Mitigating drought mortality by incorporating topography into variable forest thinning strategies

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Abstract

Drought-induced productivity reductions and tree mortality have been increasing in recent decades in forests around the globe. Developing adaptation strategies hinges on an adequate understanding of the mechanisms governing the drought vulnerability of forest stands. Prescribed reduction in stand density has been used as a management tool to reduce water stress and wildfire risk, but the processes that modulate fine-scale variations in plant water supply and water demand are largely missing in ecosystem models. We used an ecohydrological model that couples plant hydraulics with groundwater hydrology to examine how within-stand variations in tree spatial arrangements and topography might mitigate forest vulnerability to drought at individual-tree and stand scales. Our results demonstrated thinning generally ameliorated plant hydraulic stress and improved carbon and water fluxes of the remaining trees, although the effectiveness varied by climate and topography. Variable thinning that adjusted thinning

intensity based on topography-mediated water availability achieved higher stand productivity and lower mortality risk, compared to evenly-spaced thinning at comparable intensities. The results from numerical experiments provided mechanistic evidence that topography mediates the effectiveness of thinning and highlighted the need for an explicit consideration of within-stand heterogeneity in trees and abiotic environments when designing forest thinning to mitigate drought impacts.

Key words
Drought mitigation; Thinning treatments; Tree neighborhood; Topography; Ecohydrological modeling; Mortality risk

Introduction

Forests globally deliver critical ecosystem services such as provision of timber, fuel, and water, regulation of climate and hydrology, and support of biodiversity [1, 2]. Anthropogenic climate changes are threatening forests globally [3] due to increasing wildfires [4], insect outbreaks [5] and widespread tree die-offs from drought and warming climate [6-8]. Future climate projections suggest increasing drought frequency and intensity in most parts of the world [9, 10], with serious consequences on the sustainability of forest functions and services [11]. Therefore, it is crucial to develop effective mitigation strategies that minimize forest vulnerability to unprecedented moisture deficits [12-14].

Considerable research has investigated the physiological mechanisms underlying climate-induced mortality at the individual tree level [15, 16]. In particular, hydraulic damage refers to the accumulation of emboli in the xylem that disrupts water transport and leads to cell death by dehydration [17]. Models that explicitly simulate plant hydraulic impairments (e.g., percentage loss of hydraulic conductance) were able to explain the mortality of different species with contrasting vulnerability to cavitation [18], rooting depth [19], and drought treatments [20]. However, our understandings of the processes mediating mortality risks at stand or landscape scales remain limited [21, 22]. The effects of climate stressors such as drought are filtered through fine-grained attributes such as topography, soil heterogeneity, and tree neighborhoods that mediate the realized microenvironment that individual trees experience, which may link to tree-to-tree variations in mortality risks, and physiological functions such as water and carbon fluxes [14, 23-25].

Stand density reduction through prescribed forest thinning has been employed to mitigate drought impacts, promote tree- and stand-level growth and forest resilience to disturbances [26-31]. Studies have shown high levels of competition within a forest stand can compound the effects of drought and increase the probability of mortality, especially when water is a limiting resource [32-34]. There is broad consensus that thinning potentially reduces total stand water use, increases the water availability for remaining trees, and reduces inter-tree competition for resources [12, 35-37]. Yet, few process-based vegetation models explicitly account for competition for water among neighboring trees. Thinning treatments in most vegetation models have been simplified as a decrease in biomass or leaf area at the stand scale (Figure 1a) [38-40] and do not explicitly distinguish the changes in water availability experienced by an individual tree as influenced by interactions with surrounding trees (Figure 1b).

Topography interacts with broader-scale climate to create spatially heterogeneous fine-scale environments [41] that mediate individual tree responses to drought. Hydrologic processes such as lateral flows of groundwater create drier hills and wetter valleys [42]. The systematic variations in water availability driven by topography have emerged to be an important mechanism mediating the spatial patterns of vegetation biomass [43], leaf area index [44], sensitivity to drought [45], and drought-induced tree mortality [46, 47]. Despite its importance and the preponderance of forests in mountain ranges [48], most vegetation models only represent vertical flow through the soil matrix, whereas the impacts of terrain-mediated groundwater flow on forest functions are ignored [49], limiting our ability to develop realistic estimations of plant water supply. Further, topography is rarely accounted for or incorporated into thinning strategies. For example, variable thinning that adjusts the inter-tree spacing based on elevation gradients has been proposed [50], but it is not clear whether variable thinning would effectively mitigate drought impacts on forests (Figure 1cd).

Effective forest management hinges on tools that can quantify tree mortality risks and physiological functions in response to stand structure changes [6, 31]. Little research has been directed specifically toward evaluating potential forest management options under different climate scenarios, likely due to the lack of models that are able to capture relevant mechanisms. Most vegetation models simulate the functioning of an "average stand" in each model grid cell and do not account for the effects of fine-scale, within-grid cell variations in tree arrangements and the influence of topography on plant water supply and mortality risk was ignored. This leaves key knowledge gaps regarding the interactive effects of tree arrangements and topography on forest vulnerability to various climatic conditions and hampers efforts to develop climate-adapted management strategies on forested hillslopes.

