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Residual canopy cover provides buffering of near-surface temperatures, but benefits are limited under extreme conditions

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Abstract

Increasing summer temperatures and higher probabilities of extreme heat events have led to concerns about tree damage and mortality. However, insufficient attention has been given to conditions leading to heat-related regeneration failures in temperate forests. To address this, managers need to understand how microclimate varies under a range of overstory conditions. We measured air temperatures at 2 cm above-ground underneath a gradient of canopy cover on south-facing slopes in recently thinned Douglas-fir stands in western Oregon, USA. To expand the ecological relevance of these data to impacts on regeneration, we created the stress degree hours (SDH) metric, representing the amount of time—and by how much—temperatures exceeded biologically relevant stress thresholds. Overall, for every 10% increase in canopy cover, maximum temperatures at 2 cm were 1.3 °C lower, the odds of temperatures exceeding stress thresholds for conifer regeneration declined by a multiplicative factor of 0.26, and the total of SDH decreased by 40%. These reductions are large enough to be worthy of attention when managing for tree regeneration. However, data collected during the Pacific Northwest Heat Dome in June 2021 indicate that with various climate change scenarios and heatwave occurrences, temperatures will be unfavorable for regeneration regardless of overstory cover.

Key words: heatwave, microclimate, regeneration, thinning, climate change, forest management

1. Introduction

Trends of higher summer air temperatures have led to increasing concerns about a loss of tree vigor and mortality (Adams et al. 2017; Hammond et al. 2022). Over the last decade, it became evident that much of the tree mortality in selected regions was due to a combination of drought and high temperatures (Yi et al. 2022), whereby the temperatures lead to higher evaporative demand (Grossiord et al. 2020) and additional direct heat damage to cellular processes (Geange et al. 2021). Furthermore, higher probabilities of extreme events (Puettmann 2021; Hammond et al. 2022), such as the recent extreme heat event ("Heat Dome") in the US Pacific Northwest (PNW) and British Columbia in 2021, led to additional concerns of widespread leaf damage when temperatures exceeded critical thresholds (Doughty et al. 2023; Still et al. 2023). The alarming effects of hotter average conditions as well as extreme heat events on forest health have already been documented for a range of forest types (Adams et al. 2017; Hammond et al. 2022). Given future climate predictions, scientists and managers continue to explore opportunities to increase individual tree and forest level resilience to a hotter and more extreme climate.

Silviculture has a long history of using density management approaches to maintain and increase tree vigor as well as protect trees and stands from pests, pathogens, and damage from weather events such as strong winds (Chmura et al. 2011; Park et al. 2014). As global change emerged as a major threat to forests, these same principles have been used for climate change adaptation. In the past, thinning has primarily been used to improve growth of residual trees. Recently, the focus has shifted from solely promoting growth to also increasing resilience to drought and hotter temperatures (Halofsky et al. 2016; Bottero et al. 2017). Much of this shift has focused on mature trees (Sohn et al. 2016) with less attention on methods to protect or promote tree regeneration (Walck et al. 2011) and understory development (Christiansen et al. 2022) under climate change, even though regeneration failures have increasingly become an issue of interest for foresters (Dey et al. 2019), especially on drier sites (Dodson and Root 2013; Boucher et al. 2020) and whole regions (Petrie et al. 2023; Crockett and Hurteau 2024). There has also been growing interest in natural regeneration due to its inherent variability and potential to aid in the development of heterogenous stand conditions associated with late successional forests (Donato et al. 2012). Because of the different sensitivities between seedlings and larger trees (Rollinson et al. 2021), a better understanding of the ability of silvicultural actions to mitigate the effects of climate change on regeneration is needed to address concerns of regeneration failures (Dey et al. 2019; Rollinson et al. 2021) and meet multiple objectives, including creating late successional forest conditions.

The general impact of topography (Scherrer and Körner 2011; Meineri et al. 2015) and forest canopy cover (De Frenne et al. 2019) on microclimate conditions in the understory is well documented in the context of microrefugia and their impacts under normal and extreme climate conditions (Finocchiaro et al. 2024). Forest management practices have capitalized on the buffering capacity of stand structure for decades by implementing a variety of silvicultural practices. For example, shelterwood and uneven-aged silvicultural systems have long been used to modify microclimate and provide suitable conditions for seedling growth and survival through retention of overstory trees (Ashton and Kelty 2018; Palik et al. 2020), both in areas with potentially damaging summer temperatures (Childs et al. 1985; but see Valigura and Messina 1994) and areas where frost is likely to damage tree seedlings (Granberg et al. 1993; Holgén and Hånell 2000; Langvall and Ottosson Löfvenius 2002). The physical drivers of the relationship between forest canopy cover and microclimate conditions in the understory are well understood (Geiger et al. 1995; Campbell and Norman 1998), including modifying processes such as interception and attenuation of incident solar radiation, air mixing, precipitation interception and throughfall, windspeed, and humidity (Geiger et al. 1995; Kovács et al. 2017). Recently, there has been growing interest in gaining a deeper understanding on the effects of different forest management actions on microclimate conditions and the implications for regeneration and understory composition (De Frenne et al. 2013).

Studies have confirmed the importance of the fine scale-variation in microclimate on seedling establishment and tree recruitment, and in the context of climate change, this issue is gaining more attention (Halpern et al. 2012; Peck et al. 2012; Swanson et al. 2023). Larger regional variation in atmospheric processes is also a main driver of microclimate conditions and can affect the relative influence of canopy cover (Finocchiaro et al. 2024). Extreme heat events such as the Pacific Northwest June 2021 Heat Dome may overwhelm the ability of canopy cover to reduce heat stress in the understory. Areas with increases in wildfire smoke in the atmosphere may also impact this relationship by absorbing and scattering incoming solar radiation at global (Tosca et al. 2013), regional, and local scales (Price et al. 2016) as well as impacting stream temperatures (David et al. 2018). To facilitate forest management in a variety of settings in a rapidly warming world, we need to understand how microclimate conditions in forest understories change across a gradient of partial overstory cover, whether the specific location of the overstory canopy in relation to solar angle affects the microclimate, how regional conditions affect microclimate relative to canopy cover, and how the conditions relate to relevant ecological processes, such as regeneration. To gain such understanding, we set up a study with the following objectives:

1. Determine the effect of varying amounts and spatial arrangements of canopy cover on summer maximum near-surface temperatures.
2. Use previously established heat stress responses of seedlings from laboratory studies to assess potential temperature-induced stress to conifer seedlings and germinating seeds under varying overstory canopy cover conditions.
3. Describe how future climate conditions, including heat waves and wildfire smoke, may affect the influence of canopy cover on understory temperatures.

