Accounting for landscape heterogeneity improves spatial predictions of tree vulnerability to drought

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Summary

• As climate change continues, forest vulnerability to droughts and heatwaves is increasing, but vulnerability varies regionally and locally through landscape position. Also, most models used in forecasting forest responses to heat and drought do not incorporate relevant spatial processes.

• In order to improve spatial predictions of tree vulnerability, we employed a nonlinear stochastic model of soil moisture dynamics accounting for landscape differences in aspect, topography and soils. Across a watershed in central Texas we modeled dynamic water stress for a dominant tree species, Juniperus ashei, and projected future dynamic water stress through the 21st century.

• Modeled dynamic water stress tracked spatial patterns of remotely sensed drought-induced canopy loss. Accuracy in predicting drought-impacted stands increased from 60%, accounting for spatially variable soil conditions, to 72% when also including lateral redistribution of water and radiation/temperature effects attributable to aspect. Our analysis also suggests that dynamic water stress will increase through the 21st century, with trees persisting at only selected microsites.

• Favorable microsites/refugia may exist across a landscape where trees can persist; however, if future droughts are too severe, the buffering capacity of an heterogeneous landscape could be overwhelmed. Incorporating spatial data will improve projections of future tree water stress and identification of potential resilient refugia.

Introduction

As climate change continues, more frequent and intense heatwaves and droughts will likely lead to greater tree mortality (Allen et al., 2015). Instances of climate-induced tree mortality have already been documented world-wide (Allen et al., 2010). Increases in tree die-off can alter plant community composition and species distributions (Mueller et al., 2005; Engelbrecht et al., 2007; Clark et al., 2016), with consequences to biodiversity, carbon cycling, hydrology and biophysics (e.g. Ciais et al., 2005; Jackson et al., 2008; Vicente-Serrano et al., 2014). Empirical (e.g. bioclimate-envelope) or process-based models (e.g. Dynamic Global Vegetation Models, DGVMs) are two commonly used methods to predict how forests will respond to changes in climate. Spatial patterns of canopy loss often follow local stress gradients and depend on both climate and edaphic factors (Loehle & LeBlanc, 1996; Gitlin et al., 2006; McLaughlin et al., 2017). Although a few bioclimate-envelope models now account for topography (e.g. Lutz et al., 2010), they lack mechanistic representations of tree mortality. Alternatively, DGVMs include various mechanisms for modeling tree mortality; however, their algorithms are rarely tested with spatially explicit canopy loss observations (McDowell et al., 2011), and often do not account for landscape heterogeneity of abiotic factors at fine spatial resolutions, such as soil conditions, slope and aspect (Moorcroft, 2006), even though these data are readily available for many locations. Many studies have focused on improving model representations of the physiological mechanisms of tree mortality (McDowell et al., 2013; Parolari et al., 2014; Mackay et al., 2015); however, only a few have examined if including landscape heterogeneity would improve predictions of tree mortality (Tague et al., 2013; Anderegg et al., 2015; Tai et al., 2017). Spatial patterns of tree mortality are associated with changes in soil texture and depth (Bowker et al., 2012; Peterman & Waring,
model classifications are not mutually exclusive. In the present study, we combine modeling frameworks by using a statistical–
dynamic model of soil–plant water to model the probability of tree vulnerability to drought. Simplified mortality mechanisms
are incorporated (Parolari et al., 2014); the model is forced using stochastic precipitation (Laio et al., 2001; Rodríguez-
Iturbe & Porporato, 2004); and spatially explicit input parameters are included. The probability of tree mortality is then pre-
dicted given the mean intensity, duration and number of threshold crossings for percentage loss in hydraulic conductivity
(PLC) associated with tree vulnerability to embolism curves. Simulations show, for instance, that tree species impacted by
drought spend more time at higher PLC values (McDowell et al., 2013; Adams et al., 2017); chronically high PLC values
among other risk factors also can predispose a tree to mortality (Sperry & Love, 2015).

From October 2010 to September 2011, Texas experienced its most severe one-year drought since record-keeping began in 1895 (Hoerling et al., 2013). The drought killed millions of
trees across the region (Moore et al., 2016; Schwantes et al.,
2016, 2017). First, we combine a new modeling approach with
species-specific physiological parameters and a detailed spatial
dataset of tree canopy loss (Schwantes et al., 2017; Johnson et al., 2018a,b). Starting with a nonlinear stochastic model of
plot-scale soil moisture dynamics for a single watershed in cen-
tral Texas (Laio et al., 2001), we integrate plant hydraulic
thresholds and landscape processes, incorporating effects of lat-
eral redistribution of water as well as radiation and temperature
differences on dynamic soil moisture. Second, we explore the
effect of incorporating landscape heterogeneity in models, when
forecasting future drought stress, to understand whether land-
scape heterogeneity will buffer against future droughts projected
in the 21st century. We use climate projections under multiple
climate-warming trajectories and compare models with and
without landscape heterogeneity.