This study employed a state-of-the-art, integrated plant hydraulics-hydrology model to investigate how within-stand variations in tree arrangements and terrain could mediate responses to climate variability from individual-tree scales up to forest stands. Parallel Flow-Terrestrial Regional Ecosystem Exchange Simulator (ParFlow-TREES) simulates the transient, three-dimensional water flux in the subsurface and along the soil-plant-atmospheric continuum at individual-tree level [51, 52]. In addition to carbon and water fluxes, ParFlow-TREES estimates the percentage of plant hydraulic damage, which has been shown to be a proxy of drought-induced mortality risk for various vascular species by integrating the effects of water availability, atmospheric demand, and plant hydraulic traits [53, 54]. We focused on a ponderosa pine (*Pinus ponderosa*)-dominated ecosystem in northern Arizona with five-year eddy covariance measurements of ecosystem water and carbon fluxes along with detailed meteorological conditions, but the implications of our results are broadly applicable for other montane forest management. Using ParFlow-TREES as a virtual laboratory, the goal of this study is to experiment with different scenarios of tree arrangements, topography, and climate to disentangle the multiple, interacting controls on forest water use, productivity, and vulnerability to drought. Specifically, we asked: (1) How would lumped and explicit representation of thinning influence tree functions and mortality risk? (2) How does topography interact with thinning to influence forest responses to climate? And (3) Does variable thinning based on terrain result in enhanced resistance to drought?

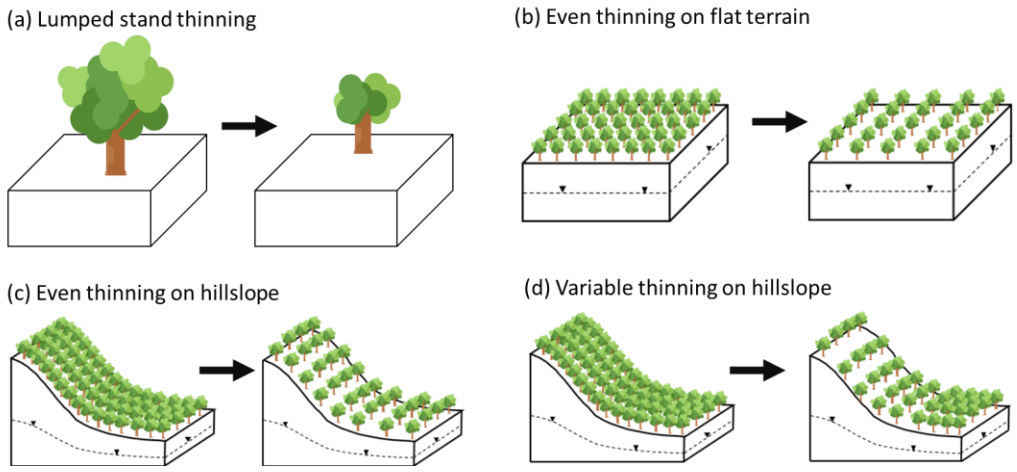

Figure 1. Conceptual diagram illustrating different representations of forest thinning with increasing complexity. (a) represents the commonly adopted modeling approach, where stand-level leaf area or basal area is decreased in a lumped mode, without explicit considerations of removing individual trees. (b) represents spatially explicit thinning that considers the location of individual trees to be removed by thinning in evenly spaced rows. (c) considers even thinning on sloped terrain, and (d) represents variably spaced thinning on sloped terrain with more trees in valleys (lower thinning intensity) and fewer trees in ridge tops (higher thinning intensity). Dashed lines represent the water table.

Materials and methods

Model

In this study, we used ParFlow-TREES, an integrated ecohydrological model that couples a plant physiology model, Terrestrial Regional Ecosystem Exchange Simulator (TREES) [55], to a variably saturated groundwater model, PARallel FLOW (ParFlow) [56]. Briefly, ParFlow solves the three-dimensional, saturated and unsaturated subsurface flow using the mixed form of Richards' equation [57, 58], and has been extensively evaluated against observations of water table depth and streamflow across continental U.S. [59]. TREES simulates canopy photosynthesis and transpiration at 30-min time steps by explicitly solving for plant hydraulic transport and hydraulic-based stomatal optimization [60, 61]. TREES has been shown to reliably capture the responses of leaf water potential, transpiration, and photosynthesis to environmental cues of soil water, vapor pressure deficit, temperature, and CO_2 [20, 62, 63]. The integrated model, ParFlow-TREES, explicitly solves the transient water fluxes through the soil-plant-atmosphere continuum vertically and across the landscape laterally. It is therefore very suitable for investigating the impacts of topography and the spatial arrangement of trees on the ecosystem mortality risk and water and carbon fluxes. Descriptions of major processes of ParFlow-TREES are provided in Supporting Information Method S1 and previous literature [51, 52, 64].

Study area and model evaluation

We focused on a ponderosa pine (*Pinus ponderosa*) forest located in the Northern Arizona University Centennial Forest (35° 5′ 20.5″ N, 111° 45′ 43.33″ W) with an elevation of 2180 m above sea level. This is the Ameriflux site US-Fuf (https://ameriflux.lbl.gov/sites/siteinfo/US-

Fuf) and observations of air temperature, precipitation, photosynthetically active radiation, wind speed, vapor pressure deficit (VPD), evapotranspiration (ET), and gross primary production (GPP) were collected during 2006-2010 at 30 min intervals. The data acquisition, processing and analysis have been described in previous publications [65, 66]. The mean annual temperature was 8.8 C° and the mean annual precipitation was 610 mm during the observation periods. The site typically experiences a bimodal precipitation pattern, with winter snowfall and rainfall occurring primarily in December through April, a pronounced drought during May and June and a rainy period associated with the North American Monsoon during July-September [65, 66]. The soil is primarily clayloam and the forest is dominated by ponderosa pine with a very sparse understory of grasses and forbs. The measured leaf area index (LAI; projected area) was 2.2 m^2 m^{-2}, basal area was 30 m^2 ha^{-1}, and tree density was 853 trees ha^{-1} [66, 67].

