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# Integrating fire effects on vegetation carbon cycling within an ecohydrologic model

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ABSTRACT

Wildfire affects landscape ecohydrologic processes through feedbacks between fire effects, vegetation growth and water availability. Despite the links between these processes, fire is rarely incorporated dynamically into ecohydrologic models, which couple vegetation growth with water and nutrient fluxes. This omission has the potential to produce inaccurate estimates of long-term changes to carbon and water cycling in response to climate change and management. In this study, we describe a fire-effects model that is coupled to a distributed ecohydrologic model, RHESSys, and a fire-spread model, WMFire. The fire-effects model has intermediate structural complexity so as to be commensurate with the ecohydrologic model. The fire-effects model includes processes for litter and coarse woody debris consumption, processes for fire-associated vegetation mortality and consumption, and takes into account canopy structure (i.e. ladder fuels) for propagation of fire effects into a forest canopy. We evaluated the model in four Western U.S. sites representing different vegetation, climate, and fire regimes. The fire-effects model was able to replicate patterns of expected fire effects across different ecosystems and stand ages without being tuned to produce them; an emergent property of the model. Fire effects of shrubland and understory vegetation varied with surface fire intensity, by design, and fire effects in forest canopies were sensitive to parameters associated with the buildup of litter and understory ladder fuels. These findings demonstrate that the fire-effects model provides an effective tool for evaluating the post-fire changes to physical and ecological processes. Future work will project future fire regimes and improve understanding of watershed dynamics under climate change and land management via the simulation of the fire-effects model with fire spread and ecohydrology.

## 1. Introduction

Ecohydrologic models simulate interactions between landscape ecological and hydrological processes. Ecohydrologic models are widely used to assess how climate, land-use change, and land management affect water resources, vegetation health (productivity, growth and mortality), carbon sequestration, and their interactions. Available models vary widely in terms of the processes that are modeled and the level of physical realism with which processes are represented (Fatichi et al., 2016). No known ecohydrologic models, however, explicitly account for disturbances such as wildfire, or such disturbances are prescribed as an exogenous forcing, despite the known strong interactions between wildfire and ecohydrology. Ecohydrologic processes both affect and are affected by wildfire. Wildfire intensity (see fire-related definitions in Table 1) is a function of fuel loads and fuel moisture, which are directly related to ecological processes such as vegetation growth and hydrologic processes such as evapotranspiration (ET). Conversely, wildfire is also a major control on vegetation, affecting species composition and structural variables such as biomass and canopy cover; this further affects ET and water yield through modifications of vegetation (Bart, 2016; Roche et al., 2018). Given this bidirectional relationship between ecohydrology and wildfire, the representation of fire effects on vegetation carbon in ecohydrologic models requires a fully coupled approach where wildfire and its effects co-evolve with ecohydrologic processes (Harris et al., 2016).

Predicting fire effects on vegetation is challenging because fire effects are often not only related to fire intensity, but also to the characteristics and structure of vegetation. Wildfire commonly spreads via surface fuels such as litter and coarse woody debris (Rothermel, 1972). For vegetation that lies in close proximity to the surface fuels (e.g.

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**Table 1**
Wildfire terms: general definitions and specific modeling usage. General definitions derived from NWCG (2006).

| Term | General Definition | Representation in model |
|---|---|---|
| Fire effects | The physical, biological, and ecological impacts of fire on the environment. | Change in carbon (canopy, surface and soil) and nitrogen resulting from simulated fire. |
| Intensity | The rate of heat release per unit time per unit length of fire front (fireline); or per area (reaction). | A surrogate for intensity, the Fire Intensity Index (*FII*) is a normalized index represented as the modeled probability of fire spread (i.e. f(fuel load, relative moisture deficit, wind speed/direction, topographic slope)). |
| Surface fuels | Fuels lying on or near the surface of the ground, consisting of leaf and needle litter, dead branch material, downed logs, bark, tree cones, and low stature living plants. | Coarse woody debris, litter and upper soil carbon stores. |
| Understory | Short stature vegetation (e.g. shrubs, grasses) and young trees. Below an overstory. | Vegetation carbon stores from canopy with height less than 'Understory Height Threshold'. |
| Overstory | Highest vegetation layer, regardless of height. | Vegetation carbon stores from canopy with height greater than 'Overstory Height Threshold'. |
| Ladder fuels | Fuels which provide vertical continuity between strata, thereby allowing fire to carry from surface fuels into the crowns of trees or shrubs with relative ease. | Combination of understory and litter fuels. Higher ladder fuel totals are assumed to more easily propagate fire to the overstory. |
| Canopy height | The vertical measurement of vegetation from the top of the crown to ground level. | Modeled height of the vegetation canopy. The canopy is represented as a big-leaf with no depth. |
| Mortality | Percent of individual plants that are killed during or after a fire. | Proportion of pre-fire vegetation carbon stores that are removed following fire. Removed carbon is either consumed or remains on the surface as fuel. |
| Consumption | The amount of a specified fuel type or strata that is removed through the fire process, often expressed as a percentage of the preburn weight. | Proportion of pre-fire carbon store (overstory, understory, surface) that is removed completely from model. |
| Residual | The amount of killed vegetation that is not consumed and remains on a landscape. | Proportion of pre-fire vegetation carbon that falls to the ground as litter or coarse woody debris. |

grasses, shrubs, forest understories), fire effects are related to vegetation properties and transient states such as moisture content. In forested ecosystems, propagation of fire to the upper forest canopy depends on the relation between understory flame lengths and the distance to the lower branches of the forest canopy, as well as the presence of intermediate height vegetation (i.e. ladder fuels) to bridge the gap. Fire effects are also dynamic; changing as vegetation structures evolve with stand age, disturbance, and management (DeBano et al., 1998).

Most ecohydrologic models treat wildfire as an exogenous forcing. Decisions on the magnitude of wildfire effects are often made subjectively (Tague et al., 2009), although in some cases the decisions could be informed by remote sensing or land surveys (Lentile et al., 2006). Recent work has generated and spread wildfire dynamically in an ecohydrologic model (Kennedy et al., 2017), but to complete the bidirectional coupling between wildfire and the ecohydrologic model, the effect of fire on vegetation needs to be represented effectively.

The design of a fire-effects model that links a fire-spread model with an ecohydrologic model needs to be compatible with both the objectives of the modeling and the data constraints of the models. Canopy structure and ladder fuels are primary controls on fire behavior and corresponding canopy-level effects in forested ecosystems. In order to utilize ecohydrologic models to assess the effects of fuel treatments or climate on fire regimes, the influence of canopy structure on fire effects must be accounted for. However, most established fire effect models that incorporate canopy structure require detailed knowledge about fire behavior, fuel structure and/or vegetation characteristics. Examples include stand-level models with empirical estimates of fuel consumption (Consume; Prichard et al., 2006) and fuel consumption and associated vegetation mortality (FOFEM; Lutes et al., 2012). These models require detailed accounting of the fuel bed commensurate with that required in semi-empirical models of fire spread, such as Rothermel (1972). Such detailed accounting is not accommodated by the existing structure of ecohydrologic models. Landscape-scale models such as Landis II (Sturtevant et al., 2009) and FireBGC (Keane et al., 2011) represent vegetation in more detail than ecohydrologic models including individual trees and age structures used to estimate fire occurrence and effects.

Ecohydrologic models do not generally predict variables at the level of complexity necessary to be represented in existing fire-effects models. Instead, vegetation growth is modeled via ecosystem carbon-cycling submodels that allow vegetation structure to respond to environmental variables and resource availability. These models typically represent vegetation as a set of carbon stores (leaves, stems, roots, non-structural carbohydrate) but do not necessarily translate these carbon stores into structure attributes. For example, individual trees are not represented in the models but rather aggregated approaches are used, as with so-called "big-leaf" models or models that have cohorts of stem size classes. In these models, detailed canopy structure variables, such as bark thickness or spacing between individuals that would be used to calculate fire effects are rarely available. Furthermore, spatially detailed information on weather variables such as wind that are important for fire behavior are not typically included. The computational and parameter costs of including substantially more complexity in canopy structure and micrometeorology submodels in order to account for fire behavior would make ecohydrologic models infeasible for larger watersheds and scenario assessments. Hence, we need a simpler way to represent canopy structure in fire-effects models that are coupled with ecohydrologic models, while retaining enough realism to replicate ecohydrologic processes effectively.

An effective watershed-scale fire-effects model for evaluating vegetation carbon change should be complex enough to respond to key drivers of fire-effects variability, such as stand age, time since most recent fire, and forest management such as fuel treatments, but generalizable enough to operate in multiple ecosystem types, including shrublands, open-canopy forests, and closed-canopy forests and across a range of scales from hillslopes to 3-4$^{th}$ order watersheds. In this paper, we document the development of a fire-effects model for use with an ecohydrologic model that accounts for the structure of vegetation, but does so in a manner that is consistent with the level of detail of the ecohydrologic model. We then use sensitivity analysis to provide insight into model processes and on-the-ground dynamics and relationships. Finally, we test whether the model can replicate expected patterns of vegetation mortality and consumption at different stand ages and in different ecosystems.

## 2. Methods

### 2.1. RHESSys and WMFire

The Regional Hydro-Ecologic Simulation System (RHESSys) is a spatially distributed ecohydrologic model that is used to simulate daily water, carbon and nutrient fluxes in watersheds (see Tague and Band

(2004) with more recent advances to model subroutines described in Tague et al. (2013) and Garcia et al. (2016)). The model is organized hierarchically. Vertical vegetation layers are simulated in patches, the finest spatial resolution. Patches can be of arbitrary size, but often modeled at 30 m, as with this study. Patches are nested within zones that define radiation and meteorological forcing. Zones are nested within hillslopes and watersheds that define lateral redistribution of water and materials.

Each vegetation canopy in RHESSys comprises fine root, coarse root, live and dead stem, and leaf carbon stores along with associated nitrogen stores that vary with species-specific organ stoichiometry. Vegetation height is a species-specific function of stem carbon stores and rooting depth is a species-specific function of root carbon stores. Vegetation canopies are assigned a cover and gap fraction. Incoming shortwave radiation is attenuated with each canopy layer based on leaf area index and canopy fraction. Vegetation photosynthesis is based on the Farquhar Model (Farquhar and von Caemmerer, 1982) and vegetation respiration is based on Ryan (1991) and Tjoelker et al. (2001). Assimilated carbon is allocated to leaves, stems, and roots according to Landsberg and Waring (1997).