Materials and Methods

Study area

Our study area is a watershed in the Edwards Plateau region of
Texas (Fig. 1). We model tree water stress for a dominant tree
species, Juniperus ashei. Our analysis only includes areas where
J. ashei is a dominant species, as defined using an ecological sys-
tems map of Texas (Elliott et al., 2014) and a percentage tree
cover threshold > 25%, using the National Land Cover Database
percentage tree cover product (Homer et al., 2015). In 2011, a
severe drought and heatwave led to 9.5% tree canopy loss overall
across Texas, with J. ashei woodlands being one of the systems
most impacted by the drought (Schwantes et al., 2017), even
though J. ashei is an extremely drought-tolerant species, with low
vulnerability to root/stem embolism compared to other species in
this region (Johnson et al., 2018b). Within the study watershed,
we acquired maps of drought-impacted area in 2011 from Sch-
wantes et al. (2017), which were used to validate our tree water
stress models.
Soil water balance model

Following Laio et al. (2001), we employ a nonlinear stochastic, ordinary differential equation of soil moisture dynamics, where rainfall follows a marked Poisson process interpreted on a daily timescale. We express the soil moisture balance at a point as:

\[ nZ_e \frac{ds(t)}{dt} = R(t) - I(t) - Q[s(t), t] - ET[s(t)] - L[s(t)] \]

Eqn 1

\( n \) (active soil depth; \( n \) (porosity; \( s(\theta) \), relative soil moisture content; \( R(\theta) \), rainfall rate; \( I(\theta) \), amount of rainfall intercepted by the canopy cover; \( Q[\theta, t] \), surface/subsurface runoff rate; \( ET[\theta] \), evapotranspiration rate; \( L[\theta] \), leakage below the root zone). The runoff, evapotranspiration and leakage rate depend on soil moisture levels through simple yet realistic representations of plant hydraulics, soil properties and topography. Under steady-state conditions, we obtain analytical solutions of the soil moisture probability density function for each 30-m grid cell across the watershed. The solution is provided in Supporting Information Eqn S1, Methods S1; however, the full derivation can be found in Laio et al. (2001) and Rodriguez-Iturbe et al. (1999). We then assess the role of climate, soil properties, plant hydraulics and topography on soil moisture dynamics and associated tree water stress, by adapting the framework for modeling dynamic water stress, originally proposed by Laio et al. (2001) and Porporato et al. (2001), Fig. 2.

Infiltration: rainfall, canopy interception and lateral water flow

Infiltration from rainfall is treated as an external random forcing factor where the occurrence of a rainfall event follows a marked Poisson process with a mean storm frequency, \( \lambda \) (\( d^{-1} \)). The depth of each rainfall event follows an exponential probability density function with a mean depth, \( \alpha \) (cm), where \( \alpha \) represents the amount of rainfall reaching the soil, while not accounting for canopy interception or lateral water flow. These distributions are commonly used to model rainfall at the daily timescale (Rodriguez-Iturbe et al., 1999; Laio et al., 2001; Porporato et al., 2001; Parolari et al., 2014). Following Daly et al. (2008), we assume that for small storm events below a certain threshold, \( \Delta \), the canopy completely intercepts all rainfall. For J. ashei, \( \Delta = 0.25 \) cm; storms below this value are typically fully intercepted (Owens et al., 2006). The process describing the frequency of a rainfall event then becomes a censored marked Poisson process, and \( \lambda \) is reduced to \( \lambda' \) as:

\[ \lambda' = \lambda e^{-\Delta/\alpha} \]

Eqn 2

For larger rainfall events above \( \Delta \), throughfall (e.g. precipitation minus interception) is linearly related to the depth of the rainfall event (Daly et al., 2008). On average about 35% of bulk rainfall is intercepted by the canopy of J. ashei per storm event and sequentially lost due to evaporation (Owens et al., 2006). The depth of each rainfall event still follows an exponential distribution; however, the mean rainfall depth is reduced to \( (k \alpha) \), where \( k = 0.65 \) (Owens et al., 2006).

In order to predict the pattern of soil moisture attributable to topographic position (e.g. describing lateral surface and subsurface flow from topographically divergent areas such as ridges to topographically convergent areas such as valleys), we further modify the mean rainfall depth \( (k \alpha) \) to depend on each pixel’s TWI, which is defined as:

\[ TWI = \log_e \left( \frac{a_c}{\tan(\beta) + 0.001} \right) \]

Eqn 3

Fig. 1 Comparison of (a) drought-impacted area, defined as pixels with > 25% canopy loss acquired from Schwantes et al. (2017), (b) soil depth and (c) soil texture, both acquired from the SSURGO database (United States Department of Agriculture, 2014), for a watershed in the Edwards Plateau region of Texas.
Upslope contributing area ($a_c$, m$^2$); local slope angle (degrees) ($b$); spatially variable inputs include potential evapotranspiration (PET) attributable to heat load (slope/aspect), lateral redistribution of water using a topographic wetness index, soil texture & depth. Species specific traits include canopy interception, soil moisture associated with incipient stomatal closure ($s_a$), complete stomatal closure ($s_w$), and vulnerability to drought stress ($s_v$), where $s_a$ = hygroscopic point and $s_v$ = field capacity.

Evapotranspiration, ET($s$), accounts for losses from both soil evaporation $E_s$ and tree transpiration $T_s$. We assume that for this system, ET($s$) has an upper limit defined by the potential evapotranspiration, PET, which depends on climate conditions and the tree species. We also assume that tree water uptake from the soil declines as a function of water stress. Under water stress, trees will partially close their stomata, and transpire at a reduced rate, up to a point where stomata close completely and transpiration ceases. Following (Laio et al., 2001), we model this process by assuming that trees transpire at a maximum rate above a soil moisture associated with a stress point ($s*$). When soil moisture drops below $s*$, transpiration decreases linearly up to a soil moisture associated with complete stomatal closure ($s_w$). Below $s_w$ only soil evaporation occurs, which we model as decreasing linearly from potential soil evaporation, PE, at $s_w$ to zero at the hygroscopic point, $s_h$, defined as follows:

$$\text{ET}(s) = \begin{cases} \text{PET} + (\text{PET}' - \text{PET}) \frac{s-s_h}{s_w-s_h}, & s_h < s \leq s_w, \\ \text{PET}', & s_w < s < s^*, \\ \text{PET}, & s^* < s \leq 1, \end{cases} \quad \text{Eqn 5}$$

Evapotranspiration also depends on the surface energy budget (Moore et al., 1991). We account for spatial variation in PET, defined as:

$$\text{PET}' = \text{PET} \times \text{HL} \quad \text{Eqn 6}$$

Losses: evapotranspiration and leakage

Rainfall • Intermittent-stochastic daily precipitation

Spatially variable inputs
• Potential evapotranspiration (PET) attributable to heat load (slope/aspect)
• Lateral redistribution of water using a topographic wetness index
• Soil texture & depth

Species specific traits • Canopy interception
• Soil moisture associated with (1) incipient stomatal closure ($s_a$), (2) complete stomatal closure ($s_w$), and (3) vulnerability to drought stress ($s_v$) where $s_a$ = hygroscopic point and $s_v$ = field capacity.

