

Disturbance effects on mountain spruce forest microclimates

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Abstract

Several forest stages can be present in a small area and their mosaic in space evolves in time. This is usually a result of small-scale disturbances. Each forest stage has a different effect on microclimate of the understorey and its surroundings. Similar effects can be observed in large scale disturbances, yet the mosaic has larger grain. We assessed the effect of six different forest stages on mean, minimum and maximum seasonal temperatures. They include salvage logged, regeneration, mature open and close canopy forest, standing dead trees (killed by bark beetle) and windthrow. There are significant differences in microclimate between many of these stages, especially during summer and autumn. The snow cover, which can last several months in the study area, homogenizes the climate near the ground for a large part of the year (winter and spring). Young regeneration can effectively protect understorey vegetation from high temperature extremes as mature forests do but cannot protect from minimum low temperatures, as mature forests do. Temperature differences are also affected by canopy cover, but not by elevation. Disturbed sites (salvage logged, standing dead wood and windthrow) have higher maximum temperatures, lower minimum temperatures and therefore higher extremity, shown by mean daily range of temperature during spring, summer, and autumn. The soil temperatures also differ between forest stages, but the differences are lower.

Key words: microclimate, forest stages, disturbances

INTRODUCTION

The forests have ability to buffer the temperature extremes, providing unique microclimatic conditions partially decoupled from macroclimate (ZELLWEGER et al. 2019), differing in many aspects, including diurnal and seasonal temperature range, light environment, air humidity, or soil moisture. The populations of many forest specialist species depend upon these specific forest microclimates (SANCZUK et al. 2023).

The degree to which forest microclimates differ from regional climate has been linked to variation in canopy cover (GILBERT et al. 2022), canopy height (KAŠPAR et al. 2021), species composition (DÍAZ-CALAFAT et al. 2023, VANDEWIELE et al. 2023), understory structure (KOVÁCS et al. 2017), management (KERMAVNAR et al. 2020, MÁLIŠ et al. 2023), wildfire (CARLSON et al. 2021) or spatial structure of disturbances (THOM et al. 2020) in interplay with topographic heterogeneity (MACEK et al. 2019). There is also known forest edge effect, that influences microclimate up to 90 m into the forest (HAIS & KUČERA 2009).

These differences result from complex processes of shading, air mixing, or evaporative cooling.

Different disturbance agents have distinct effects on forest structure and functioning and subsequent successional pathways. In consequence, the ability of disturbed forest stands to maintain specific microclimate in the understory may be lost or weakened. It was documented that recovery of microclimatic buffering function after clear cutting may last 54 years (MÁLIŠ et al. 2023). On the contrary, the persistence of the effect of natural disturbances on climate buffering was recently estimated to just two decades (VANDEWIELE et al. 2023), while BARTA et al. (2022) show that 50% thermal based recovery took 12.84 years (SD = ±3.38). While the effect of large-scale disturbances can be studied more easily, small scale disturbances can create an ever-changing mosaic of habitats within a small area, affected by its surrounding.

We aimed to quantify the effects of different forest disturbances on microclimatic conditions in the understory. We focused on climate near the ground, as the conditions in the forest floor are most relevant for forest herbs and tree regeneration (PETRÍK et al. 1986, GEIGER et al. 2009, WILD et al. 2014). Here we present results of five years of measurement of thermal microclimate of dynamically changing mountain spruce forest, undergoing multiple disturbances (windthrow, bark-beetle outbreaks, and salvage logging of various intensity), resulting in fine-scale mosaic of forest stands with contrasting structural parameters.

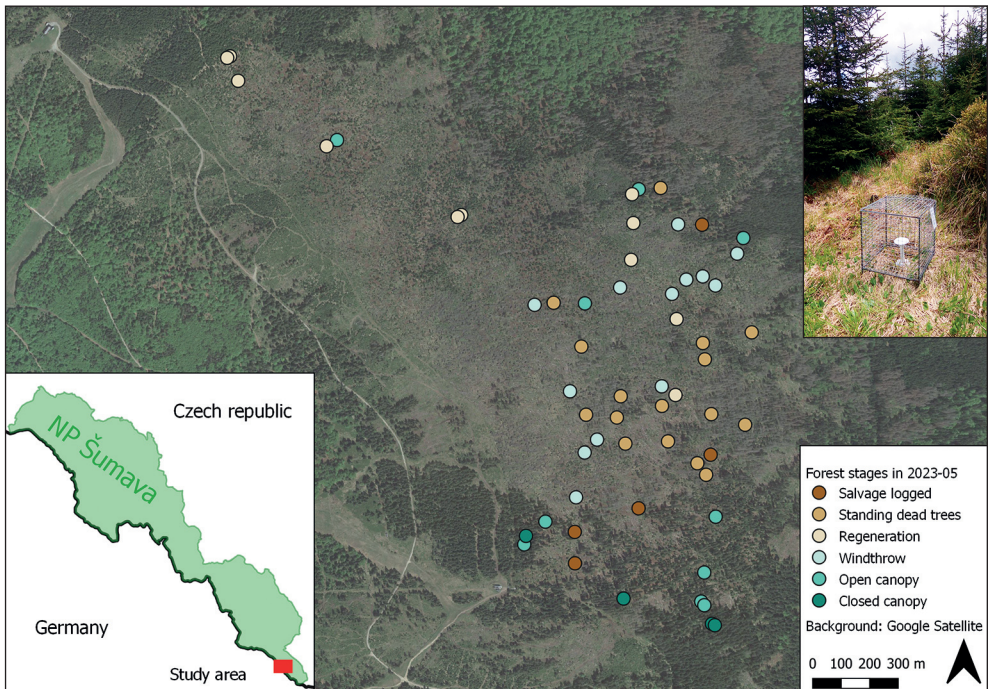


Fig. 1. Map of the study area showing locations of microclimatic loggers. The colours represent different forest stages in 2023. Inset on the right shows photograph of a single site with logger in protective cage.

METHODS

Study area

We conducted the study in the southern part of Šumava National Park at the top of the mountain ridge with the peaks of Smrčina, Alpa, and Hraničnik (Fig. 1). Study area is situated at elevations between 1 220 and 1 330 m a.s.l. and is naturally covered by spruce-dominated forests that experienced large scale wind and bark-beetle disturbances in previous decades (LAUSCH et al. 2011). This resulted in a complex mosaic of forest patches with variable tree age and density, with oldest stands over 200 years old according to old forest management maps. The study area is in a protected zone with differentiated forest management from non-intervention regime to salvage logging along the protected zone borders, aiming to prevent spread of bark-beetles into neighbouring forests and logging along the tourist paths for safety reasons (Fig. 1). In the parts with intervention regime, bark-beetle infested trees were stripped of bark and deadwood was left either standing (these were classified as standing dead trees) or laying on the ground (classified as salvage logging). This salvage logging did not disturb the ground vegetation. Tree regeneration relies mostly on natural regeneration. The forests condition in the area changed dynamically during the study period, with increasing proportion of bark beetle infested areas, salvage logged areas and regeneration at expense of area of the mature, closed-canopy forests.

Within the study area, we established 56 research sites representing different forest stages (Table 1). We established the initial 39 sites in May 2018, and added additional 17 sites later between 2019 and 2022 to retain minimal number of replicates in each forest stage class owing to reclassification of several sites due to ongoing disturbance and successional dynamics. We assigned each site to one of the six forest stages according to actual stand conditions: salvage logged, standing dead trees, regeneration, windthrow, open canopy, closed canopy (for class definitions see Table 1). Due to the ongoing forest disturbances, we have revised the forest stage classification each year before vegetation season. The salvage logged category was not typical since it includes deadwood on the ground and vegetation (Table 1).

Data collection

On each research site, we measured soil temperature 8 cm bellow the ground and near-ground air temperature 15 cm above the ground in 15-minute interval using Tomst TMS-4 dataloggers (WILD et al. 2019). Since the second year of the study, we protected loggers by wire cages. We have checked and downloaded all microclimatic loggers twice a year and replaced all malfunctioning loggers by new ones. We collected the data for this study from May 2018 until October 2023, the collection of the data continues.

