resulting in large variability in temperature and relative
97 humidity over micro- and meso-scales (Ashcroft and Gollan, 2013; Macek et al., 2019). The
98 influence of local terrain features on microclimate dynamics is even expected to be largely
99 independent from the effects brought about by local canopy characteristics (Zellweger et al.,

100 2019). However, it remains unclear whether topography-induced spatial variability of forest
101 microclimate increases after management disturbance. Fine-scale variation in microclimate and
102 associated soil properties (Kobal et al., 2015; Sewerniak et al., 2017; Jasińska et al., 2020) may
103 have important implications for habitat and species diversity and composition within intact
104 forests and canopy gaps (Suggitt et al., 2011; Jucker et al., 2018; Macek et al., 2019).
105 Microclimatic conditions in forests with diverse topography can decouple from macroclimate
106 to such degree that specific relief positions (e.g. topographic concavity caused by depressions
107 of karst surface) may even serve as potential microrefugia for some species under the climate
108 change (Lenoir et al., 2017; Kiss et al., 2020; Bátori et al., 2020).

109
110 The need for knowledge on the effects of forest management on microclimate has long been
111 recognised (Keenan and Kimmins, 1993). Microclimate has a significant impact on tree species
112 regeneration and plant growth and is a major driver of ecosystem processes such as
113 decomposition, soil respiration and nutrient dynamics (Ma et al., 2010). Previous studies have
114 either studied the main structural determinants of mature forest stands on microclimate, mainly
115 on temperature (e.g. Ehbrecht et al., 2019), or compared the below-canopy environment to that
116 of the adjacent open area (e.g. von Arx et al., 2012). Additionally, extensive work has been
117 dedicated to the quantification of how different forest management practices affect key abiotic
118 variables (e.g. Heithecker and Halpern, 2006; Heithecker and Halpern, 2007; Kovács et al.,
119 2017; Thom et al., 2020). Nevertheless, disturbance impacts on microclimate remain poorly
120 quantified, despite the importance of microclimatic conditions for future forest development.
121 Furthermore, previous studies have rarely been based on controlled manipulation experiments
122 (Thom et al., 2020). Such studies usually showed the most profound differences in microclimate
123 between intact stands (control) and conditions found in more open areas such as clear-cuts.
124 When studying forest microclimate, it is important not only to describe the average conditions
125 of cutting treatments but also the magnitude or sources of variation within them (Heithecker
126 and Halpern, 2006; Abd Latif and Blackburn, 2010). Evaluating the influence of management
127 practices on microclimatic variation and monitoring microclimate over the long term are
128 essential for improving our understanding of forest resources and effectiveness in managing
129 them (Zheng et al., 2000).

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131 In this study we examined patterns of microclimatic variation among silvicultural treatments
132 that represent a gradient in cutting intensity in mixed forests in the Dinaric Mountains. To some
133 degree, changes in microclimate due to forest management may be predictable. Although

134 considerable information has been published on the effects of different levels of overstory
135 removal upon microclimate, its topography-modulated spatial variability remains poorly
136 understood in general. Because of the accentuated karst topography of the Dinaric region, we
137 expect that variation in local topographic factors (aspect and slope) will strongly interact with
138 silvicultural measures to influence microclimatic conditions in the studied forest type.
139 Our objectives were to (1) quantify cutting treatment effects on microclimate, (2) examine fine-
140 scale spatial variation in microclimate associated with local topographic factors (i.e. slope
141 aspect and inclination) and forest structure (i.e. canopy cover), and (3) assess the potential
142 interplay between forest management and local topography. Their combined influence on
143 microclimatic conditions has received little notice so far. Effects of topographic factors upon
144 forest microclimate seems to be universal, most often evidenced by the comparisons between
145 south- and north-facing slopes in both concave and convex configurations. We aim to confirm
146 certain generalities that can be drawn from earlier studies, conducted in widely different
147 climatic regions, topographical setups and forest types. This will help to assess the impacts of
148 relatively small-scale landforms (karst sinkholes in our case) on microclimate, further
149 solidifying their prominent ecological role in shaping forest structure and vegetation
150 composition (Kobal et al., 2015), as well as concerning the post-disturbance successional
151 trajectories.

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166 2. Materials and methods

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168 2.1. Study area

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170 This study was conducted at three distinct study sites (Kočevski Rog, Snežnik and Trnovo) in
171 Slovenia, all of which are covered by Dinaric fir-beech forests. The study area at each site was
172 ca. 70 ha in size. For more details about our study area, see Kutnar et al. (2015). Despite being
173 located tens of kilometres apart, regional climatic conditions, characteristics of stand structure
174 (tree species composition, stand age, understory development) and general topographic
175 appearance (karst landscape) were similar across the study sites. In general, the climate is
176 moderate continental, i.e. warm, dry summers and cold, wet winters. The mean annual
177 temperature is 8–9 °C and mean annual precipitation is 1700–2000 mm (Kutnar et al., 2015).
178 The topography is characterized by diverse karst terrain with numerous sinkholes (bowl-shaped
179 depressions, also known as karst dolines; Aguilon et al., 2020), ridges and slopes. The diversity
180 of the karst terrain results in small-scale heterogeneity in edaphic conditions. The most frequent
181 soil types are Eutric Cambisols (calcareous brown forest soils), Leptosols (rendzinas) and
182 Luvisols (IUSS Working Group WRB, 2015) derived from limestone and dolomite parent
183 materials. The vegetation consists of uneven-aged Dinaric fir-beech forests affiliated to the
184 *Omphalodo–Fagetum* s. lat. association, with the stand growing stock ranging between 300 and
185 400 m³·ha⁻¹ (Kutnar et al., 2015). Before cutting, all of the stand overstories were dominated
186 by European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) or Norway spruce (*Picea*
187 *abies* (L.) Karst.) and were most often a mixture of these late-successional tree species.

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189 Pre-treatment forests were characterized by homogeneous mature stands with well-developed
190 vertical stratification and dense canopy cover (~ 95%) and lacked evidence of recent
191 management or natural disturbances. Local regeneration patches of irregular size and shape
192 were thus limited. The investigated forest stands have a heterogeneous structure with trees of
193 different diameters and heights. Continuous-cover and close-to-nature silvicultural approaches
194 that support structural heterogeneity have been traditionally used. Single-tree and group-
195 selection cuttings are most frequent measures to initialize tree regeneration in the studied forests
196 (Kutnar et al., 2015). Unfragmented forests in the Dinaric Mountains represent one of the few
197 large forested landscapes in Europe with continuous canopy cover, where stand-replacing
198 disturbances happen only infrequently (Nagel et al., 2017).

199 2.2. *Experimental design and sampling procedures*

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201 At each of the three study sites, nine karst sinkholes were randomly selected, amounting to 27
202 sinkholes in total for the entire study area. The basic geomorphological parameters of the
203 sinkholes (i.e. elevation, size, shape) were comparable between treatment types (see Table S1
204 in the Supplementary material). Average distances between the centres of the selected sinkholes
205 were 562.9 m (Kočevski Rog), 524.4 m (Trnovo) and 399.2 (Snežnik), respectively, with an
206 overall mean of 495.5 m.

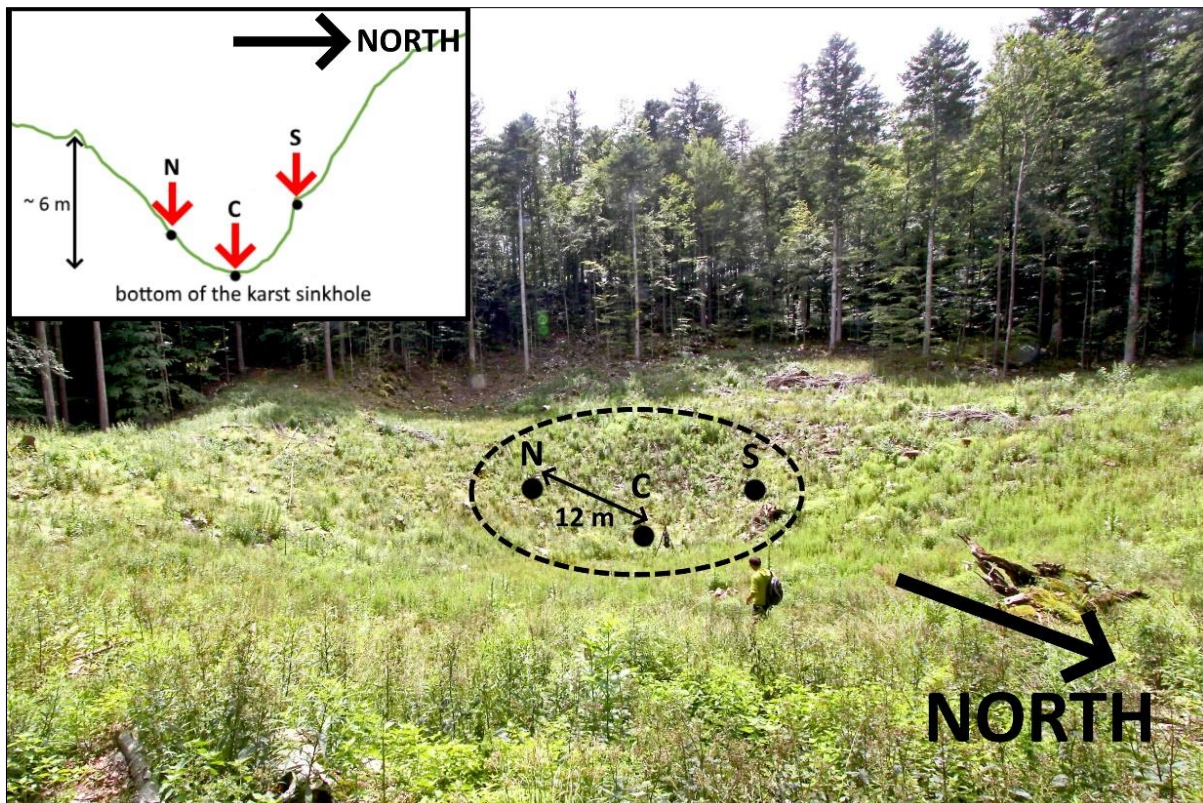
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208 In each sinkhole, a circular treatment area of 0.4 ha ($r = 35.7$ m) with the centre in the bottom
209 of the sinkhole was established. The sinkholes were randomly assigned to three different cutting
210 intensities (forest management treatments): (a) control with no cutting of the overstory trees
211 (control – CON), (b) 50% cutting of the initial stand growing stock with residual trees being
212 evenly spatially distributed across the treatment area (intermediate management intensity –
213 IMI) and (c) 100% cutting of the growing stock with no mature trees remaining (high
214 management intensity – HMI). In silvicultural terms, IMI is a form of uniform partial cutting
215 that is comparable to intensive thinning or dispersed tree retention. In the HMI treatment 0.4 ha
216 circular canopy gaps were formed within the surrounding closed canopy stands. The canopy
217 gaps created are substantially smaller than is typical in European temperate deciduous forest
218 (3–10 ha) (Kovács et al., 2018) but are in conformity with Slovenian legislation (Forest Act,
219 1993), which generally prohibits forest “clear-cuts” exceeding 0.5 ha. Within each study site,
220 the pre-treatment conditions of the sinkholes selected for the different treatment levels were
221 comparable. Cutting of trees and hauling of logs was completed in 2012.