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by using a heat load index (HL), which accounts for potential direct incident radiation and temperature differences attributable to aspect and steepness of slope (McCune & Keon, 2002; Evans et al., 2014). Higher values of PET are associated with greater radiation (e.g. south-facing slopes) and warmer afternoon temperatures (e.g. western-facing slopes).

In order to differentiate potential soil evaporation (PE) from potential transpiration, we use the fraction of solar radiation that the canopy intercepts, defined as:

\[ \psi_f = 1 - e^{-k_f \times \text{LAI}} \quad \text{Eqn 7} \]

where LAI represents leaf area index and \( k_f \) is a light extinction coefficient (Landsberg, 1986; Norman & Campbell, 1989). The higher this vegetation factor \( (h_i) \), the less PET is partitioned into PE, following:

\[ \text{PE}' = \text{PET}' \times (1 - \psi_f) \quad \text{(8)} \]

We measured LAI using a LAI-2200C Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA) during July 2016 at Colorado Bend State Park, in Central Texas. All measurements were taken at twilight, to minimize changing sky-conditions and scattering errors. We used a 45° view cap and masked out the outermost ring. Measurements were taken every 1 m, along 10 transects, each 10 m in length. The average LAI for stands of \( J. \text{ ashei} \) was 2.92 ± 0.46 (± SD). We used a \( k_f \) for juniper of 0.37 from Kiniry (1998).

The soil moisture value at which stomata start to close \( (s^*) \), and the soil moisture at which stomata close completely \( (s_w) \), both depend on tree species and soil texture. We obtain the relative soil moisture, \( s \), for a corresponding soil water potential, \( \Psi_s \), using soil water retention curves, as defined in Clapp & Hornberger (1978), as follows:

\[ \Psi_s = \Psi_{sw} s^{-b} \quad \text{Eqn 9} \]

\( (\Psi_s \text{ and } b, \text{ experimentally derived parameters that vary with soil texture). The relative soil moisture for the hygroscopic point, \( s_h \), and the field capacity, \( s_c \), can be found using Eqn 9 and the following respective soil water potentials: \( \Psi_{sh} = -10 \text{ MPa (Laio et al., 2001)} \) and \( \Psi_{sc} = -0.033 \text{ MPa (Hudson, 1994)} \). To define \( \Psi_{sw} \) we assume that stomata start to close when the soil water potential reaches a point associated with 12% loss of hydraulic conductance in the leaves, \( P_{12} \), \(-1.0 \text{ MPa for J. ashei (Johnson et al., 2016)} \). We used the \( P_{12} \) or air-entry point, because it represents the point on a leaf hydraulic vulnerability curve (see Fig. 3b) where loss of conductance increases substantially (Domenc & Gartner, 2001). We define \( \Psi_{aw} \) by assuming that stomata close completely when the soil water potential reaches the turgor loss point, TLP, for \( J. \text{ ashei} \), which is \(-3.8 \text{ MPa (Johnson et al., 2018a)} \). This TLP is associated with a 99.8% loss of leaf hydraulic conductance (see Fig. 3b). Also, \( s^* \) and \( s_w \) represent the soil moisture associated with the start of stomatal conductance reduction and near-zero stomatal conductance, respectively (Fig. 3a) using data from Johnson et al. (2018b), and described further in Methods S2 and Table S1.

Soil properties were obtained from the Soil Survey Geographic (SSURGO) database (United States Department of Agriculture 2014). We computed area- and depth-weighted averages of percentage sand, clay and silt for each soil polygon, whereas soil depth \( (Z_s) \) was acquired directly. Based on these soil texture observations, we classified each soil polygon as one of 12 United States Department of Agriculture (USDA) soil classes. The experimentally derived parameters for the soil water retention curves, \( \Psi_s \) and \( b \), the saturated hydraulic conductivity, \( K_s \), and the porosity, \( n \), were estimated using the USDA soil type classifications, following Clapp & Hornberger (1978), Daly et al. (2004) and

Fig. 3 Justification for selecting parameters associated with incipient and complete stomatal closure: (a) Field observations of average stomatal conductance for Juniperus ashei as a function of soil moisture, where soil moisture for a silty clay was derived by assuming that measured pre-dawn leaf water potential was equivalent to soil water potential. These field measurements for 5 d in summer 2013 were taken for \( J. \text{ ashei} \) in central Texas by Johnson et al. (2018b). Each point represents a daily average; error bars represent standard errors associated with variability between individuals and time of day; and the blue line shows the lagged recovery following a time-period of near zero stomatal conductance observed in July, despite rain returning in August (Johnson et al., 2018b). (b) Percentage loss of leaf hydraulic conductivity in \( J. \text{ ashei} \). The \( P_{12} \) or air entry point was chosen for the incipient stomatal closure point \( (s^*) \). The turgor loss point (TLP) was chosen to represent complete stomatal closure \( (s_w) \). Data reproduced with permission from Johnson et al. (2016).
Laio et al. (2001). Lastly, we assume that the soil hydraulic conductivity, $K_s$, follows an exponential decay from $K_s$, at $s=1$ to zero, at $s=s_0$:

$$K(s) = L(s) = \frac{K_s}{e^{P(s)}} - 1\left[e^{P(s)} - 1\right], \quad s_0 < s \leq 1$$

Eqn 10

where $\beta$ depends on the soil texture and is equal to $2b+4$ and $b$ is defined in Eqn 9 (Laio et al., 2001).