Coarse woody debris and litter stores on the ground surface are generated when vegetation undergoes phenological changes or mortality. Coarse woody debris carbon stores are generated from branch and stem turnover. Litter is produced from leaf turnover and the breakdown of coarse woody debris stores. Litter consists of four carbon stores and decay to soil carbon at varying rates. Soil carbon in RHESSys consists of four carbon stores with varying decay rates. Since the effects of wildfire on soil carbon is generally limited due to limited transfer of heat into the soil (Certini, 2005), wildfire was assumed to only affect the shallowest and fastest decaying soil store.

Precipitation in RHESSys is partitioned to rainfall and snowfall based on air temperature. Snowpack is computed from a quasi-energy budget snow model that accounts for the effects of canopy cover on sublimation and melt. Vertical water fluxes in RHESSys include interception, infiltration, and drainage through the rooting and unsaturated zones to a water table. Surface, litter and canopy evaporation, as well as vegetation transpiration, are separately calculated using the Penman-Monteith method (Monteith, 1965).

RHESSys is coupled to a fire-spread model, WMFire (Kennedy et al., 2017). The fire-spread model does not replicate specific occurrences or perimeters of historical fires, but rather aggregates spatial patterns of individual fires along with the seasonality and return intervals characteristic of contrasting fire regimes. This level of complexity is compatible with the time-space scales and process representation in RHESSys. The approach is designed to strike a balance between complexity and the uncertainty of model structure, input data, and parameters (Kennedy and McKenzie, 2016). We aim for a similar balance here in designing a coupled fire-effects model that links the fire-spread model with changes in ecosystem stores of carbon and nitrogen.

Fire spread in WMFire is organized on a pixelated grid that overlays the watershed patch structure in RHESSys. Each month, the number of potential ignitions is drawn from a Poisson distribution and these ignitions are located randomly in the watershed. Successful ignition depends on fuel load and fuel moisture deficit of the chosen pixel. If an ignition is successful, WMFire estimates the probability of subsequent pixel to pixel fire spread ($p_s$) as an aggregate multiplier that combines empirical submodels of the contributions of fuel load $p_s(l)$, fuel moisture deficit $p_s(d)$, slope $p_s(S)$, and wind $p_s(w)$:

$$p_s(l, d, S, w) = p_s(l)p_s(d)p_s(S)p_s(w). \tag{1}$$

The multiplier for fuel load is based on RHESSys patch litter carbon stores and increases with higher loads. The multiplier for fuel moisture is based on the relative moisture deficit (1 – actual evapotranspiration / potential evapotranspiration) of vegetation, making fire spread more likely with higher deficits. The multiplier for slope is based on the direction of fire movement relative to topography, with fire more likely to move upslope than downslope. The multiplier for wind increases when fire spread is oriented in the direction of the wind and at higher speeds, where a dominant wind speed and direction is selected randomly from a distribution estimated from historical weather data.

Output from WMFire includes a map of pixels that have burned and the probability of spread for each burned pixel, but provides no information on how fire alters vegetation structure as represented by RHESSys carbon and nutrient stores associated with each vertical vegetation layer in a given patch. The fire-effects model developed in this study is intended to address this deficiency and complete the bidirectional coupling between fire regimes and ecohydrology.

### 2.2. Fire-effects model

Fire effects are modeled as a function of surface fire intensity and canopy structure. Surface fire intensity is modeled classically as a function of the available fuel loading, the heat content, and the rate of spread (Byram, 1959). WMFire provides a measure of the probability of spread for a given patch, related to wind speed and direction, relative moisture deficit, fine fuel load, and topography. In our initial fire-effects implementation we use the WMFire-calculated probability of spread ($p_s$) as a normalized index of surface fire intensity, the Fire Intensity Index (*FII*). The Fire Intensity Index acts a proxy for surface fire intensity given that they are related to a similar set of variables and it increases monotonically with fire intensity. Consequently, if a patch experiences a fire with a higher probability of spread (for example, upslope movement in the direction of wind with high litter loads and high fuel deficits), we assume that the Fire Intensity Index will also be higher. We use this formulation of Fire Intensity Index as a starting point for the fire-effects model.

The general structure of the fire-effects model is shown in Fig. 1. When fire enters a patch in the model, fire effects are computed separately for surface, understory, and overstory carbon stores. As noted previously, we also alter nitrogen stores by using parameterized stoichiometric relationships in different plant organs or litter and soil organic material. For the remainder of the paper we describe changes to carbon stores but note that nitrogen stores are also modified. Surface carbon for each of the four litter stores ($L1_c$, $L2_c$, $L3_c$, $L4_c$), the top soil layer store ($S1_c$), and coarse woody debris ($CWD_c$) are consumed at a fixed proportion based on formulas adapted from the CONSUME model (Prichard et al., 2017):

$$L1_{Cons} = 1.0{*}L1_c \tag{2a}$$

$$L2_{Cons} = 1.0{*}L1_c \tag{2b}$$

$$L3_{Cons} = 0.85{*}L1_c \tag{2c}$$

$$L4_{Cons} = 0.71{*}L4_c \tag{2d}$$

$$S1_{Cons} = 0.71{*}S1_c \tag{2e}$$

$$CWD_{Cons} = 0.34{*}CWD_c \tag{2f}$$

where $L1_{Cons}$, $L2_{Cons}$, $L3_{Cons}$, $L4_{Cons}$, $S1_{Cons}$, and $CWD_{Cons}$ is the amount of carbon ($gC/m^2$) consumed in the respective carbon store.

The fire-effects model works with one or two canopy layers. As RHESSys is a multi-layer gappy big-leaf model, each vegetation canopy within a patch is associated with a single top-of-canopy height. The fire-effects model includes two height thresholds that are used to determine the proportion of a given canopy that is classified as overstory or understory vegetation (Fig. 1). Vegetation canopies with a height above the upper threshold ($h_o$) are classified as overstory vegetation. Vegetation canopies that have a height below the lower threshold ($h_u$) are classified as understory vegetation. Vegetation canopies with heights between the thresholds are considered to represent overstory and understory proportionally based on the relative distance between the height thresholds. A single vegetation canopy may be classified as an understory and an overstory at different times during its growth cycle,

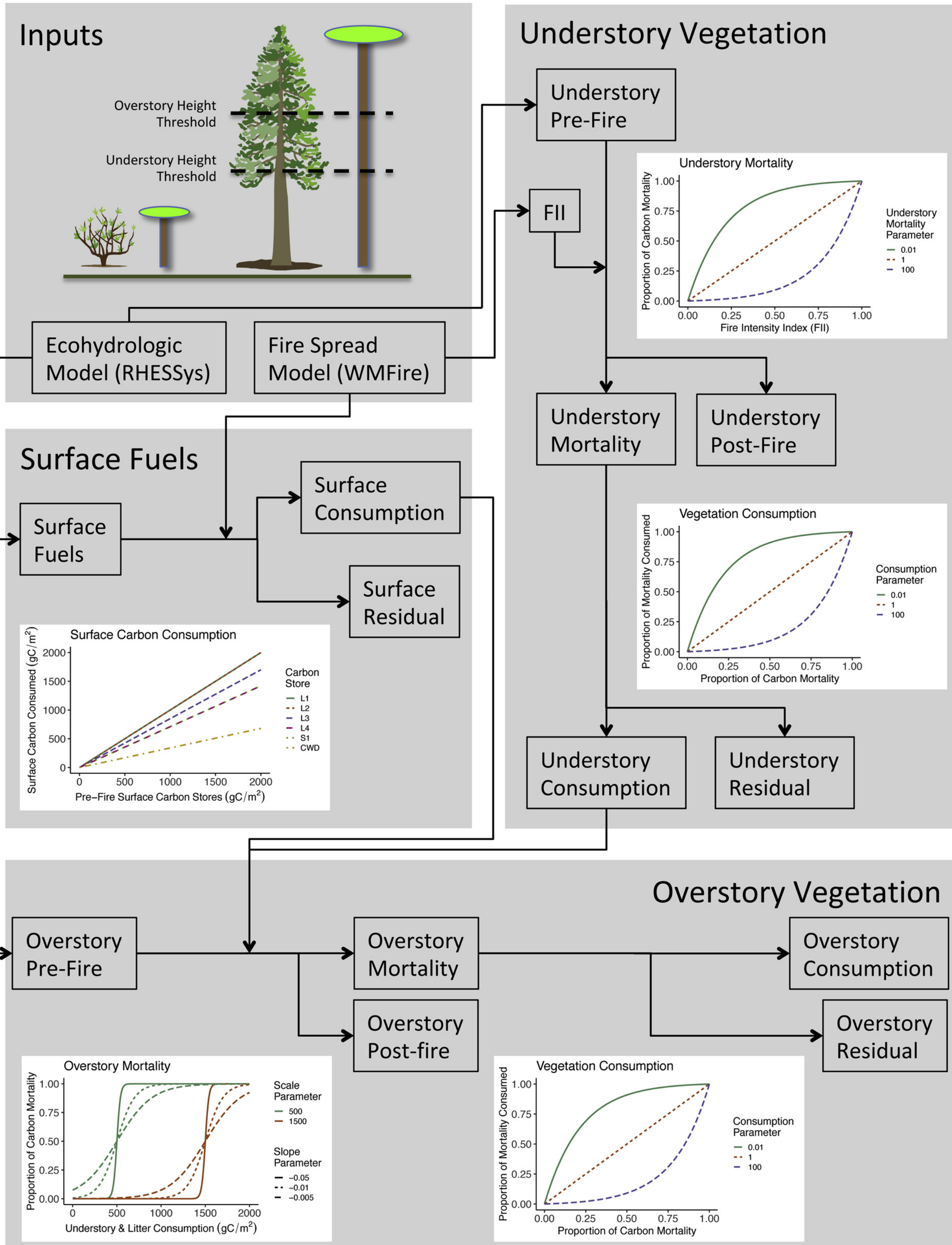


**Fig. 1.** Flow diagram of the fire-effects model.

depending on the canopies' height relative to the height thresholds. For locations with two vegetation canopies, we refer to the dominant vegetation canopy (e.g. forest) as the Primary Canopy and the sub-canopy (e.g. shrubs) as the Secondary Canopy, recognizing that the Secondary Canopy may overtop the Primary Canopy under some conditions. For locations with a single vegetation type (e.g. shrublands), the vegetation is referred to as the Primary Canopy.