By sampling across a gradient of canopy cover, our findings can be used to inform decisions regarding a variety of density management practices, including treatments that result in higher spatial variability in residual tree density (Puettmann et al. 2009; Palik et al. 2020). Thus, our findings are relevant for a wide variety of conditions, including homogenous thinning prescriptions in even-aged stands, as well as variable density treatments designed to achieve a variety of objectives (Puettmann et al. 2016; Franklin and Donato 2020).

2. Materials and methods

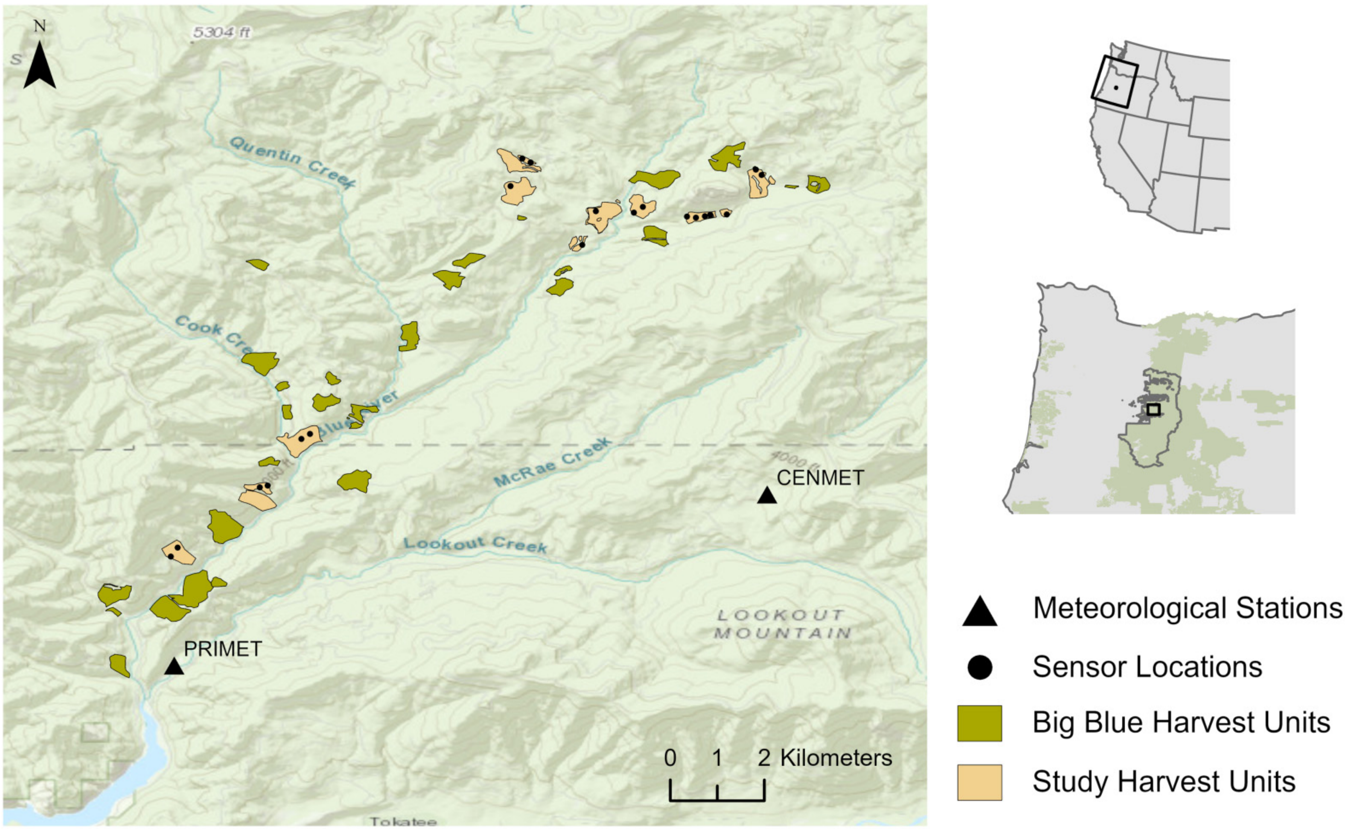
2.1. Study area

This study was conducted in 11 stands (<15 km apart) in the Big Blue Project area in the Upper Blue River Watershed on the Willamette National Forest in western Oregon (Fig. 1). The Big Blue Project area was selected due to the similarity in conditions (slope, aspect, stand histories, and conditions), the proximity to the meteorological stations at the H.J. Andrews Experimental Forest, availability of recent LIDAR data (2020), and because several stands in this area were recently commercially thinned (<5 years prior), which resulted in a variety of overstory densities and canopy covers and minimal understory vegetation. The U.S. Forest Service plant association for this area is Pseudotsuga menziesii/Acer circinatum–Berberis nervosa (Douglas-fir/vine maple–Oregon grape) (Dyrness et al. 1974).

All study sites are covered by approximately 50-year-old even-aged monoculture Douglas-fir plantations that were recently thinned. Within stands, the post-thinning tree spacing was targeted to be homogenous. However, variability in microsites, past conditions, and initial spatial arrangement of trees growing in operational settings resulted variable spatial arrangements at smaller scales. Among stands, the prescribed minimum spacing between trees post-thinning varied from 4 to 6 m (USDA Forest Service 2009 (Table S4). Similar prescriptions in these types of stands have shown to result in establishment of more and vigorous understory vegetation, including tree regeneration (Beggs et al. 2005; Kuehne and Puettmann 2008; Puettmann et al. 2016). For more detail on stand conditions and thinning prescription, see Supplementary material.

The study sites ranged in elevation from 630 to 1086 m. The mean monthly temperatures for this area ranged from 2.6 °C in January to 19.3 °C in July and annual precipitation averages 2.17 m based on 30-year normal data from 1991–2020

Fig. 1. Overall location of the study area within Oregon and locations of the 20 sensors within 11 harvest units that were part of the larger Big Blue Project area, and Primary Meteorological Station (PRIMET) and Central Meteorological Station (CENMET) meteorological stations (USDA Forest Service 2009; ESRI 2021). Figure was created using ArcGIS Pro 3.1.3 and assembled from the following data sources: USDA Forest Service, H.J. Andrews Experimental Forest, and LTER site. Base map from ESRI courtesy of Linn County, Bureau of Land Management, State of Oregon, State of Oregon DOT, State of Oregon GEO, Esri Canada, Esri, HERE, Garmin, USGS, NGA, EPA, USDA, and NPS.