222

223 Our sampling procedure was specifically designed to assess environmental variation due to both
224 management-induced canopy effects and topographic (slope exposition) variability. Within
225 each sinkhole, three measuring plots were established: in the sinkhole centre/bottom (C) and on
226 its south-facing (S) and north-facing (N) slopes (Fig. 1). Due to bowl-shaped topographic
227 concavity, northern within-sinkhole positions/plots have south-facing exposure and southern
228 within-sinkhole positions/plots have north-facing exposure. The south-facing and north-facing
229 plots were 12 m from the bottom/centre of the sinkhole (Fig. 1). In total, 81 plots (27 sinkholes
230 × three within-sinkhole positions) were established, and data on meteorological variables,
231 overstory structure and topographic factors were collected.

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233
 234 **Figure 1:** An example of the HMI treatment with the positions of three plots within a karst sinkhole, where data
 235 on microclimatic and other environmental conditions were measured. One plot was established in the centre (i.e.
 236 bottom of the sinkhole, C), one in the south-facing (S) and one in the north-facing (S) slope of the sinkhole, 12 m
 237 from the bottom/centre of the sinkhole. The dashed ellipse denotes the approx. edge of the sinkhole. The vertical
 238 profile of the sinkhole is shown in the upper left corner. Photo by Lado Kutnar, July 2014 (i.e. 2 years after cutting).

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240 2.3. Data collection

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242 Microclimatic measurements were carried out with a Voltcraft DL-120 TH (Conrad Electronic
 243 SE, Hirschau, Germany) data logger with an SHT11 integrated sensor (Sensirion Inc.) for air
 244 temperature (T, in °C) and relative humidity (RH, in %). Sensors (with typical accuracy of ±
 245 0.4 °C and ± 3%, respectively) were installed 0.5 m above the ground surface and were inserted
 246 into radiation shields to protect the instruments against direct solar radiation. Data loggers were
 247 programmed to record T and RH every 30 minutes. Measurements were deployed over three
 248 consecutive growing seasons: immediately after cutting in 2012 and in the next two years.
 249 Sensors collected meteorological data in the period of canopy leaf-out, when canopy closure
 250 was fully developed, i.e. from May to October.

251

252 To evaluate potential differences in microclimate due to variation in topography, we collected
 253 the aspect (azimuth in ° from the north) and slope inclination (in °) at each plot.

254 Percent canopy closure was determined from aerial LiDAR scanning performed in 2013. First,
255 the canopy height model (CHM) with 1 m horizontal resolution was calculated from the lidar
256 point cloud. Three concentric circular areas with radii of 2 m, 4 m and 8 m, respectively, were
257 defined. The centres of these areas were coincident with the sampling plot centres. Canopy
258 cover in each circular area was then expressed as the percentage of the area covered by CHM
259 vegetation higher than 5 m. Thus, we not only considered canopy cover in the plot but also in
260 its variously sized neighbourhoods. Based on visual estimation, there were no evident changes
261 in overstory canopy cover in the post-treatment period.

262

263 2.4. *Data preparation and processing*

264

265 Microclimate data series were first graphically and quantitatively inspected. Statistical outliers
266 and data points indicating obvious errors caused by sensor failures (e.g. unrealistic data or large
267 spikes in variables) were detected with the 'tsoutliers' function in the R package *forecast*
268 (Hyndman et al. 2019; R Development Core Team, 2018) and then omitted from the analysis.
269 The temperature data coherence for each plot was checked by comparison with daily data from
270 the nearest meteorological station at each study site for each growing season (data retrieved
271 from Slovenian Environment Agency archive, 2019); generally, the correlation coefficients
272 were above 0.9 (data not shown).

273

274 For a few plots, some minor data on T and RH were missing due to technical failures of sensors
275 or empty batteries. In the case of T, missing 30 min values were gap-filled using linear
276 regressions between the plot and nearest meteorological station because the correlations were
277 strong (Pearson's coefficients > 0.9). For RH, the correlation coefficients between our plots and
278 the nearest meteorological stations were very low (usually below 0.1). Therefore, to gap-fill
279 RH data, linear regressions between the missing RH data and complete T data from the nearest
280 plot were used.

281

282 Based on T and RH gap-filled data, the vapour pressure deficit (VPD, in kPa) was calculated
283 for each sensor (plot) at each time step (30 min) using the formula:

$$284 \quad VPD = e_{sat} - e_{air}$$

285 where e_{sat} is the saturation vapour pressure and e_{air} is the air (actual) vapour pressure (Murray,
286 1967). A combination of high T and low RH produces high VPD values (Ashcroft and Gollan,

287 2013). VPD is an eco-physiologically meaningful climate variable and a good standalone
288 indicator of the atmospheric factors influencing evapotranspiration (Jucker et al., 2018). A
289 higher VPD implies increasing water stress of plants (Thom et al., 2020). Although temperature
290 extremes have been more frequently studied, the critical role of VPD for plant growth and
291 survival is increasingly recognized (Davis et al., 2019).

292

293 To quantify the effects of topographic factors on microclimate, we derived an index called
294 “AspSlo”, which combines slope aspect and slope inclination and expresses the aspect-related
295 radiative exposure (Fleming and Baldwin, 2008). It was calculated with the following formula:

$$296 \text{ AspSlo} = ((\cos[\text{ABS}(225^\circ - \Theta)] \times \sin(\alpha))$$

297 where Θ is aspect ($^\circ$) and α is inclination ($^\circ$); both parameters need to be transformed to radians
298 before calculation. In the formula above, 225° expresses the southwestness (Heithecker and
299 Halpern, 2006); slopes in the northern hemisphere with south-western orientations are expected
300 to receive the highest amount of solar radiation. However, this also depends on slope steepness
301 – steeper slopes are more exposed to radiation than flat areas. In theory, the AspSlo index ranges
302 from -1 (aspect = 45° , slope = 90°) to 1 (aspect = 225° , slope = 90°).

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304 *2.5. Calculation of aggregated microclimatic values*

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306 For each microclimatic variable (T, RH and VPD), the data sets contained almost two million
307 individual data points (30 min records), when the data from the three study sites and three
308 growing seasons were pooled.

309 The 30 min observations were aggregated into different daily values. We focused on four main
310 variables: daily maximum temperature (T_{\max}), diurnal temperature range (DTR) as the
311 difference between T_{\max} and daily minimum temperature (T_{\min}), minimum relative humidity
312 (RH_{\min}) and maximum vapour pressure deficit (VPD_{\max}). Mean daily values (T_{avg} , RH_{avg} ,
313 VPD_{avg}) were calculated as well. For each treatment type, daily values for each sensor (plot)
314 were averaged across each growing season and also over three growing seasons to obtain the
315 overall mean plot-level value.

316

317 In addition, we calculated microclimatic differences (marked with Δ) between three cutting
318 treatments: CON vs. HMI, CON vs. IMI and IMI vs. HMI. Microclimatic differences between
319 treated and untreated stands indicate the disturbance-induced change in the buffering capacity

320 of intact forests with regard to T, RH and VPD. Control (CON) values were subtracted from
321 the treatment values. For the IMI vs. HMI comparison, IMI values were subtracted from the
322 HMI values. First, we averaged the values for each treatment, within-sinkhole position and day
323 and then subtracted the control values, producing a daily difference. Then, the daily differences
324 were averaged across the growing season. These were calculated for daily maximum
325 temperature (ΔT_{\max}), diurnal temperature range (ΔDTR), daily minimum humidity (ΔRH_{\min})
326 and daily maximum VPD (ΔVPD_{\max}). A separate analysis was done for the entire growing
327 season (May–October, 184 days), the summer period (June, July, August; 92 days), which
328 represents the most stressful portion of the growing season (e.g. summer drought, high
329 temperature amplitudes and extremes; von Arx et al., 2013; Thom et al., 2020), and the
330 transition period (May, September, October; 92 days).

331
332 Microclimatic variables were analysed in terms of their overall characteristics and patterns on
333 different temporal scales. Intra-seasonal patterns of daily differences for the selected
334 microclimatic variables were compared graphically. Second-order polynomial regression
335 curves were fitted for each comparison. Similarly, diurnal patterns of T and RH were inspected
336 with graphical visualisation, using 30 min data averaged across study sites, growing seasons
337 and within-sinkhole positions.

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339 2.6. *Statistical analyses*

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341 To test how management intensity, within-sinkhole position and their interaction affect
342 different microclimate variables over time, we constructed linear mixed-effects models. For
343 modelling, the dependent variable means of each growing season were used ($n = 243$).
344 Treatment (CON, IMI, HMI), position within the sinkhole (C, S, N) and growing season (2012,
345 2013, 2014) were regarded as fixed factors, while study site and sinkhole (nested within site)
346 were specified as random factors. We used the Shapiro-Wilk test and graphical examination
347 (histograms) to check whether each response variable significantly deviated from normal
348 distribution. If so, appropriate data transformation was used (Faraway, 2006). To detect possible
349 multicollinearity among the explanatory variables, we calculated variance inflation factors
350 (Zuur et al., 2009). The models' goodness-of-fit values were measured by a likelihood-ratio
351 test-based coefficient of determination (R^2_{LR} ; Bartoń, 2019). For post-hoc tests, the Tukey
352 procedure at $\alpha = 0.05$ significance level was used.

353 We used simple linear regression to examine the relationship between overstory structure
354 (canopy cover) and overall mean plot-level values of T_{\max} and RH_{\min} (averaged across the entire
355 measurement period). Analysis of covariance (ANCOVA) was used to test for the effect of
356 canopy cover on T_{\max} and RH_{\min} , in which treatment and study site were defined as covariates.
357 Regression analyses were also used to investigate the dependence of microclimatic variables
358 on topographic factors (AspSlo index), and this effect was tested with an ANCOVA (site and
359 treatment as covariates in the model). This was done with the mean T_{\max} and RH_{\min} values for
360 each sensor ($n = 81$) averaged across the entire measurement period.

361

362 All statistical analyses and graphing were conducted in R version 3.5.2 (R Development Core
363 Team, 2018) using the following packages: *nlme* (Pinheiro et al., 2019), *multcomp* (Hothorn et
364 al., 2019), *lsmeans* (Lenth, 2016) and *MuMIn* (Bartoń, 2019).