Canopy mortality in the fire-effects model is defined as the vegetation carbon component that is killed by wildfire (Fig. 1). A portion of the total mortality is then allocated either to carbon stores that are consumed by the fire (and counted as a net carbon flux to the atmosphere), or to residual plant material that falls to the ground as a carbon flux to surface carbon stores. For a canopy classified as understory, leaf material in a burned patch is assumed to undergo 100 % mortality. For all other canopy carbon stores classified as understory (e.g. stem carbon, root carbon), the proportion of vegetation mortality ($V_{\mathrm{pMort}}$) is a function of Fire Intensity Index in that patch,

$$V_{pMort} = \begin{cases} FII & (k_{u\_mort} = 1) \\ \dfrac{(k_{u\_mort})^{FII} - 1}{k_{u\_mort} - 1} & (k_{u\_mort} \neq 1) \end{cases} \tag{3}$$

where $k_{\mathrm{u\_mort}}$ is an canopy-specific understory mortality parameter that may be calibrated to provide a species-specific relation between *FII* and $V_{\mathrm{pMort}}$. Vegetation with high $k_{\mathrm{u\_mort}}$ values is more resistant to fire whereas vegetation with low $k_{\mathrm{u\_mort}}$ values is more sensitive to fire. The total amount of vegetation carbon mortality in a canopy ($V_{\mathrm{Mort}}$) is computed as

$$V_{Mort} = V_c{}^*V_{pMort} \tag{4}$$

where $V_{\mathrm{c}}$ is defined as the pre-fire carbon (gC/m$^2$) for a given vegetation store.

For aboveground vegetation carbon stores in a given canopy (e.g. leaves, stem), the proportion of mortality that is consumed by fire ($V_{\mathrm{pCons}}$) is

$$V_{pCons} = \begin{cases} V_{pMort} & (k_{cons} = 1) \\ \dfrac{(k_{cons})^{V_{pMort}} - 1}{k_{cons} - 1} & (k_{cons} \neq 1) \end{cases} \tag{5}$$

where $k_{\mathrm{cons}}$ is a species-specific consumption parameter specifying the relation between $V_{\mathrm{pMort}}$ and $V_{\mathrm{pCons}}$ (Fig. 1). Low values of $k_{\mathrm{cons}}$ indicate that vegetation is easily consumed by fire while high values of $k_{\mathrm{cons}}$ indicate that vegetation has a greater tendency to remain on the landscape as litter, coarse woody debris or standing deadwood. The total amount of aboveground vegetation carbon consumed ($V_{\mathrm{Cons}}$) is

$$V_{Cons} = V_{Mort}{}^*V_{pCons} \tag{6}$$

whereas the total amount of aboveground vegetation carbon that is killed but remains as litter and coarse woody debris ($V_{\mathrm{Resid}}$) is

$$V_{Resid} = V_{Mort}{}^*(1 - V_{pCons}) \tag{7}$$

Canopy mortality of vegetation classified as overstory is governed by a different relation from Eq. (3). Instead, it is a function of the combined biomass consumed from vegetation classified as an understory and litter (Fig. 1). This relation takes a sigmoidal form,

$$V_{pMort} = \frac{1}{1 + e^{-k_{o\_mort\_1}[(V_{Cons\_u} + L_{Cons}) - k_{o\_mort\_2}]}} \tag{8}$$

where $V_{\mathrm{Cons\_u}}$ is the total amount of vegetation consumption (i.e. $V_{\mathrm{Cons}}$) for canopies classified as understory in a patch, $L_{\mathrm{Cons}}$ is the total amount of litter consumed (i.e. $L1_{\mathrm{Cons}}$, $L2_{\mathrm{Cons}}$, $L3_{\mathrm{Cons}}$, and $L4_{\mathrm{Cons}}$), $k_{\mathrm{o\_mort\_1}}$ is a parameter representing the slope of the sigmoidal relation and $k_{\mathrm{o\_mort\_2}}$ is a scale parameter representing the combined amount of understory and litter consumption where $V_{\mathrm{pMort}}$ is equal to 50 %. The relation represents the role of ladder fuels in propagating fire into the overstory, with higher consumption in the understory or litter assumed to increase fire propagation. Differences in the value of the $k_{\mathrm{o\_mort\_2}}$ parameter can be implicitly used to account for location and species-specific differences in ladder fuel behavior.

### 2.3. Study sites

The fire-effects model was tested in four locations in the western U.S.; a shrubland located in southern California, open-canopy mixed-conifer forests in the southern Sierra Nevada and northern New Mexico, and a closed-canopy conifer forest in Oregon (Fig. 2). These locations provide a diverse set of land cover types and fire regimes for evaluating the robustness of the fire-effects model. An illustration of the expected patterns of vegetation mortality for each of the four sites is provided in Fig. 3 and described in more detail below.

Rattlesnake Canyon is a predominately shrubland watershed on the south side of the Santa Ynez Mountains near Santa Barbara, California. The elevation of the study site is 800 m and is composed of sclerophyllous evergreen shrubs, including ceanothus (*Ceanothus megacarpus*), chamise (*Adenostoma fasciculatum*), and manzanita (*Arctostaphylos spp.*). Mean annual precipitation for Rattlesnake is 518 mm, the mean annual maximum temperature is 21.6°C, and the mean annual minimum temperature is 12.1°C. Many wildfires in this area are wind-driven, although fuel-driven fires are also common. Chaparral shrublands are adapted for wildfire. Wildfires spread through the canopy as crown fires, which can produce high mortality regardless of stand age during extreme conditions (Keeley and Fotheringham, 2003). As a result, we would expect modeled shrubland mortality in Rattlesnake to be more sensitive to surface fire intensity than canopy structure.

The P301 watershed site near Shaver Lake, California in the southern Sierra Nevada is part of the Southern Sierra Critical Zone Observatory and Kings River Experimental Watersheds (KREW) research networks. The elevation of the site is 1950 m and the mean annual precipitation is 1308 mm. The mean annual maximum and minimum temperature is 14.4°C and 3.2°C, respectively, and it is located within the rain/snow transition zone. The open-canopy mixed-conifer forest in P301 consists of ponderosa pine *(Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), Jeffery pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana*). The understory vegetation includes young conifer species and chaparral shrubland species such as greenleaf manzanita (*Arctostaphylos patula*) and mountain whitehorn (*Ceanothus cordulatus*). Prior to fire suppression in the 1900s, the mixed-conifer forest in the Sierra Nevada had a low-severity fire regime, with frequent understory wildfire at $5-20$ year return intervals and infrequent canopy fire due to sparse ladder fuels (Kilgore and Taylor, 1979; Scholl and Taylor, 2010). Without reoccurring fire in the landscape, densities have increased in both the forest canopy and the understory over the past century (McIntyre et al., 2015), which has increased the likelihood of high-severity canopy fire. In P301, we would expect the fire-effects model to replicate this behavior, with the forest canopy resistant to fire except under extreme surface fire intensities or following a large buildup of surface and understory fuels.

The Santa Fe watershed site in New Mexico is an open-canopy forest situated at an elevation of 2760 m. The site receives monsoon rainfall during the summer, snowfall during the winter, and has a mean annual precipitation of 633 mm. The mean annual maximum temperature is 13.4°C and the mean annual minimum temperature is -0.5°C. Vegetation is mixed-conifer forest consisting of Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), ponderosa pine (*Pinus ponderosa*), quaking aspen (*Populus tremuloides*), white fir (*Abies concolor*), and white pine (*Pinus strobiformis*) (Margolis and Balmat, 2009). Natural fire-return intervals have been estimated to be between 10 and 28 years (Margolis and Balmat, 2009). Similar to P301, fire suppression over the past century has increased ladder fuel loads in the understory, increasing the risk of fire propagation into the forest canopy. Fuels management to reduce understory biomass is being conducted in the forest to decrease fire severity. A useful fire-effects model should be able to replicate these processes, with increasing forest mortality following the accumulation of ladder fuels and decreased forest mortality following fuel treatments.

The H.J. Andrews Experimental Forest site in Oregon is situated at an elevation of 975 m. The mean annual precipitation of 2266 mm is concentrated during the winter season with a mix of rain and snow. The mean annual maximum and minimum temperature is 14.4°C and 4.5°C, respectively. The mixed conifer forest consists of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), noble fir (*Abies procera*) and Pacific silver fir (*Abies amabilis*). Fire effects in H.J. Andrews are closely related to stand development (Oliver, 1981). Following a stand replacing wildfire or other major disturbance, the forest begins stand initiation. During this

