Effects of disturbance patterns and deadwood on the microclimate in European beech forests

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ABSTRACT

More frequent and severe disturbances increasingly open the forest canopy and initiate tree regeneration. Simultaneously, increasing weather extremes, such as drought and heat, are threatening species adapted to cool and moist climate. The magnitude of the microclimatic buffering capacity of forest canopies to mitigate hot and dry weather conditions and its disturbance-induced reduction remains poorly quantified. Also, the influence of disturbance legacies (e.g., deadwood) on forest microclimate is unresolved. In a unique manipulation experiment we investigated (i) the microclimatic buffering capacity of forest canopies in years with different climatic conditions; (ii) the impacts of spatial disturbance patterns on surface light and microclimate; and (iii) the effect of deadwood presence and type on microclimate.

Treatments included two disturbance patterns (i.e., aggregated and distributed), four deadwood types (i.e., standing, downed, standing and downed, removed), and one untreated control (i.e., nine treatments in total), replicated at five sites dominated by European beech (*Fagus sylvatica* L.) in southeastern Germany. We measured forest floor light conditions and derived diurnal extremes and variation in temperature (T) and vapor pressure deficit (VPD) during four consecutive summer seasons (2016 – 2019).

The buffering capacity of intact forest canopies was higher in warm and dry years. Surface light was significantly higher in spatially aggregated disturbance gaps compared to distributed disturbances of similar severity. An increase in surface light by 10 % relative to closed canopies elevated T_{max} and VPD_{max} by 0.42°C and 0.04 kPa, respectively. Deadwood presence and type did not affect the forest microclimate significantly.

Microclimatic buffering under forest canopies can dampen the effects of climate change. However, increasing canopy disturbances result in more light penetrating the canopy, reducing the microclimatic buffering capacity of forests. We conclude that forest management should foster microclimatic buffering in forests as one element of a multi-pronged strategy to counter climate change.

1. Introduction

Climate change is increasingly impacting forest ecosystems, with negative consequences for plant growth, regeneration, and survival (Anderson-Teixeira et al., 2013; D'Orangeville et al., 2018; McDowell et al., 2020). If climate change continues unabated, drought-induced stress may exceed everything that plants experienced over the past 1000 years by 2050 (Williams et al., 2013). Such extreme droughts will have dramatic consequences for biodiversity and ecosystem services supply (Choat et al., 2012). Forest canopies have the potential to buffer climate change effects through the specific microclimate they create, e.g. by providing shelter from direct insolation and increasing evaporative cooling (Bonan, 2008; De Frenne et al., 2019; Thom et al., 2017). However, climate change is also expected to decrease forest

canopy cover through increases in natural disturbance activity (Seidl et al., 2017). To date, it remains uncertain how strong the climate buffering capacity (i.e., the mitigation of hot and dry weather conditions) of undisturbed forests is, and how different disturbance patterns and processes alter microclimatic conditions.

Climate change has direct and indirect effects on plants. Direct effects include extreme heat damaging plant tissue (Guha et al., 2018) as well as water stress through the combination of heat, low humidity, and infrequent rainfall (Davis et al., 2019). Increasing activity of natural disturbances (Seidl et al., 2017) constitute an indirect effect of climate change on environmental conditions. Disturbances create canopy openings which affect the local microclimate (Schmidt et al., 2017). Previous studies have shown that the microclimate becomes warmer and drier with increasing distance from intact forests (Baker et al., 2014; Davies-Colley et al., 2000; Ewers and Banks-Leite, 2013; Wright et al., 2010). Hence, increasing disturbances will likely add to climate-induced plant stress, with consequences for future forest development. For instance, regeneration failure of the currently prevailing tree species may accelerate thermophilization (i.e., a change in the forest composition towards warm-adapted species) (De Frenne et al., 2013; Stevens et al., 2015; Zellweger et al., 2020) or in extreme cases cause a regime shift from forests to grass- or shrub-dominated ecosystems (Anderson-Teixeira et al., 2013). These transitions could have dramatic consequences for forest-dwelling species (Laurance and Bruce Williamson, 2001) and could negatively affect the services provided for human well-being (Nelson et al., 2013).

Droughts have increased over the past decades, and initiated major waves of tree mortality in Central European forests (Senf and Seidl, 2018). While droughts, often in combination with bark beetle infestations, have primarily affected Norway spruce (*Picea abies* [Karst.]) in the past, recent events have shown that also other tree species are increasingly susceptible to global change-type droughts (Breshears et al., 2009) in Central Europe. European beech (*Fagus sylvatica* [L.]) is one of the species promoted as being fairly robust to future climatic conditions (Paul et al., 2019). Furthermore, European beech is the most abundant and economically important broadleaved tree species in Central Europe, and harbors numerous forest-dwelling species (Brunet et al., 2010; Grebenc et al., 2009; Hanewinkel et al., 2012). For instance, about 70% of central European saproxylic beetles can be found in beech-dominated forests (Müller et al., 2013). With the goal to adapt forests to climate change, practitioners have intensified their efforts to convert spruce-dominated forests to beech forests. However, the high beech mortality rates of two consecutive drought years in 2018 and 2019 (Buras et al., 2019; Schuldt et al, 2020) challenge the expectation that beech will be able to cope with future climate change. A crucial element is the question of how to best mitigate the impact of severe droughts in the future. While scientists and forest managers have mainly focused on species conversion (e.g., Temperli et al., 2012; Vitali et al., 2017) and stand density regulation (e.g., D'Amato et al., 2013; Gebhardt et al., 2014) to maintain forests and their services, microclimatic conditions have received comparably little attention.