We measured local canopy cover, defined as percentage of angular sky area obstructed by vegetation, using image analysis of repeated hemispherical photographs taken at a height of 1.3 meters above ground, directly above the sensor, which defines site position. We captured the photographs following the same methods at each site every spring using a Canon 40D DSLR camera with a Sigma 4.5 mm lens following the methodology described in BRŮNA et al. (2020), and the image analysis was conducted using the WinSCANOPY software. Canopy cover values were used for distinction between the two categories of mature forests: closed canopy for stands with canopy cover greater than 80% (median 87%) and open canopy for stands with canopy cover below 80% (median 76.5%). Vegetation cover or diversity was not recorded.

Table 1. Types of studied forest stages and number of sites belonging to each class in each year with detailed description. Counts of sites with complete record for summer of each year are shown.

Forest stage	Description	2018	2019	2020	2021	2022	2023
Salvage logged	No standing tree within 30 m radius, debarked logs on ground, dense ground vegetation including ferns (<i>Athyrium</i> , <i>Dryopteris</i>) and <i>Calamagrostis villosa</i>	6	6	4	4	3	5
Standing dead trees	Standing dead trees after bark beetle attack, can also include debarked trees after salvage logging, sparse patches of <i>Vaccinium myrtillus</i>	7	7	21	20	15	14
Regeneration	Juvenile spruce trees with various heights, below 7 cm DBH	4	5	5	8	10	10
Windthrow	Windthrow or windsnap, no standing trees within 30 m radius, large amount of deadwood on ground and in the air, limited vegetation cover consisting mainly of <i>Calamagrostis villosa</i>	4	4	8	6	13	11
Open canopy	Mature stand, DBH >7cm, canopy cover <80%, sparse patches of <i>Vaccinium myrtillus</i>	8	7	6	4	9	10
Closed canopy	Mature stand, DBH >7cm, canopy cover >80%	9	8	9	5	4	4
Total		38	47	53	48	54	54

We measured the precise location of each site, defined by the position of a TMS-4 datalogger by differential GNSS Trimble GeoXH 6000 with post-processing using correction data from the nearest station of the CZEPOS network in Prachatice, resulting in sub-meter accuracy.

Data analysis

Prior to statistical analysis, we inspected temperature time-series and removed all dubious readings caused by logger malfunction or logger displacement. We aggregated the microclimatic data into meteorological seasons: a) winter (December–February), b) spring (March–May), c) summer (June–August) and d) autumn (September–November) and calculated seasonal mean of daily soil and near-ground air temperature mean, minima, maxima and range.

To test the effect of different forest stages on forest floor microclimate, we fitted generalized additive mixed-effect models for each variable and season with forest stage and site elevation as fixed effect, and effects of year and site as random intercept and random slope for elevation. Random effects deal with temporal pseudo-replication and between-year variability. If the effect of elevation was not significant, we refitted the model without elevation term. We used *gamm* function from the *mgvc* R package (WANG 1998, WOOD 2004) to fit models and *gratia* R package to visualize model results.

We created boxplot of canopy openness for each forest stage for graphical comparison and tested the differences using analysis of variance with Tukey HSD post-hoc test. The significant differences between stages are indicated directly in the boxplots using letters (Compact letter display). Categories with the same letter are not significantly different, whereas those with no matching letter are significantly different.

Statistical significance for continuous variables (canopy cover, elevation) was determined using linear regression. We have used 95% confidence level in all analyses. All data analysis were performed in R (R CORE TEAM 2020). We have tested the effect of canopy cover on each microclimate climate variable, we fitted simple linear model for each season.

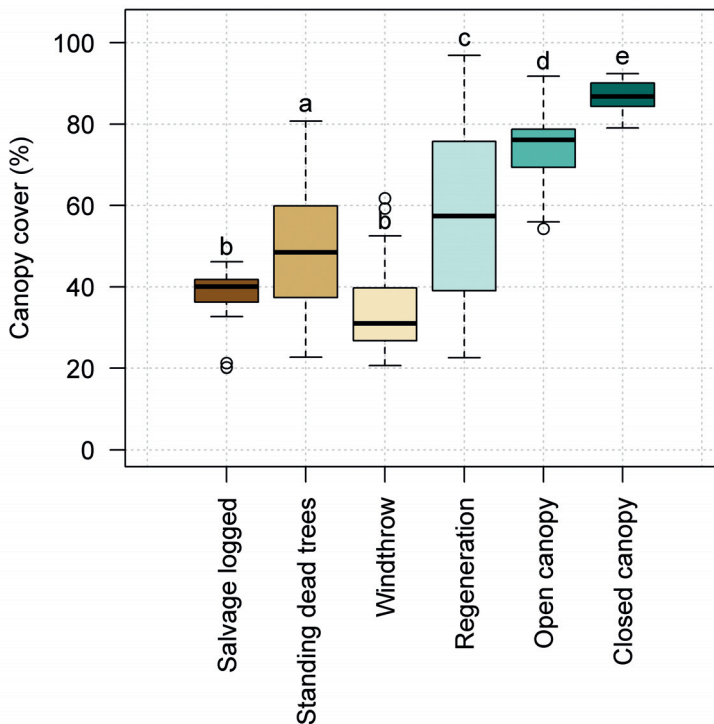


Fig. 2. Differences in canopy cover between forest stages (all years combined). Significance of difference tested by analysis of variance with Tukey HSD post-hoc test is shown by compact letter display. Box-and-whiskers plot show median and interquartile range with whiskers extending to extreme value not further than 1.5 interquartile range. Outliers are plotted as points.

RESULTS AND DISCUSSION

Canopy cover

The canopy cover of studied sites ranged from 20.2% to 96.9% (Fig. 2). Stands with living canopy trees (*open* and *closed canopy*) had cover values between 54.3% to 92.4%, separated by the threshold of 80% canopy cover. Canopy cover in *regeneration* class was highly heterogeneous, ranging between 22.6% and 96.9%, with median value of 61.8%. The *standing dead trees* provided intermediate canopy cover, depending upon the state of canopy disintegration with median value 48.3% and the highest value (80.7%). Disturbed stand categories *salvage logged* and *windthrow* showed lowest values of canopy cover, with median value 32.4% for *windthrow* and 40.1% for *salvage logged* stage and the lowest value (20.2%) observed in *salvage logged* stage. Fine-scaled mosaic of different forest stages in the study area causes diffuse boundaries between these stages when part of sky region in the logged stand may be obscured by neighbouring trees in a mature forest patch.

The effect of canopy cover on mean, minimum and maximum temperature was significant when testing most seasons except winter. Canopy is effectively lowering mean temperature beneath canopy except for autumn when it prevents heat loss. Denser canopy usually led to higher minimum temperatures, but in winter it may prevent snow from melting resulting in longer snow cover with temperatures around 0°C. Denser canopy also prevents temperature extremes near the ground.

Our results confirm the role of canopy cover in microclimate buffering as shown by KERMAVNAR et al. (2020), GILBERT et al. (2022), VANDEWIELE et al. (2023). In contrast with MÁLIŠ et al. (2023) and MENGE et al. (2023), our results show that microclimate heterogeneity in unmanaged forest can be very high, when affected by small scale disturbances. This affects not only the mean temperatures, but also daily temperature range and minimum and maximum temperatures.

Areas with regeneration (young stands with low height and heterogeneous canopy) can effectively reduce maximum temperatures by shading the surface, affected by direct solar radiation. This agrees with VANDEWIELE et al. (2023), who showed that regeneration had similar buffering capacity as the mature forest after two decades. In contrast, we found that the regeneration does not protect against low temperature extremes which are more influenced by overall air circulation in the vicinity. Our results are also in contrast with KOPÁČEK et al. (2020) who found no significant return of original soil and air temperature after a decade of rapid forest recovery after large scale disturbances near the Plešné Jezero lake.