To ensure the model reliably captures the water and carbon fluxes, we evaluated the predictions of ParFlow-TREES against the observed evapotranspiration (ET) and gross primary production (GPP) within the tower footprint by simulating the entire forest stand in a lumped, one-dimensional mode. We focused on ET and GPP because of their critical role in the terrestrial water and carbon cycle [1, 68], and their wide usage in ecosystem model evaluations [69-71]. Key model parameters of plant traits and soil properties were estimated based on previous literature as described in Table 1. Five years of meteorological conditions of air temperature, VPD, radiation, wind speed, and precipitation at 30-min time steps were used to run the simulation. Pearson's correlation (R) and Root Mean Square Error (RMSE) were calculated to quantify the agreement between model predictions and data observations of ET and GPP.

Table 1. Major inputs of ParFlow-TREES and associated values used in this study.

Model variable or parameter	Values	Sources
(a) Plant hydraulics parameters		
Weibull vulnerability curve parameter [b, c][1]	[1.56, 1.41] for root [3.81, 2.5] for stem [2.08, 3.72] for leaf	[72]
Leaf-specific hydraulic conductance (LSC)	10 mmol s^{-1} m^{-2} MPa^{-1}	[72]
Maximum carboxylation rate at 25 degree C (Vmax)	32 μmol m^{-2} s^{-1}	[72]
Rooting depth	1.7 m	Assumed
Leaf area index	2.2 m^2 m^{-2}	[65]
(b) Hydrologic parameters		
Number of vertical soil layers	10	Assumed
Thickness of soil layers (from top to bottom)	0.02, 0.1, 0.2, 0.2, 0.4, 0.8, 1.6, 3.2, 6.4, 7.1 (m)	Assumed
Van Genuchten parameters [a, n]	Clayloam [1.9, 1.31]	[65]
Saturated permeability	Clayloam [0.0026 m h^{-1}]	[65]
Saturated soil moisture	0.450 m^3 m^{-3}	
Residual soil moisture	0.095 m^3 m^{-3}	
(c) Initial & boundary condition		

Boundary condition	No flow except for the surface allowing overland flow when the water table rises to the land surface
Initial condition	-10 m
(d) Spatial Setup	
Grid size	96 m*24 m for one dimension (lumped) simulation 1 m*1 m for three dimension (spatially explicit) simulation
Domain	1*1*10 for one dimension 96*24*10 for three dimension

[1] The vulnerability curve is characterized using Weibull function $f(\varphi) = e^{-(\frac{-\varphi}{b})^c}$, where φ is xylem pressure, and b and c are curve parameters.

Numerical experiments and hypothesis testing

Using the evaluated model, we performed four sets of numerical experiments (Table 2) to investigate how topography and thinning interact to influence tree water use, carbon uptake, and mortality risk at individual tree and whole stand levels, across a range of climate conditions and thinning intensities. We considered three different meteorological scenarios (Figure S1): a wet year at the study area (2007) with annual precipitation of 653 mm, a dry year (2009) with annual precipitation of 296 mm, and an extreme dry year with the same weather variables as 2009 except the precipitation was reduced by half (148 mm). Although the wet year had higher total precipitation, it had a long dry period before the onset of monsoon rains in late summer. We also considered six levels of thinning intensities, corresponding to 0%, 33%, 50%, 66%, 75%, and 80% of tree removal. Since this study focused on the impacts of tree spatial arrangement and topography, all trees were assumed to have the same traits (Table 1) and the grid cell became bare soil when trees were removed in spatially explicit simulations. For every simulation with different climate, thinning treatments, and topography, we reported the maximum percentage loss of whole-plant hydraulic conductance (PLK), which has been used as an indicator of tree mortality risk with higher PLK associated with higher mortality risk [20, 64]. We further reported the annual transpiration and productivity per leaf area (individual tree performance proxy) and per ground area for the entire forest stand (aggregated effect).

In the first experiment, we ran one-dimensional simulations that reduced stand leaf area from 2.2 to 1.46, 1.1, 0.73, 0.55, and 0.44 to represent different thinning intensities in a lumped mode (Figure 1a). This configuration mimicked the commonly adopted approaches by current ecosystem models that represent thinning through reduced leaf area index (LAI) at the stand scale. In the second to fourth experiments, we ran spatially explicit, three-dimensional simulations with a model domain of 96 by 24 grid cells and a grid size of 1 m by 1 m. Every grid cell was covered by a ponderosa pine tree and evenly spaced row thinning was used to achieve different thinning intensities (Figure 2). For example, every third row was removed in 33% thinning and every second row was removed in 50% thinning. Terrain was assumed to be flat in the second experiment. To evaluate the influence of topography-induced lateral flow, we ran a third experiment that simulated the forest stand on an idealized hillslope (Figure S2) and applied the same thinning treatments as in Experiment 2.

Table 2. Descriptions of numerical experiments and how they were used to test hypotheses about explicit thinning, topography, and variable thinning.

Experiments	Description of the procedure	Hypothesis
Experiment 1 (3 climate scenarios * 6 thinning treatments for a total of 18 simulations)	1D model domain; vary leaf area index values from 2.2 to 1.46, 1.1, 0.73, 0.55, and 0.44.	Lumped thinning overestimates the benefits of water savings, compared to explicit thinning
Experiment 2 (3 climate scenarios * 6 thinning treatments for a total of 18 simulations)	3D model domain; vary the percentage of bare soil covered grid cells from 0% to 33%, 50%, 66%, 75%, and 80%. Evenly spaced row thinning was used to achieve a given thinning intensity. Terrain is flat	Lateral flow buffers tree stress on hillslopes, and impacts the effectiveness of thinning
Experiment 3 (3 climate scenarios * 6 thinning treatments for a total of 18 simulations)	Same as Experiment 2, except a sloped terrain is prescribed.	Variable thinning better reduces tree mortality risk and improves stand-scale productivity
Experiment 4 (3 climate scenarios * 1 variable thinning treatment for a total of 3 simulations)	Same as Experiment 3, except variably spaced row thinning was developed to minimize the total number of trees to be removed while keeping the mortality risk to the minimum or under 60%.	