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387 **3. Results**

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389 *3.1. The effects of cutting and within-sinkhole position on microclimate*

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391 According to the linear mixed models, treatment intensity had a highly significant effect on all
392 of the microclimatic variables considered (Table 1). Treatment most significantly affected
393 DTR, T_{\max} , VPD_{\max} and RH_{\min} , whereas it showed a less strong effect on T_{\min} , T_{avg} , RH_{avg} and
394 VPD_{avg} . Mean and maximum T and VPD were on average highest in the HMI treatment and
395 lowest in the CON treatment (Fig. 2). In contrast, mean and minimum daily RH were lowest in
396 the HMI treatment. Daily T_{\max} and VPD_{\max} in the HMI treatment were up to 5.9 °C (overall
397 average: 3.5 °C) and 1.4 kPa (0.6 kPa) higher than in the CON treatment, respectively, whereas
398 daily RH_{\min} was up to 22.7 (13.0) percentage points lower (Fig. 2). DTR was on average 4.2 °C
399 higher in the HMI compared to the CON treatment. When comparing different treatments, the
400 largest differences were between CON and HMI. Overall, for the analysed microclimatic
401 variables, differences between IMI and HMI tended to be smaller than differences between IMI
402 and CON (Fig. 2). Differences between treatments were higher for maximum and minimum
403 variables compared to daily mean values.

404

405 The within-sinkhole position had a significant effect on some temperature variables (DTR, T_{\max} ,
406 T_{\min}) and vapour pressure deficit (VPD_{\max}) (Table 1), but not in the CON treatment. The
407 interaction between treatment and position showed a significant effect on DTR, T_{\min} and T_{\max}
408 (Table 1). Along the cutting intensity gradient, differences between positions increased for all
409 microclimatic variables (Fig. 2), with south-facing plots in the IMI and HMI treatments
410 exhibiting the highest T_{\max} and VPD_{\max} . For example, the significance of the interaction term
411 implies that there were larger temperature differences between the within-sinkhole positions in
412 the IMI treatment, and particularly in the HMI treatment, compared to the CON treatment.
413 North-facing plots in IMI and HMI tended to be colder and more humid compared to south-
414 facing plots. Overall, the most extreme microclimatic conditions, i.e. high T and low RH
415 resulting in high VPD, were in south-facing HMI plots (Fig. 2).

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420 **Table 1:** The results of the linear mixed-effects models performed for the selected microclimatic variables: T – air
 421 temperature, RH – relative humidity, VPD – vapour pressure deficit, DTR = diurnal temperature range (T_{\max} minus
 422 T_{\min}). Interaction between position and growing season is not shown as it was not significant in any of the models.
 423 Captions: “avg” refers to mean, “max” to maximum and “min” to minimum.

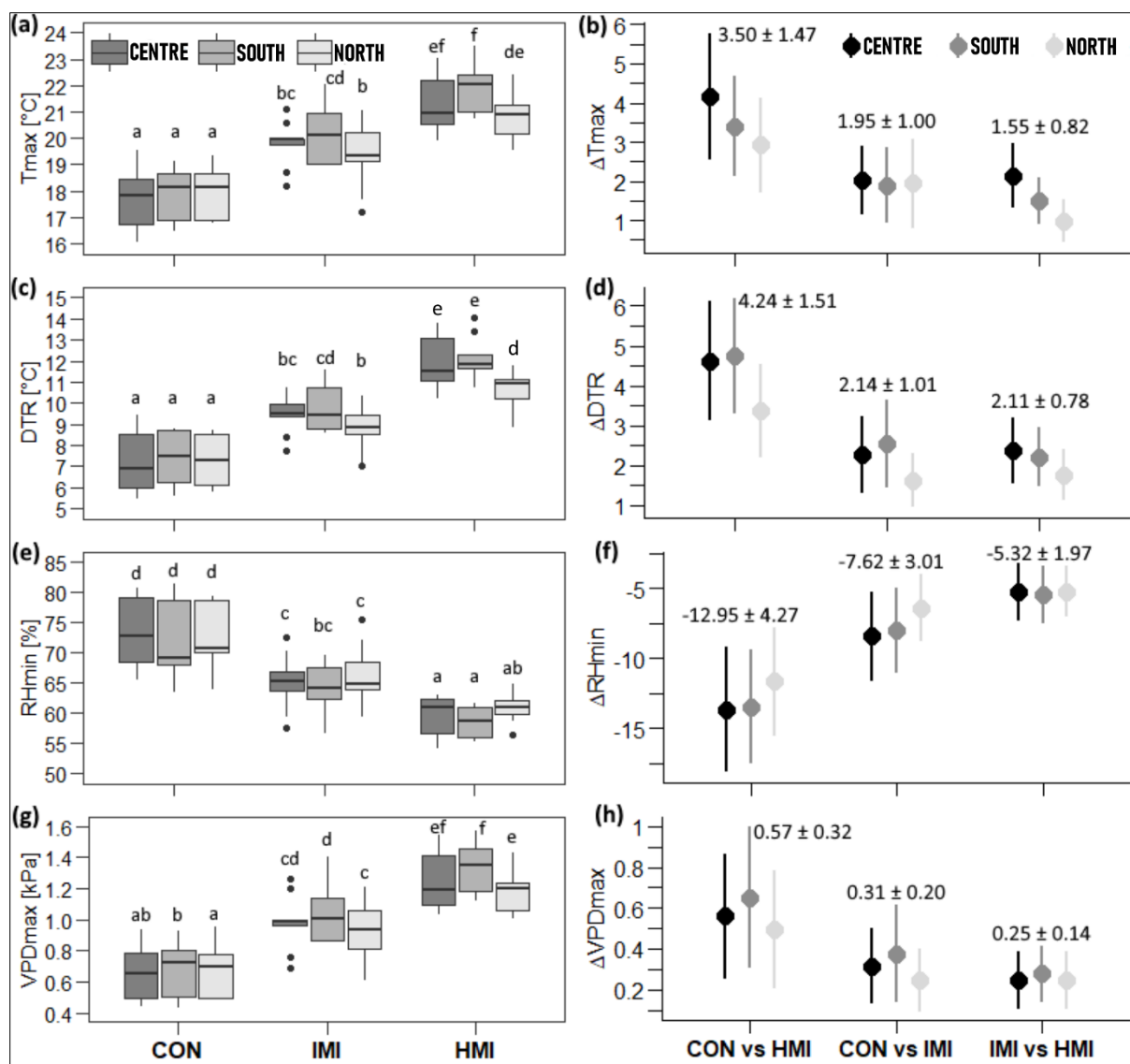
Dependent variable	Model		Treatment		Position		G. season		Treat:Posit		Treat: g. season		
	Chi ²	p	R ² _{LR}	F	p	F	p	F	p	F	p	F	p
T _{avg}	355.06	***	0.799	32.94	***	2.47	ns	447.01	***	0.83	ns	-2.28	ns
T _{max}	287.45	***	0.845	261.97	***	11.31	***	72.74	***	3.32	*	4.92	***
T _{min}	321.82	***	0.734	32.29	***	6.30	**	291.94	***	3.69	**	3.28	*
DTR	233.45	***	0.836	376.34	***	15.93	***	10.56	***	4.19	**	5.35	***
RH _{avg}	277.25	***	0.742	48.37	***	0.76	ns	216.90	***	0.10	ns	2.08	ns
RH _{min}	222.91	***	0.777	141.84	***	2.77	ns	61.04	***	0.39	ns	3.20	*
VPD _{avg}	379.42	***	0.845	61.53	***	1.31	ns	440.60	***	0.49	ns	1.42	ns
VPD _{max}	335.87	***	0.846	217.30	***	7.32	**	149.24	**	1.70	ns	6.90	***

* p < 0.05, ** p < 0.01, *** p < 0.001, ns – not significant.

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 425
 426 Treatment had a more prominent effect on the maxima and minima of the variables, while for
 427 the variable means (T_{avg}, RH_{avg}, VPD_{avg}), growing season proved to be more important (Table
 428 1).

429 With respect to treatment effects, the largest differences in the investigated variables were
 430 detected between the CON and HMI treatments. These differences on average amounted to 3.5
 431 °C (T_{max}), 4.2 °C (DTR), –13.0 percentage points (RH_{min}) and 0.6 kPa (VPD_{max}), respectively.
 432 The smallest differences were observed between the IMI and HMI treatments. Differences in
 433 microclimatic conditions were on average smaller between the IMI and HMI treatments than
 434 between CON and IMI treatments (Figs. 2b, 2d, 2f, 2h).