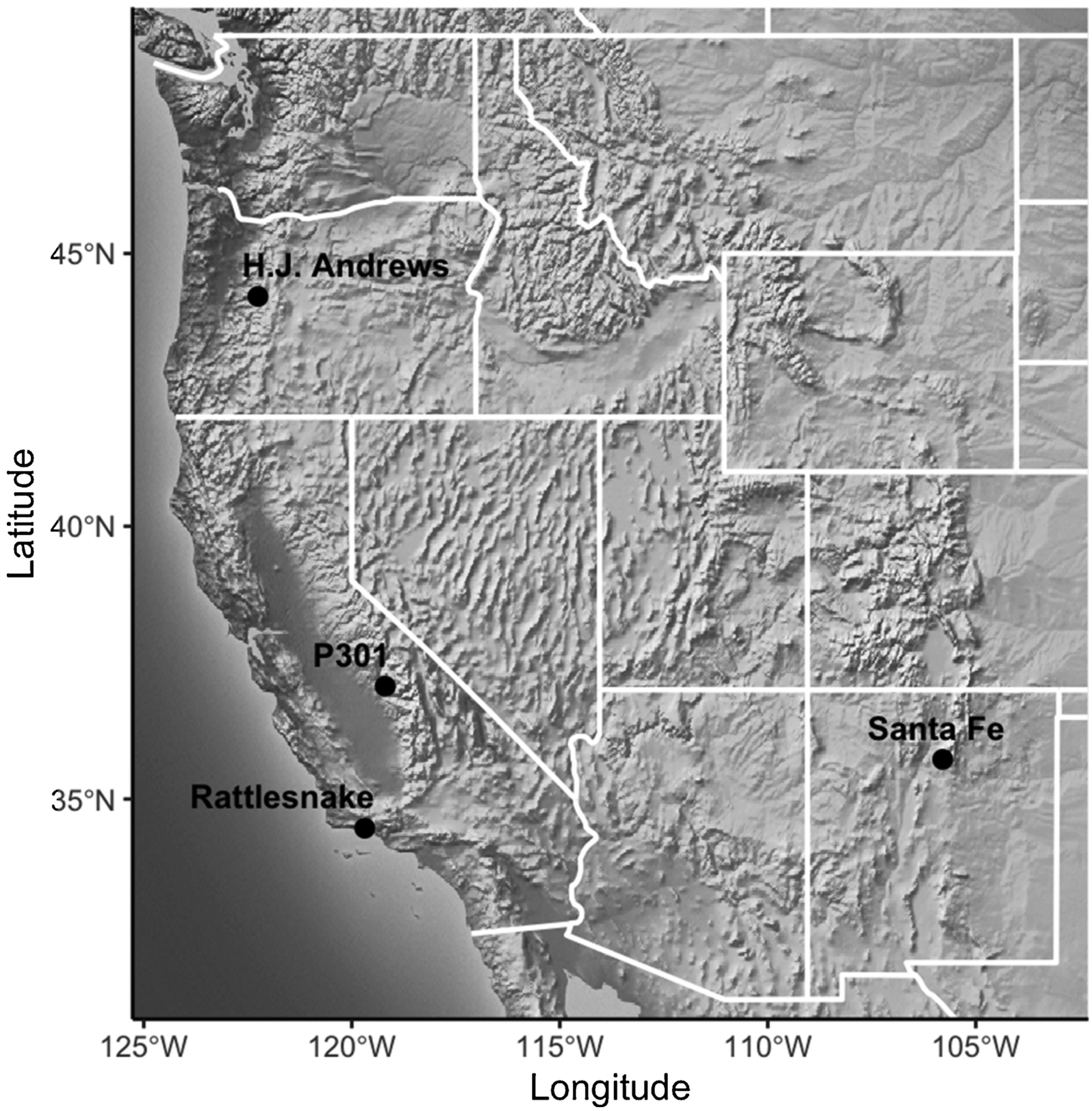


**Fig. 2.** Map of study locations.

period, small stature trees are vulnerable to fire, though in many cases, surface fuels may be insufficient for fire spread. As the forest canopy becomes taller and closed, a stem exclusion phase begins where understory growth cannot establish and a lack of ladder fuels protects the forest canopy from crown fire. After a period of time, small disturbances and increased forest mortality create gaps in the forest canopy that allow understory vegetation and young trees to reinitiate. This understory growth can act as a ladder fuel, increasing the fire risk for the forest canopy. We expect that the model should replicate fire effects at each phase of stand development in H.J. Andrews, with forest vulnerability to fire decreasing during the transition from the stand initiation phase to the stem exclusion phase, and then increasing during the transition to the understory reinitiation phase.

Assembled datasets for Rattlesnake, P301, Santa Fe, and H.J. Andrews are described in detail in Shields and Tague (2012); Bart et al. (2016); Kennedy et al. (2017), and Garcia et al. (2013), respectively. For Rattlesnake, daily precipitation data were obtained from Santa Barbara County Flood Control District gauge 228 located 4 km south of the study site and daily temperature data from a National Climate Data Center (NCDC) monitoring station located 9 km south of the study site. The combined precipitation and temperature dataset extends from water year 1989 to 2009, with the water year defined as October 1 of the previous year to September 30 of the present year. Daily precipitation and temperature data for P301 (water years 1942–2005) were generated by extending the short record from a KREW meteorological station located near the outlet of the P301 watershed (Hunsaker and Safeeq, 2018) with a longer record from the Grant Grove Climate station located 40 km to the southeast. Daily precipitation was adjusted using a scaling factor, and daily temperature was adjusted using a linear regression model (Son and Tague, 2019). Santa Fe daily precipitation and temperature data (water years 1942–2008) were obtained from two National Weather Service Cooperative Network climate stations in the City of Santa Fe, located approximately 14 km to the west of the study site. Daily precipitation, minimum temperature and maximum temperature data for H.J. Andrews (water years 1958–2004) were taken from a climatic station at Watershed 2 (CS2MET). For all of the sites, we repeated the observed climate sequences for simulations requiring time series that were longer than the observed records.

### 2.4. Analysis

At each study site, we tested the fire-effects model at the patch scale using a three-step approach. First, we simulated the ecohydrologic

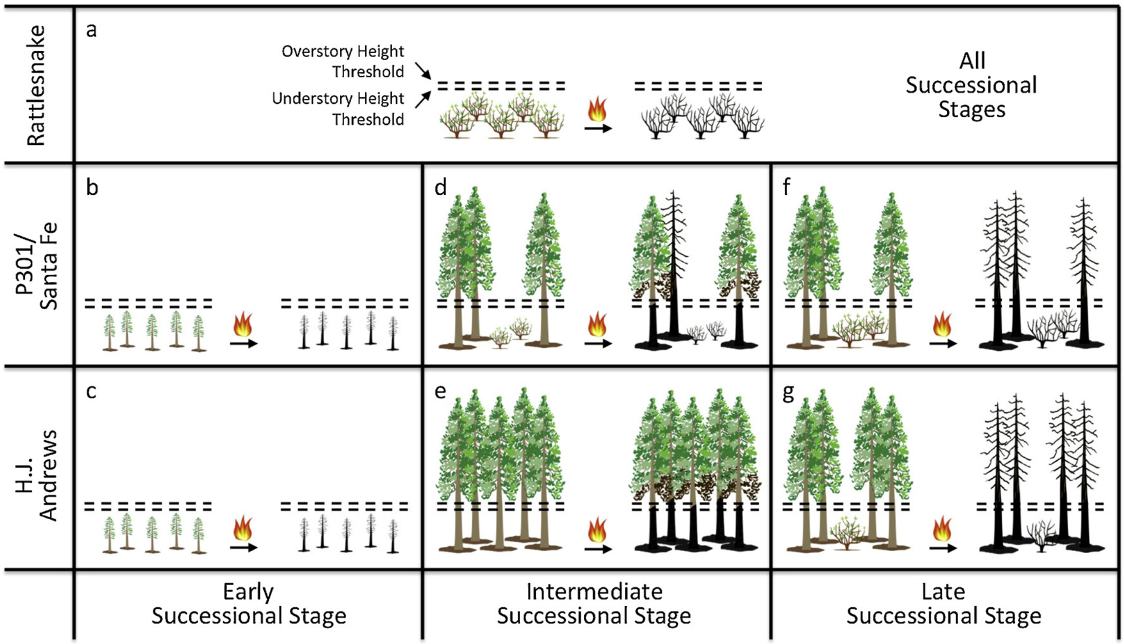


**Fig. 3.** Expected patterns of fire effects for the Primary Canopy at the four study sites at three stages of succession, assuming no previous fire since stand initiation. a) At Rattlesnake, the shrub canopy is below the understory height threshold and fire effects are related to surface fire intensity. b–c) At the other sites in early succession, the forest canopy is below the understory height threshold and fire effects are related to surface fire intensity. d–e) In intermediate succession, the forest canopy is above the overstory height threshold and ladder fuels in the understory are small in the open canopy systems (P301/Santa Fe) or not present in the closed canopy systems (H.J. Andrews). Since fire effects are related to understory biomass (i.e. ladder fuels) consumed, the forest canopy is expected to experience only occasional or no fire effects. f–g) In late succession, the forest canopy is above the overstory height threshold and the ladder fuels are more developed. Fire effects in the forest canopy are expected to be more severe.

**Table 2**
Parameter values selected from simulating RHESSys vegetation and litter carbon pools.

| Parameters | Units | Rattlesnake | P301 | Santa Fe | HJ Andrews |
|---|---|---|---|---|---|
| Subsurface | | | | | |
| Soil air entry pressure | m | 6.77 | 1.15 | 1.39 | 4.18 |
| Pore size index | – | 0.78 | 0.77 | 0.85 | 0.67 |
| Percent of infiltration to groundwater | % | 0.33 | 0.24 | 0.29 | 0.23 |
| Soil depth | m | 3.35 | 4.47 | 3.64 | 2.16 |
| Primary Canopy | | | | | |
| New coarse root to new stem C allocation | – | 0.44 | 0.33 | 0. 31 | 0.20 |
| New fine root to new leaf C allocation | – | 1.4 | 1.4 | 1.2 | 1.32 |
| New livewood to total wood C allocation | – | 0.90 | 0.63 | 0.14 | 0.074 |
| New stem to new leaf C allocation | – | 0.2 | 0.4 | 0.8 | 1 |
| Annual turnover of leaf C to litter | $yr^{-1}$ | 0.39 | 0.25 | 0.16 | 0.14 |
| Annual turnover of livewood C to deadwood | $yr^{-1}$ | 0.075 | 0.48 | 0.46 | 0.65 |
| Annual turnover of stem C to CWD | $yr^{-1}$ | 0.032 | 0.0028 | 0.0023 | 0.0058 |
| Height to stem carbon relation coefficient | $mKgC^{-1}$ | 2.74 | 10.77 | 13.64 | 10.45 |
| Secondary Canopy | | | | | |
| New coarse root to new stem C allocation | – | – | 0.40 | 0.41 | 0.33 |
| New fine root to new leaf C allocation | – | – | 1.4 | 1.4 | 1.4 |
| New livewood to total wood C allocation | – | – | 0.82 | 0.93 | 0.92 |
| New stem to new leaf C allocation | – | – | 0.2 | 0.2 | 0.2 |
| Annual turnover of leaf C to litter | $yr^{-1}$ | – | 0.41 | 0.42 | 0.36 |
| Annual turnover of livewood C to deadwood | $yr^{-1}$ | – | 0.090 | 0.28 | 0.13 |
| Annual turnover of stem C to CWD | $yr^{-1}$ | – | 0.019 | 0.011 | 0.027 |
| Height to stem carbon relation coefficient | $mKgC^{-1}$ | – | 3.16 | 3.74 | 3.71 |

*Note*: C, carbon; CWD, coarse woody debris.

model in the absence of fire and selected a single set of soil and vegetation parameters that satisfactorily produced typical long-term (100 − 150 year) trajectories of vegetation growth, including height and biomass of the Primary and Secondary Canopies. Second, we used a global sensitivity analysis to assess the performance of the model structure, to improve understanding of potential fire-watershed dynamics, and to guide the selection of calibration parameters. Finally, we applied the fire-effects model to vegetation at various stand ages to evaluate whether the modeled fire effects occurring at different times in a stand growth trajectory conform to expected fire-effect patterns. For each of these analyses, the fire-effects model was evaluated decoupled from the fire-spread model. In this paper, we focus on fire effects from individual fires of different intensities. The evaluation of fire regimes using the fully coupled model will be addressed in subsequent papers.