Forest canopies have a cooling effect on the local environment. The phase change from liquid water transpired by forests to water vapor causes an energy flux from the surface to the atmosphere (i.e., latent heat flux) resulting in an evaporative cooling effect (Bonan, 2008). Given sufficient water supply, an intact forest's evapotranspiration (and thus its cooling effect) increases under higher temperatures (Thom et al., 2017). However, resulting from an intense forest management history and increasing natural disturbances, large landscapes with continuous forest canopy have become rare in Central Europe (McGrath et al., 2015). Instead, landscapes are mosaics of different land-use systems and forest canopies are fragmented by management practices such as gap and shelterwood cutting as well as by natural disturbances. Thus the resultant forest edges are exposed to stronger winds, lower humidity and higher air temperatures than the interior of

undisturbed forests (Magnago et al., 2015). These conditions will likely amplify climate-induced stress for trees. Forest regeneration will be most strongly affected, as their root systems do not yet reach deep into the soil (E Silva et al., 2012) while, at the same time, regeneration density is usually highest in canopy gaps (Vodde et al., 2015).

Despite the importance of microclimate for future forest development, the number of studies investigating disturbance impacts on microclimatic conditions remains limited. Previous studies have analyzed the spatial extent of forest effects on microclimate from edges into open (disturbed) areas (Aragón et al., 2015; Baker et al., 2014; Pinto et al., 2010; Wright et al., 2010) or from open areas into the forest (Chen et al., 1999; Davies-Colley et al., 2000; Ewers and Banks-Leite, 2013). Others have tested the correlation between canopy closure and microclimate (Brown, 1993; Davis et al., 2019; Hardwick et al., 2015). However, to our knowledge, no study has yet assessed the effects of different spatial patterns of disturbance on microclimate. Most disturbances in Central European forests are characterized by mortality at the level of individuals or small groups of individuals, while stand-replacing disturbances happen only infrequently (Nagel et al., 2017; Panayotov et al., 2015; Splechtna et al., 2005; Standovár and Kenderes, 2003). Whether disturbance patterns are distributed (i.e., with several spatially segregated individual trees being affected by the disturbance) or aggregated (i.e., clusters of trees affected) within a stand can potentially lead to different microclimatic outcomes.

Disturbances not only cause variable openings in the canopy but also create important biological legacies. An important disturbance legacy is standing and downed deadwood. Deadwood is an important pool of carbon in natural forests (Jacob et al., 2013), and is crucial for the occurrence of a large number of saproxylic organisms (Seibold et al., 2016). However, the potential deadwood effect on forest microclimate has received little attention to date (Kovács et al., 2017). For instance, moisture stored in deadwood within the first few years after a disturbance could induce an evaporative cooling effect. Further, standing deadwood can still shield the ground from insolation, and thus reduce energy input, potentially modifying local temperature and moisture conditions. Understanding the role of deadwood on microclimate is important because management frequently removes disturbance-killed trees by salvage logging (Thorn et al., 2018).

Here, we conducted a replicated manipulation experiment with a factorial design of nine treatments. Previous microclimate studies have rarely been based on manipulation experiments, despite the fact that controlled experiments are best suited to control for the noise that is introduced by the inherent heterogeneity in ecosystems (Hurlbert, 1984). Our treatments were specifically designed to assess the effects of different disturbance patterns and deadwood types on microclimate. Disturbance sizes and severities were chosen to reflect patterns that are characteristic for the natural disturbance regime of forests dominated by European beech (Drößler and Von Lüpke, 2005; Kenderes et al., 2008). They also span a typical management gradient from single-tree to group-selection harvesting, in effect, management systems that are frequently used to initialize regeneration in Central European forests (Lorenz et al., 2018). We investigated (i) the climatic buffering capacity of forest canopies in years with different climatic conditions, (ii) the effects of different spatial patterns of disturbance on surface light and microclimate, and (iii) the effect of deadwood presence and type on microclimate. We expected a higher microclimatic buffering capacity of undisturbed forests in warm and dry years due to increases in evapotranspiration causing additional cooling and wetting of the air (de Frenne et al., 2019). We also expected a change towards warmer and drier conditions with disturbances that more strongly increase surface light (i.e., aggregated > distributed disturbances), as openings are more exposed to direct solar radiation, warming and drying the surface (Ritter et al., 2005). Finally, we hypothesized deadwood retention to mitigate the effects of increasing surface light on the forest microclimate as the evaporation of moisture stored in deadwood increases evaporative cooling, and as standing deadwood
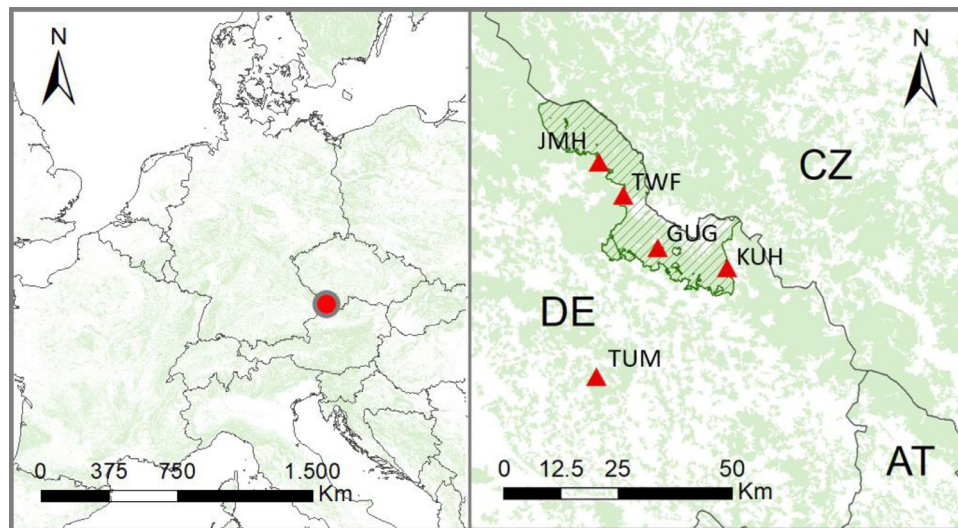
Figure 1. Study area. The red dot marks the study location in Central Europe. Red triangles represent the five experimental sites. Shaded areas delineate the Bavarian Forest National Park, and green areas denote forest cover.

provides shelter from the sun (Marcolin et al., 2019).