435

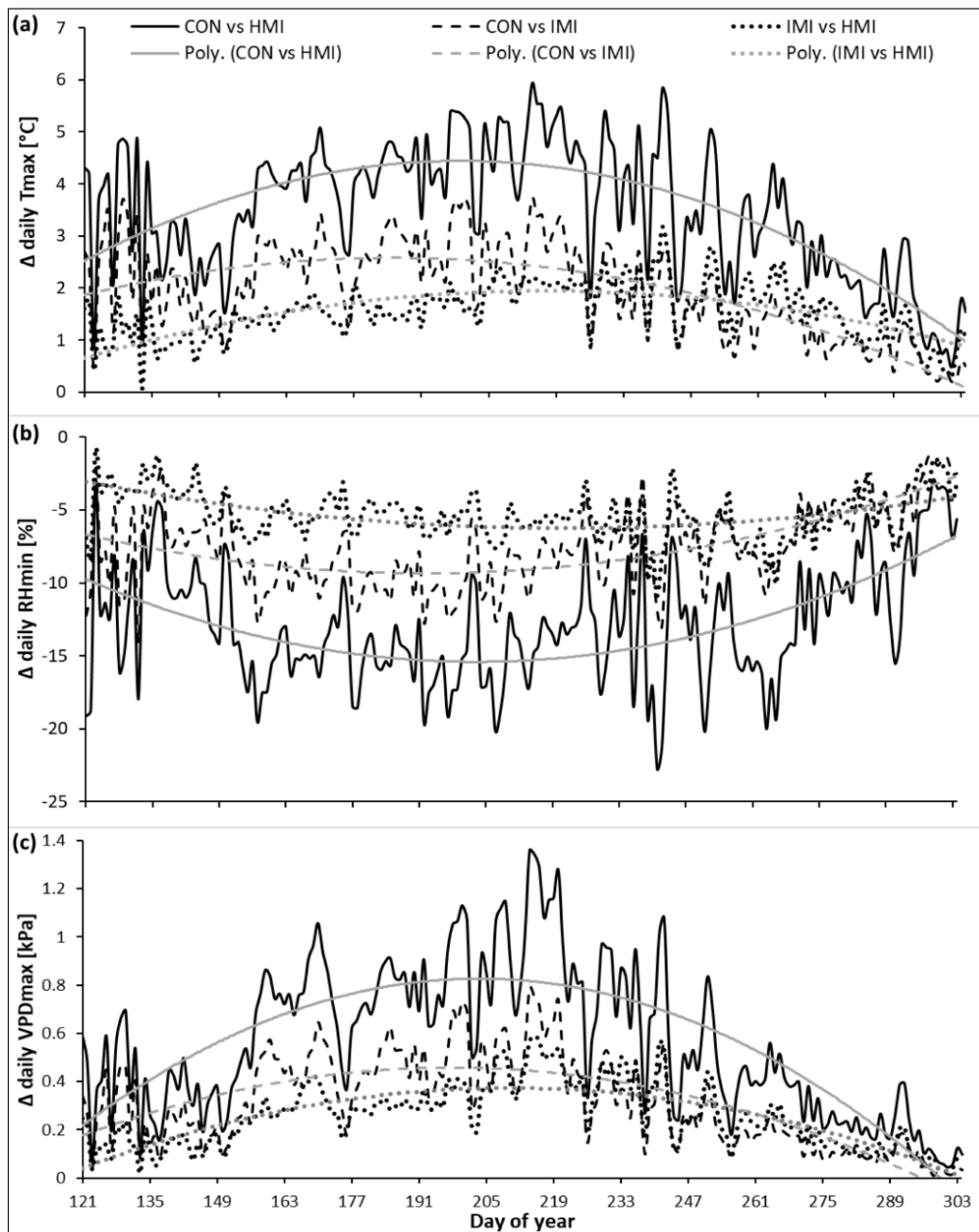


436
 437 **Figure 2:** Plot-level values, averaged across three growing seasons, of four selected microclimatic variables: (a)
 438 daily maximum temperature (T_{\max}), (c) diurnal temperature range ($DTR = T_{\max}$ minus T_{\min}), (e) daily minimum
 439 relative humidity (RH_{\min}) and (g) daily maximum vapour pressure deficit (VPD_{\max}). Results are shown for each
 440 treatment (CON = control, IMI = 50% cut, HMI = 100% cut) and within-sinkhole position (centre – central plots,
 441 south – south-facing plots, north – north-facing plots). Letters designate significant differences between treatments
 442 and position. Panels b, d, f and h show differences (Δ , mean \pm SD) in microclimatic variables between treatments.
 443

444 **3.2. Differences in microclimate between treatments: intra-seasonal variation**

445
 446 Differences between treatments in T_{\max} , RH_{\min} and VPD_{\max} were largest during the summer
 447 months, especially in July and August (Fig. 3, Fig. S1 in the Supplementary material). These
 448 differences were in most cases smallest during the transition period (Fig. S1 in the
 449 Supplementary material). The strength of the cooling and humidifying effect of the canopy
 450 depended on the absolute value of T_{\max} ; the warmer the temperature, the stronger the canopy
 451 effect. For example, in the case of T_{\max} , during a hot summer day with temperatures exceeding
 452 30 °C, the difference between HMI and CON treatments reached 5 °C or even more. During

453 colder days (e.g. temperatures between 10 and 15 °C), this difference was normally lower than
 454 2 °C (data not shown). Similar patterns were observed for RH_{\min} and VPD_{\max} (Fig. 3).
 455



456
 457 **Figure 3:** Mean temporal profile of differences between cutting treatments (CON = control, IMI = 50% cut, HMI
 458 = 100% cut) in (a) daily maximum temperature (T_{\max}), (b) daily minimum relative humidity (RH_{\min}) and (c) daily
 459 maximum (VPD_{\max}) during the growing season (May 1 – Oct 31). The fitted curves (in grey) are second-order
 460 polynomial regression lines.
 461

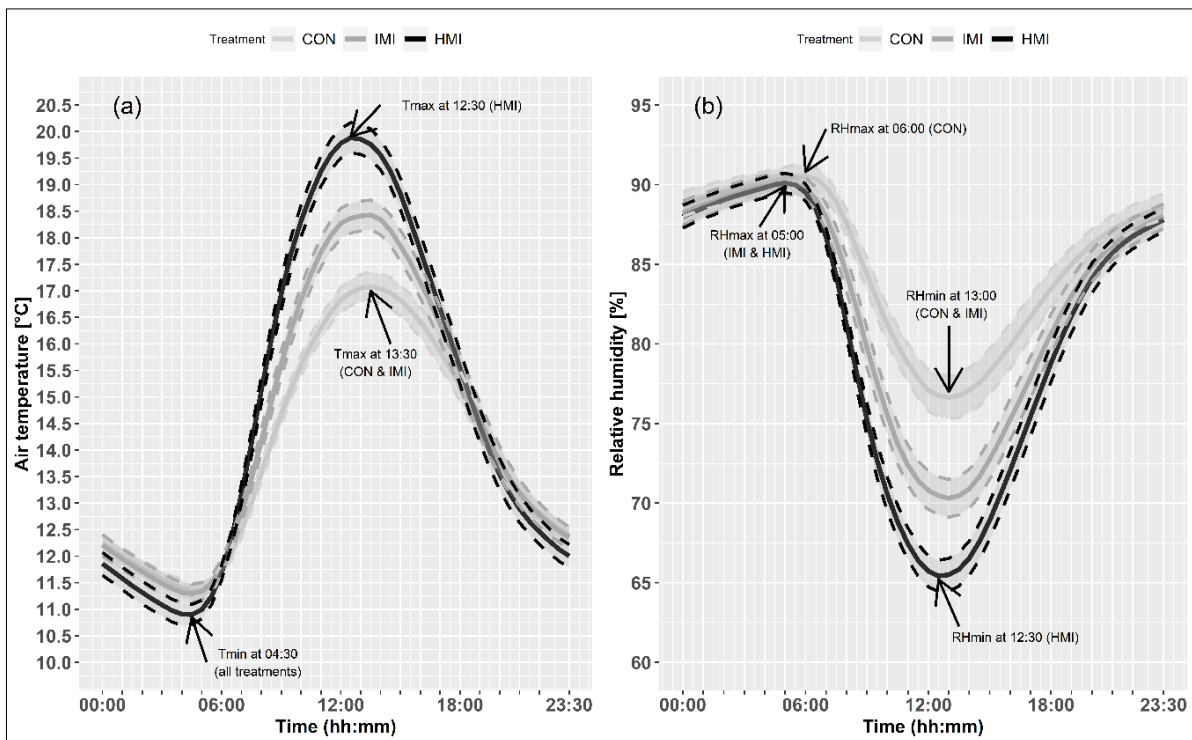
462 3.3. Diurnal course of air temperature and relative humidity

463
 464 Intermediate management intensity and particularly HMI treatment experienced larger diurnal
 465 variation in T and RH values compared to the CON treatment (Fig. 4). Despite lower night-

466 time temperatures in HMI treatment, the time of day when T_{\min} was reached (at 04:30) did not
 467 differ between treatments. In contrast, air temperature in the HMI treatment reached its
 468 maximum ca. one hour before (at 12:30) peaking in the other two treatments (CON and IMI; at
 469 13:30) (Fig. 4a). At peak time, T_{\max} values (averaged across all days and across all growing
 470 seasons) reached 17.1 °C in the CON treatment, 18.4 °C in the IMI treatment and 19.9 °C in
 471 the HMI treatment (Fig. 4a).

472
 473 Relative humidity, because of its coupling with T, showed a more or less inverse diurnal course
 474 compared to temperature (Fig. 4b). Its maximums were reached at 05:00 (IMI and HMI) and
 475 06:00 (CON), respectively. Minimums of RH were reached almost at the same time as T
 476 peaked, i.e. at 12:30 (HMI) and 13:00 (CON and IMI). On average, at the time of the lowest
 477 daily RH (averaged across all days and across all growing seasons), values dropped to 76.7%
 478 in the CON treatment, 70.3% in the IMI treatment and 65.4% in the HMI treatment (Fig. 4b).
 479 Within-sinkhole position showed no effect on diurnal patterns of T and RH.

480



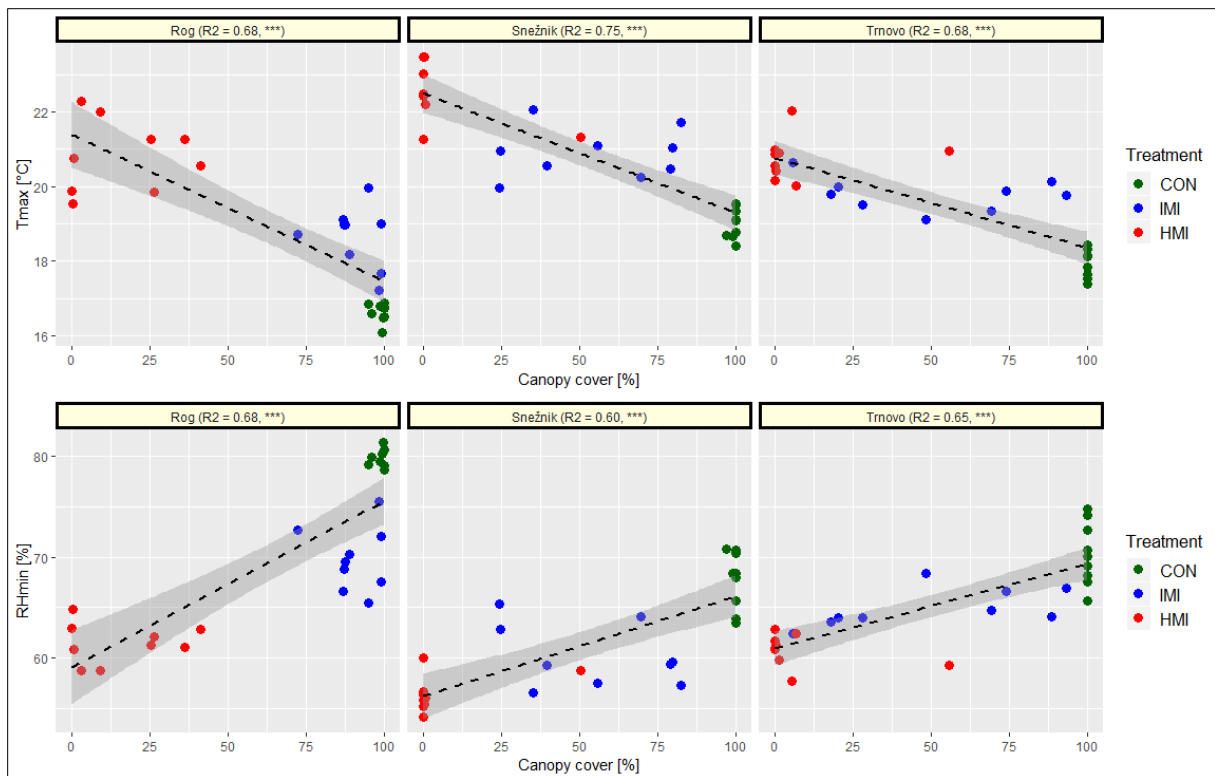
481
 482 **Figure 4:** Diurnal course of (a) air temperature and (b) relative humidity for different cutting treatments (CON =
 483 control, IMI = 50% cut, HMI = 100% cut). Solid lines represent means averaged over the study sites, entire
 484 measurement period and within-sinkhole positions (i.e. central, south-facing and north-facing plots). Bands
 485 (dashed lines) represent 95% confidence intervals. Arrows indicate the time of day when peak values (maxima –
 486 max and minima – min) of microclimatic variables were reached for each treatment type.
 487
 488

489 3.4. Relationship between overstory canopy cover and microclimatic variables

490

491 Overstory vegetation characteristics (canopy cover) had a strong influence on T_{\max} (ANCOVA:
492 $n = 81$, $F_{1,75} = 342.3$, $p < 0.001$, $R^2 = 0.59$) and RH_{\min} (ANCOVA: $n = 81$, $F_{1,75} = 262.5$, $p <$
493 0.001 , $R^2 = 0.53$). Plots, which were subjected to different cutting treatments, exhibited wide
494 variation in the degree of canopy closure (Fig. 5). There was a significant linear relation
495 between canopy cover and daily T_{\max} . Plots with higher overstory canopy cover (i.e. vegetation
496 higher than 5 m) showed lower maximum temperatures and vice-versa. In contrast, we found a
497 statistically significant positive linear relation between canopy cover and daily RH_{\min} . Plots
498 with higher canopy cover experienced higher humidity values and vice-versa (Fig. 5). Canopy
499 cover also significantly affected other microclimatic parameters, i.e. T_{avg} , T_{\min} , DTR, RH_{avg} and
500 VPD_{avg} (ANCOVA results not shown).