Static and dynamic water stress

Our objective was to model tree water stress in a semi-arid ecosystem and evaluate factors contributing to tree mortality. Although some isohydic species tend to have greater mortality following periods of near-zero gas exchange, Juniperus mortality likely occurs with hydraulic failure, especially in the absence of pathogens (Plaut et al., 2012); therefore, we define a new soil moisture level below the point of near-zero gas exchange, at which a tree is under severe stress and vulnerable to mortality, $s_m$. We define $P_{sm}$ as the soil water potential associated with a 50% loss in hydraulic conductivity in the roots, root $P_s$ which is $-9.5$ MPa for J. ashei (Johnson et al., 2016). Brodribb et al. (2010) found that stem $P_s$ correlated with lethal water potential thresholds across four conifer species. Instead of using stem $P_s$, we used the root $P_s$ as $P_{sm}$, because roots are often more vulnerable to cavitation compared to shoots, especially in conifers (Kavanagh et al., 1999). Moreover, the root $P_s$ acquired from Johnson et al. (2016) was nearly identical to modeled critical soil water potential, representing the point to which J. ashei could no longer transport water, as modeled by Johnson et al. (2018b) using the Terrestrial Regional Ecosystem Exchange Simulator model (Sperry et al., 1998; Mackay et al., 2015). The stem $P_s$, $-13.1$ MPa, (Willson et al., 2008), and root $P_s$, $-9.5$ MPa, are much lower than the leaf $P_s$ of $-1.66$ MPa (Johnson et al., 2018b), likely due to the hydraulic vulnerability segmentation hypothesis, which suggests that distal portions (e.g., leaves) will embolize first at less negative pressures to avoid hydraulic impairment in the stems/roots (Tyree & Ewers, 1991; Johnson et al., 2016).

We adapt the static water stress equations developed by Porporato et al. (2001), and define static water stress, $\zeta$, as zero at $s>s_m$ to approaching 1 as $s$ approaches the hygroscopic point, $s_h$:

$$\zeta(t) = \frac{s_m - s(t)}{s_m - s_h}, \quad s_b < s(t) \leq s_m$$

Eqn 11

We expect that larger deviations from $s_m$ would result in higher probabilities of tree mortality. Derivatives for computing the probability distribution for the static water stress, $\zeta$ (Eqn S3), as well as the mean static water stress, $\bar{\zeta}$ (Eqn S6), and the mean static water stress given that the tree was under stress, $\bar{\zeta}^s$ (Eqn S7), can be found in the Supporting Information.

In order to predict tree vulnerability to drought-induced tree mortality, we calculate the dynamic water stress $\tilde{\theta}$ as follows:

$$\tilde{\theta} = \left\{ \begin{array}{ll} \left(\frac{s_{sm}}{s_{sm}}\right)^{1/\bar{m}} & \text{if } \zeta \geq T_{sm} < T_{seas} \\ 1 & \text{otherwise,} \end{array} \right.$$  

Eqn 12

$\tilde{\theta}$ was adapted from the original equation proposed by Porporato et al. (2001) by incorporating $\zeta$ and two crossing properties below the soil moisture threshold associated with severe water stress and potential mortality, $s_m$. The two crossing properties include: $\bar{m}$, the average number of crossings below $s_m$, and $T_{sm}$ the average time spent below $s_m$. As such, dynamic water stress incorporates mean intensity, duration and frequency of soil water deficits associated with crossings below root $P_s$. We can obtain analytical solutions for both $T_{sm}$ and $\bar{m}$. Full solutions are in the Supporting Information, Eqns S8 and S9, respectively. We used the full year as the duration of the growing season ($T_{seas}$), because J. ashei is an evergreen species, and the model was run at a 30-m spatial resolution.

Historical and future projections of water stress

Historical, 1980–2015, spatially interpolated 4-km gridded daily precipitation and monthly potential evapotranspiration calculated using Penman–Monteith for a grass reference surface, PET, were acquired from gridMET (Abatzoglou, 2013). We used spatial averages across the watershed for annual PET, the mean rainfall depth, $z$, and the average time between rainfall events, $1/\lambda$. For a similar juniper-dominated woodland/savannah in the Edwards Plateau of Texas, Heilman et al. (2014) found an average annual PET of $69$ cm from 2005 to 2009, whereas PET estimates in this region were $176$ cm according to gridMET; therefore, we applied a plant correction coefficient of $0.39$. This value was similar to expected crop coefficients for trees, which range from $0.4$ to $1.0$ (Allen et al., 1998). The PET for J. ashei was calculated by multiplying the crop coefficient, $0.39$, by PET acquired from gridMET (Abatzoglou, 2013).

We also acquired downscaled (4-km) climate projections from the coupled model intercomparison project, CMIP5, under two representative concentration pathways, RCP, 4.5 and 8.5 trajectories from 2006 to 2099 for PET and precipitation (Abatzoglou & Brown, 2012). Of 20 global climate models (GCMs) that we considered, we selected 10 GCMs that showed the best performance in projecting historical annual precipitation values (1980–2005) for our study watershed, considering mean absolute error (MAE) in annual precipitation. We again took spatial averages across the watershed for future annual projections of PET, $z$ and $\lambda$. We then examined historical (1980–2015) and future projections of dynamic water stress (2006–2099) for models with and without landscape heterogeneity.