(PRISM Climate Group 2022). This area is also characterized by highly seasonal precipitation and a mostly dry growing season. During this study, conducted from 29 June 2021–25 September 2021, the mean daily near-surface air temperature ranged from 11.3 to 22.2 °C at the Primary Meteorological Station (PRIMET) of the H.J. Andrews Experimental Forest (located at 430 m elevation approximately 6.5 km south of the study sites) (Daly and McKee n.d.). The study area experienced an unprecedented heat wave ("Heat Dome") between 25 June and 3 July 2021, with maximum air temperatures at 1.5 m reaching 46 °C, as well as several subsequent smaller heat waves with maximum air temperatures ranging from 38 to 40.5 °C. During the Heat Dome event, maximum near-surface temperatures at our study sites was 44.1 °C on average and the absolute maximum temperature recorded was 57.4 °C. In upper tree canopies at the Andrews Forest, foliar temperatures exceeded 50 °C and stayed above 40 °C for at least 26 h (Still et al. 2023).

The study area was also heavily impacted by smoke in early and mid-August of 2021 due to the Middle Fork Complex and Washington Ponds Fires. While these events complicate the interpretation of our data, such conditions may be indicative of future climate conditions of this area given the predicted increase in duration and severity of heatwaves (Mazdiyasni and AghaKouchak 2015) and large wildfires (Abatzoglou 2013). This event allowed us to quantify the impacts of wildfire smoke on near-surface air temperatures as an illustrative example for the future.

2.2. Study design

To capture the microclimate conditions at locations relevant to germinating seeds and young seedlings, we used Tomst TMS-4 temperature sensors (Wild et al. 2019), which capture climate and soil moisture conditions near ground level. These sensors also had a small radiation shield installed (Wild et al. 2019). For this study, we only used the air temperature measured at 2 cm above ground, since this height is heavily influenced by the soil surface temperature and reasonably represents the climate experienced by newly germinated and very young seedlings, which are the life stages most susceptible to heat damage (Bell et al. 2014).

We installed TMS-4 sensors at 20 locations (1 sensor per location) in 11 different stands with specific locations selected by a stratified random sample and nested design. Sampling was stratified by levels of overstory canopy cover. The range of each level was 10% canopy cover, resulting in seven levels from 15% to 85%. There were three sensors per level apart from the 46%–55% level containing four sensors and the 75%–85% level with only one sensor. This was done to ensure that the full range of canopy cover was sampled while accounting for the larger variability in conditions at the mid-levels compared to higher canopy cover (Table S1). Slope, aspect, and elevation also affect the potential direct incident radiation and therefore the microclimate conditions, but we did not have sufficient resources to cover all those gradient combinations and thus focused on a restricted set of conditions. Sites were nested within stands and limited to slopes of less than 25 degrees, with a southern aspect (S or SW), and between 600 and 1100 m of elevation. South- or southwest-facing slopes were chosen because they receive the highest amount of incident radiation in the Northern Hemisphere and are therefore more likely to be warmest and have the most limiting microclimates for tree regeneration. Mid-slope positions were chosen to limit the effect of cold-air drainages or hill-shade. See Table S1 for additional site-specific information.

One hundred potential sensor locations within areas with the target topographic conditions were randomly generated and stratified by canopy cover within a GIS. Each of the potential locations were randomly assigned a priority level of 1–5 such that each priority level contained the full range of canopy cover conditions. Levels 2–5 were backup locations and were only used if the level 1 site was determined to be unsuitable in the field due to excessive slash, microtopography conditions such as seeps, or other factors that might have affected the near-surface temperature other than canopy cover and therefore might have biased the results. To limit spatial autocorrelation in relation to microclimate variables, the minimum distance between sites was 100 m (Chen et al. 1995; Baker et al. 2016). The stratified sampling design resulted in 20 sensor locations in 11 different stands. Apart from one stand (Big B 660), which had four, there were only one or two sensors per stand, as the focus of this study was to examine microclimate conditions across a gradient of overstory cover and not within-stand microclimate variability.

2.3. Temperature data processing

Our primary interest was to understand how canopy cover influences air temperatures in understory conditions in the context of tree regeneration. Specifically, we were interested in differences in daily maximum air temperatures and relating those conditions to potential seedling/germinating seed stress. We summarized the data to weekly averages of daily maxima air temperature (°C). To estimate the impact of heat on seedling stress, we used a novel application of the degree-day concept: stress degree hours (SDH). Instead of calculating the accumulation of heating units above a minimum threshold that reflects physiological processes and the initiation of plant growth, we used a high temperature threshold above which photosynthetic damage typically occurs in tree seedlings and calculated the accumulation of heating units above this threshold over time (Baskerville and Emin 1969). The base temperature in these calculations (40 °C) was derived from photosynthetic responses of Douglas-fir seedlings exposed to simulated heatwaves of temperatures from 25 to 61 °C (Marias et al. 2017). We calculated weekly averages of daily accumulated SDH by subtracting 40 °C from hourly average temperatures. Negative values were reassigned to 0, and the positive values were summed to a daily accumulation. The daily accumulation of SDH was then averaged for each week (Cook et al. 2024). The last 2 weeks of the study (14–28 September) were removed since temperatures were significantly cooler due to changing seasons and seedlings were not stressed based on our definition. The resulting metric used in our analysis was the weekly average of daily accumulated SDH. It represents a combination of the number of hours over 40 °C, as well as how much higher than 40 °C the hourly average temperature was during these periods.

2.4. Calculating explanatory variables

To investigate our primary objectives, canopy cover was measured using two different approaches. First, we used canopy closure values from convex spherical densiometer measurements, which integrate across the sky ignoring the azimuth to represent total canopy cover (referred to as 360° measurement in tables and figures). This was selected as it was a simple method that foresters can apply easily in the field. Second, to examine the effect of direct shading and sun flecks due to canopy gaps and the orientation of canopy cover relative to the sun position, we used LiDAR data from a June 2020 flight to isolate the canopy cover that shades the sensor based on time of day, solar angle and azimuth, aspect, slope, and average tree height (Fig. S1). For this, we quantified canopy cover that provided shade during three time periods, from 9 am to 12 pm, from 12 pm to 3 pm, and from 9 am to 3 pm. This resulted in four canopy cover variables: one 360° field measurement using a densiometer and the three LiDAR-derived metrics (Table 1).

Additional explanatory variables that varied by sensor location included heat load and elevation. Heat load was calculated following McCune (2007) using latitude, slope, and aspect of each sensor location to represent the potential incoming solar radiation at each sensor in the absence of canopy cover and assuming clear skies. Elevation was determined using the digital elevation model from LiDAR. The weekly average of the daily maximum air temperature from Central Meteorological Station (CENMET) at the H.J. Andrews Experimental Forest was included in the models to account for regional climate conditions and autocorrelation among weeks (Daly and McKee n.d.).