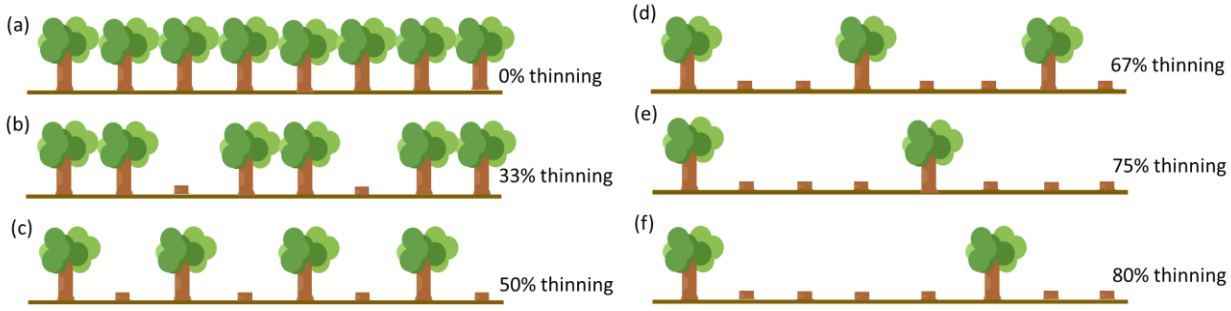

Figure 2. Diagram illustrating the evenly spaced thinning at different intensities with 0% thinning (a), 33% thinning (b, remove one of every three trees), 50% thinning (c, remove one of every two trees), 67% thinning (d, remove two of every three trees), 75% thinning (e, remove three of every four trees), and 80% thinning (f, remove four of every five trees).

In the fourth experiment, we simulated variable thinning that adjusts thinning intensity depending on the hillslope position to better take advantage of the laterally redistributed water. Based on simulations from Experiment 3, we plotted the mean PLK for upslope trees (distance in the uphill direction > 40 m) versus even thinning intensity (Figure 3). PLK kept declining as thinning intensity increased until a certain tipping point (red circles in Figure 3). This tipping point was used to determine the highest thinning intensity at upslope locations (Figure 3a). In some cases, PLK would drop below 60% before approaching the tipping point (Figure 3b), the

lowest thinning intensity that keeps PLK under 60% will be used. We used 60% loss in plant hydraulic conductance as the mortality threshold, informed by previous synthesis work showing 60% best distinguishes trees that survived from those that died from droughts [15, 54]. For lower slope positions, the thinning intensity is determined by maintaining as many trees as possible while keeping the mortality risk of every individual tree under 60%. For example, 0% thinning will be applied in downslope locations where PLK is always under 60% due to lateral flow subsidy, and intermediate thinning intensities will be selected in the middle, transitional zone, accounting for the effects of both topography and neighboring tree distance.

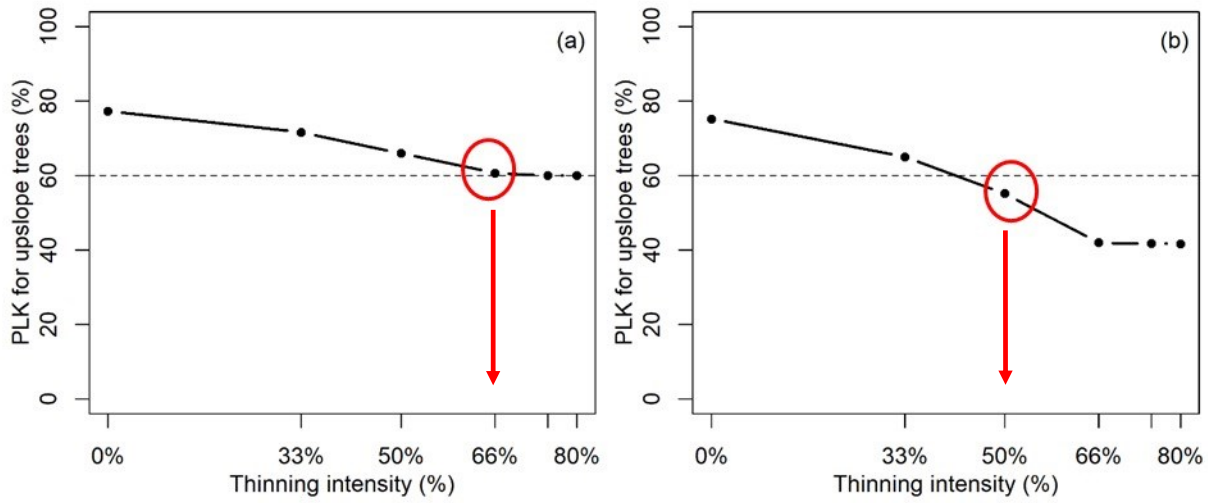

Figure 3. Changes in the PLK of upslope trees (Distance in the uphill direction > 40 m) versus thinning intensity. PLK generally declines as thinning intensity increases until a certain tipping point. If PLK levels off before reaching 60% PLK (a), the tipping point was used to determine the highest thinning intensity in upslope positions (66% thinning, highlighted by the red circle in a). If PLK levels off after reaching 60% PLK (b), the lowest thinning intensity that keeps PLK under 60% will be used (50% thinning, highlighted by the red circle in b).

Results

Model evaluation

A comparison between the observed and simulated daily values of ET and GPP showed that ParFlow-TREES reasonably captured the stand-scale responses of water and carbon fluxes during the five years from 2006 to 2010 (Figure 4, S3). Throughout the five years, the Pearson's correlation coefficient between observation and simulation was 0.66 for ET and 0.83 for GPP, and the regression slope between observed and predicted values was 0.72 for ET and 1.03 for GPP (Figure 4ab). For days when ET is likely dominated by transpiration such as growing season days without precipitation, the Pearson's correlation coefficient was 0.85 for ET and 0.81 for GPP and the regression slope was 0.81 for ET and 0.96 for GPP.