The ecohydrologic model, RHESSys, was used to simulate vegetation succession at each of the four sites to identify parameter combinations that were consistent with known patterns of vegetation succession. Comparisons were based on qualitative descriptions of stand development at each site. Qualitative calibration of the model was used due to a lack of century-scale vegetation data to compare modeled vegetation dynamics. Simulations began with no vegetation, reflecting conditions following a stand replacing wildfire. Vegetation in Rattlesnake, P301, and Santa Fe was simulated for 100 years without fire and vegetation conditions were evaluated at stand ages 5, 12, 20, 30, 40, 60 and 80 years. Vegetation in H.J. Andrews was simulated for 150 years without fire due to its longer growth cycle; with vegetation conditions evaluated at stand ages 5, 12, 20, 40, 70, 100 and 140 years. Two vegetation canopies were simulated for the three forested ecosystems, with a Primary Canopy representing the trees and a Secondary Canopy representing smaller shade-tolerant vegetation. The Secondary Canopy at these sites was restricted to grow no higher than the understory height threshold, $h_u$. The shrubland site, Rattlesnake, was modeled with a single Primary Canopy. Simulations were conducted using a latin hypercube selection of 250 parameter sets across plausible ranges of a number subsurface and vegetation parameters that were expected to be important for growth (Garcia et al., 2016) (see Table 2 for parameter list). Other vegetation and hydrologic parameters were chosen from RHESSys parameter libraries. The runs were evaluated visually to assure that most runs conformed to expected succession dynamics at each site. However, since the objective of the study was to evaluate the fire-effects model and not succession dynamics, a single parameter set that provided representative dynamics was selected from among all the simulations in order to reduce dimensionality of the subsequent sensitivity tests. We selected the parameter set that produced most consistently the rank median height for each canopy and the rank median litter load across the selected stand ages at each site.

A global sensitivity analysis was conducted to evaluate the contribution of individual components of the fire-effects model and evaluate whether the model could be simplified or parameters in the model fixed (Song et al., 2015). We used the variance-based Sobol' approach, which uses input parameter contributions to the modeled output variance as an estimate of parameter sensitivity (Pianosi et al., 2016). The Sobol' approach has the advantage of working with non-linear and non-monotonic models. It can also be used on models with interacting parameters and can estimate interaction effects (Song et al., 2015). The Sobol' model produces two types of output, first-order and total-order indices. First-order indices quantify the direct contribution of a parameter to the output variance. Total-order indices quantify the combined direct contributions and the indirect contributions of a parameter on the output variance. Indirect contributions are generated from interactions with other parameters. The sensitivity analysis was implemented using the *sobol2007* function (Saltelli et al., 2010; Sobol' et al., 2007) in the R *sensitivity* package (Pujol et al., 2017). The sensitivity of the fire-effects model was tested separately for each of the seven stand ages. Inputs to the sensitivity model included the two parameters that define the height thresholds for each patch, $h_o$ and $h_u$, and four parameters for each vegetation canopy, $k_{u\_mort}$, $k_{cons}$, $k_{o\_mort\_1}$ and $k_{o\_mort\_2}$ (Table 3). We also included the Fire Intensity Index in the sensitivity test. Although the Fire Intensity Index is an input variable passed to the fire-effects model rather than an adjustable parameter, we were interested in understanding the relative contribution of the Fire Intensity Index to model output variability compared to the other parameters. As with all global sensitivity tests, results using the Sobol' approach can vary depending on the variability space of the input parameters (Pianosi et al., 2016). We selected broad parameter ranges that encompassed most of the plausible parameter space (Table 3). The sensitivity analysis was run with 1000 unique parameter sets for each stand age. Sensitivity output was evaluated for the relative post-fire change in four model variables for each canopy, $V_{\mathrm{pMort}}$, $V_{\mathrm{pCons}}$, $V_{\mathrm{Cons}}$ and $V_{\mathrm{Resid}}$.

Fire effects were evaluated separately for all combinations of the four study sites, the seven stand ages, and for ten levels of the Fire Intensity Index, to assess whether the fire-effects model conformed to expected behavior (Fig. 3). The levels of the Fire Intensity Index ranged from 0.1 to 1, by 0.1, representing a range of very low intensity to very high intensity fire. For each site/ stand age/ Fire Intensity Index combination, we simulated fire effects using a latin hypercube selection of 100 parameter sets based on the parameters that were previously identified to be sensitive in the sensitivity test (see Table 3), for a total of 28,000 fire effects simulations.

## 3. Results

### 3.1. Vegetation simulation

Vegetation in the model was simulated in order to produce a representative example of vegetation growth at each site. The simulated canopy heights and litter carbon stores for each of the 250 fire-free runs are displayed in Fig. 4, along with the representative run that was used for the subsequent sensitivity test. The parameter values corresponding to the representative run are displayed in Table 2. For Rattlesnake, shrub height increased rapidly during the first 12 years and then began to level off, peaking at a little over 2.5 m of height. Litter accumulation shows the cyclical signature of the looped 21-year climate sequence, but overall, litter accumulation was fairly steady over the growth cycle of the shrubs.

The two open canopy sites, P301 and Santa Fe, had similar behavior to one another in the absence of fire. Following an initial period of slow growth, the Primary Canopy had a short period of rapid growth, followed by a long period of slower but steady growth. The height of the Secondary Canopy in P301 stabilized after about 40 years while the height of the Secondary Canopy in Santa Fe showed consistent growth throughout the 100-year simulation period. Litter carbon, on the other hand, showed consistent accumulation during the simulation period in P301, while litter carbon in Santa Fe was more variable and did not display a trend. Litter carbon accumulation in Santa Fe was lower than P301, reflecting the smaller forest size in Santa Fe due to drier conditions and potentially higher rates of decomposition with summer precipitation.

For the closed canopy forest at H.J. Andrews, strong Primary Canopy growth during the stem exclusion phase prevented the Secondary Canopy from becoming established. However after 60 years, understory initiation began when forest gaps in the Primary Canopy allowed the understory to become established. Litter carbon in H.J. Andrews showed a steady increase with stand age when fire was excluded from the system.

### 3.2. Sensitivity test

A global Sobol' sensitivity test was used to compare the relative influence of model parameters and the model input variable Fire Intensity Index on fire effects. The tests were performed separately for each site and stand age combination. We found that the sensitivities (first-order indices) of the shrublands at Rattlesnake were very similar to the sensitivities of the Secondary Canopies at P301, Santa Fe and H.J. Andrews. We also observed that the first-order indices of the two open-canopy sites, P301 and Santa Fe, were similar. Accordingly, we show only first-order indices for the Primary Canopy in the three sites that showed distinct behavior, Rattlesnake, P301 and H.J. Andrews (Fig. 5). First-order indices for the Primary Canopy of Santa Fe and all Secondary Canopies are provided in Supplemental Material. Total-order indices for all sites were not substantially different from first-order indices, indicating that interactions among the parameters and the Fire Intensity Index were not a substantial contributor to the output variance. These results are also available in Supplemental Material.

In Rattlesnake, the sensitivity results did not vary by stand age since

**Table 3**
Parameter ranges for Sobol' sensitivity test and fire effect simulations.

| Parameters/Variable | Description | Units | Sensitivity Test | Simulations | | | |
|---|---|---|---|---|---|---|---|
| | | | All sites | Rattlesnake | P301 | Santa Fe | H.J. Andrews |
| Input Variable | | | | | | | |
| FII | Fire Intensity Index | – | 0.001 to 1 | – | – | – | – |
| Patch | | | | | | | |
| $h_o$ | Overstory height threshold | m | 6 to 8 | 7 | 7 | 7 | 7 |
| $h_u$ | Undertory height threshold | m | 4 to 5 | 4 | 4 | 4 | 4 |
| Primary Canopy | | | | | | | |
| $k_{u\_mort}$ | Understory mortality parameter | – | 0.01 to 100 | 0.01 to 100 | 0.01 to 100 | 0.01 to 100 | 0.01 to 100 |
| $k_{cons}$ | Vegetation consumption parameter | – | 0.01 to 100 | 0.01 to 100 | 0.01 to 100 | 0.01 to 100 | 0.01 to 100 |
| $k_{o\_mort\_1}$ | Overstory slope parameter | $m^2$/Kg | −20 to -1 | −10 | −20 to -1 | −20 to -1 | −20 to -1 |
| $k_{o\_mort\_2}$ | Overstory scale parameter | Kg/$m^2$ | 0.2 to 2 | 1 | 0.4 to 1.7 | 0.4 to 1.1 | 0.4 to 1.7 |
| Secondary Canopy | | | | | | | |
| $k_{u\_mort}$ | Understory mortality parameter | – | 0.01 to 100 | – | 0.01 to 100 | 0.01 to 100 | 0.01 to 100 |
| $k_{cons}$ | Vegetation consumption parameter | – | 0.01 to 100 | – | 0.01 to 100 | 0.01 to 100 | 0.01 to 100 |
| $k_{o\_mort\_1}$ | Overstory slope parameter | $m^2$/Kg | −20 to -1 | – | −10 | −10 | −10 |
| $k_{o\_mort\_2}$ | Overstory scale parameter | Kg/$m^2$ | 0.2 to 2 | – | 1 | 1 | 1 |