Temperatures on sites with *standing dead trees* were significantly different from sites with living trees with *closed canopy*, but they did not differ from *salvage logged* areas. This suggests no significant effect of standing deadwood on near-ground temperatures. This agrees with previous study from Bavarian Forest National Park which did not find any significant effect of deadwood on microclimate (THOM et al. 2020). This study report found weak indication that standing and downed deadwood together influence microclimate, but not alone. Our *salvage logged* sites did not include standing deadwood but did include vegetation and our standing dead trees did not include downed deadwood. However, our results are in contrast with HAIŠ & KUČERA (2008) who used Landsat land surface temperature and found that decayed spruce forests and clear-cut areas showed a significant average increase in surface

temperature by 5.2°C and 3.5°C, respectively. The difference may be due to the methods used because we generally measure below trees or ground vegetation.

Elevation

The effect of elevation was insignificant in all models. We expected weak effect of elevation given the limited variation of site elevations in this study (sd = 24 m, total range = 110 m). The differences between forest stages are more significant and therefore, we dropped elevation term from the final models presented below (Table 2). Other topographic conditions were not tested because the differences between sites were low.

Near ground air temperature

The near ground air temperature displays a large diurnal variation during days without snow cover (Fig. 3). The length of continuous snow cover is very variable in the study area between years, with the snowmelt usually in April or May, but the formation of continuous snow cover occurred from November to January. In the winter 2020/2021, there was a limited snow cover. Minimum air temperatures dropped below zero even during the summer months (June to August) on 34 stations, but never in the closed canopy forest stage.

By analysing the differences in mean, minimum and maximum temperatures in each season, we determined significant differences for all forest stages (Table 2). Daily mean temperatures were less affected by forest stage than daily extremes. We observed the lowest temperature variability in the winter season. In winter, near-ground air temperature sensors are usually under the snow which effectively decouples near-ground temperatures from

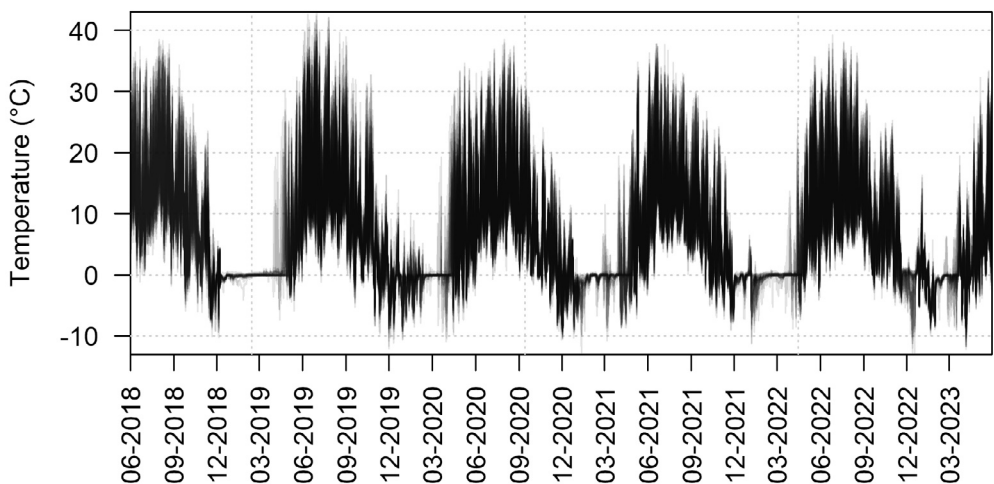


Fig. 3. Air temperature (15 cm above ground) during the whole 5-year study period on all research sites. Notice the parts with low variability that signify snow cover above 15 cm.

Table 2. Average values of temperature variables over 5-year period (stage class mean and sd). Periods with significant differences ($p < 0.05$) from closed canopy stage are marked in bold.

Season	Forest stage	Soil temperatures (°C)						Air temperature (°C)					
		Tmean	sd	Tmin	sd	Tmax	sd	Tmean	sd	Tmin	sd	Tmax	sd
Winter	Closed canopy	1.056	0.276	0.990	0.275	1.119	0.275	-0.864	0.449	-1.645	0.857	-0.053	0.438
	Open canopy	1.077	0.197	1.015	0.204	1.136	0.191	-0.776	0.409	-1.479	0.862	0.002	0.244
	Regeneration	0.877	0.296	0.828	0.299	0.925	0.292	-0.83	0.470	-1.591	0.983	-0.08	0.231
	Standing dead trees	1.244	0.302	1.191	0.293	1.294	0.307	-0.64	0.307	-1.24	0.641	0.006	0.187
	Windthrow	0.993	0.32	0.956	0.312	1.031	0.327	-0.592	0.337	-1.139	0.668	-0.035	0.227
	Salvage logged	0.963	0.457	0.927	0.446	0.998	0.469	-0.684	0.422	-1.307	0.859	-0.05	0.171
Spring	Closed canopy	2.200	0.603	1.98	0.565	2.432	0.64	2.638	0.875	0.753	0.831	5.367	1.611
	Open canopy	2.492	0.454	2.238	0.399	2.782	0.514	2.831	0.693	0.451	0.745	6.474	1.358
	Regeneration	2.100	0.484	1.889	0.454	2.336	0.516	2.63	0.742	0.32	0.551	5.668	1.613
	Standing dead trees	2.645	0.388	2.397	0.376	2.913	0.404	3.121	0.68	0.164	0.623	7.505	1.402
	Windthrow	2.537	0.579	2.242	0.503	2.849	0.66	3.057	0.904	0.221	0.428	7.191	2.224
	Salvage logged	2.524	0.644	2.219	0.56	2.845	0.731	2.858	0.866	0.175	0.631	6.746	2.148
Summer	Closed canopy	10.961	0.566	10.414	0.539	11.531	0.571	13.535	0.72	9.931	0.543	19.491	1.244
	Open canopy	11.194	0.489	10.637	0.429	11.812	0.54	13.534	0.685	8.954	0.479	21.439	1.586
	Regeneration	10.886	0.421	10.35	0.417	11.457	0.421	13.08	0.673	8.173	0.339	19.643	1.34
	Standing dead trees	11.391	0.658	10.811	0.598	12.000	0.739	13.713	0.835	7.804	0.313	22.803	1.871
	Windthrow	11.456	0.543	10.784	0.521	12.165	0.569	14.028	0.769	7.848	0.477	23.355	1.381
	Salvage logged	11.604	0.483	10.968	0.469	12.253	0.52	13.537	0.601	7.462	0.475	22.39	1.364
Autumn	Closed canopy	6.843	0.576	6.481	0.582	7.21	0.573	5.989	0.366	3.557	0.387	9.53	0.762
	Open canopy	6.885	0.425	6.534	0.438	7.249	0.408	5.759	0.425	2.734	0.600	10.642	0.802
	Regeneration	6.610	0.470	6.273	0.486	6.961	0.461	5.255	0.498	2.028	0.468	9.409	0.952
	Standing dead trees	6.891	0.354	6.566	0.354	7.225	0.362	5.363	0.427	1.716	0.445	11.02	0.596
	Windthrow	6.534	0.416	6.200	0.415	6.880	0.414	5.219	0.464	1.626	0.423	10.396	0.583
	Salvage logged	6.576	0.38	6.240	0.405	6.925	0.356	4.869	0.505	1.041	0.713	10.608	0.576

free-air temperatures and minimize differences between different forest stands. In contrast, we observed the most pronounced differences between forest stages in summer. In spring, forest stages had stronger effect on maximum temperatures, while in autumn, forest stages affected minimum temperatures more strongly. This discrepancy might be related to different effects of ground vegetation, which is not yet formed in the spring, but provide shading from direct sunlight until late autumn and variability in snowmelt date during spring between forest stages. Similar effect is under deciduous trees, but these were not present.

Mean temperature

Estimated effects of forest stage on mean air temperatures were moderate, with the highest negative difference to mean temperature under closed canopy for autumn temperatures in salvage logged stands (Fig. 4). Since we use average temperatures from every 15 minutes, there is a combined effect of buffering by vegetation and heat loss during the night.