501



502

503 **Figure 5:** Linear relationship between overstory canopy cover (%), data derived from LiDAR and daily maximum
504 temperature (T_{\max} , upper panels) for different cutting intensities (CON = control, IMI = 50% cut, HMI = 100%
505 cut). Bottom-row panels show linear regressions between canopy cover and daily minimum relative humidity
506 (RH_{\min}). Results are reported separately for each study site (Kočevski Rog, Snežnik, Trnovo). Significant
507 regression lines and corresponding 95% envelopes are given. *** $p < 0.001$, R^2 – explained variance by the
508 regression model.

509

510

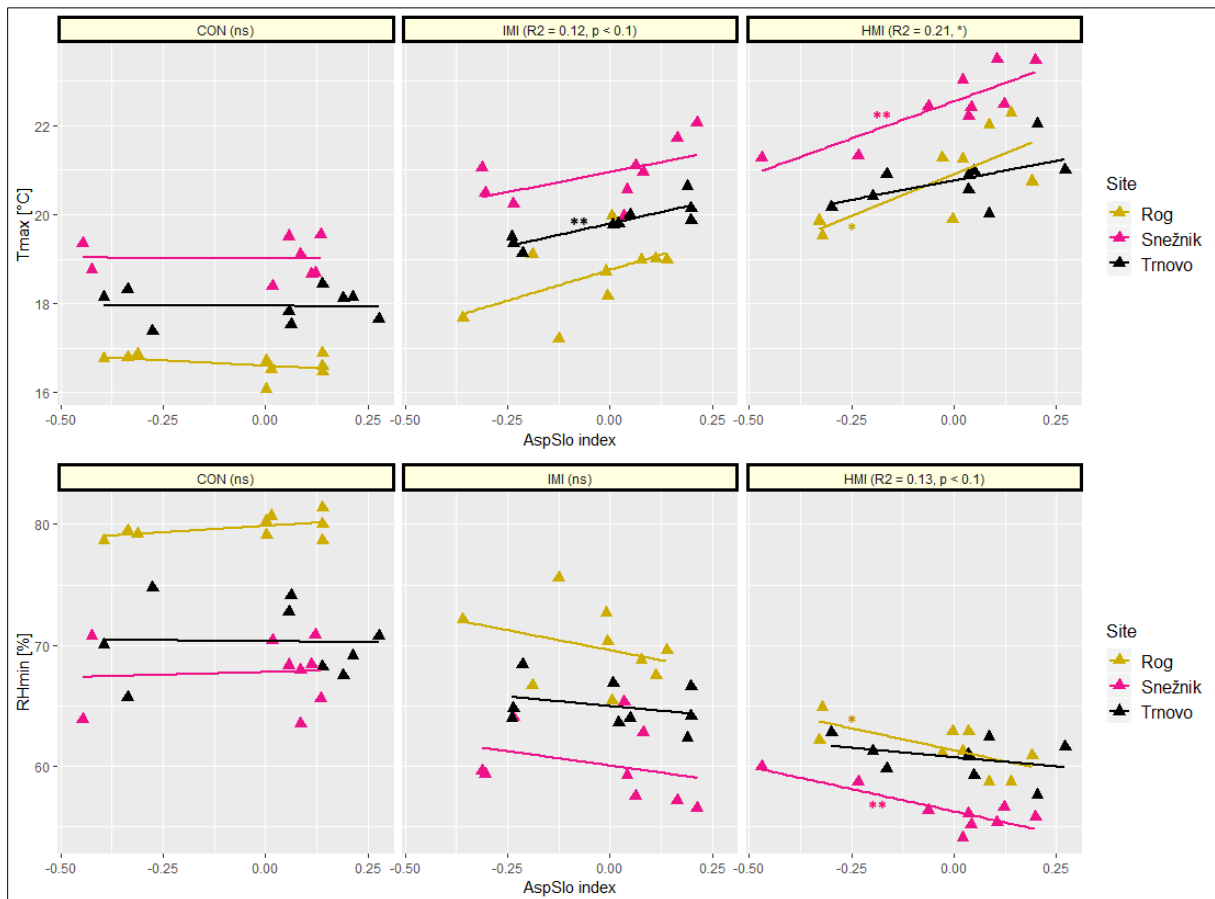
511 3.5. Microclimate in relation to topographic factors

512

513 We found significant relations between microclimatic variables and the AspSlo index for plots
 514 where cutting was performed (IMI and HMI treatments), whereas the dependence of T_{\max} and
 515 RH_{\min} on the AspSlo index in CON plots was not significant (Fig. 6). There was a significant
 516 ($p < 0.05$) positive linear relation between the AspSlo index and T_{\max} in HMI plots. In IMI plots
 517 this regression was marginally significant ($p < 0.1$). The relationship between the AspSlo index
 518 and RH_{\min} was negative, but only marginally significant in HMI plots. In general, more exposed
 519 steep south-facing plots experienced high T_{\max} and low RH_{\min} values (Fig. 6).

520

521



522

523 **Figure 6:** Linear regression between the AspSlo index and maximum daily temperature T_{\max} (upper panels) and
 524 minimum daily relative humidity RH_{\min} (bottom panels). The AspSlo index combines both slope aspect and slope
 525 inclination. Regressions are made separately for each cutting treatment (control = CON, 50% cut = IMI, 100% cut
 526 = HMI) and study site (Kočevski Rog, Snežnik, Trnovo). Asterisks beside the regression lines indicate that the
 527 slope of the regression line is significantly different from zero (** $p < 0.01$, * $p < 0.05$). R^2 – explained variance
 528 by the regression model.

529

530

531

532 4. Discussion

533

534 4.1. *Response of microclimate to overstory removal at different time scales*

535

536 Our experimental research in Dinaric fir-beech forests in Slovenia gave us an opportunity to
537 observe differences in microclimate between forest stands subjected to different management
538 intensities, and our results are in agreement with those of numerous studies (e.g. Chen et al.,
539 1993; Heithecker and Halpern, 2006; Kovács et al., 2018). Differences in microclimatic
540 variables between treatments corresponded to the intensity of stand growing stock (canopy
541 cover) removal. Kovács et al. (2018) showed that clear-cuts in oak-hornbeam stands induced
542 extreme light increment and consequently substantially increased air temperature and vapour
543 pressure deficit. In our study, closed-canopy forests also had a cooling effect, expressed as
544 lower T_{\max} , and a humidifying effect, expressed as higher RH_{\min} , due to the dense canopy cover
545 which intercepted a substantial proportion of solar radiation.

546

547 We found that the IMI treatment (50% cut) resulted in significant divergence from the uncut
548 controls in all investigated microclimatic variables. Differences in microclimate were on
549 average lower between the IMI and HMI treatments than between the IMI and CON treatments.
550 Even though the mean and maximum values of microclimatic variables in IMI treatment were
551 consistently lower than those in HMI treatment, the overall observation is that IMI treatment
552 acted slightly more similarly to the HMI treatment than to the CON treatment. These results are
553 in contrast to some previous studies which quantified the effects of partial cutting on forest
554 microclimate. Heithecker and Halpern (2006) reported that T_{avg} and T_{\max} did not differ
555 significantly between a treatment with 40% dispersed retention of stand basal area and control.
556 Kovács et al. (2018) illustrated that uniform partial cutting in oak-hornbeam forest, where 30%
557 of the initial total basal area of the upper canopy layer was cut (plus complete sub-canopy and
558 shrub layer removal), significantly differed from uncut stands with respect to T_{avg} only, but not
559 with respect to RH_{avg} and VPD_{avg} . The significant deviation of the IMI treatment from the CON
560 treatment in our case is most likely because of more intensive cutting compared to other similar
561 studies (e.g. Heithecker and Halpern, 2006; Kovács et al., 2018).

562

563 High management intensity was characterized by the highest T and VPD, as well as the lowest
564 RH values. Daily T_{avg} in HMI plots was on average ca. 1 °C higher compared to CON plots.

565 This is in line with previous studies of Carlson and Groot (1997), von Arx et al. (2013) and
566 Kovács et al. (2018). However, mean differences in daily T_{\max} and VPD_{\max} (CON vs. HMI: 3.5
567 °C and 0.6 kPa, respectively) were significantly higher and also consistent with those reported
568 in other studies (e.g. mean buffering capacity for T: 1.5 °C to 5 °C) spanning different forest
569 types (Morecroft et al., 1998; von Arx et al., 2013; Davis et al., 2019). For instance, von Arx et
570 al. (2013) showed that the long-term mean buffering capacity of 11 different temperate forest
571 types was up to 3.3 °C for daily T_{\max} and 0.52 kPa for daily VPD_{\max} . Renaud et al. (2010)
572 highlighted that in beech and beech-silver fir forests, T_{\max} during summer was 6 to 8 °C lower
573 below-canopy compared to open-field, and RH_{\min} was most often 10% to 20% higher in forest
574 than in the open-field. A recent study of understory temperature buffering in temperate
575 deciduous forests across Europe (Zellweger et al., 2019) demonstrated that the maximum
576 temperature during the summer was on average cooler by 2.1 °C inside than outside forests.
577 Moreover, a global analysis of understory versus open temperature offset showed that the mean
578 and maximum understory temperatures were, on average, cooler by 1.7 °C and 4.1 °C,
579 respectively. Conversely, the minimum temperatures were 1.1 °C warmer under forest canopies
580 than outside the forest (De Frenne et al., 2019).