the shrubs remained below the understory height threshold across all stand ages. We note that this does not imply that fire intensity does not vary with stand age and associated fuel accumulation, but rather that the effects of fire of a given intensity with a given parameter set do not change across stand ages. Fire effects in Rattlesnake were sensitive to parameters $k_{u\_mort}$ and $k_{cons}$, as well as the Fire Intensity Index (Fig. 5a). Changes in the response variable for vegetation mortality, $V_{pMort}$, and the response variables for consumption, $V_{pCons}$, and $V_{Cons}$, were most sensitive to the Fire Intensity Index. The parameter $k_{u\_mort}$ acted as a secondary control for these response variables and the parameter $k_{cons}$ as a tertiary control. The response variable for the proportion of residual carbon that falls to the ground, $V_{Resid}$, had the $k_{cons}$ parameter as was the most sensitive parameter. Fire effects in Rattlesnake were not sensitive to the two height threshold parameters or the two parameters that control the fire effects in the overstory, $k_{o\_mort\_1}$ and $k_{o\_mort\_2}$. Similar patterns of sensitivity were observed for the understory canopies at each of the forested sites (See Supplementary Material). The sensitivity of fire effects in the open-canopy forest, P301, varied across stand age (Fig. 5b). At stand age 5, sensitivity was similar to that of an understory, since the height of the Primary Canopy was well below the understory height threshold (Fig. 4c). At stand age 12, Primary Canopy height was close to the understory height threshold ($h_u$) and fire effects showed sensitivity to this parameter. By stand age 20, Primary Canopy height was greater than the overstory height threshold and sensitivity in the model shifted. Sensitivity to parameters $k_{u\_mort}$ and $k_{cons}$, as well as the input variable Fire Intensity Index, was greatly diminished while the sensitivity to $k_{o\_mort\_2}$, which defines how much understory and litter biomass is needed to be consumed to generate 50 % mortality in the overstory, was greatly increased. Fire effects were generally much more sensitive to the parameter $k_{o\_mort\_2}$ than the parameter $k_{o\_mort\_1}$, except for the response variable, $V_{Resid}$, where both parameters were similarly sensitive. Fire-effects sensitivity in H.J. Andrews was similar to P301, shifting from understory-sensitive parameters and the Fire Intensity Index at stand age 5 to overstory-sensitive parameters in older stands (Fig. 5c).

In summary, the sensitivity results indicate that for vegetation that is shorter than the understory height threshold, fire effects are most sensitive to the $k_{u\_mort}$ and $k_{cons}$ parameters. In addition, we have shown that fire effects are also very sensitive to the Fire Intensity Index. For vegetation that is taller than the overstory height threshold, fire effects are most sensitive to the $k_{o\_mort\_2}$ parameter. For the simulation of fire effects in the following section, we only allowed the parameters $k_{u\_mort}$ and $k_{cons}$ to vary for vegetation canopies that were a shrubland or an understory. For forest canopies, we allowed $k_{u\_mort}$, $k_{cons}$, $k_{o\_mort\_1}$ and $k_{o\_mort\_2}$ to vary, since depending on stand age, forest canopies may behave like both an understory and an overstory. All other parameters were fixed, including $h_o$ and $h_u$, since these parameters were not consistently sensitive across stand age or site. The parameter ranges for the fire effect simulations are found in Table 3.

### 3.3. Fire effects

We evaluated the fire-effects model to understand how well it could replicate the expected temporal dynamics of fire-effect behavior at each of the four sites (Fig. 3). Fire effects at each site were simulated across 7 stand ages and 10 levels of Fire Intensity Index. A time series of the aboveground carbon stores (Primary Canopy, Secondary Canopy, Litter) for each site is presented in the top panels of Fig. 6 and Fig. 7. The vertical lines indicate the stand ages that fire effects were investigated. The remaining panels show the associated percentage change in mortality, consumption, and residual carbon for the Primary Canopy at each site. The distribution of responses for each site/stand age/Fire Intensity Index combination was generated using 100 parameter sets.

Fire effects in Rattlesnake were similar across all stand ages since the height of the vegetation never exceeded the understory height threshold. Mortality was roughly linear with the Fire Intensity Index, with some variability based on different parameter values of $k_{u\_mort}$ (Fig. 6b). Canopy consumption increased non-linearly with the Fire Intensity Index, with lower levels of consumption for a given level of the Fire Intensity Index except when for the Fire Intensity Index goes to 1 (Fig. 6c). The carbon that is killed but not consumed falls to the ground as residual litter carbon. In Rattlesnake, residual carbon increased with the Fire Intensity Index until peaking at intermediate levels of the Fire Intensity Index, at which time residual carbon began to decrease (Fig. 6d). The initial increase in residual carbon is a result of fractionally less canopy consumption for a given level of mortality at lower levels of mortality (Fig. 1). This reverses at higher levels of mortality, when consumption becomes a fractionally higher component of mortality and levels of residual carbon begin to decline. The fire effect results for Rattlesnake were similar to those of the Secondary Canopy at the forested sites.

For P301 at stand ages 5 and 12, the forest canopy remained below the understory height threshold of 4 m (Fig. 4c). Consequently, fire effects at these stand ages were similar to the shrubs in Rattlesnake. However, beginning at stand age 20, the forest canopy grew beyond the overstory height threshold and the controls on mortality in the Primary Canopy shifted to being a function of the combined understory and litter consumption (Fig. 6f). For stand ages 20 and 30, understory and litter biomass consumption was insufficient to propagate fire into the Primary Canopy except at the highest levels of the Fire Intensity Index. However, litter accumulation with stand age in the absence of fire

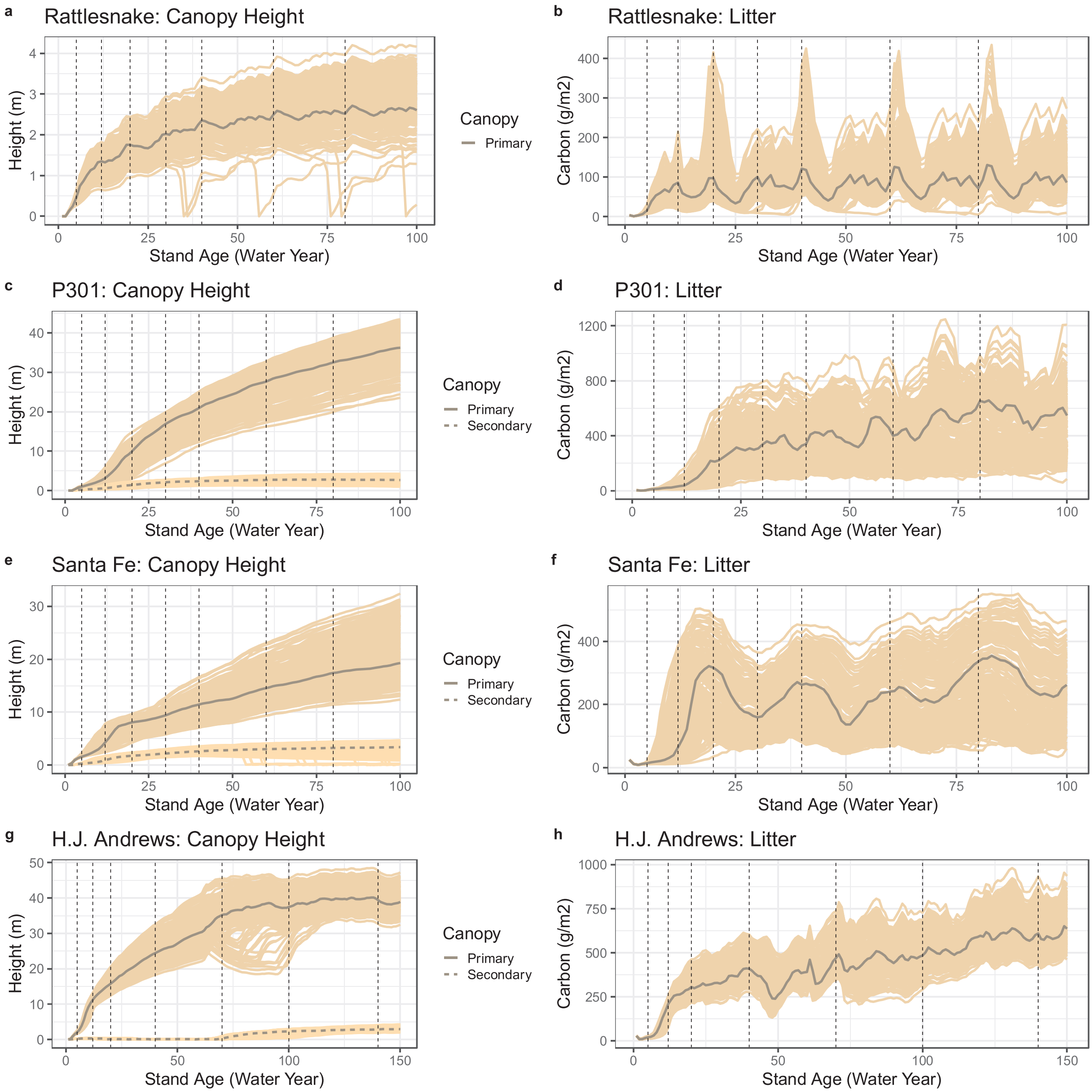


**Fig. 4.** Distribution of canopy heights and litter carbon following the simulation of 250 vegetation and subsurface parameter sets. Each simulation was initiated with no vegetation or litter stores and run in the absence of fire. Dark line indicates the representative parameter set used for fire-effects modeling. Vertical dotted lines correspond to selected stand ages.

increased the amount of fuels available to burn and by stand age 80, mortality in the Primary Canopy had increased for fires at lower levels of intensity. Changes in Primary Canopy consumption and residual carbon mirrored the patterns observed with Rattlesnake, with consumption in P301 increasing non-linearly with mortality and residual carbon levels peaking at intermediate levels of the Fire Intensity Index, although the total amount of carbon that becomes litter is a smaller percentage for stand ages greater than 20 years (Fig. 6g and h).