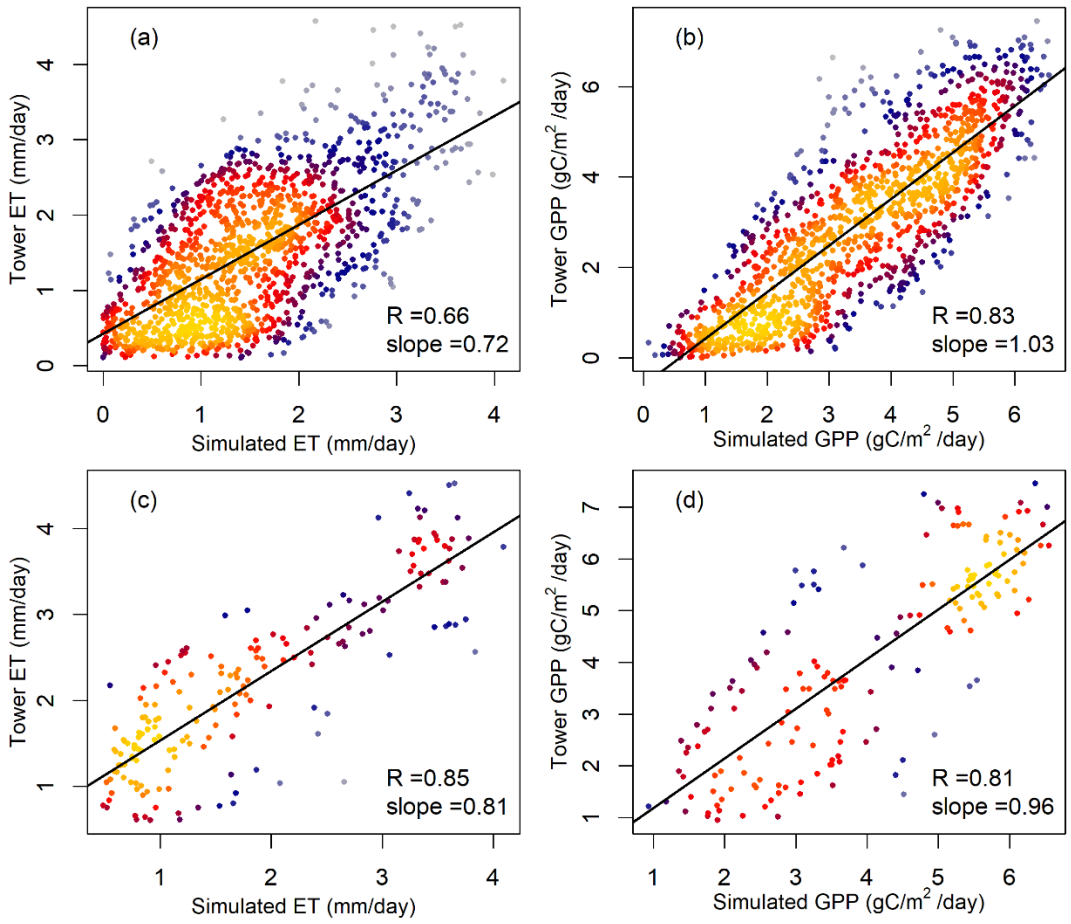

Figure 4. Scatter plot between ParFlow-TREES simulated and observed daily values of evapotranspiration (ET, a, c) and gross primary productivity (GPP, b, d) from an eddy covariance flux tower at an Ameriflux Site US-FUF, in a ponderosa pine forest near Flagstaff, Arizona during the period of 2006 to 2010. a and b include data points for the entire five year period. c and d only include days when ET is likely dominated by transpiration, determined as days during the growing season from June to August and had no precipitation. Warmer dot colors indicate a higher point density, and the black lines indicate the linear regression fit. R is the Pearson's correlation coefficient and slope is the regression slope between observed and modeled values.

Lumped versus spatially explicit representation of stand thinning

We compared the transpiration, productivity, and mortality risks of the remaining trees using model representations of lumped (Experiment 1) versus explicit tree removal (Experiment 2) across different thinning intensities and climate scenarios (Figure 5, S4). Reducing tree densities generally improved transpiration and productivity per leaf area, for both lumped and explicit thinning (Figure 5ab). While lumped and spatially explicit simulations had the same transpiration and productivity with 0% thinning, their discrepancies increased with thinning intensity (gray versus white bars in Figure 5), and was significant at a thinning intensity of 66% ($p<0.1$). Lumped thinning tended to overestimate water savings from thinning, with higher increases in transpiration and productivity per unit leaf area and reductions in PLK. Further, lumped thinning predicted continued decrease in PLK with thinning intensity, whereas spatially explicit thinning

predicted PLK to level off at intensities of 66%. Finally, increased transpiration and productivity at leaf-scale was not sufficient to compensate for tree removal at stand scale, leading to decreased transpiration and productivity of the entire stand (Figure 5de).