Air T_{mean}

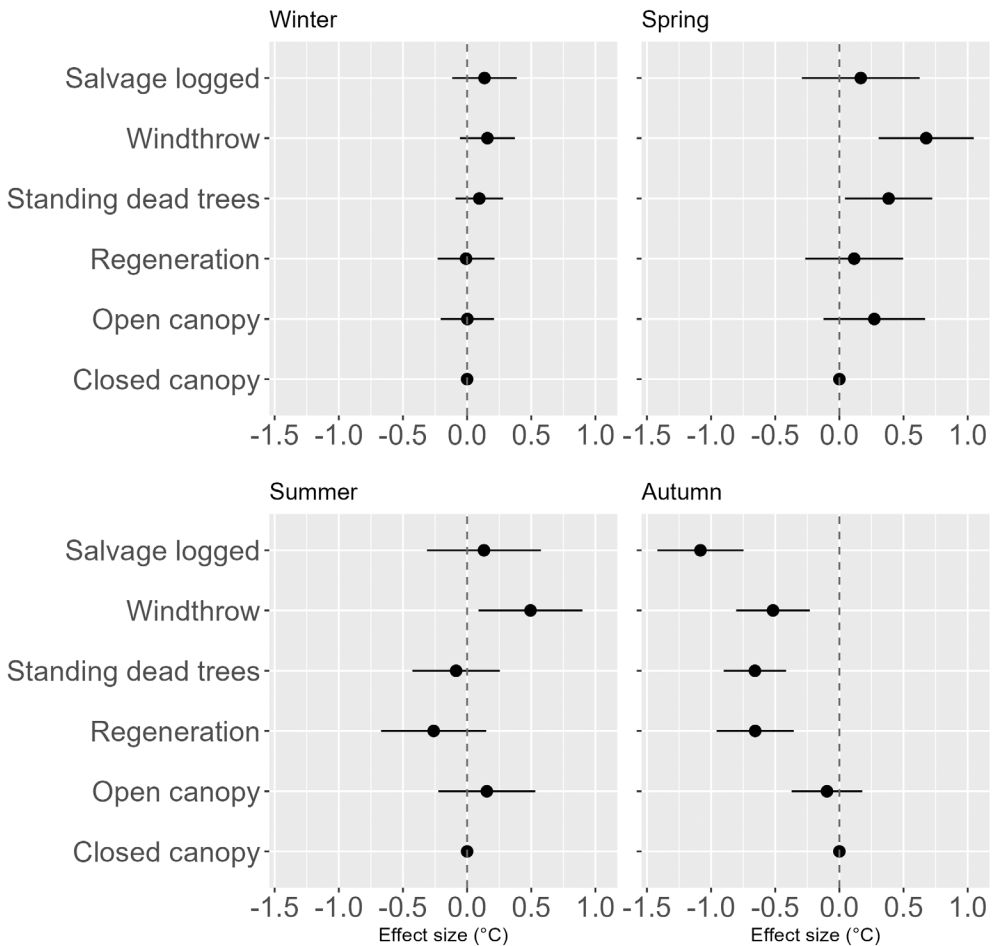


Fig. 4. Effect of forest stage on mean seasonal near-ground air temperatures compared to *closed canopy* forest as stage (reference value). Estimated effect is represented by the dots and 95% confidence interval by whiskers. See also Table 1 for description of individual stages. The *salvage logged* stage has the largest amount of ground vegetation, which influences mean and maximum temperatures.

Minimum temperature

The effects of forest stage on minimum temperatures were significant in all disturbed and regeneration stages throughout the year except for winter. We detected the strongest effect on summer and autumn minimum temperatures in salvage logged areas, with temperatures lower by 1.53°C and 1.8°C compared to closed-canopy forest (Fig. 5). The lower minimum air temperatures in salvage logged sites is due to higher heat loss during the night.

Air T_{\min}

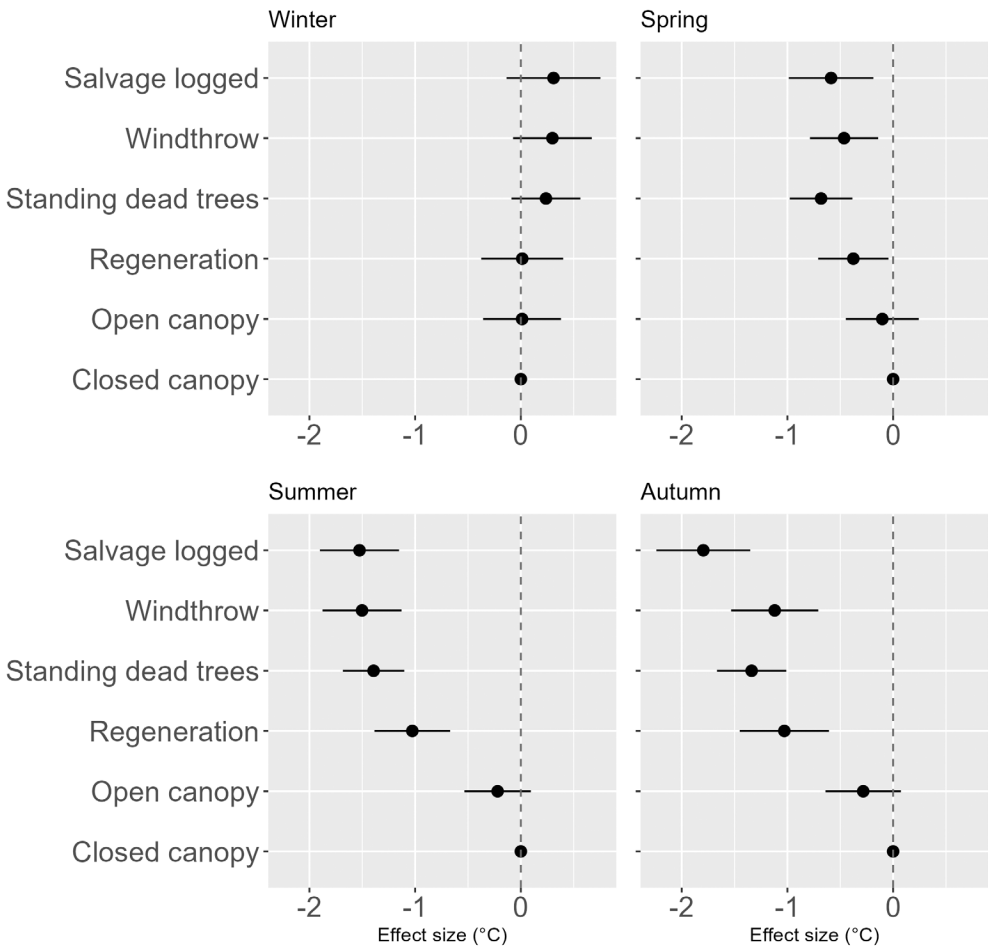


Fig. 5. Effect of forest stage on seasonal average for daily minimum of near-ground temperature (15 cm) compared to closed canopy as a reference.

Maximum temperature

Disturbed forest stages experienced significantly higher maximum temperatures compared to *closed canopy* stage in the spring and summer (Fig. 6). In contrast to its effect on minimum temperatures, effect of *regeneration* stage on maximum temperatures was not statistically significant. This suggests that shading provided by spruce regeneration is sufficient to effectively buffer maximum temperatures near the ground, comparably to mature forest stands. Disturbed areas (*salvage logged*, *windthrow* and *standing dead trees*) have higher maximum air temperatures.