581
582 Our field data were analysed for the buffering capacity of the canopy with respect to seasonal
583 and diurnal patterns. The prevailing seasonal pattern revealed that (1) differences between
584 treatments were highest during the summer months and (2) largely depended on the general
585 weather conditions. A greater buffering effect of forest canopy in summer, particularly when
586 considering T_{\max} , has also been reported by Morecroft et al. (1998), von Arx et al. (2012) and
587 Baker et al. (2014). Summer is a period of maximum leaf canopy development when the
588 presence of foliage enhances the difference between closed forests and canopy gaps. During
589 clear, hot and dry summer days, when conditions are physiologically most demanding for plant
590 growth, differences in T_{\max} between the CON and the HMI treatments were on average
591 significantly higher (~ 5 °C) than during more cloudy, cold and wet days in autumn (~ 1 °C).
592 There is also a significant inter-seasonal variation in the buffering capacity of intact forest
593 canopies. Thom et al. (2020) showed higher microclimatic buffering capacity of undisturbed
594 European beech forest in warm and dry years due to increase in evaporation causing additional
595 cooling and wetting of the air. Our results and those of other studies confirm that the
596 temperature offset is magnified as temperatures become more extreme (De Frenne et al., 2019).
597

598 Clear differences in the diurnal cycles of T and RH were found between silvicultural measures.
599 Buffering capacity below dense canopy (CON treatment) was strongest in early afternoon when
600 maximum temperatures in HMI plots evidently exceeded those in the other two treatment types.
601 In addition, we showed that the microclimate in the forest interior would track open area
602 (canopy gap) conditions with some time lag. This is contrary to von Arx et al. (2013), who
603 showed that the timing of T_{\min} , T_{\max} , RH_{\min} and RH_{\max} in forest stands and nearby open areas
604 more or less coincided, i.e. time lags were generally less than 30 min. Such time lags were also
605 not confirmed in the study by Holst et al. (2004) in a Central European beech forest and by
606 Morecroft et al. (1998) in an oak woodland.

607

608 *4.2. Canopy cover and local topography as drivers of microclimate at a fine* 609 *spatial scale*

610

611 We found that forest stand structure factors played an important role in driving evident
612 differences in microclimate between stands subjected to different management intensities.
613 Microclimate buffering was most strongly related to canopy cover, which is consistent with
614 other studies (von Arx et al., 2013; Hardwick et al., 2015; Kovács et al., 2017; Greiser et al.,
615 2018). Davis et al. (2019) found that canopy buffering of T and VPD was greater at higher
616 levels of canopy cover. Zellweger et al. (2019) concluded that local canopy cover was a strong
617 non-linear driver of the maximum temperature offset during summer. Furthermore, topographic
618 factors (slope exposition and steepness) contributed to spatial variability in microclimate, which
619 is in line with many previous studies (e.g. Grimmond et al., 2000; Ma et al., 2010; Macek et al.,
620 2019). Jucker et al. (2018) found that canopy structure and topography jointly constrain the
621 local microclimate of human-modified tropical landscapes.

622

623 Our results pointed to the significant dependence of T_{\max} and RH_{\min} on the degree of canopy
624 closure, suggesting its clear dampening effect on microclimate extremes. The air temperature
625 in plots with higher canopy cover was lower and the air was more humid. Canopy cover is a
626 major determinant of the amount of solar radiation reaching the forest floor (Morecroft et al.,
627 1998). Previous studies demonstrated that, in general, the buffering capacity of the forests is
628 mainly related to factors associated with overstorey structure, e.g. leaf area index or canopy
629 cover, tree height and structural heterogeneity (Renaud et al., 2010; Hardwick et al., 2015;
630 Ehbrecht et al., 2019). Ehbrecht et al. (2019) concluded that structural characteristics of forest

631 stands other than canopy openness marginally contribute to variation in forest microclimate.
632 The results of Kovács et al. (2017) suggested that structural elements have a stronger influence
633 on microclimate conditions than the tree species composition of the overstory layer.

634
635 The effects of cutting treatments were, at least to some degree, modified due to the specific
636 topographic features of karst sinkholes. Within-sinkhole position had a significant impact on
637 microclimatic conditions. The more exposed south-facing plots in the HMI treatment
638 experienced the most extreme microclimatic conditions (i.e. highest T and lowest RH overall).
639 Slope aspect is also important within forests with closed canopy, as shown by Grimmond et al.
640 (2000). However, position within the sinkhole did not significantly affect microclimate in our
641 control stands. In contrast, the spatial variability of microclimate increased along the cutting
642 intensity gradient, meaning that differences between within-sinkhole positions were more
643 pronounced in treated stands. All of these results suggest that overstory removal increased the
644 dependence of microclimate on local topographic factors.

645
646 In general, south-facing and north-facing plots differed the most for the majority of
647 meteorological variables. However, for T_{\max} (Fig. 2b), the largest differences were between
648 central and north-facing plots. This could be explained either by cold air accumulation in the
649 centre of the sinkholes or by slight differences in the slope and shape (DDratio) of the sinkholes
650 between treatment types (Table S1 in the Supplementary material). The observed pattern could
651 also be attributed to environmental factors (e.g. soil properties, ground vegetation cover, bare
652 soil cover) which were not measured in our study but described in other studies (e.g. Sewerniak
653 and Puchałka, 2020).

654
655 *4.3. Ecological relevance of the observed microclimatic patterns for forest*
656 *vegetation and management implications*

657
658 Our results and other empirical evidence (Heithecker and Halpern, 2007; Abd Latif and
659 Blackburn, 2010; Ma et al., 2010; Hardwick et al., 2015; Kovács et al. 2018; Thom et al., 2020)
660 highlight how management and natural forest disturbances drive changes in microclimate. The
661 highest value for each microclimatic variable was more likely to occur in disturbed stands,
662 indicating that cutting can induce more extreme microclimatic conditions. Based on
663 experimental (e.g. Lenzion and Leuschner, 2008; Will et al., 2013) and observational studies

664 (e.g. Leuschner and Lenzion, 2009; Park Williams et al. 2013), we can assume that the
665 magnitude of the described differences in microclimate between treatments has an eco-
666 physiologically meaningful effect on forest-dwelling organisms and a marked impact on many
667 bioecological processes. Macek et al. (2019) demonstrated that maximum air temperature,
668 which is controlled by landscape topography, affects plant species composition in temperate
669 forests. Topographically induced variation in microclimate and soil conditions similarly drive
670 ground vegetation diversity in secondary forest ecosystems, such as managed *Pinus sylvestris*
671 mono-stands on inland dunes (Sewerniak and Puchałka, 2020).

672

673 An increase in temperature and especially VPD directly affect plant survival, growth and
674 reproduction (Davis et al., 2019). If extreme microclimatic conditions, such as higher
675 temperatures in the daytime (or summer months) and cooler ones in the night-time (or winter
676 months), exceed tolerance thresholds for certain species, growth patterns and species
677 composition will likely be altered (Ma et al., 2010; Jucker et al., 2018; Buras and Menzel, 2019).
678 High T_{\max} and VPD_{\max} during the warmest and driest time of the day, coupled with high short-
679 term fluctuations and diurnal variation in microclimatic conditions can cause stress for plants,
680 potentially resulting in regeneration failure of the currently prevailing tree species (Thom et al.,
681 2020). There seems to be a critical threshold canopy density below which the buffering capacity
682 of forest ecosystems switches from supportive (buffering capacity of forest canopy strongest
683 when conditions most demanding) to unsupportive (buffering capacity on microclimate small
684 to negative when conditions most demanding) (von Arx et al., 2013) for tree species
685 regeneration and growth of forest-dependent herbaceous understory plant communities (De
686 Frenne et al., 2013). Stressful microclimatic conditions can act as a strong filtering force,
687 especially for shade-tolerant, late-successional plant species with low drought tolerance, which
688 are adapted to a more stable and less stressful microclimate, and thus induce significant control
689 over early succession pathways in post-cutting forest stands (Taylor et al., 2020).

690

691 Under karstic conditions with a high number of sinkholes, forest management practices must
692 be adapted to very rough and sensitive terrain (Kobal et al., 2015; Aguilon et al., 2020). Forest
693 managers and silviculturalists could benefit from our findings. For example, when planning
694 artificial tree regeneration to restore damaged or open forest areas, the planting of sensitive
695 climax tree species (such as *Abies alba*) should be avoided in microsites within canopy gaps
696 (HMI treatment) with the highest heat load and most extreme microclimate (steep south-facing
697 slopes), as indicated by high VPD. Young trees are most strongly affected by microclimate-

698 induced stress, as their root systems do not yet reach deep into the soil (Thom et al., 2020).
699 Even partial reduction of the canopy cover (IMI treatment) induced significant differences in
700 microclimate compared to the CON treatment. Lower levels of canopy removal should be
701 implemented on south-facing slopes to mitigate the effects on ground microclimate. In contrast,
702 north-facing slopes receive less insolation than surrounding areas and usually have more
703 favourable microclimatic conditions (lower T and higher RH) for typical forest plant species
704 with affinity to shadier microsites. Such effects can facilitate *in situ* persistence of pre-
705 disturbance compositional legacy, positive response of shade-tolerant trees and general co-
706 existence of ecological divergent plant species in post-treatment conditions. Greater focus on
707 these relationships may contribute not only to more effective forest management, but also to
708 reduced loss of soil organic matter and maintenance of high diversity of plant communities
709 (Jasińska et al., 2020; Sewerniak and Puchałka, 2020; Kiss et al., 2020).

710

711 We emphasize the importance of canopy cover for the buffering capacity of forest microclimate.
712 The provision of this basic stand structural feature is expected to be seriously at risk as forest
713 disturbances around the globe are likely to have a strong impact on canopy structure in the
714 future (Lenoir et al., 2017). Variety of anthropogenic disturbances alter the conservation value
715 of karst dolines (Bátori et al., 2020). Kiss et al. (2020) concluded that intensive logging, the
716 main driver of changes in forest cover, decrease the capacity of depressions to support beech
717 and ravine forest species. The buffering capacity of temperate forests might decrease due to the
718 increasing impacts of more frequent and intense disturbances as well as extreme weather events
719 resulting in drought- and heat-stress (Park Williams et al., 2013; Thom et al., 2017; Davis et
720 al., 2019). High disturbance severity paired with a large disturbance extent will have
721 particularly strong impacts on forest microclimate (Baker et al., 2014; Davis et al., 2019).
722 Practitioners should in general intensify their efforts to foster the microclimatic buffering
723 capacity of forest canopies to mitigate hot and dry weather conditions. Strategies to improve
724 the microclimate need to be adapted locally considering the specific stand and site conditions
725 (Thom et al., 2020). Moreover, due to the combination of specific site conditions and
726 unfavourable factors, such as reduced mechanical and biological stability of forest stands as a
727 consequence of intense large-scale disturbances, prolonged summer droughts, water-permeable
728 karst terrain and associated shallow soils with low water storage capacity, Dinaric fir-beech
729 forests are presumed to be highly susceptible to global climate change (Kutnar and Kobler,
730 2011).

731

732 *4.4. Conclusions*

733

734 The short-term responses of microclimatic conditions in Dinaric fir-beech forests to various
735 forest management intensities showed that the greatest differences were observed between the
736 most intensive treatment and the uncut controls. Obtained results corroborate the widespread
737 microclimatic patterns recognized in forested areas with highly diversified land terrain,
738 spanning from lowland to mountain regions. The effects of overstory removal might interact
739 with local topographic factors, as shown by our results, where spatio-temporal variations in
740 temperature and relative humidity were jointly driven by canopy cover and terrain topography
741 (slope aspect and slope inclination). Overstory removal increased the dependence of
742 microclimate upon local topographic factors. In general, the results highlight the intricate
743 interplay between many environmental factors in forest ecosystems which might significantly
744 affect understory species occurrence, tree seedling growth and thereby overall forest structure
745 and composition. The main findings of our research should be considered in forest management
746 planning and forest biodiversity protection.