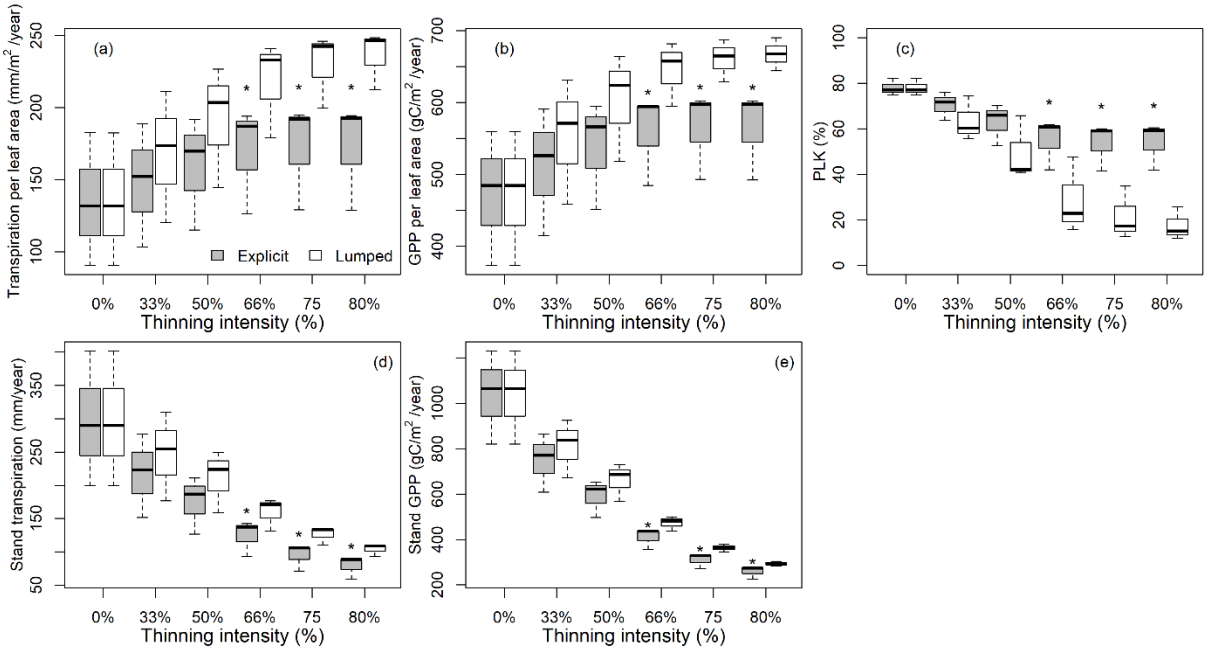

Figure 5. Boxplots of transpiration per unit leaf area (a), productivity (GPP) per unit leaf area (b), maximum percentage loss of whole-plant hydraulic conductance (PLK) (c), stand transpiration per ground area (d), and stand GPP per ground area (e) across different thinning intensities of 0%, 33%, 50%, 66%, 75%, and 80%, using lumped (while bars, Experiment 1) versus explicit (grey bars, Experiment 2) representations of tree removal. For explicit simulations, only mean values are presented in a-c. Stars represent significant ($p < 0.1$) differences between lumped and explicit simulations based on t test.

Forest thinning on flat versus sloped terrains

We compared forest responses to explicit thinning at even distances between flat (Experiment 2) and sloped terrains (Experiment 3). Trees on the flat terrain showed little spatial variation, whereas trees on the hillslope demonstrated large spatial gradients in PLK, transpiration, and productivity (Figure 6, S5-S7). As soil water laterally redistributed from topographic high to low, trees on the lower hillslope received additional water subsidy, and therefore had higher transpiration and productivity and lower PLK (Figure 6, uphill distance < 30 m). Trees on the dry upslopes had lower transpiration, productivity and higher PLK (Figure 6, uphill distance > 30 m). Averaged across the stand, transpiration and productivity were higher and PLK was lower for forests on hillslopes, compared to flat terrains (Figure S8-S10). Further, the differences between flat and sloped forest stands were greater at lower thinning intensities (greater forest density) when the total demand for water was higher.

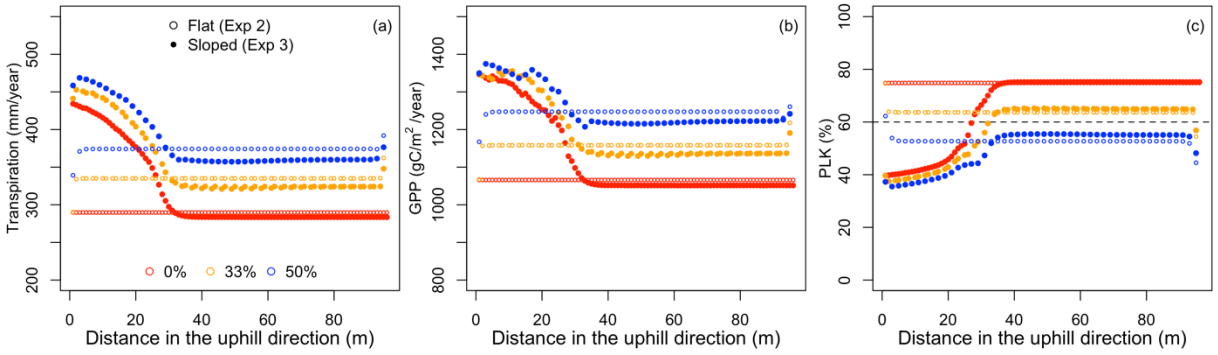

Figure 6. Spatial variations in transpiration (a), productivity (GPP, b), and mortality risk (PLK, c) along the uphill direction of a forested stand during the dry year and for different terrains with solid dots representing sloped terrain (Experiment 3) and open dots representing flat terrain (Experiment 2). Every dot represents a grid cell that has tree coverage. Only three thinning intensities were shown for easier visualization (red: 0%, orange: 33%, and blue 50%).