Air T_{max}

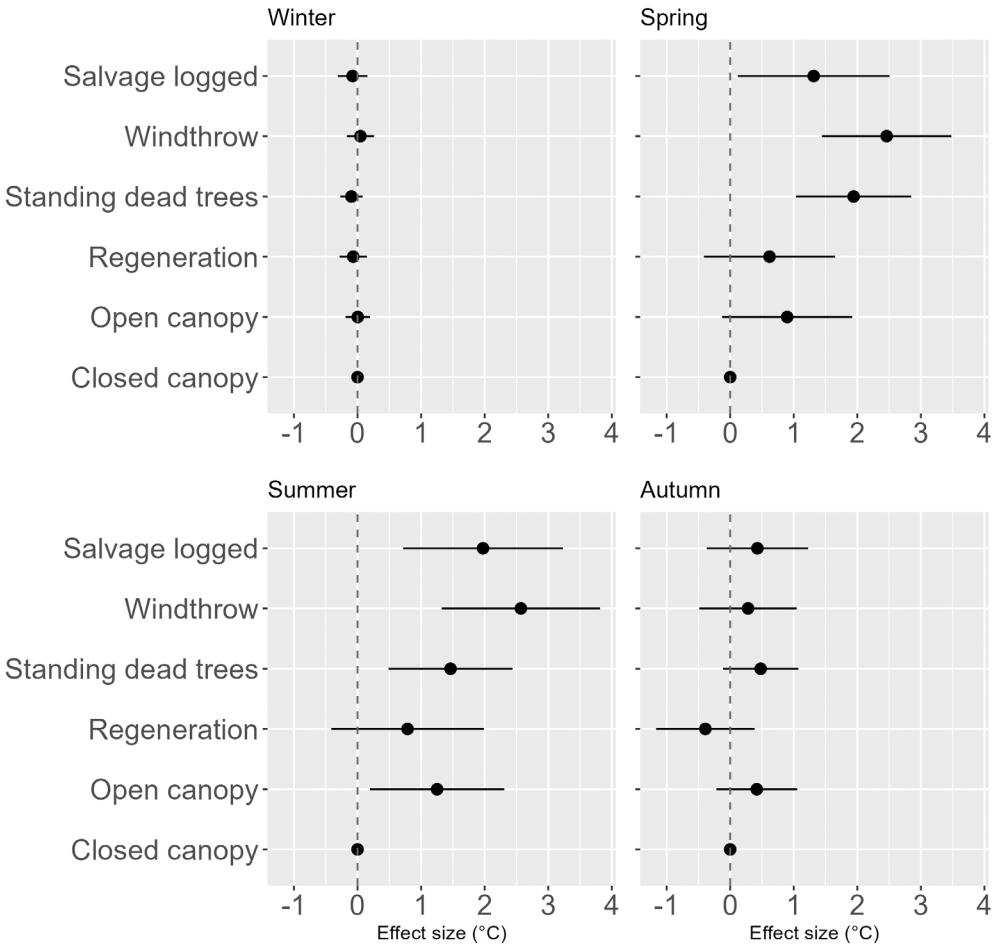


Fig. 6. Effect of forest stage on seasonal average for daily maximum of near-ground temperature (15 cm) compared to closed canopy as a reference.

The effect of forest stages on microclimate is visible also on average daily range of air temperature for each season (Fig. 7). *Salvage logged*, *windthrow* and *standing dead trees* have high daily range when compared to closed canopy forest with exception of winter. This shows the extremity of these stages, which is not so clear from comparing single microclimate variables.

Air T_{range}

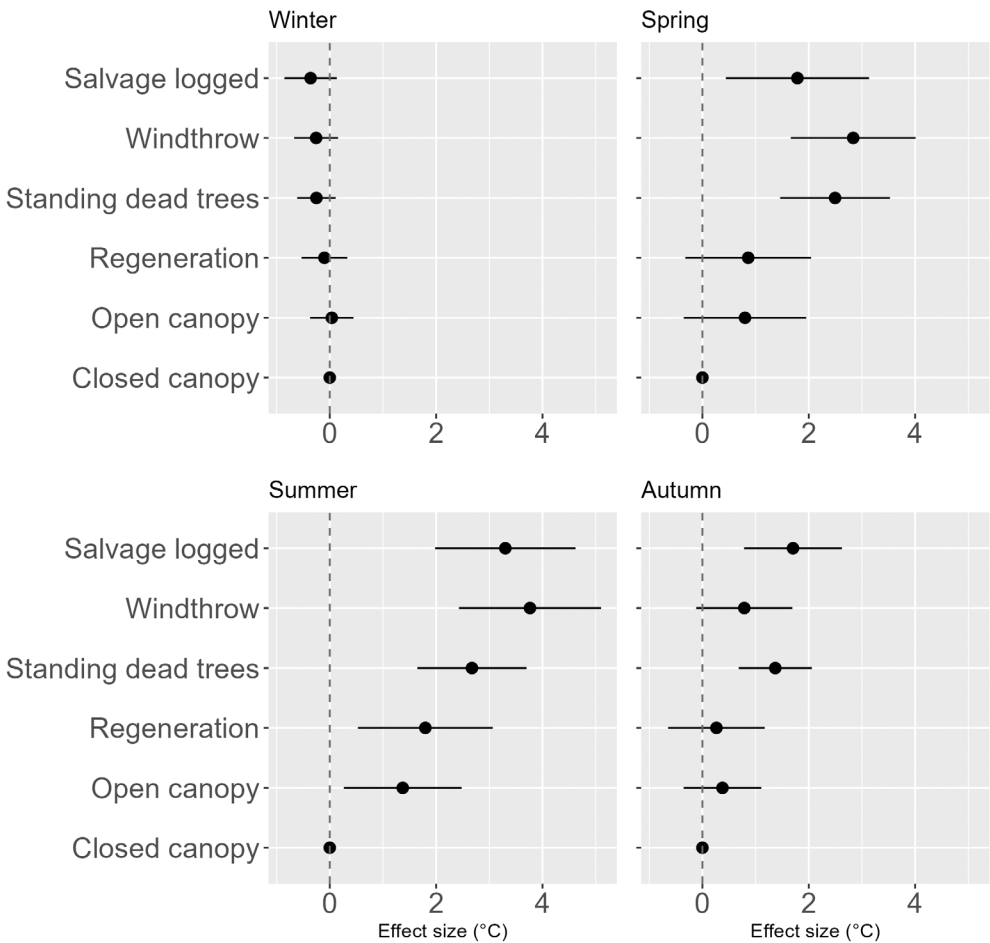


Fig. 7. Effect of forest stage on average daily range of air temperature (near-ground temperature (15 cm) compared to closed canopy as a reference.

Soil temperature

Soil temperatures were less variable compared to air temperatures. Due to attenuated daily variation, effects of forest stage on daily mean, minima and maxima were comparable (Fig. 8, 9, 10, 11). Winter soil temperatures 8 cm below ground are quite stable and rarely reach freezing temperatures (absolute minimum for soil temperature recorded over 5-year period was -1°C) thanks to isolation effect of the snow (Fig. 3). Accordingly, we have not detected any significant effect of forest stages on winter soil temperatures (Fig. 9, 10, 11). The differences between forest stages were most pronounced in the spring when disturbed forest stages warmed faster than *closed canopy* forests. This effect is probably amplified by earlier snowmelt in disturbed forest stages with remnant deadwood (*standing dead trees*, *windthrow*) which initiate formation of thaw circles.

We have shown that the effect of different forest disturbances on microclimate is season specific. Effects of different disturbance agents (bark-beetle, windthrow, salvage logging) on microclimate were comparable, while *open canopy* and *regeneration* stages showed intermediate response. Differences between these categories were not conclusive owing to the large heterogeneity within these categories, driven by fine-scaled variation in disturbance severity, vegetation in the herb layer and effects of site surrounding affecting the resulting canopy cover and exposure to solar radiation and potential confounding effects of local topography.

The effect of forest stages on microclimate is visible also on average daily range of soil temperature for each season (Fig. 12). Salvage logged and windthrow have large daily range when compared to closed canopy stage in Spring and Summer.