747

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758

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760

761 5. References

- 762
763 Abd Latif, Z., Blackburn, G.A., 2010. The effects of gap size on some microclimate variables during late summer
764 and autumn in a temperate broadleaved deciduous forest. *Int. J. Biometeorol.* 54, 119-129.
765
- 766 Aguilon, D.J., Vojtkó, A., Tölgyesi, C., Erdős, L., Kiss, P.J., Lőrinczi, G., Juhász, O., Frei, K., Bátor, Z., 2020.
767 Karst environments and disturbance: evaluation of the effects of human activity on grassland and forest
768 naturalness in dolines. *Biologia*, <https://doi.org/10.2478/s11756-020-00518-7>
769
- 770 Ashcroft, M.B., Gollan, J.R. 2013. Moisture, thermal inertia, and the spatial distributions on near-surface soil and
771 air temperatures: Understanding factors that promote microrefugia. *Agric. For. Meteorol.* 176, 77-89.
772
- 773 Aussenac, G., 2000. Interactions between forest stands and microclimate: Ecophysiological aspects and
774 consequences for silviculture. *Ann. For. Sci.* 57 (3), 287-301.
775
- 776 Baker, T.P., Jordan, G.J., Steel, E.A., Fountain-Jones, N.M., Wardlaw, T.J., Baker, S.C., 2014. Microclimate
777 through space and time: Microclimatic variation at the edge of regeneration forests over daily, yearly and
778 decadal time scales. *Forest Ecol. Manag.* 334, 174-184.
779
- 780 Bátor, Z., Vojtkó, A., Keppel, G., Tölgyesi, C., Čarni, A., Zorn, M., Farkas, T., Erdős, L., Kiss, P.J., Módra, G.,
781 Breg Valjavec, M., 2020. Anthropogenic disturbances alter the conservation value of karst dolines.
782 *Biodiversity and Conservation* 29: 503-525.
783
- 784 Bartoń, K., 2019. MuMIn: Multi-Model Inference, R Package Version 1.43.6. Available online: [https://cran.r-](https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf)
785 [project.org/web/packages/MuMIn/MuMIn.pdf](https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf)
786
- 787 Buras, A., Menzel, A., 2019. Projecting Tree Species Composition Changes of European Forests for 2061-2090
788 Under RCP 4.5 and RCP 8.5 Scenarios. *Front. Plant Sci.* 9, 1986.
789
- 790 Cantlon, J.E., 1953. Vegetation and microclimates on north and south slopes of Cushtunk Mountain, New Jersey.
791 *Ecol. Monogr.* 23, 241-270.
792
- 793 Carlson, D.W., Groot, A., 1997. Microclimate of clear-cut, forest interior, and small openings in trembling aspen
794 forest. *Agric. For. Meteorol.* 87, 313-329.
795
- 796 Chen, J., Franklin J.F., Spies, T.A., 1993. Contrasting microclimates among clearcut, edge, and interior of old-
797 growth Douglas-fir forest. *Agric. For. Meteorol.* 63, 219-237.
798
- 799 Davis, K.T., Dobrowski, S.Z., Holden, Z.A., Higuera, P.E., Abatzoglou, J.T., 2019. Microclimatic buffering in
800 forests of the future: the role of local water balance. *Ecography* 42, 1-11.
801
- 802 De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-
803 Römermann, Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S.,
804 Hédli, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf,
805 T., Newman, M., Peterken, G., Petřík, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.-
806 R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J., Verheyen, K., 2013. Microclimate moderates plant
807 responses to macroclimate warming. *PNAS* 110 (46), 18561-18565.
808
- 809 De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M.,
810 Verheyen, K., Lenoir J., 2019. Global buffering of temperatures under forest canopies. *Nat. Ecol. Evol.* 3, 744-
811 749.
812
- 813 Ehbrecht, M., Schall, P., Ammer, C., Fischer, M., Seidel, D., 2019. Effects of structural heterogeneity on the
814 diurnal temperature range in temperate forest ecosystems. *Forest Ecol. Manag.* 432, 860-867.
815
- 816 Faraway, J.J., 2006. *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric*
817 *Regression models.* Chapman and Hall/CRC: Boca Raton, FL, USA.
818

819 Fleming, R.L., Baldwin, K.A., 2008. Effects of harvest intensity and aspect on a boreal transition tolerant
820 hardwood forest. I. Initial postharvest understory composition. *Can. J. Forest Res.* 38 (4), 685-697.
821
822 Forest Act, 1993. The Law on Forests (Official Gazette of RS, Nos. 30/93 , 56/99 - ZON, 67/02 , 110/02 - ZGO-
823 1 115/06 - ORZG40, 110/07 , 106/10 , 63/13 , 101/13 - ZDavNepr, 17/14 , 22/14 - dec. US, 24/15 , 9/16 -
824 ZGGLRS and 77/16. Available online: <http://pisrs.si/Pis.web/pregledPredpisa?id=ZAKO270> (accessed 13
825 August 2019).
826
827 Frey, S.J.K., Hadley, A.S., Johnson, S.L., Schulze, M., Jones, J.A., Betts, M.G., 2016. Spatial models reveal the
828 microclimatic buffering capacity of old-growth forests. *Sci. Adv.* 2 (4), e1501392.
829
830 Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., Hylander, K., 2018. Monthly microclimate models in a managed
831 boreal forest landscape. *Agric. For. Meteorol.* 250-251, 147-158.
832
833 Grimmond, C.S.B., Robeson, S.M., Schoof, J.T., 2000. Spatial variability of micro-climatic conditions within a
834 mid-latitude deciduous forest. *Clim. Res.* 15, 137-149.
835
836 Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, C.E., Nilus, R., Ewers, R.M., 2015. The relationship between leaf
837 area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in
838 microclimate. *Agric. For. Meteorol.* 201, 187-195.
839
840 Heithecker, T.D., Halpern, C.B., 2006. Variation in microclimate associated with dispersed-retention harvests in
841 coniferous forests of western Washington. *Forest Ecol. Manag.* 226, 60-71.
842
843 Heithecker, T.D., Halpern, C.B., 2007. Edge-related gradients in microclimate in forest aggregates following
844 structural retention harvest in western Washington. *Forest Ecol. Manag.* 248, 163-173.
845
846 Holst, T., Mayer, H., Schindler, D., 2004. Microclimate within beech stands-part II: thermal conditions. *Eur. J.*
847 *Forest Res.* 123, 13-28.
848
849 Hothorn, T., Bretz, F., Westfall, P., 2019. Multcomp: Simultaneous Inference in General Parametric Models, R
850 Package Version 1.40-10. Available online: <https://cran.r-project.org/web/packages/multcomp/multcomp.pdf>
851 (accessed 15 June 2019).
852
853 Hyndman, R., Athanasopoulos, G., Bergmeir, C., Caceres, G., Chhay, L., O'Hara-Wild, Petropoulos, F., Razbash,
854 S., Wang, E., Yasmeeem, F., 2019. forecast: Forecasting functions for time series and linear models, R Package
855 version 8.9. Available online: <https://cran.r-project.org/web/packages/forecast/forecast.pdf> (accessed 22
856 January 2019).
857
858 IUSS Working Group WRB, 2015. World reference base for soil resources 2014, updated 2015. International soil
859 classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No.
860 106, 192 p., Rome, Italy: FAO.
861
862 Jasińska, J., Sewerniak, P., Puchałka, R., 2020. Litterfall in a Scots Pine Forest on Inland Dunes in Central Europe:
863 Mass, Seasonal Dynamics and Chemistry. *Forests* 11, 678.
864
865 Jucker, T., Hardwick, S.R., Both, S., Elias, D.M.O., Ewers, R.M., Milodowski, D.T., Swinfield, T., Coomes, D.A.,
866 2018. Canopy structure and topography jointly constrain the microclimate of human-modified tropical
867 landscapes. *Glob. Change Biol.* 24, 5243-5258.
868
869 Keenan, R.J., Kimmins, J.P., 1993. The ecological effects of clear-cutting. *Environ. Rev.* 1 (2), 121-144.
870
871 Kiss, P.J., Tölgyesi, C., Bóni, I., Erdős, L., Vojtkó, A., Maák, I.E., Bátor, Z., 2020. The effects of intensive logging
872 on the capacity of karst dolines to provide potential microrefugia for cool-adapted plants. *Acta Geogr. Slov.*
873 60-1, 37-48.
874
875 Kobal, M., Bertoneclj, I., Pirotti, F., Dakskobler, I., Kutnar, L., 2015. Using Lidar Data to Analyse Sinkhole
876 Characteristics Relevant for Understory Vegetation under Forest Cover – Case Study of a High Karst Area in
877 the Dinaric Mountains. *PLoS ONE* 10(3): e0122070.
878