Accuracy assessments

The soil water balance model was run for each 30-m grid cell within the watershed, to obtain spatially explicit estimates of tree water stress. We then compared our modeled results forced using PET, $z$ and $\lambda$ values for 2011 to remotely sensed 30-m drought-impacted area maps for 2011 from Schwantes et al. (2017), where
areas of drought-impact were defined as having > 25% canopy loss. We first aggregated both modeled results and observations of drought-impacted area to hydrologically similar but noncontiguous stands of *J. ashei*, similar to Tai *et al.* (2017). Hydrologically similar stands, $n = 24$, were defined as stands with similar aspects, NE, $-45^\circ$ to $135^\circ$ vs SW, $135^\circ$ to $315^\circ$; soil depths, $< 100$ cm vs $> 100$ cm; soil texture, silty clay, clay loam or other; and topographic divergence vs convergence, TWI below or above the mean, respectively. Following aggregation, we used linear regressions to compare modeled outputs to observations of drought-impacted areas.

We also identified stands of spatially contiguous pixels of two classes: drought-impacted vs homogenous live canopy. Pixels were considered contiguous if one of eight neighboring cells was the same class. We then compared explanatory power (e.g. Cragg and Uhler’s pseudo $R^2$) for logistic regressions in predicting whether a stand was either drought-impacted or homogenous live canopy, using dynamic water stress as the continuous predictor variable. Dynamic water stress represents a probability of tree vulnerability to drought. Therefore, in order to select a threshold of dynamic water stress that best distinguished drought-impacted stands from live canopy stands, we used receiver operating characteristic (ROC) curves (Sing *et al.*, 2005). For multiple cut-off values of modeled dynamic water stress, ROC curves plot true positive rate (TPR, accurately predicting a drought-impacted stand) against true negative rate (TNR, accurately predicting a homogenous live canopy stand). The cut-off value that balanced TPR and TNR was chosen, using 10-fold cross-validation. To test whether accuracy improved when considering average dynamic water stress in larger stands, we sequentially removed stands below a certain size threshold. Other studies have found that aggregation up to a 100-m pixel (i.e. 1 ha) was necessary to improve correlations between modeled and observed soil moisture (Pellenq *et al.*, 2003). The water stress model was solved using MATLAB; statistical analysis was conducted in R; and spatial analysis was performed using ArcGIS and PYTHON.

**Results**

Comparing modeled water stress to observations of drought-impacted area

Using our dynamic water stress model for each 30-m pixel across a watershed in central Texas, we found that canopy loss from drought was greatest in areas of shallow soils, on hillslopes with low values of TWI, and on southwestern-facing aspects (Fig. 4). We started with models that only had spatially explicit soil conditions, and then added parameters associated with lateral

*Fig. 4* Comparison of spatially explicit input variables of (a) soil depth, (b) topographic wetness index (TWI) and (c) heat load index to (d) a 30-m remotely sensed drought-impacted area map. We also present modeled estimates of mean dynamic water stress for scenarios including processes specific to (e) heterogeneous soil inputs, (f) lateral redistribution of water using TWI ($f = 1$) and (g) spatially variable potential evapotranspiration using a heat load index, accounting for radiation and temperature differences attributable to aspect. Using a cut-off value of dynamic water stress (defined in Table 2), we also show a binary water stress map (h), which is directly comparable to observed canopy loss (d).
Redistribution and then spatially explicit PET driven by radiation and temperature differences attributable to aspect. Spatially distributed inputs, characterizing soil conditions, lateral water flow, and PET, all drove patterns of dynamic water stress across the landscape. By increasing model complexity, modeled dynamic water stress had higher spatial concordance with remotely-sensed observations of drought-impacted area (Fig. 4).

Modeled dynamic water stress varied across two important environmental gradients. As expected, dynamic water stress decreased with increasing soil depth, as simulated with the following assumptions: constant clay loam soil texture, constant PET and no lateral flow of water (Fig. 5a). Directly matching model predictions, observations of drought-impacted area also decreased with increasing soil depth. Furthermore, dynamic water stress decreased with increasing values of TWI (Fig. 5b). The model was forced using a constant clay loam soil texture and average soil depth. Observations of drought-impacted area aggregated up to 2-unit bins of TWI, also decreased with increasing TWI, following modeled dynamic water stress.

In order to test the accuracy in predicting observed values of canopy loss during the 2011 drought year, we first aggregated modeled results and observed drought-impacted area in 24 hydrologically similar but noncontiguous stands (Table 1). We compared explanatory power for linear regressions of observations of percentage drought-impacted area and four modeled outputs. We found that the explanatory power for dynamic water stress increased, as model complexity increased. When only considering spatial variability of soils, adjusted $R^2$ was equal to 0.76; however, when including lateral flow of water and spatially variable PET from radiation and temperature differences, the explanatory power increased to 0.82 (Table 1).

Second, we tested how well modeled dynamic water stress differentiated spatially contiguous J. ashei drought-impacted stands compared with homogenous live canopy stands. We compared Cragg and Uhler’s pseudo $R^2$ for logistic regressions and percentage accuracy for a threshold distinguishing the two types of stands using ROC curves (Fig. 6; Table 2). We also tested the
influence of only including stands above a certain stand size class. There seemed to be an inflection point, where percentage accuracy and explanatory power increased dramatically for stands >1 ha and started to level off at around 2 ha (Fig. 6). Also, increasing model complexity resulted in higher accuracy and higher explanatory power. For example, models that only included spatially variable soil conditions reached an accuracy of 60%, when considering stands >2 ha; however, when including spatially variable inputs related to soil, lateral flow of water and radiation/temperature effects, the accuracy increased to 72% (Table 2). Furthermore, increasing the amount of lateral redistribution of water, by increasing \( f \), led to improvements in model accuracy and higher explanatory power. However, as \( f \) got larger and approached 1, large changes in \( f \) only led to minimal improvements in model accuracy (Fig. 6). A cut-off value of 0.28 for dynamic water stress was most successful at distinguishing homogenous live canopy stands from drought-impacted stands (Table 2). We therefore used this cut-off value and \( f = 1 \), to determine the percentage of the landscape that surpassed a dynamic water stress value associated with canopy loss for both historical and future climate projections. The cut-off value was not dependent on the size of stands considered (Fig. 6c).