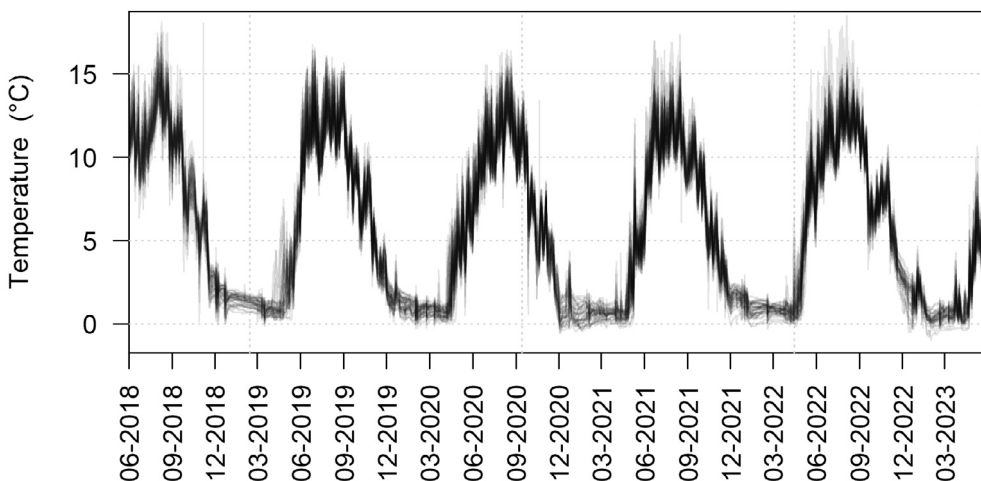


Fig. 8. Variation in soil temperature (measured in 8 cm depth) measured on 54 sites during the whole 5-year study period. Each line represents microclimatic time-series from one TMS logger.

We assume, that differences in microclimate were primarily driven by variability in canopy cover, controlling the attenuation of incoming and outgoing radiation. The deadwood, remaining on disturbed sites in different quality and quantity, have limited potential to modify ground microclimate, with possible positive effects on mean and maximum

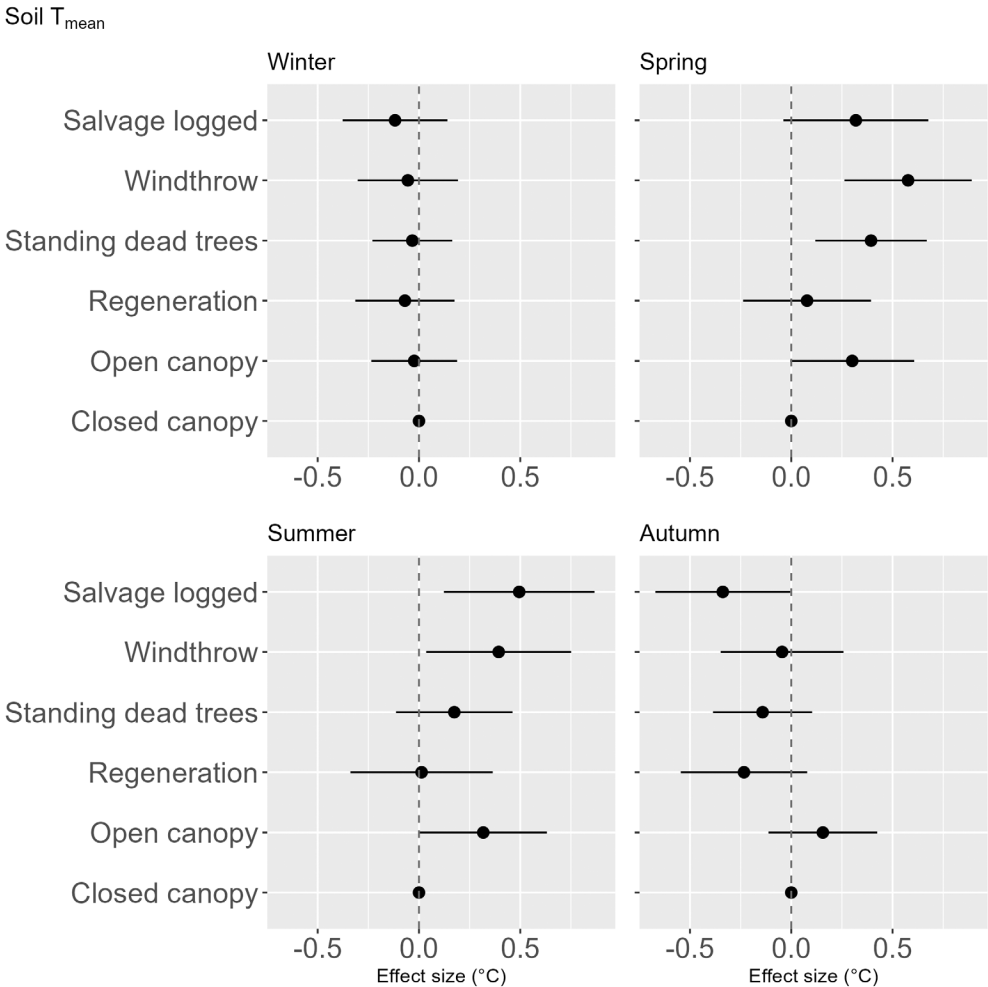


Fig. 9. Effect of forest stage on seasonal mean soil temperature (8 cm) compared to closed canopy as reference level. Largest effect of canopy disturbance was detected in spring, when soils in *windthrow* and *standing dead trees* stages warmed more rapidly than in *closed canopy* stage. Estimated effect in Figs 4–6 is represented by the dots and 95% confidence interval by whiskers.

temperatures visible mostly in the spring, when snowmelt is accelerated around tree trunks and snags (GEIGER et al. 2009, WILD et al. 2014). There is a clear effect of ground vegetation, that was not included in the models, that is most visible on salvage logged stage in spring and summer.

Soil T_{\min}

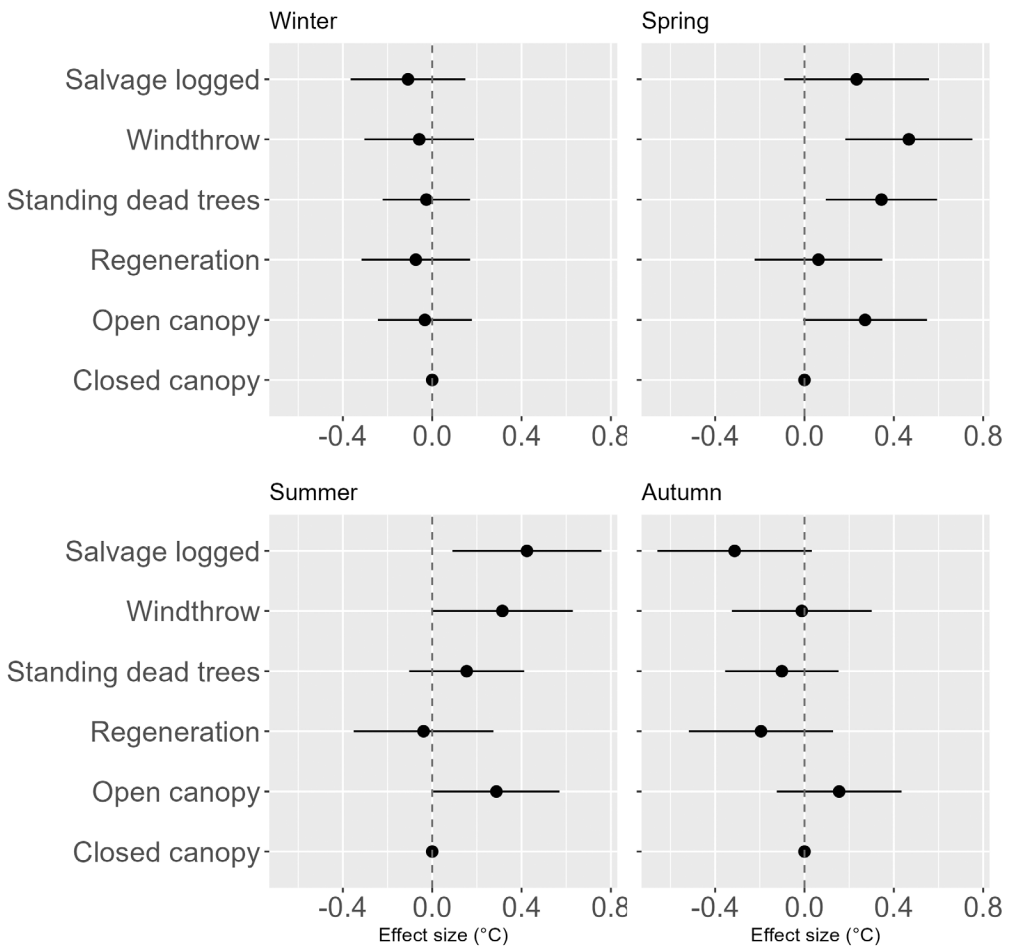


Fig. 10. Effect of forest stage on seasonal average for daily minimum of soil temperature (8 cm) compared to *closed canopy* as reference level.