In the initial model fitting temporal autocorrelation was not accounted for by using a correlation structure, indicating the variables in the models did not sufficiently explain the trend through time. We hypothesized that this was due to the timing of nearby wildfires, as the study area was impacted by smoke throughout most of August. Smoke and high particulate concentrations in the air increases scattering of incoming solar radiation and decreases the amount of direct radiation on the sensor (Rastogi et al. 2022). Since the TMS-4 only had a small radiation shield, this change in conditions likely affected the temperature recorded by the sensor, especially the maximum daily temperature. Additionally, temper-

Table 1. Model parameters of the three different model types and 12 models fit in the analysis to address the two objectives.

Objective	Response variable	Model type	Canopy cover	Continuous fixed effects	Random effects
1	Weekly average daily maximum	Linear mixed model with AR1 correlation structure	360° AM PM AM + PM	1. Canopy cover (%) 2. Open air temperature (°C) 3. Elevation (m) 4. Heat load 5. Weekly average daily accumulation of incoming shortwave radiation (J/m^2/week)	Sensor nested in harvest unit
2	Presence/absence of stress degree hours	Binomial generalized linear mixed model with logit link	360° AM PM AM + PM		
2	Log of weekly average daily accumulation of stress degree hours	Linear mixed model with log transformation and AR1 correlation structure	360° AM PM AM + PM		

Note: Each model type had four individual models with the same response variable. These four models only differed in which measurement of canopy cover was used (360° measurement from spherical densiometer and three LiDAR-derived canopy cover estimates for different time periods). AM time period corresponds to shade from 9 am to 12 pm, PM time period corresponds to shade from 12 pm–3 pm, and AM + PM is 9 am to. Refer to Fig. S1 for how these variables were calculated. For each response variable, weather station screen height air temperature used in the models was summarized to match the response variable.

ature at 2 cm is heavily influenced by the radiative heating of the soil surface and was likely impacted by changes in direct radiation (Campbell and Norman 1998). Consequently, we included the weekly average daily accumulation of incoming shortwave radiation (J/m^2/day) measured at CENMET to account for the reduction in shortwave radiation due to wildfire smoke and subsequently the temporal autocorrelation. Although heat load and incoming shortwave radiation represent the amount of solar radiation received, both variables were included in the analysis since heat load accounted for site differences, while measured incoming shortwave radiation accounted for differences through time and the impact of smoke. See Tables S1 and S2 for additional information on how the variables varied by sensor location and week.

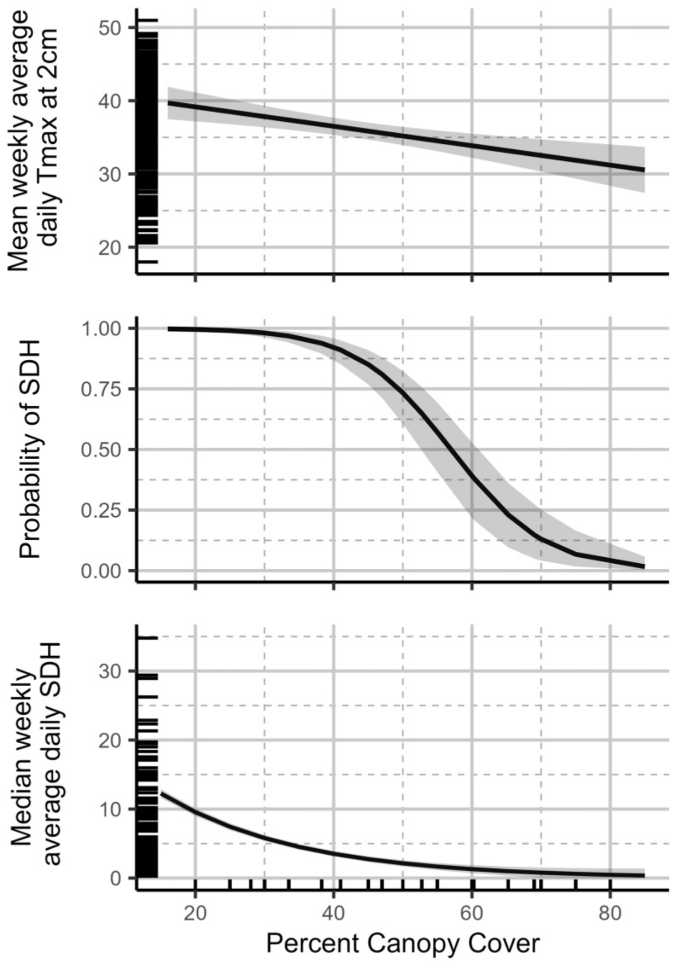
2.5. Statistical analysis

To develop an understanding of the relationship between canopy cover and maximum near-surface temperatures, we used weekly average daily maximum temperature (°C) at 2 cm above the ground as the response variable in four linear mixed models. These models used canopy cover, CENMET weather station 1.5 m screen height air temperature, elevation, heat load, and incoming shortwave radiation as continuous explanatory variables, with sensor location nested in harvest unit as a random effect. Each of the four models used a different canopy cover measurement described above and in Table 1. To avoid overfitting due to the relatively small number of sites, we limited the number of explanatory variables in the models. To account for this and still test whether average canopy cover from the densiometer or the LiDAR-derived canopy cover measurements better explain near-surface air temperature, we used a model comparison approach.

All linear mixed models were extended to allow for among-week correlations of the errors within sensor locations nested in harvest unit using an autoregressive correlation of lag 1 (AR1). This correlation structure estimated a single correlation used to describe how errors within weeks become less similar with increasing time between measurements. Assumptions of constant variance and normality of errors for each model were assessed visually using plots of the normalized residuals (Fig. S2). No problems were noted. Sensor locations were assumed to be independent of each other due to the minimum intersampling distance of 100 m (Chen et al. 1995; Baker et al. 2016). Harvest unit was included in the models as a random effect to account for any within unit spatial autocorrelation (distance between sensors in different harvest units was >1 km). Delta Akaike's corrected information criteria values (ΔAICc) were used to compare evidence for model support following Burnham et al. (2011) where a ΔAICc value less than 7 indicates no difference in model support. Pseudo R^2 were calculated following Efron (1978) and regression coefficients were also used to interpret model fit and the relationship between each response variable and the four canopy cover measurements (Fig. 2).