Projecting dynamic water stress through the 21st century
In order to understand how dynamic water stress is projected to change in the future, we selected 10 GCMs that showed the lowest MAE in predicting mean annual precipitation (Table S2). For several years in the 21st century and across several of the GCMs, the mean rainfall depth, \( a \), and the time between rainfall events, \( 1/k \), surpassed drought conditions that were more severe than the 2011 drought year (Fig. 7a,b). PET for \( J. ashei \) increased dramatically compared to historical averages for both RCP 4.5 and even more so for RCP 8.5 (Fig. 7c). Ensemble means of dynamic water stress across 10 GCMs showed that average dynamic water stress increased over the 21st century (Fig. 8a) for both RCP 4.5 and 8.5 scenarios. Furthermore, the percentage of the landscape surpassing a threshold of dynamic water stress associated with mortality increased through the 21st century (Fig. 8b). For models forced using no landscape heterogeneity, the maximum percentage of the area impacted by model construction was 100% for the most severe droughts projected in the 21st century. However, when landscape heterogeneity was included, the maximum percentage area impacted in the future was c. 90% for both RCP 4.5 and 8.5 (Table 3).

Fig. 6 Accuracy in distinguishing drought-impacted stands from homogenous live canopy stands of Juniperus ashei above a certain patch area threshold (x-axis): (a) Cragg and Uhler’s pseudo R² for logistic regressions, (b) percentage accuracy and (c) the dynamic water stress cut-off defined using receiver operating characteristic (ROC) curves. Each line represents a different model with multiple levels of complexity, including only spatially variable soil conditions (soils), lateral redistribution of water (soils + topographic wetness index (TWI)) with the constant, \( f \), ranging from 0.4, 0.6, 0.8 and 1.0, and spatially variable potential evapotranspiration (PET) due to radiation/temperature differences (soils + TWI + heat load). The number of stands ranged from c. 42 000 when including all size patches to c. 1000 when including only patches > 8 ha.
Table 2 Summary of logistic regression coefficients and outputs of the receiver operating characteristic (ROC) curve analysis for models of increasing complexity, testing the capacity of model outputs in distinguishing drought-impacted stands from homogenous live canopy stands

<table>
<thead>
<tr>
<th>Model output</th>
<th>Soils</th>
<th>Soils + LR</th>
<th>Soils + LR + H</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$R^2$</td>
<td>$P$</td>
<td>AIC</td>
</tr>
<tr>
<td>&gt;1 ha</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\theta$</td>
<td>0.08</td>
<td>***</td>
<td>7715</td>
</tr>
<tr>
<td>$\zeta^c$</td>
<td>0.08</td>
<td>***</td>
<td>7717</td>
</tr>
<tr>
<td>$n_{lm}$</td>
<td>0.08</td>
<td>***</td>
<td>7718</td>
</tr>
<tr>
<td>$t_{sm}$</td>
<td>0.08</td>
<td>***</td>
<td>7722</td>
</tr>
<tr>
<td>&gt;2 ha</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\theta$</td>
<td>0.10</td>
<td>***</td>
<td>4570</td>
</tr>
<tr>
<td>$\zeta^c$</td>
<td>0.10</td>
<td>***</td>
<td>4574</td>
</tr>
<tr>
<td>$n_{lm}$</td>
<td>0.10</td>
<td>***</td>
<td>4573</td>
</tr>
<tr>
<td>$t_{sm}$</td>
<td>0.10</td>
<td>***</td>
<td>4577</td>
</tr>
</tbody>
</table>

Model outputs included dynamic water stress ($\theta$), static water stress given a tree was under stress ($\zeta^c$), the average number of crossings ($n_{lm}$) below root $P_{50}$ (50% hydraulic conductivity lost), and the average time spent ($t_{sm}$) below root $P_{50}$, where $f=1$, and the size of drought-impacted or homogenous live canopy stands of J. ashei was either > 1 ha or > 2 ha. *** $P <$ 0.001; Soils, soil texture and depth; LR, lateral redistribution using topographic wetness index (TWI); H, heat load. $R^2$, Cragg and Uhler’s pseudo $R^2$; % acc, percentage accuracy in differentiating drought-impacted vs live canopy stands using ROC curve analysis and 10-fold cross-validation.

Discussion

Incorporating topography in models of tree water stress

Model estimates of dynamic water stress compared well with remotely-sensed observations of drought-impacted area from the 2011 drought. When using dynamic water stress to distinguish between drought-impacted stands vs homogenous live canopy stands > 2 ha, we found that accuracy increased from 60% for models including only spatially variable soil conditions to 72% for models considering soils and topography, including lateral redistribution of water using a topographic wetness index (TWI) and spatially variable potential evapotranspiration (PET) attributable to radiation/temperature differences (Table 2). Tai et al. (2017) also found that including topography to approximate lateral redistribution improved predictions of Aspen, Populus tremuloides, mortality in Colorado. Our approach expands upon Tai et al. (2017), by providing an alternative framework that cohesively integrates plant physiological thresholds limiting hydraulic capacity (Fig. 3b) and landscape processes. In the absence of widespread observations of leaf water potential thresholds for tree vulnerability to drying soil, the prediction of large-scale response to drought seems difficult. Our model requires simple physiological traits that are consistent with known mechanisms of plant hydraulic failure and that are routinely measured when investigating plant response to drought (e.g. air entry, 50% loss in hydraulic conductivity in the roots (root $P_{50}$) and turgor loss points derived from cavitation and pressure–volume curves, respectively).