Soil T_{\max}

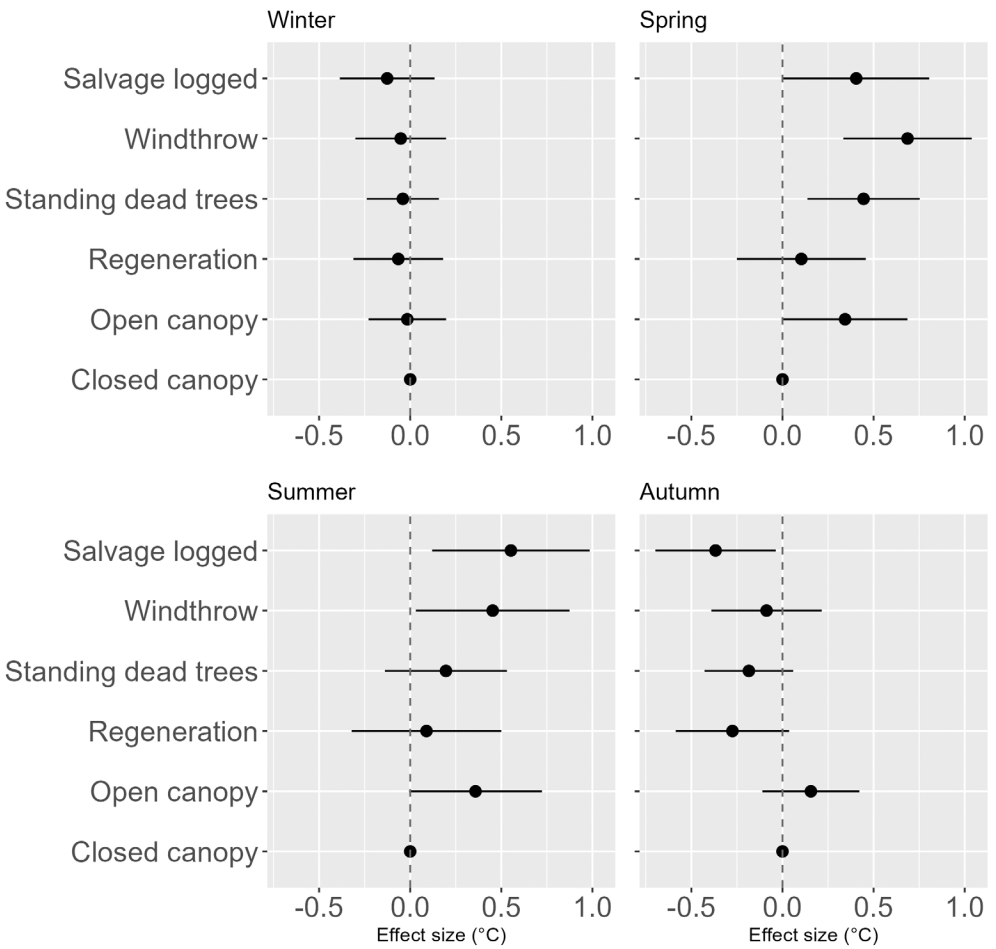


Fig. 11. Effect of forest stage on seasonal average for daily maximum soil temperature (8 cm) compared to *closed canopy* as reference level. Patterns in canopy disturbance effect on daily minima in soil follow patterns in daily mean and max temperature.

Soil T_{range}

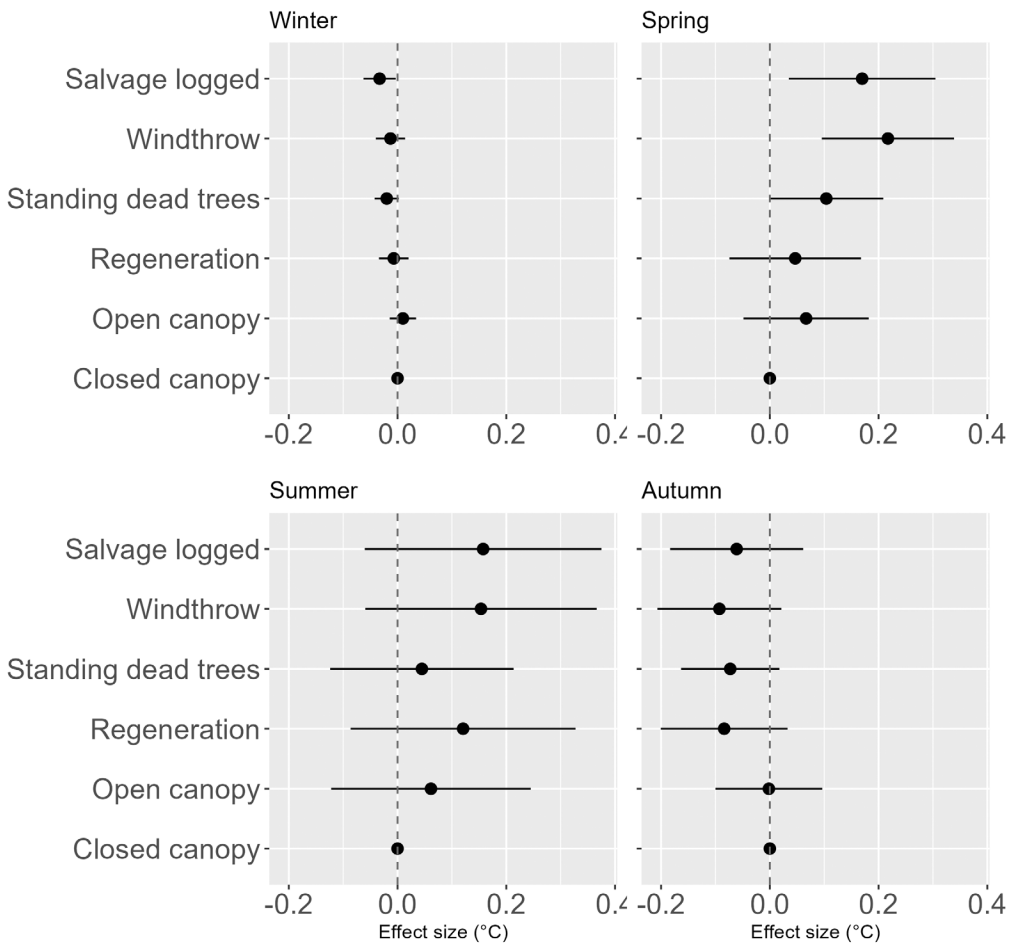


Fig. 12. Effect of forest stage on average daily range of soil temperature (8 cm) compared to *closed canopy* as a reference.

CONCLUSION

The effect of forest disturbance on thermal microclimate in mountain spruce forest is controlled by the extent of canopy loss and is season specific. The effects on air temperature extremity are most pronounced during summer, while effectively disappear during winter, when temperature variation is suppressed by snow insulation effect. Soil temperatures are less affected by forest stage, with highest effect on spring temperatures.

Closed forests exhibit a balanced diurnal temperature pattern, with the canopy cover reducing maximum daily temperatures above the soil surface and conversely increasing minimum daily temperatures. The influence of both effects adds up to the daily temperature amplitude but cancel out each other in their effect on average daily temperatures. The disturbance forest stages exhibit higher diurnal range which illustrates the extremity of these stages.

Tree regeneration can effectively reduce maximum temperatures near the ground by shading, however it does not protect understory from low temperatures. Areas with disturbed canopy (windthrows, areas with standing dead trees following bark beetle attack, and salvage logged areas) exhibited similar values in all observed parameters. To conclude, the removal of the canopy layer by any means increases maximum daily temperatures and decrease minimum daily temperatures during growing season, with long-lasting effect on low temperatures, prevailing even during regeneration phase, and increasing the risk of ground frost even during the summer months in the mountain spruce forests.