- 879 Kovács, B., Tinya, F., Ódor, P., 2017. Stand structural drivers of microclimate in mature temperate mixed forests.
880 Agric. For. Meteorol. 234-235, 11-21.
881
- 882 Kovács, B., Tinya, F., Guba, E., Németh, C., Sass, V., Bidló, A., Ódor, P., 2018. The Short-Term Effects of
883 Experimental Forestry Treatments on Site Condition in an Oak-Hornbeam Forest. Forests 9, 406.
884
- 885 Kutnar, L., Kobler, A., 2011. Prediction of forest vegetation shift due to different climate-change scenarios in
886 Slovenia. Sumar List. 135, 113-126.
887
- 888 Kutnar, L., Eler, K., Marinšek, A., 2015. Effects of different silvicultural measures on plant diversity – the case of
889 the Illyrian *Fagus sylvatica* habitat type (Natura 2000). iForest 9, 318-324.
890
- 891 Lenzion, J., Leuschner, C., 2008. Growth of European beech (*Fagus sylvatica* L.) saplings is limited by elevated
892 atmospheric vapour pressure deficits. For. Ecol. Manag. 256, 648-655.
893
- 894 Lenoir, J., Hattab, T., Pierre, G., 2017. Climatic microrefugia under anthropogenic climate change: implications
895 for species redistribution. Ecography 40, 253-266.
896
- 897 Lenth, R.V., 2016. Least-Squares Means: The R Package lsmeans. J. Stat. Soft. 69.
898
- 899 Leuschner, C. Lenzion, J., 2009. Air humidity, soil moisture and soil chemistry as determinants of the herb layer
900 composition in European beech forests. J. Veg. Sci. 20, 288-298.
901
- 902 Ma, S., Concilio, A., Oakley, B., North, M., Chen, J., 2010. Spatial variability in microclimate in a mixed-conifer
903 forest before and after thinning and burning treatments. Forest Ecol. Manag. 259, 904-915.
904
- 905 Macek, M., Kopecký, M., Wild, J., 2019. Maximum air temperature controlled by landscape topography affects
906 plant species composition in temperate forests. Landscape Ecol. 34, 2541-2556.
907
- 908 Morecroft, M.D., Taylor, M.E., Oliver, H.R., 1998. Air and soil microclimates of deciduous woodland compared
909 to an open site. Agric. For. Meteorol. 90, 141-156.
910
- 911 Murray, F.W., 1967. On the computation of the saturation vapor pressure. J. Appl. Meteorol. 6, 203-204.
912
- 913 Nagel, T.A., Mikac, S., Dolinar, M., Klopčič, M., Keren, S., Svoboda, M., Diaci, J., Bončina, A., Paulić, V., 2017.
914 The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. For. Ecol. Manag.
915 388, 29-42.
916
- 917 Park Williams, A., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W.,
918 Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M.,
919 McDowell, N.G., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nat.
920 Clim. Change 3, 292-297.
921
- 922 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2019. nlme: Linear and Nonlinear Mixed Effects
923 Models. R Package Version 3.1-141. Available online: <https://cran.r-project.org/web/packages/nlme/nlme.pdf>
924 (accessed 23 July 2019).
925
- 926 R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for
927 Statistical Computing. 2018, Vienna, Austria. URL <https://www.R-project.org/>.
928
- 929 Renaud, V., Innes, J.L., Dobbertin, M., Rebetez, M., 2010. Comparison between open-site and below-canopy
930 climatic conditions in Switzerland for different types of forests over 10 years (1998-2007). Theor. Appl.
931 Climatol. 105 (1-2), 119-127.
932
- 933 Sewerniak, P., Jankowski, M., Dąbrowski, M., 2017. Effect of topography and deforestation on regular variation
934 of soils on inland dunes in the Toruń Basin (N Poland). Catena 149, 318-330.
935
- 936 Sewerniak, P., Puchałka, R., 2020. Topographically induced variation of microclimatic and soil conditions drives
937 ground vegetation diversity in managed Scots pine stands on inland dunes. Agric. For. Meteorol. 291, 108054.
938

939 Slovenian Environment Agency archive, 2019. Archive of measurements – observed and measured meteorological
940 data in Slovenia. <http://meteo.arso.gov.si/met/sl/archive/> (accessed November 2018).
941

942 Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., Thomas, C.D., 2011. Habitat
943 microclimates drive fine-scale variation in extreme temperatures. *Oikos* 120, 1-8.
944

945 Taylor, A.R., Endicott, S., Hennigar, C., 2020. Disentangling mechanisms of early succession following harvest:
946 Implications for climate change adaptation in Canada's boreal-temperate forests. *Forest Ecol. Manag.* 461,
947 117926.
948

949 Thom, D., Rammer, W., Seidl, R., 2017. The impact of future forest dynamics on climate: interactive effects of
950 changing vegetation and disturbance regimes. *Ecol. Monogr.* 87 (4), 665-684.
951

952 Thom, D., Sommerfeld, A., Seibald, J., Hagege, J., Müller, J., Seidl, R., 2020. Effects of disturbance patterns and
953 deadwood on the microclimate in European beech forests. *Agric. For. Meteorol.* 291, 108066.
954

955 von Arx, G., Dobbertin, M., Rebetez, M., 2012. Spatio-temporal effects of forest canopy on understory
956 microclimate in a long-term experiment in Switzerland. *Agric. For. Meteorol.* 166-167, 144-155.
957

958 von Arx, G., Graf Pannatier, E., Thimonier, A., Rebetez, M., 2013. Microclimate in forests with varying leaf area
959 index and soil moisture: potential implications for seedling establishment in a changing climate. *J. Ecol.* 101,
960 1201-1213.
961

962 Will, R.E., Wilson, S.M., Zou, C.B., Hennessey, T.C., 2013. Increased vapor pressure deficit due to higher
963 temperature leads to greater transpiration and faster mortality during drought for tree seedlings common to the
964 forest-grassland ecotone. *New Phytol.* 200, 366-374.
965

966 Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S., Wulf, M., Kirby, K.J., Brunet, J., Kopecký, M., Máliš,
967 F., Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K., De Frenne,
968 P., 2019. Seasonal drivers of understory temperature buffering in temperate deciduous forests across Europe.
969 *Global Ecol. Biogeogr.* 28, 1774-1786.
970

971 Zheng, D., Chen, J., Song, B., Xu, M., Sneed, P., Jensen, R., 2000. Effects of silvicultural treatments on summer
972 forest microclimate in southeastern Missouri Ozarks. *Clim. Res.* 15, 45-59.
973

974 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed effect models and extensions in
975 ecology with R.* 574 p., New York, NY: Springer.
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986 **Supplementary material, Table S1:**

987 Selected geomorphological parameters (calculated based on LiDAR data for north-south and
 988 east-west transects) of karst sinkholes, averaged across three study sites for each treatment type
 989 (CON = control, IMI = 50 % cut, HMI = 100 % cut): elevation (m), depth of the sinkhole (m,
 990 i.e. elevation difference between the bottom and edge of the sinkhole), radius (distance between
 991 the centre and edge of the sinkhole), slope (%) and DDratio (diameter vs. depth ratio). The latter
 992 describes the ratio between the diameter (radius \times 2) and depth of the sinkhole. It gives a very
 993 rough estimation of the shape of the sinkhole. The higher the DDratio, the more “open” the
 994 sinkhole is. Sinkholes with a lower DDratio are more “closed”, i.e. their depth is relatively large
 995 compared to their diameter. Potential differences between treatments were tested with a non-
 996 parametric Kruskal-Wallis Rank sum test (alpha = 0.05).

997 The values are mean \pm SD. n.s. – non-significant differences between treatments.

TREATMENT	Elevation (m)	Depth (m)	Radius (m)	Slope (%)	DDratio
CON	803.8 \pm 42.7	9.8 \pm 3.0	32.7 \pm 10.9	32.6 \pm 4.0	6.7 \pm 1.0
IMI	788.0 \pm 42.4	9.3 \pm 2.2	32.8 \pm 7.8	30.6 \pm 3.5	7.1 \pm 1.1
HMI	789.7 \pm 48.1	7.9 \pm 3.3	29.9 \pm 9.6	26.6 \pm 6.9	8.1 \pm 2.0
Kruskal-Wallis test	n.s.	n.s.	n.s.	n.s.	n.s.

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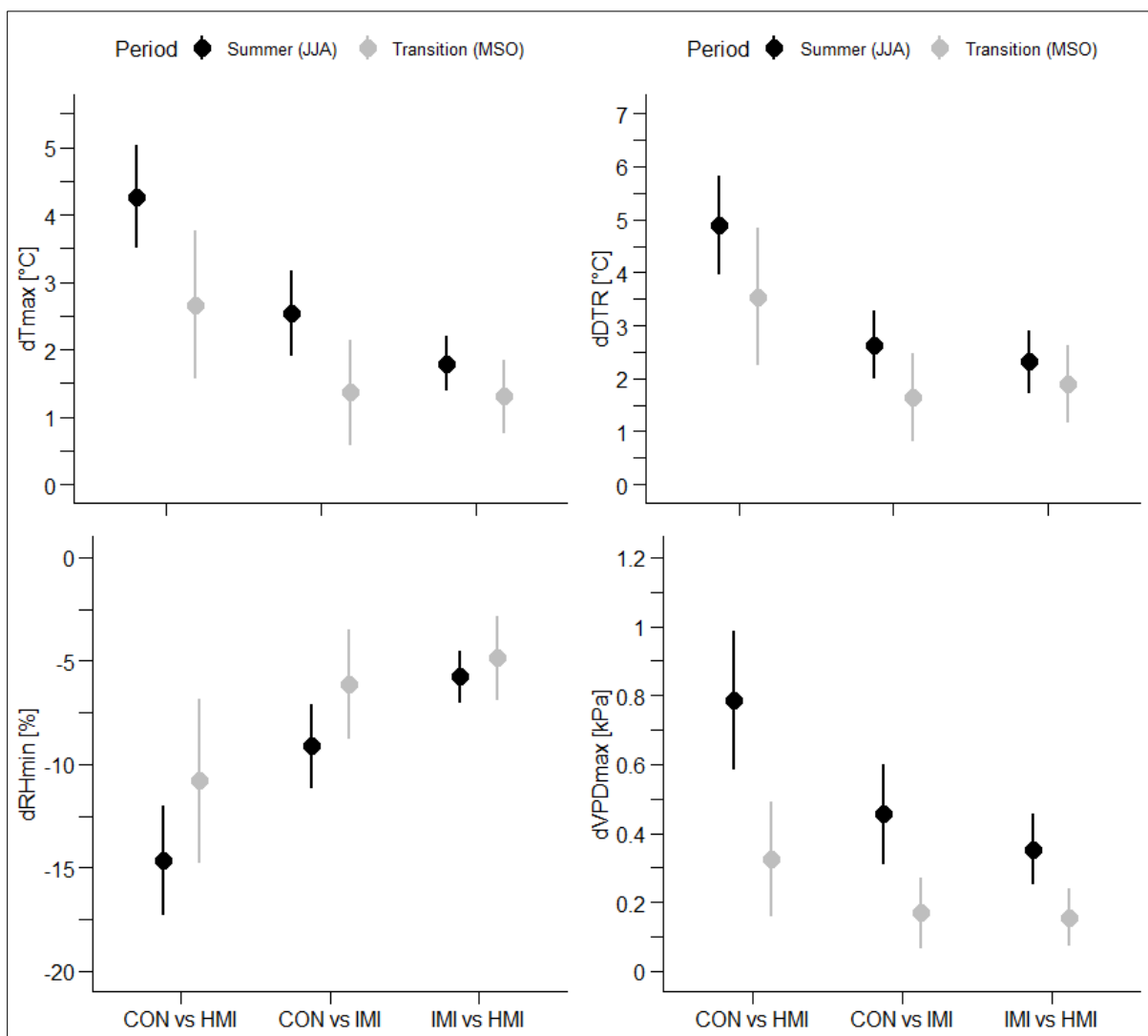
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1010 **Supplementary material, Figure S1:**

1011 Daily differences (mean \pm SD) in maximum temperature (T_{\max} , upper left), diurnal temperature
1012 range (DTR, upper right), minimum relative humidity (RH_{\min} , bottom left) and maximum
1013 vapour pressure deficit (VPD_{\max} , bottom right) between cutting treatments: CON vs. HMI,
1014 CON vs. IMI and IMI vs. HMI (CON = control, IMI = 50% cut, HMI = 100% cut). Colours
1015 denote two different periods: black – summer (JJA) = summer months (June, July and August),
1016 grey – transition period (MSO) = May, September and October. Daily differences were
1017 averaged across the entire measurement period (three growing seasons), three study sites and
1018 within-sinkhole positions (i.e. central, south-facing, north-facing plots).
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