To assess the likelihood and amount of temperature-induced stress that seedlings and germinating seeds may experience, we used a hurdle model approach. This was necessary given that SDH calculations resulted in positive continuous data with a point mass at zero, which make fitting a single statistical model difficult and prone to bias (Brooks et al. 2017). The hurdle model consisted of two models: one to examine whether the threshold for SDH accumulation (>40 °C for 1 h) was passed and another to examine the amount of SDH accumulation (positive values only) (Table 1). For the first model, the SDH weekly average daily accumulation was transformed into a binary variable with values of 1 for weeks above 0.25 SDH and 0 for weeks below 0.25 SDH. These small values of SDH (<0.25) negatively affected the interpretability of the second component of the hurdle model. Given the accuracy level of the sensor (0.5 °C) (Wild et al. 2019), we determined that values less than 0.25 were not different than zero. From a plant physiological perspective, these small values are negligible (Marias et al. 2017), thus setting the values to zero allowed for increased interpretability of the results while keeping the variables tied to plant physiological principles.

Fig. 2. Estimated relationship and associated 95% confidence intervals between the three response variables and canopy cover. To isolate the effect of canopy cover, all other fixed effects (see Table 1) were held at their observed median values. SDH, stress degree hours.



This binary variable of presence or absence of SDH, which represented whether a biologically relevant amount of stress (SDH > 0.25) accumulated, was used as the response variable in four binomial generalized linear mixed models using a logit link (also referred to as logistic regression). This type of model was chosen because of the ability to estimate the probability of an event (SDH accumulation) occurring and because binomial distributions were appropriate for presence/absence data. Standardized continuous explanatory variables of canopy cover, open air temperature, elevation, heat load, and incoming shortwave radiation and a random effect of sensor nested in harvest unit were also included in the models (Table 1). The continuous fixed effects were standardized by subtracting the mean from each value and dividing by the standard deviation to accommodate for the difference in scales between variables. Plots of simulated residuals relative to fitted values were examined and no unusual patterns or overdispersion were noted (Fig. S2).

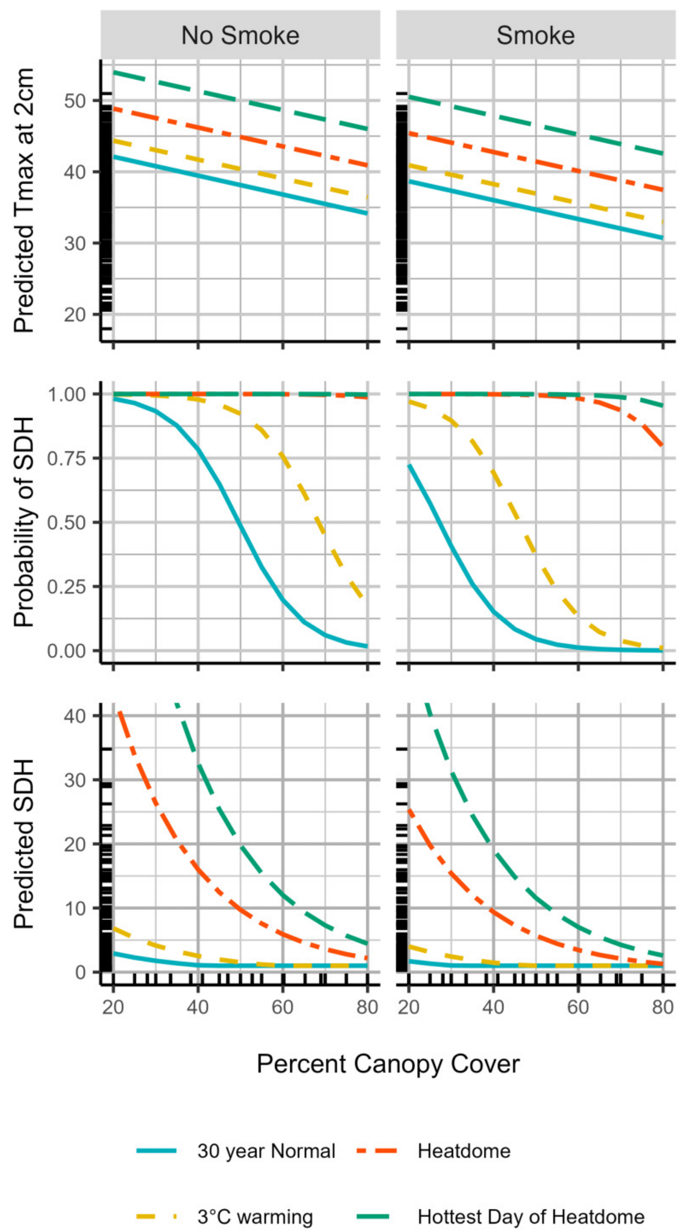
In the second component of the hurdle model, the weekly average daily accumulation of SDH for weeks when the average was greater than 0.25 was log transformed and used as a response variable in a family of four linear mixed models with the same fixed and random effects as previous models (Table 1). Based on a graphical assessment of residual plots, a natural logarithm transformation of weekly average daily accumulation of SDH adequately stabilized the variance and residuals were sufficiently symmetric and approximately normal (Fig. S2). The ΔAICc, pseudo R^2, and coefficients were used to interpret model support and fit and the relationships between each response variable, and the four canopy cover measurements. Pseudo R^2 was calculated following Nakagawa and Schielzeth (2013). The nlme package was used to fit the linear mixed models (Pinheiro et al. 2022) and the lme4 package was used to fit the binomial generalized linear mixed models (Bates et al. 2015). Analyses were done with R version 4.1.2 (2021) (R Core Team 2021).

To portray how these relationships are biologically relevant under varying regional climate scenarios (objective 3), the models containing canopy cover measured with a densiometer were used to describe the relationship between canopy cover and the three response variables (weekly average daily maximum temperature, presence of SDH, and accumulation of SDH) under four different climate scenarios: 30-year normal, 3 °C of warming added to the normals, the daytime average conditions during the June 2021 Heat Dome, and the average air temperature during the hottest day of the Heat Dome (Fig. 3). For all scenarios a prediction dataset was created using the models developed in objectives 1 and 2 (See Supplement for more details). These 24 prediction datasets (3 response variables, 4 climate change scenarios, 2 smoke conditions) were then used to predict maximum temperature, probability of SDH accumulation, and the amount of SDH accumulation across the range of canopy cover for each scenario.

3. Results

The study results demonstrate that—after accounting for the influences of topography—canopy cover reduces near-surface temperatures. We found a reduction in maximum (and mean temperatures) in the understory with increasing canopy cover (Fig. 2). The model comparison results suggest that accounting for the specific location of trees that provide shade did not improve the ability to predict the impact of canopy cover in reducing near-ground temperatures (Table 2). Low ΔAICc values (<7) for models used to address objective 1 suggest that there is no difference in support among all models (Burnham et al. 2011), suggesting that the method used to collect canopy cover (i.e., LiDAR versus densiometer-derived data) did not influence model support. However, the model containing densiometer canopy cover better predicts the mean weekly average daily maximum air temperature at 2 cm, as indicated by a slightly higher pseudo R^2 (0.82) (Table 2). Thus, the selected model used weekly average daily maximum air temperature as a response with fixed effects of densiometer-derived canopy cover, open air temperature at 1.5 m, elevation, heat load, and weekly average daily accumulation of incoming shortwave radia-

Fig. 3. Estimated relationships between the three response variables and canopy cover, as measured by densiometer, for four different climate scenarios and the presence/absence of smoke. Fitted lines were plotted using a prediction dataset where all elevations and heat loads were held at their observed median. For each climate scenario open-air temperature was held at the associated temperature. To account for the effect of smoke incoming, shortwave radiation was held at the value for the week of 27 July without the presence of smoke and the smoke used the value from the week of 3 August (see Table S2 for weekly values of each variable). SDH, stress degree hours.



tion and sensor location nested in harvest unit as a random effect.