Fine scale forest microclimate grids are increasingly available (BRŮNA et al. 2023, HAESSEN et al. 2021). However, these grids still lack detailed effect of different forest stages because they rely on coarse forest maps with information about density or species and do not differentiate forest stages or structure. The temperature buffering is not only influenced by canopy density which can be retrieved by laser scanning (BRŮNA et al. 2023), but also by other forest structure parameters connected to the forest stage, as we have shown here.

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REFERENCES

- BARTA K.A., HAIS M. & HEURICH M., 2022: Characterizing forest disturbance and recovery with thermal trajectories derived from Landsat time series data. *Remote Sensing of Environment*, 282: 1–14.
- BRŮNA J., WILD J., HEDEROVÁ L., KLINEROVÁ T. & MACEK M., 2020: Metodika zpracování hemisférických fotografií [Methodology of processing hemispheric photographs]. Průhonice, 20pp. Online: https://asep.lib.cas.cz/ar1-cav/cs/detail-cav_un_epca-0540271-Metodika-zpracovani-hemisferickych-fotografii (accessed on 25 January 2024) (in Czech).
- BRŮNA J., MACEK M., MAN M., HEDEROVÁ L., KLINEROVÁ T., MOUDRÝ V., HEURICH M., ČERVENKA J., WILD J. & KOPECKÝ M., 2023: High-resolution microclimatic grids for the Bohemian Forest Ecosystem. Online <https://zenodo.org/records/6352641> (accessed on 25 January 2024).
- CARLSON A.R., SIBOLD J.S. & NEGRÓN J.F., 2021: Wildfire and spruce beetle outbreak have mixed effects on below-canopy temperatures in a Rocky Mountain subalpine forest. *Journal of Biogeography*, 48: 216–230.
- DÍAZ-CALAFAT J., URÍA-DÍEZ J., BRUNET J., DE FRENNE P., VANGANSBEKE P., FELTON A., ÖCKINGER E., COUSINS S.A.O., BAUHAUS J., PONETTE Q. & HEDWALL P.-O., 2023: From broadleaves to conifers: The effect of tree composition and density on understory microclimate across latitudes. *Agricultural and Forest Meteorology*, 341: 1–12.

- GEIGER R., ARON R.H. & TODHUNTER P., 2009: *The Climate near the ground*. Rowman & Littlefield Publishers, Lanham, Maryland, 623 pp.
- GILBERT N.A., ANICH N.M., WORLAND M. & ZUCKERBERG B., 2022: Microclimate complexities at the trailing edge of the boreal forest. *Forest Ecology and Management*, 524: 3–11.
- HAESSEN S., LEMBRECHTS J.J., DE FRENNE P., ... & VAN MEERBEEK K., 2021: ForestTemp – Sub-canopy microclimate temperatures of European forests. *Global Change Biology*, 27: 6307–6319.
- HAIS M. & KUČERA T., 2008: Surface temperature change of spruce forest as a result of bark beetle attack: remote sensing and GIS approach. *European Journal of Forest Research*, 127: 327–336.
- HAIS M. & KUČERA T., 2009: The influence of topography on the forest surface temperature retrieved from Landsat TM, ETM+ and ASTER thermal channels. *ISPRS Journal of Photogrammetry and Remote Sensing*, 64: 585–591.
- KÁŠPAR V., HEDEROVÁ L., MACEK M., MÜLLEROVÁ J., PROŠEK J., SUROVÝ P., WILD J. & KOPECKÝ M., 2021: Temperature buffering in temperate forests: Comparing microclimate models based on ground measurements with active and passive remote sensing. *Remote Sensing of Environment*, 263: 1–10.
- KERMAVNAR J., FERLAN M., MARINŠEK A., ELER K., KOBLEK A. & KUTNAR L., 2020: Effects of various cutting treatments and topographic factors on microclimatic conditions in Dinaric fir-beech forests. *Agricultural and Forest Meteorology*, 295: 1–12.
- KOPÁČEK J., BAČE R., HEJZLAR J., KAŇA J., KUČERA T., MATĚJKA K., PORCAL P. & TUREK J., 2020: Changes in microclimate and hydrology in an unmanaged mountain forest catchment after insect-induced tree dieback. *Science of The Total Environment*, 720: 1–13.
- KOVÁCS B., TINYA F. & ÓDOR P., 2017: Stand structural drivers of microclimate in mature temperate mixed forests. *Agricultural and Forest Meteorology*, 234–235: 11–21.
- LAUSCH A., FAHSE L. & HEURICH M., 2011: Factors affecting the spatio-temporal dispersion of *Ips typographus* (L.) in Bavarian Forest National Park: A long-term quantitative landscape-level analysis. *Forest Ecology and Management*, 261: 233–245.
- MACEK M., KOPECKÝ M. & WILD J., 2019: Maximum air temperature controlled by landscape topography affects plant species composition in temperate forests. *Landscape Ecology*, 34: 2541–2556.
- MÁLIŠ F., UJHÁZY K., HEDEROVÁ L., UJHÁZYOVÁ M., CSÖLLEOVÁ L., COOMES D.A. & ZELLWEGER F., 2023: Microclimate variation and recovery time in managed and old-growth temperate forests. *Agricultural and Forest Meteorology*, 342: 1–11.
- MENGE J.H., MAGDON P., WÖLLAUER S. & EHBRECHT M., 2023: Impacts of forest management on stand and landscape-level microclimate heterogeneity of European beech forests. *Landscape Ecology*, 38: 903–917.
- PETŘÍK M., HAVLÍČEK V. & UHRECKÝ I., 1986: *Lesnícka bioklimatológia [Forest bioclimatology]*. Príroda, Bratislava, 346 pp.
- R CORE TEAM, 2020: A language and environment for statistical computing. R foundation for Statistical Computing.
- SANCZUK P., DE PAUW K., DE LOMBAERDE E., LUOTO M., MEEUSSEN C., GOVAERT S., VANNESTE T., DEPAUW L., BRUNET J., COUSINS S.A.O., GASPERINI C., HEDWALL P.-O., IACOPETTI G., LENOIR J., PLUE J., SELVI F., SPICHER F., URÍA-DIEZ J., VERHEYEN K., VANGANSBEKE P. & DE FRENNE P., 2023: Microclimate and forest density drive plant population dynamics under climate change. *Nature Climate Change*, 13: 840–847.
- THOM D., SOMMERFELD A., SEBALD J., HAGGE J., MÜLLER J. & SEIDL R., 2020: Effects of disturbance patterns and deadwood on the microclimate in European beech forests. *Agricultural and Forest Meteorology*, 291: 1–11.
- VANDEWIELE M., GERES L., LOTZ A., MANDL L., RICHTER T., SEIBOLD S., SEIDL R. & SENF C., 2023: Mapping spatial microclimate patterns in mountain forests from LiDAR. *Agricultural and Forest Meteorology*, 341: 1–10.
- WANG Y., 1998: Mixed Effects Smoothing Spline Analysis of Variance. *Journal of the Royal Statistical Society Series B (Statistical Methodology)*, 60: 159–174.
- WILD J., KOPECKÝ M., SVOBODA M., ZENÁHLÍKOVÁ J., EDWARDS-JONÁŠOVÁ M. & HERBEN T., 2014: Spatial patterns with memory: tree regeneration after stand-replacing disturbance in *Picea abies* mountain forests. *Journal of Vegetation Science*, 25: 1327–1340.
- WILD J., KOPECKÝ M., MACEK M., ŠANDA M., JANKOVEC J. & HAASE T., 2019: Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. *Agricultural and Forest Meteorology*, 268: 40–47.

- WOOD S.N., 2004: Stable and Efficient Multiple Smoothing Parameter Estimation for Generalized Additive Models. *Journal of the American Statistical Association*, 99: 673–686.
- ZELLWEGER F., COOMES D., LENOIR J., DEPAUW L., MAES S.L., WULF M., KIRBY K.J., BRUNET J., KOPECKÝ M., MÁLIŠ F., SCHMIDT W., HEINRICHS S., DEN OUDEN J., JAROSZEWICZ B., BUYSE G., SPICHER F., VERHEYEN K. & DE FRENNE P., 2019: Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, 28: 1774–1786.

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