2. Material and Methods

2.1. Study area

Our experiment was conducted in southeastern Germany close to the boarder of Czechia and Austria (Fig. 1). In particular, four sites are located in the Bavarian Forest National Park (GUG, JMH, KUH, TWF), and one is in Thurmansbang (TUM) in the vicinity of the National Park. The sub-montane forests studied here are all dominated by European beech (Table 1), with minor shares of Norway spruce and other tree species. Forests originated from secondary succession, and are of low structural diversity, characterized by only one canopy layer and limited age variation. They are in a mature development stage with similar basal area, stand density and tree dimensions across study sites. Active forest management ceased several decades ago. While the national park has experienced the largest unimpeded bark beetle outbreak in European forests in recent decades, our sites have not been affected by these disturbances (Heurich and Englmaier, 2010).

2.2. Experimental design

We manipulated canopy cover and deadwood at five experimental sites. In a randomized factorial block design, we selected eight plots per site and assigned different treatments to them, with an additional plot

serving as the untreated control (i.e., 5 sites × (8 treatments + 1 control) = 45 plots in total) (Fig. 2). Plots were randomly distributed within each site, and consisted of squares of 50 m × 50 m (i.e., 2,500 m^2). In October 2015, gaps were created to mimic disturbances of individual trees and groups (Figs. 2, 3). At all treated plots, disturbance severity was held constant at approximately 25 % of basal area removed. Trees were cut either in spatially aggregated groups of 25 m x 25 m (625 m^2) around the plot center or as individual trees distributed randomly across the plot (two different treatments regarding the spatial pattern of disturbance, cf. the rows in Fig. 2). In these gaps we retained downed, standing or both downed and standing deadwood, or removed deadwood altogether (four different deadwood treatments, cf. the columns in Fig. 2). To create standing deadwood trees were cut below the first strong branch of the crown, which was on average at a height of 8.3 m. Resulting from the factorial design of our manipulation experiment, the average amount of standing and downed deadwood was similar across sites (Table 1). Remaining differences can be partly attributed to differences in deadwood before treatments and local variation in stand structure.

2.3. Data collection

In May 2016, we installed an automatic data logger (model UT 330C) in the center of each plot on a pole ca. 1.2 m above the ground. Data loggers measured temperature and relative humidity every hour during the summer seasons (June, July, August) of the years 2016 –

Table 1
Site topography and forest attributes after treatment. Presented are means and standard deviations (in parentheses) across all plots and treatments per site. H' (Shannon) diversity is based on the basal area of live trees.

Site	GUG	JMH	KUH	TUM	TWF
Coordinates (UTM)	32 U 824074 5429269	32 U 815223 5440885	32 U 834390 5426884	32 U 816421 5410171	32 U 819000 5436191
Elevation (m)	837	857	852	483	1055
Slope (°)	7.1	13.0	18.1	10.9	11.0
Aspect	W	N	E	N	NE
Live basal area (m^2 ha^{-1})	32.4 (5.6)	30.9 (5.3)	34.3 (5.5)	31.6 (4.0)	41.4 (4.5)
Stand density (N ha^{-1})	540 (164)	418 (159)	388 (89)	443 (89)	864 (173)
Mean DBH (cm)	24.3 (5.2)	29.1 (4.9)	30.7 (2.5)	26.3 (3.6)	23.4 (2.3)
Mean Height (m)	26.1 (2.5)	29.4 (3.9)	28.3 (1.7)	25.9 (2.0)	21.9 (3.1)
Beech basal area share (%)	83.4 (14.0)	92.0 (3.1)	70.4 (18.1)	77.5 (16.7)	81.2 (8.2)
H' diversity	0.5 (0.3)	0.3 (0.1)	0.6 (0.2)	0.5 (0.3)	0.5 (0.1)
Standing deadwood basal area (m^2 ha^{-1})	3.3 (3.4)	3.4 (3.1)	2.9 (3.0)	3.1 (2.5)	4.0 (3.4)
Downed deadwood volume (m^3 ha^{-1})	21.8 (27.2)	30.1 (36.7)	27.0 (32.2)	19.8 (20.8)	23.6 (30.9)

Figure 2. Experimental design. Two spatial disturbance patterns were created while keeping disturbance severity constant at ~25 % basal area removed. For each spatial disturbance pattern four different deadwood treatments were studied. Including the untreated control plot each of the five experimental sites comprised nine factorial combinations of spatial disturbance patterns and deadwood types.

2019 (four years). We focused on summer because forests have been shown to have a particularly strong effect on the microclimate during this particular season (Baker et al., 2014). The summer season is also of crucial importance for the growth and survival of tree recruits (Chen et al., 1999).

As we expected the modulation of the light regime to be the main process through which canopy openings influence forest microclimate, we collected information about the light regime throughout our experimental plots. We measured light as the total site factor (TSF) (i.e., the total solar radiation including direct and diffuse light, relative to open conditions) at the same height as data loggers at four locations using hemispherical photography (Solariscope SOL 300B) in the first summer after implementing the treatments. The instrument measures the shading of forest canopies relative to open field conditions. Accounting for the theoretical path of the sun (depending on geographical orientation and latitude) it obtains an accurate sub-canopy light estimate (Canham et al., 1990). Light measurements were taken at the four corners of a 10 m × 10 m square centered around the plot center (see Figure S1 in the Supplementary material). For further analysis we aggregated these measurements to plot averages.

2.4. Analysis

First, we harmonized and cleaned the collected data. To that end, the data logger records were inspected for unrealistic values and missing measurements. For instance, we omitted days in which hourly records were incomplete to avoid aggregation bias.