The controls on fire effects in Santa Fe were similar to P301 (Fig. 7). At a young stand age, the Primary Canopy behaved as an understory and fire effects were primarily a function of the Fire Intensity Index. Fire effects were depressed initially after the Primary Canopy height exceeded the overstory height threshold, but with time, the Primary Canopy again became vulnerable to fire following a buildup of fuels in the Secondary Canopy.

Fire effects in H.J. Andrews followed the pattern of stand development (Fig. 7). During the stand initiation phase (stand age 5), the Primary Canopy was vulnerable to fire since its height was below the understory height threshold. For stand ages 12, 20 and 40, the forest grew into the stem exclusion phase and the closed Primary Canopy inhibited the Secondary Canopy from becoming established. Fire did not spread effectively into the Primary Canopy during this period, making the forest Primary Canopy resistant to fire. After stand age 60, the Primary Canopy in H.J. Andrews entered the understory reinitiation phase and was parameterized to become an open canopy forest by decreasing the canopy cover fraction, representing the expected gap dynamics that occur in maturing forests in this region (Spies et al., 1990). During this phase, the Secondary Canopy was able to reestablish and accumulate sufficient levels of biomass to act as ladder fuels to the Primary Canopy.

## 4. Discussion

The fire-effects model was specifically designed to be used with an established ecohydrologic model, RHESSys, and to be compatible with carbon cycling and 'big leaf' models, in general. Due to constraints on


**Fig. 5.** Sensitivity results (Sobol' first-order indices) for the Primary Canopy of Rattlesnake, P301, and H.J. Andrews. Horizontal panels correspond to fire-effects model parameters/ input variable. Vertical panels on right correspond to fire-effects model response variables. Uncertainty bars represent standard errors. The Rattlesnake results are representative of forest Secondary Canopies.

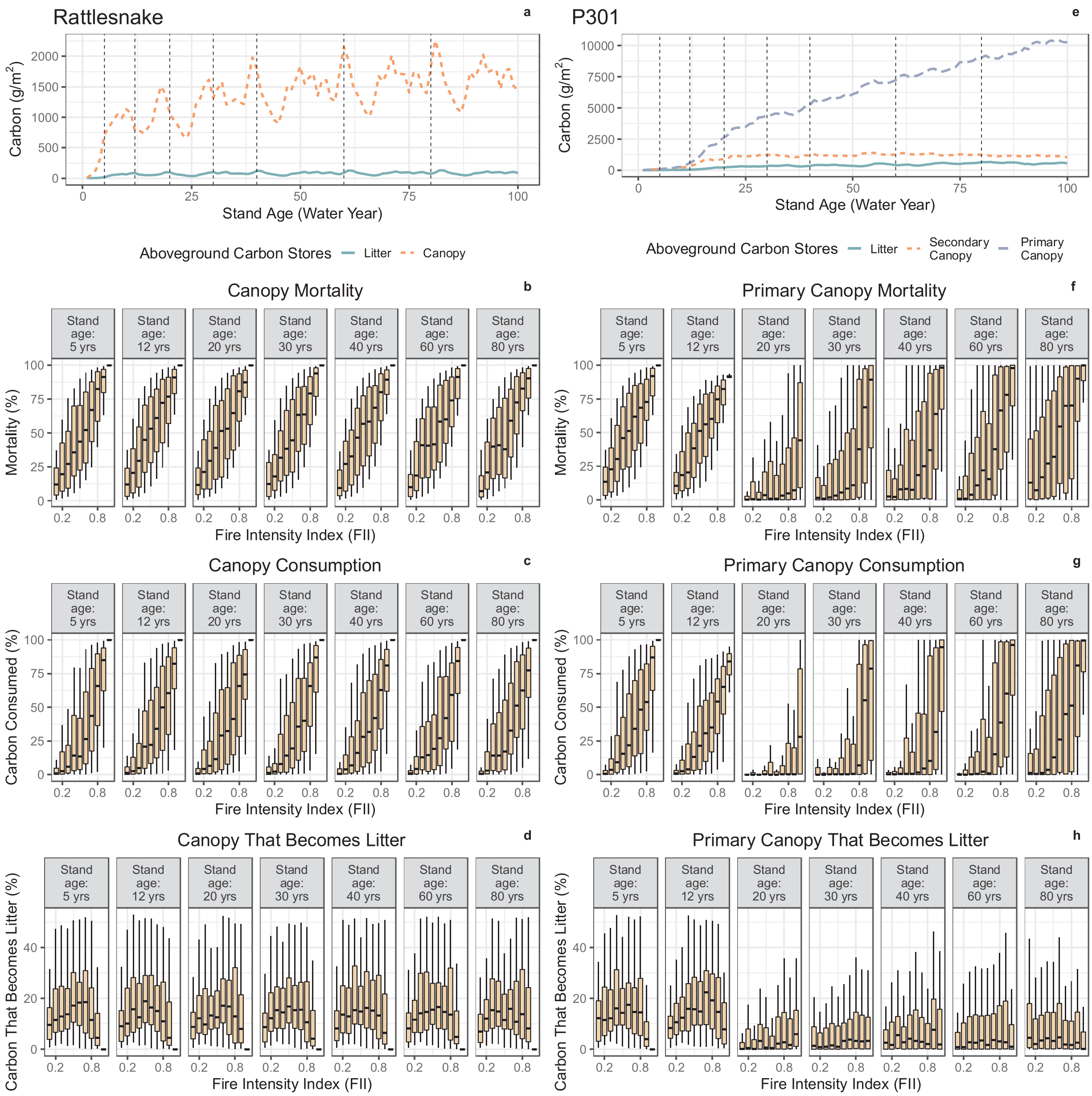


**Fig. 6.** Simulation of fire-effects model across multiple stand ages and surface fire intensities (*FII*) for Rattlesnake and P301. a,e) Simulation time series of aboveground carbon stores for the Primary and Secondary Canopy, as well as the litter carbon store. b,f) Box plots showing percent mortality at different stand ages and intensities. Range of response derived from 100 parameter sets. c,g) Percent canopy carbon consumed. d,h) Percent canopy carbon that becomes ground litter.

the data and processes that can be incorporated into the model, our objective was a parsimonious design that still included canopy structure as a key process controlling fire effects.

The results of this study demonstrated that the fire-effects model containing two height parameters per patch and four additional parameters per canopy was able to replicate broad expected patterns of fire-effect dynamics across different ecosystems (Fig. 3). For shrubland ecosystems dominated by canopy fires, such as California's chaparral, the model produced fire effects that were independent of stand age, which agrees with observed fire effects in the ecosystem (Moritz et al., 2004). In the open-canopy forests of P301 and Santa Fe that historically had a low-severity fire regime, the forest canopy showed little fire effects unless the stand age of the forest canopy was very young or a prolonged fire-free period allowed litter and understory ladder fuels to build up to sufficient levels to allow fire to spread into the forest canopy. This behavior conforms to observed fire effects in low-severity fire regimes forests (Agee, 1998). In the closed-canopy forest at H.J. Andrews, fire during the stem exclusion phase had little effect on the forest canopy. It was only during stand initiation and following understory reinitiation that the forest canopy showed noticeable fire effects. The fire-effects model captured the distinct patterns of vegetation growth and fire vulnerability at each of these sites without being designed explicitly to replicate these patterns; this was an emergent property of the model.

### 4.1. Fire effects and shrubland/understory vegetation

Fire effects in shrublands and forest understory were more responsive to variability in the Fire Intensity Index than the model parameters, regardless of watershed. The Fire Intensity Index is a proxy for surface fire intensity that in this modeling system is calculated by the fire-spread model and is passed to the effects model. This responsiveness was expected and emphasizes the importance of generating an adequate measure of fire intensity in order to correctly model fire