Similarly, the results indicate that any stress, as quantified by SDH, that seedlings may experience due to heat is not influenced by the orientation of cover relative to solar position of the shading trees. The ΔAICc (7.4) for the first component of the hurdle model suggested there was no difference in support for any individual model in estimating the probability of SDH accumulation (Table 2). As with the analysis of temperature reductions due to overstory canopy cover, utilizing data collected with a densiometer for assessment of stress appears to be just as valid as using LiDAR data, which is much more challenging to collect and use. The pseudo R^2 for the model with densiometer-based measurement data was slightly higher (0.72) (Table 2). In regard to the amount of SDH accumulation, the second component of the hurdle model, the model containing the densiometer measurement was better supported by the data than the LiDAR-based measurements (ΔAICc 14.48). The difference in pseudo R^2 between models is also larger for this comparison (Table 2).

Based on these results, we quantified the impact of residual trees in terms of mediating high temperature conditions using the models containing the densiometer (360°) measurement. After accounting for elevation, heat load, incoming shortwave radiation, and regional, i.e., weather station screen air temperature at 1.5 m, every 10% increase in canopy cover (measured using a densiometer) was predicted to decrease the mean weekly average daily maximum at 2 cm by 1.3 °C (95% CI 0.4–2.2 °C), the odds of accumulating SDH by a factor 0.26 (95% CI 0.06–0.59), and the median weekly average daily accumulation of SDH by 40% (95% CI 20%–55%) (Table 3; Fig. 2). These results are based on the range of temperatures observed during the summer of 2021, which, as mentioned above, was hotter than normal. See Table S5 for estimates for elevation and heat load index.

The results can also be used to quantify how higher canopy cover led to lower potential for heat stress in vegetation near the ground under current conditions. The relationship between the probability of accumulating stress and canopy cover indicated that on south-facing slopes, maintaining at least 60% canopy cover under normal temperature regimes may avoid temperature stress for seedlings. In stands with higher canopy cover plant stress in the understory is less likely (probability of stress) and less intense (accumulation of stress hours). Distinguishing the probability and absolute amount of stress provides additional insights. For example, in stands with 40% canopy cover the probability of SDH is much higher than at 60% cover but the median average daily accumulation only 4 SDH (Fig. 3). The high probability, but low amounts of SDH in such stands, indicates that the temperature buffering as experienced by seedlings may be quite substantial in terms of reducing heat stress.

Simulations of potential future climates indicated that under 3 °C of warming of average summertime temperatures and during extreme events, such as the 2021 Heat Dome, the buffering effect of canopy cover was not strong enough to prevent temperatures at 2 cm from crossing the biologically relevant 40 °C threshold even at high canopy cover (Fig. 3). However, the presence of wildfire smoke during the study period resulted in lower near-surface temperatures, suggesting additional buffering effects. The smoke impact on the near-surface temperature maxima (and means) was similar

Table 2. Results of model comparison using ΔAICc and pseudo R^2 to evaluate which model and associated canopy cover variable better predicted each of the three response variables.

Objective	Response variable	Model type	Canopy cover	AICc	ΔAIC	Pseudo R^2
1	Weekly average daily maximum	Linear mixed model with AR1 correlation structure	**360°**	**1084.67**	**0.00**	**0.82**
			AM + PM	1086.15	1.48	0.76
			AM	1088.38	3.71	0.74
			PM	1091.72	7.05	0.76
2	Presence/absence of stress degree hours	Binomial generalized linear mixed model with logit link	**360°**	**146.59**	**0.00**	**0.72**
			AM + PM	153.33	6.74	0.62
			AM	153.72	7.13	0.62
			PM	154.01	7.42	0.62
2	Log of weekly average daily accumulation of stress degree hours	Linear mixed model with log transformation and AR1 correlation structure	**360°**	**339.85**	**0.00**	**0.50**
			AM + PM	353.26	13.44	0.26
			AM	353.52	13.67	0.25
			PM	353.95	14.09	0.17

Note: The model with the lowest ΔAIC was then used (in bold). For each of the three response variables, this was the 360° measurement from a convex spherical densiometer.

Table 3. Estimates and 95% confidence intervals for relationships between the three response variables (weekly average daily maximum, presence/absence of SDH, and amount of SDH accumulated) associated with the two objectives.

Objective		Model type	Canopy cover	Lower 95% CI	Estimate	Upper 95% CI
1	Change in mean weekly average daily maximum temperature at 2 cm for 10 % change in canopy cover	Linear mixed model with AR1 correlation structure	**360°**	**0.41**	**1.32**	**2.24**
			AM + PM	0.48	1.25	2.03
			AM	0.26	0.95	1.63
			PM	0.08	0.64	1.20
2	Factor for the multiplicative change in odds of accumulation of SDH for a 10% change in canopy cover	Binomial generalized linear mixed model with logit link	**360°**	**0.07**	**0.26**	**0.62**
			AM + PM	0.12	0.48	1.48
			AM	0.13	0.53	1.51
			PM	0.27	0.65	1.59
2	Factor for the multiplicative change in median weekly average daily accumulation of SDH for a 10% change in canopy cover	Linear mixed model with log transformation and AR1 correlation structure	**360°**	**0.46**	**0.61**	**0.81**
			AM + PM	0.68	0.96	1.36
			AM	0.70	0.91	1.18
			PM	0.84	1.06	1.33

Note: Objective column connects estimates to hypotheses and provides context to which relationship the estimate applied to. For the binomial GLMM estimates and confidence intervals were exponentiated from the link scale (log odds) to the odds scale.

to the temperature reduction caused by an increase of 15% in canopy cover (Brackett et al. 2022).