Subsequently, we used temperature and relative humidity to derive vapor pressure deficit (VPD). VPD is the difference between saturated and actual vapor pressure and quantifies the amount of water vapor in the air. VPD constitutes an important driver of plant hydraulic functioning (Ficklin and Novick, 2017). As VPD acts as mediator between atmospheric conditions and stomatal conductance, it also represents the drying capacity of the air. A higher VPD thus implies increasing water stress of plants (Williams et al., 2013).

Next, we aggregated hourly observations to daily values. In particular, we derived extreme values (maxima), and the variation (standard deviation, SD) of temperature and VPD within a day. These microclimatic parameters were selected as they provide important information for growth and survival of tree recruits. High maximum temperature (T_{max}) and VPD (VPD_{max}) induce stress during the warmest and driest time of the day, potentially limiting growth (e.g., due to stomata closing) and resulting in mortality (e.g., due to water stress). Besides weather extremes, high variation in temperature (T_{SD}) and VPD (VPD_{SD}) can cause stress for plants as microclimate variation influences ecosystem processes, including plant and soil respiration rates (Chen et al., 1999). For instance, a sudden rise in temperature close to lethal limits requires plants to keep pace in producing heat-shock proteins to protect their tissue (Lambers et al., 2008). The ability to produce such proteins differs among species. The effects of diurnal fluctuations in microclimatic conditions on ecosystem processes can thus, *inter alia*, alter forest regeneration dynamics (Brown, 1993). We assessed the dependencies among microclimate parameters using Pearson's correlation coefficients. In particular, we were interested in the association between extremes and variations in microclimate as they could cause compounding effects on plants (with higher maxima and
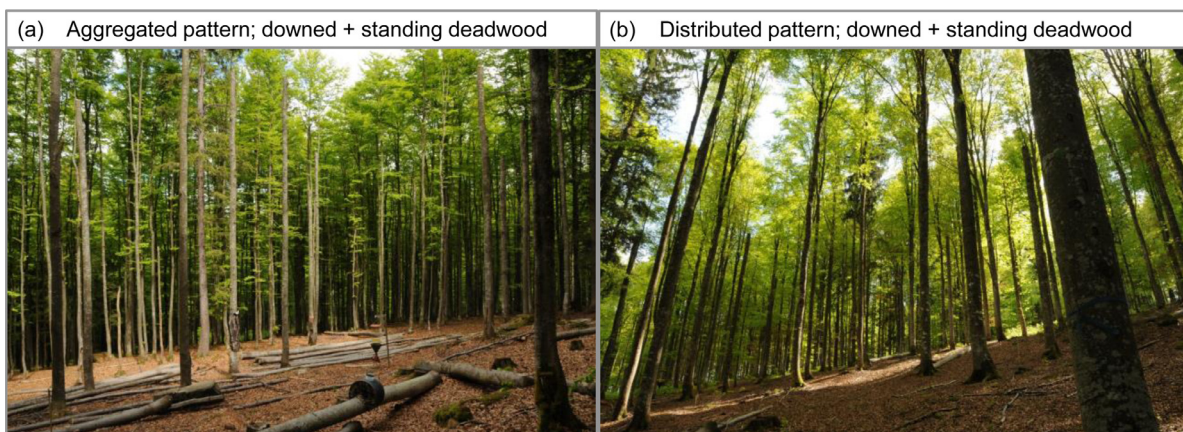
Figure 3. An example of the aggregated and distributed disturbance treatment with both downed and standing deadwood.

higher variation indicating particularly challenging conditions for the growth and survival of seedlings and saplings).

We derived the difference between treated and untreated plots at each site to assess the overall treatment effects on microclimate. The difference between treated and untreated plots indicates the disturbance-induced change in the buffering capacity of intact forests with regard to temperature and VPD, respectively. We also compared the interannual variation in the buffering capacity to test for differences with climate variability (e.g., in warm and dry years). Based on the data of Germany's National Meteorological Service (Deutscher Wetterdienst), there was a trend towards warmer and drier conditions from 2016 to 2019, with 2019 being the warmest and driest year of the observation period (Figs. S2, S3). On average over the five experimental sites, T_{max} was 0.6°C, 1.4°C, and 2.7°C higher in the summer of 2019 compared to the summers of 2018, 2017, and 2016, respectively. Concurrently, summer precipitation was 11 mm, 29 mm, and 57 mm lower in 2019 compared to 2018, 2017, and 2016, respectively. We tested annual differences in the buffering capacity of microclimate parameters for statistical significance employing Tukey's Honest Significant Difference ($\alpha = 0.05$).

Using the full dataset including untreated plots (i.e., 45 observations), we investigated the effects of spatial disturbance patterns and deadwood type on light conditions using a Bayesian analysis framework. Bayesian models capture parameter uncertainty when estimating the probability distribution of treatment effects on the response variable and allow the integration of prior information (McElreath, 2016). In contrast to maximum likelihood approaches that provide point estimates of the highest likelihood of model parameters, Bayesian inference involves the full range of parameter values and their probabilities. Prior information is used to restrict parameters to plausible ranges (McElreath, 2016). Incorporating Markov Chain Monte Carlo (MCMC) sampling, Bayesian approaches achieve accurate results when assessing complex (e.g., multi-hierarchical) data and are not restricted by the model's degrees of freedom (Rossi and Allenby, 2003). We expected more light to penetrate the canopy in aggregated compared to distributed disturbance patterns, and hypothesized an interaction effect between aggregated disturbance patterns and standing deadwood on light conditions. However, as the model with spatial disturbance pattern as only fixed effect clearly outperformed models including deadwood type (see evaluation criteria below), we omitted the latter from the final model. In effect, we fitted a multi-hierarchical Bayesian model with site as random effect and spatial disturbance pattern as the only fixed effect. Surface light was log-transformed prior to the analysis to normalize the data distribution.