Variable thinning effects on ecosystem responses

We developed a variable thinning strategy (Experiment 4) that adjusted thinning intensity (or inter-tree spacing) based on hillslope positions and climate conditions (Figure 7, black versus colored dots). Compared to even thinning, variable thinning achieved lower PLK for upslope trees (Figure 7ac), except for the dry year where 50% thinning was selected as the PLK for upslope trees was lower than 60% (Figure 7b). Further, variable thinning maintained more trees in the lower hillslope to better utilize the water subsidy at hillslope bottoms through lateral subsurface flow while keeping PLK less than 60%. At the whole stand scale, variable thinning resulted a thinning intensity of 50% for the wet year, 36% for the dry year, and 54% for the extreme dry year. Compared to even thinning at similar intensities, variable thinning had similar stand transpiration and productivity but more mitigated PLK (Figure 8, red versus grey bars). Compared to even thinning at the highest intensity of variable thinning (66% for wet year, 50% for dry year, and 75% for extremely dry year), variable thinning had similar reduction in PLK, but higher stand transpiration and productivity by maintaining more trees (Figure 8, blue versus grey bars).

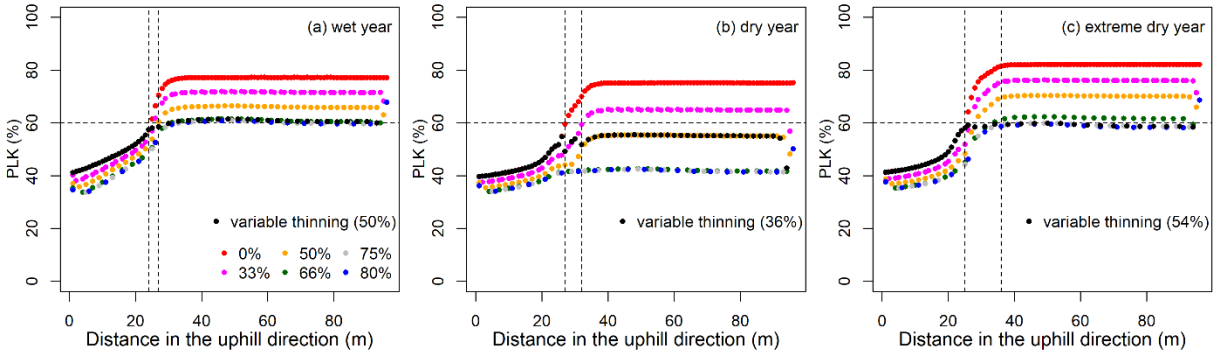

Figure 7. Variations in individual tree mortality risk (PLK) along the uphill direction of a hypothetical hillslope, for even thinning at various intensities (different colors) and variable thinning (black), during wet (a), dry (b), and extreme dry (c) years. Every dot represents an

individual model grid with tree coverage. Numbers in the parentheses indicate the stand-scale thinning intensity. Dashed lines represented 60% mortality risk threshold (horizontal) and the location to change thinning intensities (vertical).

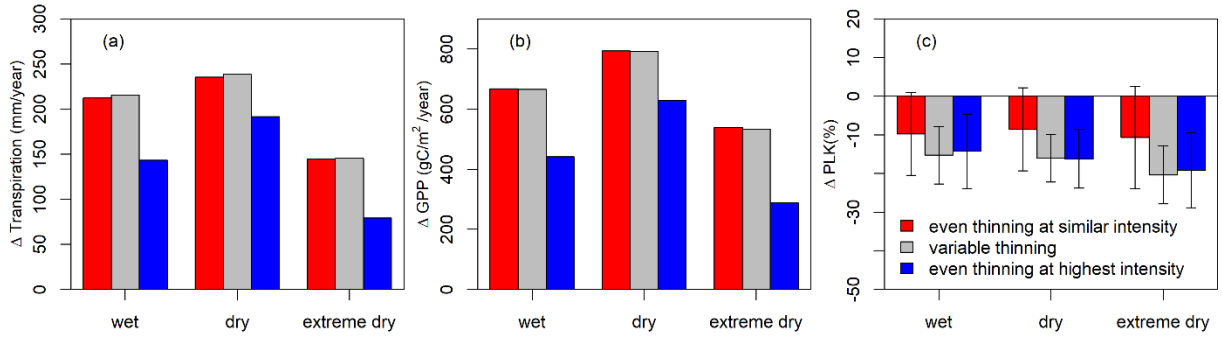

Figure 8. Changes in stand transpiration (ΔT, a), productivity (ΔGPP, b) and mortality risk (ΔPLK, c) from variable thinning (grey bars), even thinning at similar intensities (red bars), and highest intensities (blue bars), across different years. Variable thinning intensity was 50% for wet year, 35% for dry year, and 54% for extremely dry year. Even thinning at similar intensity was 50% for wet year, 33% for dry year, and 50% for extremely dry year. Even thinning at upslope intensity was 66% for wet year, 50% for dry year, and 75% for extremely dry year. 0% thinning on sloped terrains was used as the baseline to calculate the changes. Error bars in c represented the standard deviation among trees within the forest stand.

Discussion

Developing effective strategies that mitigate forest vulnerability to drought has become a major research frontier to inform forest management [6, 12, 36, 73]. In this study, we evaluated the sensitivity of forest functions and mortality risks to within-stand variations of tree arrangement and topography using a coupled plant hydraulics-hydrology model, across thinning intensities and over highly variable climate. Our results showed that the explicit consideration of water transport among neighboring trees and along hillslope within a forest stand strongly influence the estimated effectiveness of thinning in reducing water stress and mortality risk to drought. Further, topography could be leveraged to develop variable thinning treatments that can enhance both stand productivity and individual level resistance against drought stress. Our numerical experiments highlighted the need for an explicit consideration of within-stand heterogeneity in trees and abiotic environment when designing mitigation strategies.