4. Discussion

This study confirmed the large role of overstory trees in influencing the understory temperature regime in stands without much understory vegetation (Rambo and North 2009). It demonstrated that greater canopy cover resulted in reductions of maximum temperatures and heat-related stress levels that were sufficiently large to be ecologically relevant to tree germinating seeds and other understory plants (Jansen et al. 2014; Marias et al. 2017). However, under climate change and heatwave scenarios, conditions on south-facing slopes in our study region will likely be unfavorable for regeneration. The spatial variability in conditions (Macek et al. 2019) as well as variability in species and individual responses to heat and moisture stress (Marias et al. 2017; Guha et al. 2018) indicate that while growth and survival rates may decline, large-scale regeneration failure is still unlikely in this region (De Lombaerde et al. 2022). Forest managers whose goal is to create structural diversity through lower stand densities and understory regeneration will need to develop decision and risk analysis tools that can incorporate the buffering capacity of higher tree cover and topography to create sufficient spatial variability in microclimate conditions for regeneration success to occur at the stand and landscape level. We also found that the presence of wildfire smoke reduced near-surface temperatures. The reduction in radiative heating as particles in wildfire smoke reflect and absorb incoming solar radiation (Stone et al. 2011), apparently reduced temperature near the soil surface.

Our study documented the buffering effect of canopy cover in regard to high temperatures and specific biological relevance by sampling near the soil surface, where seedlings and germinating seeds are most sensitive to heat (Harper 1977;

Rollinson et al. 2021). The low sensor height of 2 cm above ground made direct comparison of our results with those of other studies difficult. At first glance, the 1.3 °C decrease in maximum temperatures for every 10% increase in canopy cover found in this study is larger than effects found in most other studies. For example, in western Washington, conditions at 1 m above ground show only a reduction of approximately 4 °C under an unthinned control (90% canopy cover) and ∼50% canopy cover (Heithecker and Halpern 2006). The current results suggest a difference of 5.2 °C in near-surface temperatures for the same canopy cover difference. This discrepancy was partially due to the differences in sampling height (2 cm vs 1–2 m), as large air temperature gradients commonly occur in the first few meters above the soil surface, and our sampling was limited to south-facing aspects only (Geiger et al. 1995). Other studies found maximum air temperatures to be lower under closed canopy versus stands thinned to various degrees or canopy gaps anywhere from 0.6 to 5 °C, measured between 1 and 5 m above ground (Heithecker and Halpern 2006; Kovács et al. 2020). Additionally, studies that examined the effect of thinning and shelterwood treatment on soil temperatures at 20 mm below ground found a larger difference of ∼7 °C between controls and treatments (Childs et al. 1985; Peck et al. 2012). Our results provide support to these findings, as they fell in between those results, confirming that maximum air temperatures near the surface are expected to be lower than soil surface temperatures but higher than air temperatures further from the ground due to the conductive heating from the soil surface (Geiger et al. 1995; Campbell and Norman 1998).

Much of the research that quantifies seedling survival and performance following retention harvests has focused on availability of light as a limiting factor (Gagnon et al. 2003; Powers et al. 2008; Peck et al. 2012), although selected research on shelterwood systems has examined soil temperature effects on seedling survival and growth (Childs et al. 1985; Man and Lieffers 1999) and many have looked at climate conditions alone (Granberg et al. 1993; Valigura and Messina 1994; Langvall and Ottosson Löfvenius 2002). Childs et al. (1985) found that on south or west aspects in southwest Oregon where temperatures are generally higher than our study sites, shade from shelterwoods was beneficial in protecting seedlings from heat damage. While we did not directly examine regeneration rates or seedling survival or performance, the interpretation of the temperatures near the soil surface and SDH was based on physiological studies (Marias et al. 2017; Rank et al. 2022) and thus reflected their ecological relevance, especially for germinating seeds and seedlings and other understory plants. The relationships between canopy cover and SDH in our study confirm results from studies that examined the probability of regeneration after varying fire severity and climate scenarios (Willms et al. 2017; Davis et al. 2023). The associated lower post-fire canopy cover will result in limited temperature buffering and associated higher temperature stresses of the regenerating vegetation. For example, Davis et al. (2023) showed that the benefits of retained canopy cover on natural tree regeneration were likely due to a combination of shading and seed availability. Retained canopy cover may provide additional benefits to natural tree regeneration through reducing competition from understory vegetation (Devine and Harrington 2008; Dodson et al. 2014).

The emphasis on light availability as a limiting factor on seedling survival and performance following retention harvests highlights a key tradeoff of leaving higher canopy cover to buffer understory temperatures (Peck et al. 2012; Käber et al. 2023). Many commercially valuable species are shade-intolerant, and higher overstory canopy cover can negatively impact regeneration through reduction of light availability, potentially outweighing benefits of reduced microclimate temperatures (Gray and Spies 1997; Brandeis et al. 2001; Ashton and Kelty 2018). This tradeoff can be addressed through incorporating topographical conditions (Scherrer and Körner 2011; Meineri et al. 2015) and diversification of management goals. If high temperatures are the main concern for understory establishment following a harvest, foresters should target north-facing or other topographically buffered areas (Carnicer et al. 2021), leave higher canopy cover initially to provide shading during initial stages of regeneration that are most temperature-limited followed by a second entry to improve light availability (Devine and Harrington 2008; Shatford et al. 2009), retain higher canopy cover and shift goals toward establishment of a shade-tolerant cohort, or a combination of these approaches (Kuehne and Puettmann 2008).

Additionally, there may also be tradeoffs associated with water availability and competition between residual trees and understory regeneration following retention harvests (Gray et al. 2002; Devine and Harrington 2008). Water availability for seedlings is influenced by competition from overstory trees and other understory vegetation (Devine and Harrington 2007), overstory canopy interception of precipitation, evaporative demand on soil moisture, and the interaction of these effects (Aussenac 2000). The presence of an overstory canopy reduces through fall of precipitation (Geiger et al. 1995) but may also reduce soil evaporation rates through shading and litter deposition (Aussenac 2000; Floriancic et al. 2023). In this study, we examined the most extreme topographical positions for microclimate conditions where it is likely that the benefit of reduced evaporative demand outweighs reduction in throughfall. While overstory trees may negatively affect regeneration through direct competition (Balandier et al. 2006; Devine and Harrington 2008; Riegel et al. 2013), there is evidence that under partial canopies competition from other understory vegetation, which has a larger effect on regeneration, is reduced (Smidt and Puettmann 1998; Montgomery et al. 2010; Dodson et al. 2014). Therefore, the overall competition regeneration experience following retention harvests may be lower than in clear cut settings without vegetation management (Montgomery et al. 2010).