Subsequently, we used all daily records aggregated from data loggers (i.e., 7,487 observations) in multi-hierarchical Bayesian models to analyze the impacts of surface light (expecting a direct link between light conditions and microclimate) and deadwood type (expecting an additional evaporative cooling effect from deadwood evaporation) on each microclimate parameter. Consequently, each model included

surface light and deadwood type as fixed effects. We specified a conservative prior to regulate the inference of surface light effects to a reasonable range (i.e., a weakly informative prior) (McElreath, 2016). Random effects for site and year allowed for variable intercepts and slopes of the response variables. Both VPD variables were square-root-transformed to normalize their data distributions. As microclimate models were based on time-series data, we modelled the first-order autoregressive effects of residuals.

All Bayesian models were evaluated with posterior predictive checks. The leave-one-out (LOO) adjusted R^2 was calculated to avoid an overestimation of the variance explained by adding explanatory variables to the model, and residuals were tested for normality. Additionally, residuals of the microclimate parameter models were tested for temporal autocorrelation using generalized Durbin-Watson statistics. All analyses were performed using the R language and environment for statistical computing (R Development Core Team, 2019). In particular, we employed the packages tidyverse (Wickham, 2017) and reshape2 (Wickham, 2017) for data organization; brms (Bürkner, 2018) and loo (Vehtari et al., 2019) for Bayesian models and their evaluation; car (Fox et al., 2019) to test temporal autocorrelation; and ggplot2 (Wickham, 2009) for visualizations.

3. Results

3.1. High correlation between variation and extremes in microclimatic

Variation and extreme values of microclimate parameters were highly positively correlated. In particular, we identified a strong association between VPD_{SD} and VPD_{max} (r = 0.948), indicating that days with a high fluctuation in aridity were also driest. Also T_{SD} and T_{max} were clearly positively correlated (r = 0.777), indicating that days with a high temperature variation were also hottest, but their association was weaker than the one between VPD_{SD} and VPD_{max}. As temperature is one of the two components defining VPD (see above), hot and dry conditions interact inherently. Consequently, days with a high T_{SD} and T_{max} generally also experienced a high VPD_{SD} and VPD_{max}.

3.2. Climate buffering capacity increases in warm and dry years

The importance of intact forest canopies for the microclimate increased under warm and dry conditions (Table 2). The buffering capacity of intact canopies (i.e., the difference between all treated and untreated plots) was higher in warm and dry years (2018 and 2019) compared to relatively cold and wet years (2016 and 2017). In 2019, T_{max} and VPD_{max} in undisturbed forests were 2.25°C and 0.53 kPa higher compared to 2016. At the same time, the buffering capacity of undisturbed forests increased statistically significantly by 0.45°C and 0.08 kPa on average between those two years. Consequently, intact forests compensated on average 20.0 % and 15.1 % of elevated summer T_{max} and VPD_{max}, respectively. Moreover, the buffering capacity of T_{SD}

Table 2

Microclimate buffering capacity of intact forest canopies. Presented are the average summer conditions across all data loggers in undisturbed and disturbed forests, as well as the average buffering capacity. Note that the buffering capacity is the average across diurnal differences between disturbed and undisturbed plots, in effect, subtracting one control plot from eight treatments per day and site. As missing observations alter the weight of control plots (e.g., if one control plot is compared against seven instead of eight treatments) subtracting microclimate parameters after aggregation to annual averages would result in slightly different buffering capacities than presented in the table. T_{SD} and VPD_{SD} represent the daily standard deviation of temperature and vapor pressure deficit, respectively. T_{max} and VPD_{max} denote maximum temperature and vapor pressure deficit, respectively. Letters indicate significant differences between years ($\alpha = 0.05$). All measurements were taken hourly by data loggers during the summers of 2016 – 2019, and were aggregated to daily values.

	Average microclimate conditions in undisturbed forests				Average microclimate conditions in disturbed forests				Average buffering capacity			
Year	T_{SD}	T_{max}	VPD_{SD}	VPD_{max}	T_{SD}	T_{max}	VPD_{SD}	VPD_{max}	T_{SD}	T_{max}	VPD_{SD}	VPD_{max}
2016	2.81 [a]	21.69 [a]	0.25 [a]	0.82 [a]	3.00 [ab]	22.70 [a]	0.30 [a]	1.05 [a]	0.26 [a]	1.08 [a]	0.05 [ab]	0.22 [a]
2017	2.73 [a]	22.23 [ab]	0.30 [ab]	1.14 [b]	2.95 [a]	22.60 [a]	0.31 [a]	1.19 [b]	0.41 [b]	1.45 [b]	0.05 [ab]	0.23 [a]
2018	2.74 [a]	23.25 [bc]	0.32 [b]	1.23 [bc]	3.08 [b]	24.30 [b]	0.37 [b]	1.46 [c]	0.35 [b]	1.46 [b]	0.05 [a]	0.25 [a]
2019	2.98 [a]	23.94 [c]	0.36 [c]	1.35 [c]	3.31 [c]	25.00 [c]	0.41 [c]	1.56 [d]	0.41 [b]	1.53 [b]	0.06 [b]	0.30 [b]
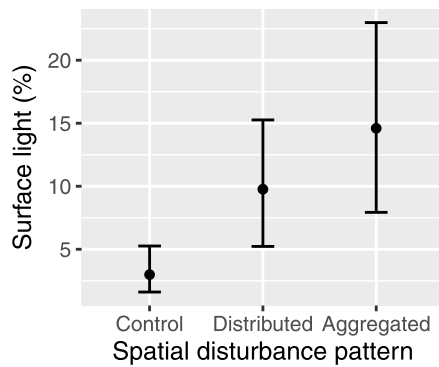
Figure 4. Disturbance effects on surface light conditions. Presented are means (dots) and 95% credibility intervals (whiskers).

increased significantly by 0.16°C from year 2016 to 2019, compensating 54.8 % of the higher diurnal variation in temperature in 2019. In contrast, changes in the buffering capacity of VPD_{SD} between those two years were not significant, and the buffering capacity of closed canopies reduced VPD_{SD} only marginally (9.1%).