When aggregating modeled results to larger stands (> 1 ha; Fig. 6), we observed improved accuracy, which could be attributable to hydrological processes acting across pixels. The topographic index, TWI, was used to directly relate the land surface to lateral water flow; however, the land surface may not be the best predictor of belowground processes. As an example, variations in the water table depth could be lower compared to variations in the land surface elevation (Wolock & Price, 1994). Also, the minimum size map delineation for the SSURGO soil database ranges from 0.4 to 4 ha; a much coarser resolution than the 30-m digital elevation maps used to derive TWI. Moreover, soil maps often show sharp, unrealistic changes of soil texture and soil depth between neighboring soil polygons (Zhu & Mackay, 2001); aggregating across stands may smooth these transitions. Lastly, at fine spatial scales, tree mortality could appear stochastic due to a variety of mechanisms that are not included in most models (e.g. insects and pathogens, harvesting/land management and plasticity of plant traits). For these reasons, accuracy improved as we aggregated modeled results to larger stands, until a threshold of c. 2 ha was reached. Past this threshold of 2 ha and up to 8 ha, accuracy did not increase substantially (Figs 5, 6).

Limitations

The modeling framework had a few important limitations. Juniperus ashei is an evergreen species; therefore, we defined the growing season as the full year, but did not include seasonal differences when modeling rainfall stochastically. Incorporating seasonality could improve our ability to model tree water stress (Viola et al., 2008; Feng et al., 2017). We did not consider water inputs from the deep regolith, which could provide additional sources of water (Fellows & Goulden, 2013). A few J. ashei individuals have been observed to access water in caves up to 8-m below the soil surface in central Texas (Jackson et al., 1999). When examining tree water stress in the future, we did not consider effects associated with increased water use efficiency (WUE) from elevated atmospheric CO$_2$ concentrations. However, an experiment examining the interactive effects between elevated CO$_2$ and drought found that elevated CO$_2$ did not delay time to mortality for two gymnosperm species (Duan et al., 2015). If
Fig. 7 Comparison of how climate parameters vary with annual precipitation: (a) $\mu$, mean rainfall depth (mm), (b) $1/\tau$, time (days) between rainfall events, and (c) potential evapotranspiration (PET) for *Juniperus ashei*, using spatial averages across all areas in the watershed. We include both historical gridMET climate data: 1980–2015 (Abatzoglou, 2013) and future MACA climate projections: 2020–2099, from two representative concentration pathway trajectories, RCP 4.5 and 8.5, acquired from Abatzoglou & Brown (2012). Each point represents climate parameters for each year from 2020 to 2099, for each of the 10 global climate models (GCMs).

Fig. 8 Comparison of how dynamic water stress has changed over the past 35 yr (1980–2015) (Abatzoglou, 2013) and was projected to change in the future 2006–2099, using climate data from two representative concentration pathway trajectories, RCP 4.5 and 8.5 (Abatzoglou & Brown, 2012): (a) spatial averages of dynamic water stress across the watershed with *Juniperus ashei* cover and (b) percentage area drought-impacted (e.g. percentage of the landscape that surpassed the dynamic water stress threshold of 0.28 associated with canopy loss during the 2011 drought year, defined in Table 2). The dark line represents the average of 10 global climate models (GCMs), the colored shading: the standard deviation, and the gray shading: the range.
projected future droughts are too severe and cause complete closure of stomata, then the benefit of elevated CO₂ will have no effect on photosynthesis (Franks et al., 2013). Also, in some species, elevated CO₂ can cause changes in plant hydraulics that lead to greater potential for drought stress (Domec et al., 2017). Although we found that stomatal conductance was linearly related to soil moisture (Fig. 3a), J. ashei showed a lagged recovery in gas exchange, despite an increase in rainfall during August (Johnson et al., 2018b); our model does not account for delayed recovery from any hydraulic impairment. By not accounting for memory of impairment, we could be underestimating water stress, especially given the potential for consecutive droughts to increase in frequency with climate change. Lastly, models that can also account for re-growth/recovery of vegetation could provide additional insight on how landscape heterogeneity influences tree survival and recovery following drought (Tague et al., 2013; Vicente-Serrano et al., 2015).

**Table 3** Comparison of future water stress projections of dynamic water stress for models with and without landscape heterogeneity, compiling dynamic water stress across 10 model runs, each forced with climate projections from 10 global climate models (GCMs) from 2006 to 2099, and two representative concentration pathways (RCP), 4.5 and 8.5

<table>
<thead>
<tr>
<th>Landscape heterogeneity</th>
<th>No landscape heterogeneity</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>RCP 4.5</strong></td>
<td></td>
</tr>
<tr>
<td>Dynamic water stress</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>0.096</td>
</tr>
<tr>
<td>SD</td>
<td>0.079</td>
</tr>
<tr>
<td>Range</td>
<td>[0.000, 0.379]</td>
</tr>
<tr>
<td>Landscape past threshold (%)</td>
<td>5.5%</td>
</tr>
<tr>
<td>Mean</td>
<td>17.0%</td>
</tr>
<tr>
<td>Range</td>
<td>[0%, 90.5%]</td>
</tr>
<tr>
<td>No. of crossings at 100%</td>
<td>0</td>
</tr>
<tr>
<td><strong>RCP 8.5</strong></td>
<td></td>
</tr>
<tr>
<td>Dynamic water stress</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>0.104</td>
</tr>
<tr>
<td>SD</td>
<td>0.078</td>
</tr>
<tr>
<td>Range</td>
<td>[0.000, 0.362]</td>
</tr>
<tr>
<td>Landscape past threshold (%)</td>
<td>5.4%</td>
</tr>
<tr>
<td>Mean</td>
<td>16.2%</td>
</tr>
<tr>
<td>Range</td>
<td>[0%, 90.0%]</td>
</tr>
<tr>
<td>No. of crossings at 100%</td>
<td>0</td>
</tr>
</tbody>
</table>