The spatially explicit simulation of individual tree removal was compared with the lumped reduction in stand leaf area that is commonly employed in process-based ecosystem models [38, 39]. Our results showed the lumped thinning tended to overestimate the amount of water savings for a given thinning intensity (Figure 5). This discrepancy was primarily because water saved by thinning became immediately available to the remaining biomass in the lumped reduction in leaf area, whereas in a spatially explicit manner, water would have to laterally transport from inter-tree spaces into tree locations before the extra water could subsidize the neighboring tree. Further, the extra water could be consumed by increased evapotranspiration from bare soil or understory after overstory tree removal [74, 75]. As thinning intensity increases, spatially explicit thinning suggested minimal changes in transpiration, productivity, and mortality risk beyond a certain point, whereas lumped thinning suggested continued increases in transpiration

and productivity and decreases in mortality risk as more biomass was being removed (Figure 5a-c).

By explicitly solving plant hydraulics for each individual tree within the stand, our results showed that thinning improved leaf-level gas exchanges and reduced PLK to drought (Figure 5a-c), while the stand-scale productivity and transpiration decreased due to the removal of trees (Figure 5d, e). These results are consistent with earlier leaf-level observations from nearby sites [65, 76, 77] and stand-scale estimations from other places [26, 50]. Further, thinning was more effective to decrease mortality risk when drought was mild such as the dry year, and less effective when total precipitation was very low (e.g., extreme dry year) or when there was a long drought period (e.g., the wet year, Figure S1). Overall, our results support the view that density management has the potential to compensate for the deleterious effects of drought and to promote resilience to drier future climates [12, 28] and that management strategies need to be tailored to specific local context and environmental conditions [6].

By simulating forest stands on a sloped terrain, our study showed topography creates fine-scale spatial heterogeneities of plant responses within the same forest stand through lateral groundwater flow (Figure 6, S5-7). While topography is generally recognized in empirical studies [78-80], topography-mediated water supply is more rarely considered in ecosystem models (but see [52, 81]) or incorporated into forest management design. Trees in lower topographic positions received the water subsidy via lateral flow from higher positions at the cost of reducing water supply for trees at higher topographic positions (Figure 6). But the stand-scale productivity and transpiration were higher and mortality risk was lower compared to forests on flat terrains (Figure S8-10), suggesting a net benefit of lateral water redistribution at the stand scale [41]. Further, the differences between flat and sloped terrains increased with water stress when stand density is high or climate condition is dry (Figure S8-10). This result was in line with previous studies suggesting complexities in topography complicated the prediction of forest mortality from climate variables [22, 46].

Based on the changes of PLK to various even thinning intensities, a variable thinning scheme (Figure 3) was developed to demonstrate how sloped terrain might be incorporated into forest treatment design. Our results demonstrated topographically-informed variable thinning could lead to higher stand productivity and lower mortality risk compared to even thinning (Figure 8). Keeping more trees in lower hillslope positions took better advantage of the extra water made available through groundwater redistribution, whereas increasing inter-tree distance in the dry upslope helped to release water stress (Figure 7). Variable thinning requires solving for water dynamics that are modulated by climate, tree neighborhood, and topography. This dynamic response cannot be predetermined, and can only be captured by models solving transient water fluxes through soil-plant atmosphere continuum and across the landscape, such as ParFlow-TREES [51]. Previous research on variable thinning focused on the creation of structurally complex stands by creating different gap sizes, age or species compositions [28, 82]. Our work adds to this body of literature by providing a paradigm to incorporate terrain into forest management and predictive models [50].

While this study illustrated the potential influence of tree arrangements and topography in affecting forest health, there were several caveats that are worth further investigations. First, this study was based on idealized experiments with hypothetical terrain and density treatments.

Future work should combine numerical modeling with more realistic and detailed topography and pre- and post-treatment forest structure and incorporate the differences in plant functional traits associated with variations in tree size, age, and species that are important for modulating ecosystem responses [83, 84]. Second, we relied on the eddy covariance measurements of ecosystem water and carbon fluxes to evaluate model performance. Although this approach has been commonly used [69-71], it does not explicitly consider the separate water fluxes of transpiration, soil evaporation, and canopy evaporation. Long-term, simultaneous, and accurate measurements of these water balance components and their dynamics following thinning treatments will be critical to better constrain model uncertainty [85]. Similarly, additional processes that modify the water dynamics and microclimate such as radiation, temperature and vapor pressure deficit might be equally important [26, 86, 87] and should be incorporated to comprehensively understand the impacts of thinning on forest functions. Third, we used the maximum percentage loss of hydraulic conductivity as a proxy of drought-induced mortality risk. While this metric has been successful in predicting several episodes of mortality [18, 54, 64], future work should evaluate its potential in explaining observed tree mortality across sites with and without treatments. Finally, while this study focused on short-term changes in water and carbon fluxes and drought mortality risks after thinning, dynamics of forest composition and structure after thinning treatments might influence ecosystem resilience to drought and other compounded disturbances in the long term [88-90].

Conclusion

Developing effective adaptation strategies to changing climate hinges on an adequate understanding of the mechanisms governing drought vulnerability of forests. Using a coupled plant hydraulics-hydrology model, this study quantified the effects of within-stand variations in tree arrangement and topography on ecosystem functions and mortality risks and demonstrated the potential of ecohydrological models to estimate forest vulnerability to climate change under alternative management scenarios. Our results suggested inter-tree spacing and topography could strongly modulate ecosystem functions and mortality risks at individual tree and stand scales. Further, variable thinning that adjusts tree densities with topography could result in enhanced forest functions and health. These findings provide mechanistic evidence that density management has the potential to compensate for the deleterious effects of drought. They also underscore the important interaction between tree location and terrain in mediating drought-related mortality risk, and thus should be incorporated when designing forest management strategies.

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Data availability statement

The eddy covariance flux data can be accessed from https://ameriflux.lbl.gov/sites/siteinfo/US-Fuf. The model experiment results that support the findings of this study are available upon request from the authors.

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