3.3. Disturbance impacts on surface light

Disturbances increased light penetration through the canopy (Fig. 4). On average, only 3.0 % of the sunlight reached the ground in control plots. Where disturbances were distributed, on average 9.8 % of light reached the ground (i.e., an increase of 226.7 % relative to control plots). With on average 14.6 % (i.e., + 386.7 % relative to control plots) the highest light levels were observed under the aggregated disturbance pattern. Although disturbance treatments were standardized, their effects on light conditions varied considerably within each disturbance pattern (due to the variable distribution of trees at each plot). Credibility intervals were especially wide for the effect of aggregated disturbances. Overall, spatial disturbance patterns explained 56.7 % of the variation in surface light in the multi-hierarchical Bayesian model as indicated by the LOO-adjusted R^2.

3.4. Light regime drives microclimate

An increase in light close to the forest floor was associated with a warmer and drier microclimate (Fig. 5). Surface light was positively correlated with all four microclimate variables. A 10 % increase in light on the ground increased the variation in microclimatic conditions throughout the day by 0.11°C (T_{SD}) and 0.02 kPa (VPD_{SD}). The same increase in light intensified daily extreme values by 0.42°C (T_{max}) and 0.04 kPa (VPD_{max}). The Bayesian multi-hierarchical models explained between 58.5 % (T_{SD}) and 68.1 % (VPD_{SD}) of the variance in microclimatic parameters. The generalized Durbin-Watson statistics were between 2.3 and 2.4, indicating low residual autocorrelation of the models.

3.5. Minor deadwood effects on microclimate

Deadwood effects on microclimate were small and ambiguous (Fig. 6). Across all microclimatic parameters, we found no significant effect of retaining deadwood on the variation and extremes of microclimatic parameters relative to the removal of all deadwood. Our data show only a weak indication that retaining both downed and standing deadwood after disturbance is more beneficial for the microclimate than only retaining one deadwood type or removing all deadwood.

4. Discussion

4.1. Forest microclimate can partially compensate climate change

Forest canopies alter microclimate, and their microclimatic buffering capacity increases in warmer and drier years (Table 2). Based on our findings, it is conceivable that the microclimatic buffering capacity of forest canopies could partly offset the impacts of global climate change on subcanopy processes. On average, intact forest canopies mitigated increases in temperature and VPD extremes by 20.0 % and 15.1 % compared to disturbed forests. It is important to note that the disturbances studied here opened the forest canopy only moderately, with maximum surface light levels remaining below 30 % of open conditions in all plots. We thus assume that the microclimate effect of intact canopies is considerably greater when compared against high severity disturbances or other land-use systems. For instance, the Atlantic tropical forest of Brazil mitigates up to 62 % of T_{max} increases using the air temperature outside of forests as reference (Ewers and Banks-Leite, 2013). Further, it is possible that our analysis underestimates the increase of the microclimate buffering effect of intact forest canopies in warmer and drier years. Light measurements were only available for the year 2016, and we assumed surface light not to change significantly in the following three years. However, European beech forest canopies can recover quickly after disturbance (Valverde and Silvertown, 1997). Thus, the difference in light regimes between disturbed and undisturbed forests have likely become smaller over time, and it can be expected that the buffering capacity of disturbed sites has already increased.

Microclimatic buffering of weather extremes might be of great importance to sustain forest ecosystems in the future (Davis et al., 2019; De Frenne et al., 2019, 2013). However, climate change could also result in tipping points, exceeding the microclimatic buffering capacity of forest ecosystems. If the water available for evaporative cooling is increasingly limited under climate change, for instance, microclimatic buffers might be lost. Also, additional evapotranspiration in a warmer and drier environment could lead to drought-induced mortality (Greenwood et al., 2017) or increase the predisposition towards other disturbance agents (Anderegg et al., 2015; Krams et al., 2012), which could result in canopy loss and reduce the microclimatic buffering effect of forests.

4.2. Increasing disturbance activity dampens microclimatic buffering

Disturbances increase surface light (Fig. 4) and alter the forest microclimate towards warmer and drier conditions (Fig. 5). Our findings highlight that even disturbances of small spatial extent (2,500 m²) and relatively low severity (25 % of basal area disturbed) can change the microclimate considerably. This is important because the area disturbed has doubled since the mid-1980s in Central Europe, with low-severity disturbances increasing more strongly than stand-replacing disturbances (Senf et al., 2018). Nonetheless, high severity disturbances of larger size are likely to have a stronger impact on the microclimate (Schmidt et al., 2017). Disturbance activity is expected to increase in many parts of the world as a result of climate change (Seidl et al., 2017), which will expose the forest floor more frequently to the full force of weather extremes without the buffering effect of forest canopies.