While long-term trends of increasing average temperatures have and will continue to impact forest ecosystems, extreme events pose a larger threat to forest health and the provision of ecosystem services (Breshears et al. 2021; Puettmann 2021; Hammond et al. 2022). The June 2021 Northwest Heat Dome shattered temperature records and caused significant foliar damage and mortality throughout the PNW (Still et al. 2023) and occurred during our study period. The results of our analysis also indicated that even under high residual canopy cover, temperatures at 2 cm are well above thresholds for heat-stress impacts on plants (Jansen et al. 2014). This is of major concern as it indicates that during extreme events, understory conditions will likely not be sufficiently protected from damaging and potentially lethal temperatures on south-facing slopes by canopy cover alone. In fact, the Heat Dome conditions led to substantial seedling mortality in the region as well as damage to adult trees due to the heat (Still et al. 2023). Assuming such heat events are becoming more common, managers planning retention harvests with the goal of recruiting a second age cohort through regeneration and (or) of establishing vigorous understory vegetation (Puettmann et al. 2016; Franklin and Donato 2020) may need to retain a higher canopy density after harvests in the future, especially in topographically vulnerable areas (Meineri et al. 2015; Finocchiaro et al. 2024). However, leaving more canopy may shift the species composition of the regeneration to more shade-tolerant species (Kuehne and Puettmann 2008) and will reduce the establishment of light demanding early successional species (Puettmann et al. 2016). This may be problematic, as light demanding, early successional tree species are also more likely to be drought-tolerant (Niinemets and Valladares 2006).

The concerns around extreme events coupled with the reduction in microclimate temperatures due to wildfire smoke highlights that as disturbance regimes and regional climate conditions shift under global change, new dynamics and interactions will arise that demand different approaches (Puettmann 2011; Tosca et al. 2013). Despite the increasing presence of wildfire smoke across the western U.S., little is known about how smoke affects plants directly through chemical and physical interactions or indirectly through altering climate and atmospheric patterns from microclimate to global scales (Tosca et al. 2013; Price et al. 2016; McKendry et al. 2019). However, recent studies have documented increases in forest photosynthesis due to diffuse light (Rastogi et al. 2022) but also stomatal occlusion and suppression of gas exchange and photosynthesis (Riches et al. 2024). Wildfire smoke has also been shown to disrupt global air circulation patterns and affect precipitation along the equatorial zone (Tosca et al. 2013).

It is important to note that the variability in microclimate temperatures at a landscape scale was not captured in this study, as we limited our sampling to south-facing slopes. However, the general principles of temperature buffering should apply to north-facing slopes, where absolute temperatures and thus the stress vegetation experiences will be lessened (Geiger et al. 1995). Also, since forest structure, including canopy height, layers, and composition influence temperatures (Rambo and North 2009), e.g., through air mixing, our findings may not be applicable to old-growth (Wolf et al. 2021) or very young stands (Kovács et al. 2017). However, the stands selected for this study were representative of the age class and structure at which the first commercial thinning is typically conducted on managed forests in the PNW as well as in other regions (Ashton and Kelty 2018; Franklin and Donato 2020). Even if not specifically desired after thinning operations, regeneration of tree seedlings and other vegetation, is a major factor in forest development as the start of understory reinitiation (Oliver and Larson 1996; Kuehne and Puettmann 2008; Dodson et al. 2014) and the associated habitat conditions (Hagar 2007).

For a more comprehensive understanding of the implications of the canopy cover on germination and early growth of tree seedlings, it is important to keep in mind that growing conditions are influenced by complex interactions between air temperature, tissue temperature, and both atmospheric and soil moisture (McLaughlin et al. 2017; Davis et al. 2019) (Table S3). Future research should also monitor microclimate conditions before and after harvesting to better assess the effects of forest management independent of site conditions. Additionally, we sampled the harshest topographical position by focusing on south-facing aspects at a mid-slope position where incoming solar radiation is highest. Further research on possible interaction effects of canopy cover and protected topographical positions on microclimate conditions should also be conducted (Meineri et al. 2015; Finocchiaro et al. 2024).

Our results raise concern about the temperature conditions these regenerating plants will experience. However, if the establishment of the first understory cohort is successful, the additional shading by understory vegetation and advance regeneration will increase the amount of near-surface temperature reduction (Kovács et al. 2017; Prévosto et al. 2020). This raises concerns about a positive feedback loop where the increase in temperature stress immediately after partial harvest slows or prevents the establishment and growth of tree and other understory vegetation, leading to arrested succession driven by continuing high temperatures and evaporative demand that further affect growth and establishment of understory layers (Dey et al. 2019; Soto and Puettmann 2020).

5. Implications for management

The tradeoffs discussed above can be used to inform management actions to mitigate climate change effects and promote natural regeneration. Current climate change adaptation and forest restoration treatments focus on reducing stand density for drought and fire resilience (Sohn et al. 2016; Bottero et al. 2017; Stephens et al. 2020), creation of structural complexity (Puettmann et al. 2016; Stephens et al. 2020), and recently promoting natural regeneration (Dey et al. 2019). Sampling across a gradient of canopy cover allows our findings to be relevant to a wide variety of these treatments from homogenous thinning prescriptions in even-aged stands to variable density treatments (Puettmann et al. 2016; Franklin and Donato 2020). Thus, how managers may use the results of this study to mitigate impacts on forest ecosystems will vary based on the management goal and the available resources. For example, if the goal is to regenerate a cohort of shade-intolerant species and there are sufficient resources to allow for multiple entries or treatments, managers may retain more overstory cover to provide shading and temperature buffering during the early stages of seedling establishment. Once the new cohort has established and has greater heat tolerance (Harper 1977), a larger portion of the overstory could be removed to improve light availability (Ashton and Kelty 2018; Palik et al. 2020).

When there are fewer resources available for multiple entries, which is often the case for federally managed lands in the western US, the results from this study can be used to guide post-harvest canopy cover percentages based on topography and the desired understory composition. For example, consider a project area with variable topography and a goal of creating structurally complex multi-aged stands over half the area and on the other half regenerating stands focused on timber production, relying on regeneration from seed to achieve both goals. Results from this study suggest identifying the harshest sites based on topographical condition for leaving higher post-harvest canopy cover. Due to the lower light availability but buffered temperature conditions in the understory, this would provide opportunity for recruitment of shade-tolerant species, which are often less heat-tolerant, eventually resulting a structurally complex and diverse overstory (Kuehne and Puettmann 2008; Puettmann et al. 2016). When the desired future stand condition requires less overstory canopy cover, such as establishment of shade-intolerant species for timber production, our results suggest avoiding south-facing aspects for these prescriptions. Our results show that, on harsh topographic positions, regenerating seedlings with little shading from overstory canopy cover is likely to experience heat stress and is vulnerable to extreme heat events. Thus, results of this study can be used to mitigate climate change impacts while achieving a variety of management goals by balancing the tradeoffs associated with overstory canopy cover with topographic conditions and the desired understory condition and composition.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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The authors declare there are no competing interests.

Supplementary material

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