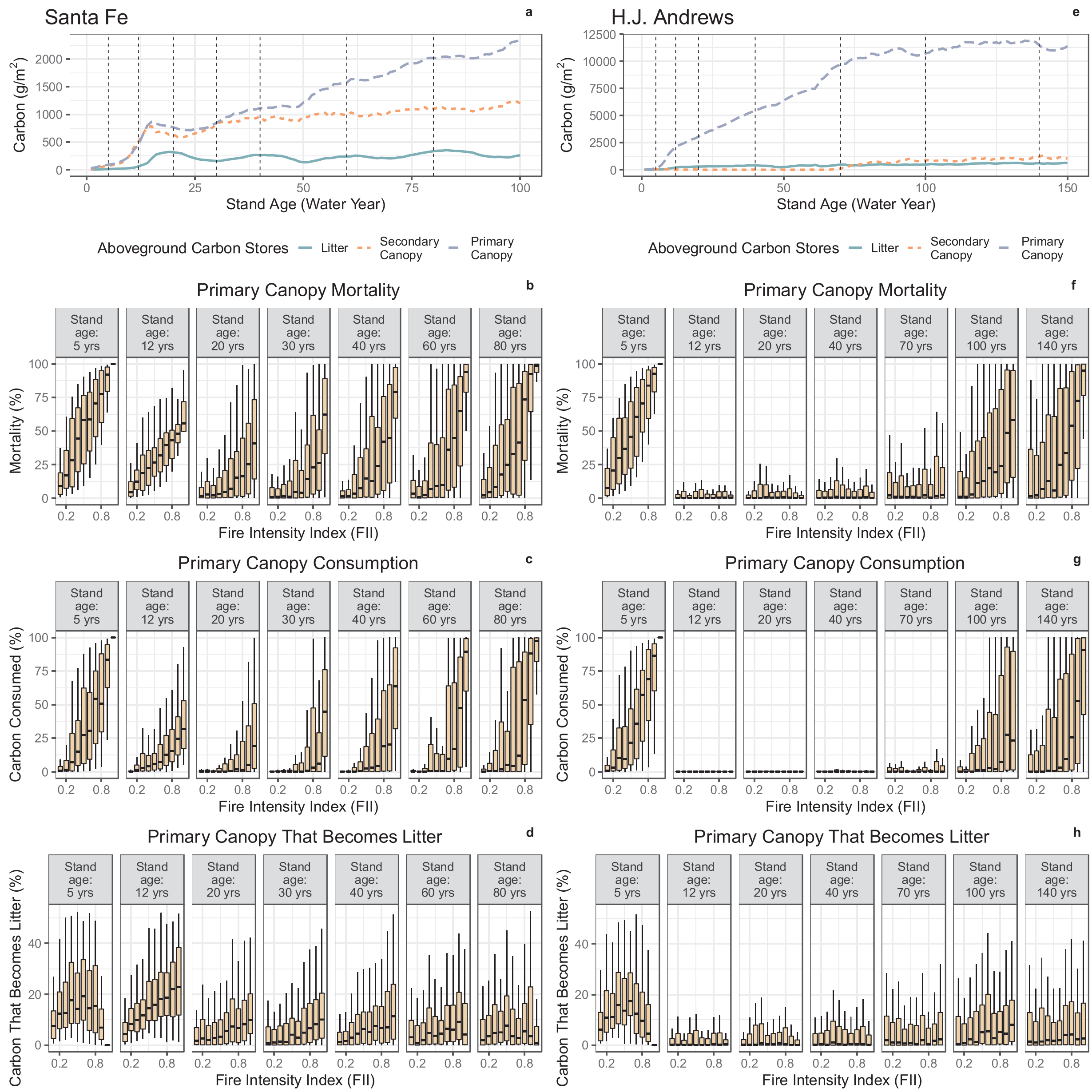


**Fig. 7.** Simulation of fire-effects model across multiple stand ages and surface fire intensities (*FII*) for Santa Fe and H.J. Andrews. a,e) Simulation time series of aboveground carbon stores for the Primary and Secondary Canopy, as well as the litter carbon store. b,f) Box plots showing percent mortality at different stand ages and intensities. Range of response derived from 100 parameter sets. c,g) Percent canopy carbon consumed. d,h) Percent canopy carbon that becomes ground litter.

effects. In shrublands where the understory is the only canopy layer, the sensitivity of fire effects to fire intensity can be interpreted as fire intensity distinguishing between low severity fire and stand-replacing fire (i.e. high severity fire regimes). A high-intensity fire in these systems will result in removal of live vegetation, with potential second-order consequences on slope stability, soil erosion and hydrology (Shakesby and Doerr, 2006). A low-intensity fire, in contrast, will result in more shrub survival and less carbon removed from the landscape.

Fire effects in shrublands and forest understory were also sensitive, though less so, to the parameter that controls how fire intensity relates to mortality ($k_{u\_mort}$) and the parameter that scales the proportion of mortality that is consumed ($k_{cons}$). These parameters may be refined if vegetation species are known to be more or less susceptible to mortality or combustion, which might vary by species average stem diameter or bark thickness.

### 4.2. *Fire effects and forests*

For forested canopies, the fire-effects model was successfully able to replicate expected fire effects at multiple stand ages (Fig. 3). In young forests, fire effects were similar to those estimated for shrublands and understory vegetation, with fire intensity being the primary control on fire effects. At this stage of stand development, forests function effectively as an understory, and a high intensity fire early in stand development may represent a stand-replacing event. This may have implications for reburn potential (Thompson et al., 2007) and type conversion (Boisramé et al., 2017) that may be accommodated by the coupled modeling system. Prior ecohydrologic modeling with RHESSys has shown that the local microclimatological conditions can have a strong impact on the rate of vegetation regeneration after disturbance (Tague and Moritz, 2019). We expect that the coupling of an ecohydrologic model with fire effects may be better able to predict such local microclimatological conditions (e.g. water status) for regeneration that are missing from non-coupled models of future fire regimes in a changing climate.

In intermediate and late-aged forests, when the canopy exceeds the overstory height threshold, fire effects were less responsive to the Fire Intensity Index but were very responsive to the parameter that controls how much understory and litter consumption is necessary to produce overstory mortality ($k_{o\_mort\_2}$). In this context, the understory and litter biomass act as mediators between fire intensity and overstory fire effects. A low value for the $k_{o\_mort\_2}$ parameter means that fire propagation to the overstory is such that even low understory and litter consumption results in high-severity overstory fire. This may be representative of forest species with low hanging branches or with thin, non-fire resistant bark. A higher value requires larger amounts of understory and litter consumption for the same severity in the overstory. We emphasize, however, that understory consumption captures many of the first-order controls on fire propagation to the overstory, including fuel moisture and understory biomass effects. Thus, establishing general plant function type related ranges for this parameter might be feasible.

At the watershed scale, implementation of the fire-effects model will necessitate understanding how $k_{o\_mort\_2}$ varies for different forest types and under different conditions. For example, if the value of $k_{o\_mort\_2}$ is too low, fire effects in the forest overstory may be predicted to be too severe. In ecosystems with forest species that are relatively resistant to fire, such as *Pinus ponderosa*, this may hinder the establishment of larger old-growth open forests that are characteristic of many dry forests with frequent fire regimes in the Western U.S. (Fulé et al., 1997). In contrast, if the value of $k_{o\_mort\_2}$ is too high, the forest canopy may be invulnerable to fire regardless of how much understory and litter is consumed. While this issue necessitates further investigation at the watershed scale with the fully coupled ecohydrologic model, we note that our results in the two dry forest systems (i.e. Santa Fe and P301) showed suitable behavior over a range of $k_{o\_mort\_2}$ parameter values (Table 3). Thus, we anticipate that the fire-effects model is likely robust under many watershed conditions.

### 4.3. Fire effects and fire regimes

In this study, we simulated fire effects at different stand ages (effectively variable fire return intervals, or reburn intervals), assuming that the vegetation was free of fire during the period prior to that stand age. However, in some forests, particularly those with a historically low severity fire regime (e.g. P301 and Santa Fe), the understory could be subject to repeated fire. Under this scenario, we expect the model will function well. For example, once a forest overstory is established in P301, a fire return interval of $5-20$ years (Scholl and Taylor, 2010) would prevent a substantial build up of understory and litter biomass. This lack of ladder fuels would hinder fire movement into the forest canopy except under the most extreme fire conditions. The model is also able to account for changes in forest structure due to forest management. Fire suppression in a low severity fire regime forest such as P301 allows ladder fuels to accumulate, increasing fire risk to the forest canopy, similar to what is currently observed in many locations of the fire-suppressed Sierra Nevada (Collins et al., 2011). Forest management tools such as mechanical understory thinning and prescribed fire can be represented in the ecohydrologic model and thus the potential for decreasing the likelihood of fire propagation into the forest canopy. The coupled ecohydrologic approach is particular important here because it can account for differences in the effectiveness of these treatments associated with interaction among climate and fuel moistures, forest growth rates and overstory/understory relationships that evolve over time.

### 4.4. Model limitations and further development

The fire-effects model was designed to be structurally less complex than some established fire-effects models (e.g. FOFEM (Reinhardt et al., 1997)), and capture first-order effects that are important for representing long-term averages or fire regimes. However, because of this simplicity, the model cannot capture many of the details that are important for replicating fire effects of specific wildfires. For example, the model doesn't account for the structure of the understory vegetation (e.g. grass, shrub) that is consumed, which can be an important second-order control on how effectively the vegetation functions as ladder fuel. In a similar manner, the model also doesn't differentiate between consumption during the flaming front or post-frontal combustion (Finney et al., 2003). However, incorporation of these more sophisticated fire effects elements would require a more complicated model structure that would not be compatible with the ecohydrologic-modeling framework established in RHESSys. We have shown that the fire-effects model can represent the major controls on fire effects, namely different levels of intensity and stand structure.

Wildfire is a contagious process, and the physics of combustion and heat transfer confer autocorrelation in fire effects and observed fire severity (Kennedy and Prichard, 2017; Prichard and Kennedy, 2014). The fire effects in a stand with a given fuel profile and structure are expected to differ depending on the fire intensity and behavior of neighboring stands (Johnson and Kennedy, 2019). When the fire-effects model is integrated with a model of fire spread and an ecohydrologic model, this coupled system will provide a spatial representation of fire spread and effects as they interact with the underlying topography, wind, and vegetation structure. Future development may consider longer correlation lengths between Fire Intensity Index with commensurate representation of neighboring fire characteristics. This would require careful consideration of scale in the framework of WMFire and considerable advancement in the representation of the physical process of heat transfer in models of intermediate complexity.

The performance of the fire-effects model results will be sensitive to the performance of other submodels connected to the fire-effects model, particularly the fire-spread model and models of both overstory and understory growth. While previous studies have evaluated fire spread and general growth models in RHESSys (Garcia et al., 2016; Kennedy et al., 2017), the ability to capture both understory and overstory growth has not been extensively evaluated. Evaluations of carbon cycling models in general often focus on aggregate responses through comparison with flux tower data (Friend et al., 2007) or remote sensing products such as MODIS that lump overstory and understory biomass (Wu et al., 2019). Given the importance of overstory and understory distinctions as controls on fire effects, additional evaluation of the ability of carbon cycling models to capture these layers is warranted.

Ecohydrologic models are valuable tools that inform potential consequences of climate change, land-use change, and forest management. They incorporate dynamic physical and biological feedbacks that are essential to understand watershed processes. As fire is an important physical and ecological driver in many watersheds (McKenzie et al., 2011), our understanding of future ecosystem services requires fully coupling fire spread and effects with ecohydrologic modeling. We show here that this is possible within the existing model complexity framework of an ecohydrologic model, and that we can achieve good replication of patterns of fire effects. This will both improve our ability to understand future watershed dynamics, but also to better project future fire regimes under climate change and land management. Littell et al. (2018) showed that empirical projections of future fire regimes do not adequately represent feedbacks between climate and fuels. The integration of the fire-effects model developed in this study within an ecohydrologic model will allow us to explore those feedbacks.

**Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2019.108880.

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