On average, an additional 10 % of surface light increased T_{max} by 0.42°C and VPD_{max} by 0.04 kPa during summer. Similar results have also been reported from other parts of the world (Schmidt et al., 2017). For instance, a study conducted in tropical forests of Borneo found a positive correlation between surface light (using leaf area index as a substitute) and daily temperature and VPD extremes as well as the variability in microclimatic conditions (Hardwick et al., 2015). Another analysis assessing the effect of a small gap (mean diameter 24 m) on the microclimate of European beech dominated forests confirms the strong
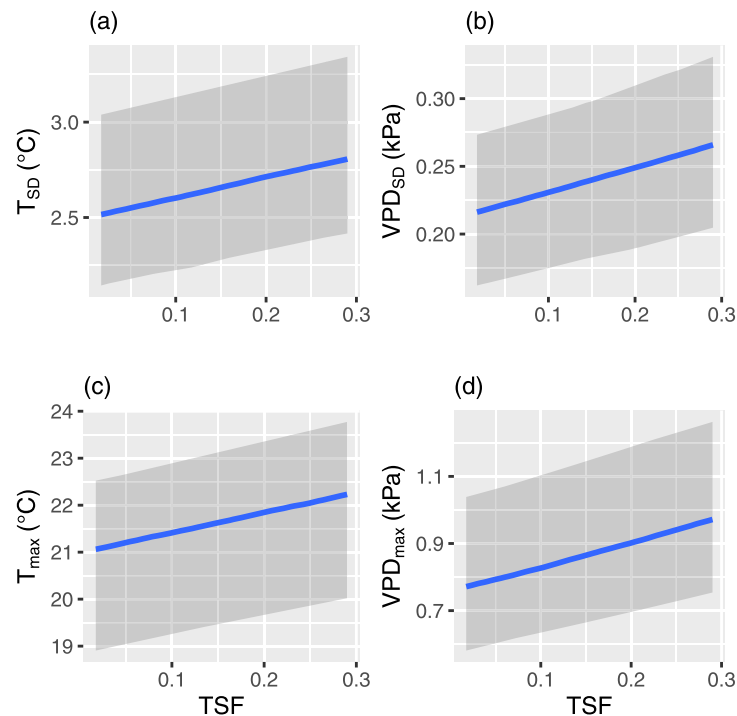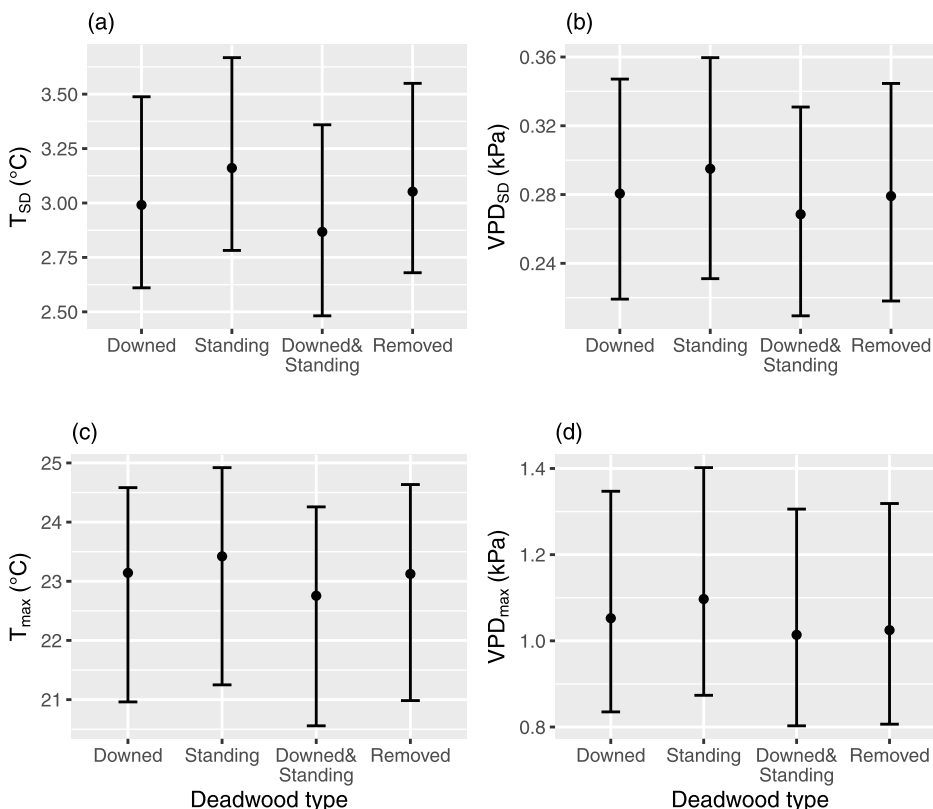
Figure 5. Effects of surface light conditions on microclimate. (a) T_{SD}: Standard deviation of daily temperature; (b) VPD_{SD}: Standard deviation of daily vapor pressure deficit; (c) T_{max}: maximum daily temperature; (d) VPD_{max}: maximum vapor pressure deficit. Shaded areas denote the 95 % credibility interval.

disturbance impact on local summer temperatures (Ritter et al., 2005). They found daily T_{max} to be increased in the gap center by up to 10°C compared to adjacent intact forests. Our study documented a linear trend between surface light and microclimatic parameters. This suggests a stand-replacing disturbance event could increase T_{max} by 4.2°C and VPD_{max} by 0.4 kPa. In addition, disturbances also affect the diurnal variation in microclimatic conditions. Microclimatic extremes and variations were positively correlated, and increased simultaneously with surface light. Interactions between microclimatic extremes and variations may amplify the effects of future disturbance regimes on forest floor vegetation, and could severely impede the recovery after disturbances (Johnstone et al., 2016).

Figure 6. Deadwood effects on microclimate. (a) T_{SD}: Standard deviation of daily temperature; (b) VPD_{SD}: Standard deviation of daily vapor pressure deficit; (c) T_{max}: maximum daily temperature; (d) VPD_{max}: maximum vapor pressure deficit. Presented are the means (dots) and 95% credibility intervals (whiskers) of microclimate parameters for each deadwood type.

The spatial patterns of disturbance had a strong modulating effect on their microclimatic impacts. At similar severities (here: basal area removed), aggregated spatial disturbance patterns caused a stronger increase in surface light, and consequently resulted in warmer and drier conditions, than distributed disturbance patterns. Thus we conclude that the influence of disturbance on forest microclimate depends on the combination of different components of the disturbance regime, such as disturbance size, severity, and frequency (cf. Turner, 2010). High disturbance severity paired with a large disturbance extent will have particularly strong impacts on forest microclimate (Baker et al., 2014; Davis et al., 2019). The combined effects of disturbance severity and size on the microclimate could be multiplicative and non-linear. Also increases in disturbance frequency will play a critical role for future microclimate, as it may take decades to recover intact forest canopies (and thus to reinstate microclimatic buffers) after disturbance (Baker et al., 2014). A limitation of our analysis is that we here only studied the initial treatment effect, and did not consider the dynamic changes in the forest canopy after disturbance. Future work should thus analyze the change in microclimatic buffering with time since disturbance, particularly since European beech invests into additional branch growth after disturbance to fill available canopy space (Bayer and Pretzsch, 2017).