Failure to capture landscape heterogeneity in models could limit our capacity to accurately predict forest response to a changing climate. Tree mortality is often observed across local stress gradients within a species range, rather than at trailing range edges (Gitlin et al., 2006). Therefore, when projecting future water stress, it is important to account for the fact that not all landscape positions are equally stressful. For our watershed in central Texas, models only predicted minimal buffering of tree water stress through the 21st century. However, different watersheds would likely have different buffering capacities, depending on the landscape complexity.

**Modeling future tree water stress**

Using projected climate data from 10 global climate models (GCMs), we found that dynamic water stress was forecasted to increase through the 21st century due to both projected increases in PET and changes in the timing and amount of rainfall. Future projections of rainfall are highly uncertain; regional processes are often not included in many GCMs, causing projections of precipitation extremes to be less accurate at regional scales (Burke et al., 2006; Jentsch et al., 2007). However, there is high confidence in projected temperature increases; this warming also will lead to higher atmospheric moisture demand and PET (Fig. 7c). Higher projected PET values are likely the main driver of dynamic water stress increasing throughout the 21st century (Fig. 8a). When comparing models with and without landscape heterogeneity, it is important to consider that landscape heterogeneity allows for the existence of both stressful (e.g. drier, hotter) and favorable (e.g. wetter, cooler) landscape positions for tree growth. Not considering landscape heterogeneity results in the whole landscape experiencing the same level of water stress and requiring a more severe drought to cause stress. With landscape heterogeneity across a gradient of drought severity, some stress appears more readily, compared to the uniform landscape, (e.g. in hotter, drier landscape positions even under moderate drought). However, some refugia still remain under the most severe droughts. Therefore, when landscape heterogeneity is included, the range of water stress is lower due to buffering from cooler, mesic landscape positions during severe drought.

By including landscape heterogeneity in models, we identified microrefugia capable of buffering against water stress, allowing tree survival even during the most severe drought projected in the 21st century. For this study area, these microsites included areas with deep soil, substantial contributing area and northeastern-facing aspects. When considering outputs from 10 GCMs across the 21st century (2006–2099), the maximum percentage area of the watershed surpassing a dynamic water stress threshold associated with canopy loss was 100% for models with no landscape heterogeneity, compared to c. 90% for models including landscape heterogeneity (Table 3). For the most severe drought, only c. 10% of the landscape did not pass a dynamic water stress threshold associated with tree mortality in 2011. This supports the hypothesis of Allen et al. (2015) that the potential for microsites to buffer may be overwhelmed under the severe droughts and heatwaves projected under climate change. Alternatively, microsites might exist across the landscape that are too small to be adequately captured by the spatially distributed input variables of soil conditions and topography included in this model. For example, the SSURGO soil database does not identify areas with unique soil conditions below the minimum size map delineation of 0.4–4 ha. By using finer-scale digital elevation models (DEMs) and soil maps we could potentially identify additional microsites, capable of providing buffering against future water stress.
seeds can disperse from surviving trees (Lloret et al., 2012); these sites could then be prioritized for conservation (McLaughlin et al., 2017). However, if droughts become too severe and leave only isolated stands, this isolation may limit dispersion and the potential for a species to migrate to keep pace with changing climate conditions (Hewitt & Kellman, 2004; Gitlin et al., 2006; Lazarus & McGill, 2014).

Conclusion

We modeled dynamic water stress across a landscape at a 30-m spatial resolution by incorporating plant hydraulic thresholds in relation to water deficit and spatial heterogeneity of soil conditions (e.g. texture and depth), surface/subsurface lateral water flow using a topographic index, and PET attributable to radiation and temperature differences. Our model simplifies the plant hydraulics to maintain analytical tractability. As such, the model is currently computationally efficient to run at regional scales, while still accounting for local water stress gradients. Landscape heterogeneity typically is not considered in DGVMs, with coarse spatial resolutions of c. 10^3 to 10^5 km^2 (e.g. Moorcroft, 2006). Local water stress gradients with high spatial variability, combined with the nonlinear nature of mortality processes, suggest that modeling an average tree growing in an average environment will not give the same water stress predictions as a model that incorporates spatial heterogeneity of the environment (Levin et al., 1997; Moorcroft, 2006). We found that including topographically variable input parameters improved our ability to predict spatial patterns of canopy loss observed during the 2011 drought. Furthermore, the model projected increases in mean dynamic water stress throughout the 21st century with the use of key physiological parameters of drought-induced vascular damage. Models with landscape heterogeneity showed some buffering capacity, but it was limited. The landscape can act as a buffer against water stress, but depending on the topography of the watershed, the buffering capacity has the potential to be overwhelmed if future droughts are too severe. By incorporating landscape heterogeneity in models, we can test whether landscapes can act as effective buffers against future droughts and heatwaves projected under climate change.

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Author contributions

A.M.S., A.J.P., N.P. and A.P. contributed to model development; A.M.S., D.M.J. and J-C.D. assisted with model parameterization; and A.M.S., A.J.P., J.J.S., D.M.J., J-C.D., R.B.J., N.P. and A.P. contributed to the design of the study and writing of the manuscript.

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