Downed and standing deadwood did not notably influence the microclimatic buffering effect in our study system. Specifically, we could not detect an interaction effect between deadwood type and spatial disturbance pattern on surface light conditions. Moreover, our results did not support the hypothesis of deadwood legacies partially mitigating disturbance effects on microclimate. We found a weak indication for a positive buffering effect on microclimate on plots where both downed and standing deadwood remained after disturbance. However, this effect was very uncertain. We note that we removed the crown in topping trees to create standing deadwood in our manipulation experiment. Disturbances that do not remove all branches could provide a higher level of shading, resulting in a stronger microclimatic buffering effect. We thus suggest that disturbance effects on microclimate depend on disturbance type and agent. For instance, many biotic disturbance agents (e.g., insects and fungi) cause a protracted loss of twigs and branches, whereas abiotic disturbances (e.g., fire, wind, snow) may remove the entire canopy, and thus are likely to have a stronger impact on the forest microclimate.

4.3. Integrating considerations of microclimate into adaptive forest management

Climate change and novel disturbance regimes will increasingly challenge the sustainable supply of ecosystem services to society (Albrich et al., 2018; Duveneck and Scheller, 2015; Schröter et al., 2005). Ensuring the functional and structural recovery of forests after disturbance could be increasingly challenging, as tree recruits are very susceptible to hot and dry conditions (Anderson-Teixeira et al., 2013; E Silva et al., 2012). A central aim of future forest management is thus to mitigate the coupled impacts of changing climate and disturbance regimes (Lindner et al., 2010; Millar et al., 2007; Seidl, 2014). Based on our findings, management should aim to reduce large-scale high-severity disturbances, as these have the strongest negative impacts on microclimatic buffering in forests. Homogeneous monocultures experience these disturbances more frequently than mixed forests of higher structural complexity (Felton et al., 2016). Thus, increasing tree species and structural diversity will likely reduce disturbance size and severity, and sustain a more suitable microclimate for many forest-dwelling species. Moreover, tree species and structural diversity are highly correlated with functional diversity (Cadotte et al., 2011). Increasing functional diversity will provide ecosystems with greater flexibility to react on future changes (Aubin et al., 2016; Silva Pedro et al., 2015). For instance, enriching ecosystems with drought-tolerant species will support forest regeneration after disturbance (O'Brien et al.,

2017), and thus facilitates the establishment of a suitable microclimate for species with lower drought tolerance. Strategies to reduce disturbances and their effects on ecosystems should also account for landscape heterogeneity. A central European study has shown that disturbance risk and management effectiveness to reduce disturbances can differ considerably within a landscape (Seidl et al., 2018). Thus, strategies to avoid canopy disturbances should be adapted locally. For instance, managing for deep rooting tree species at wind exposed sites can lower disturbance predisposition considerably (Mitchell, 2013).

In addition to managing natural disturbances tree harvesting should not create large canopy openings in order to retain the microclimatic buffering effect for the regenerating tree cohort. Forest management practices that maintain a continuous canopy cover are likely better able to prevent regeneration from drought stress and heat than clear-cut systems (Hlásny et al., 2014). For instance, the ecosystem-based silvicultural systems that have been developed in recent years (Puettmann et al., 2015) are likely to sustain suitable microclimate conditions for regeneration. In particular, single-tree selection systems minimize harvesting effects on the forest microclimate. If gaps are cut into forests in drought-prone regions, their direction should be considered to reduce surface light. An east-west facing gap (e.g., in the form of an ellipse that is long from east to west, but narrow from north to south) is better sheltered from the sun by surrounding trees than a comparable gap in north-south direction. Accounting for gap direction is particularly important for south-exposed slopes in the northern hemisphere (north-exposed slopes in the southern hemisphere), where canopy openings alter surface light conditions, and thus the microclimate, most strongly.

Fostering specific forest types is another potential strategy to improve the microclimate. Broadleaf-dominated forests generally have a higher evaporative cooling effect than conifer-dominated forests of similar stand age in central Europe (Schume et al., 2004; Thom et al., 2017), which is, *inter alia*, related to differences in leaf area and hydraulic architecture between conifers and broadleaves (Oksanen et al., 2018). For instance, in single-canopy, mature forests in Austria, the evapotranspiration rate of European beech-dominated stands is up to 84 % higher than of Norway spruce-dominated stands (Schume et al., 2004). Depending on water availability, management should thus aim for a high share of broadleaved trees to buffer the effects of climatic extremes in summer. Further, microclimate varies with forest development stages. Norris et al. (2012) showed that biomass-rich, cool temperate old-growth forests in Germany, Ukraine, and the UK attenuate temperature more efficiently than young and mature plantation forests of similar species composition. Hence, managing forest structure for late-development conditions may provide another option to buffer future climate change. In recent decades, silvicultural methods have been developed to create old-growth forest structures early in stand development (Bauhus et al., 2009; Keeton, 2006). These approaches could be beneficial for the microclimate, while fostering biodiversity and ecosystem services at the same time (Ford and Keeton, 2017; Franklin et al., 2002). However, if climate conditions of European cool temperature forests become increasingly Mediterranean, evaporative cooling may even decrease with stand development. Delzon and Loustau, 2005 found a decrease in evapotranspiration in even-aged maritime pine (*Pinus pinaster* Ait.) stands, driven by drought-related decreases in leaf area and canopy conductance. In conclusion, managing microclimatic buffering has the potential to partially offset negative consequences of climate change, but strategies to improve the microclimate need to be adapted locally considering the specific stand and site conditions.

Declaration of Competing Interests

None.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108066.

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