FINAL PROJECT SUMMARY

Title: Mortality reconsidered: Testing and extending models of fire-induced tree mortality across the US

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Sharon M. Hood USDA Forest Service, Rocky Mountain Research Station

J. Morgan Varner Tall Timbers Research Station

C. Alina Cansler USDA Forest Service, Rocky Mountain Research Station

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List of Acronyms/ Abbreviations

AUC – area under the curve BCH – bark char height CLK – crown length killed CLS – crown length scorched CMD – climatic moisture deficit CVS – crown volume scorched DBH – diameter at breast height DGVM – dynamic global vegetation model FFE-FVS – Fire and Fuel Extension to the Forest Vegetation Simulator FITM – Fire-Induce Tree Mortality dataset FOFEM – First Order Fire Effects Model NPV – negative predictive value PPV – positive predictive value ROC – receiver operating characteristic

Keywords – post-fire mortality, fire-caused mortality, survival curves, model validation, model evaluation, fire-insect interactions, salvage, modeling, prescribed burn plans, fire-climate interactions

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Abstract

Predictive models of tree mortality and survival are vital for management planning and understanding fire effects in forests and woodlands, yet the underlying mechanisms of firecaused tree mortality remain poorly understood. This shortcoming limits the ability to accurately predict mortality and develop robust modelling applications, especially under novel future climates. Our project reviewed the current understanding of the mechanisms of fire-induced tree mortality, recommended standardized terminology, and described model applications and limitations. We evaluated accuracy of the fire-induced tree mortality models from the First Order Fire Effects Model (FOFEM; https://www.firelab.org/project/fofem) software system using a national dataset we developed. Lastly, we explored if climate data can improve prediction of fireinduced tree mortality and conclude with key knowledge gaps and future directions for research.

We used a post-fire tree mortality dataset built from 40 contributed datasets from across the USA to formally evaluate the accuracy of fire-induced tree mortality models from the FOFEM software system. The Fire-Induced Tree Mortality (FITM; https://www.firelab.org/project/fire-induced-tree-mortality) database includes 173,120 tree-level observations of fire injury and survival or mortality. The database includes 160 tree species from 435 prescribed fires and wildfires occurring from 1981 to 2016.

Using the FITM database, we evaluated mortality models available in FOFEM, including the general and species-specific formulations for 45 tree species. These models are also included in FFE-FVS (https://www.firelab.org/project/ffe-fvs) and BehavePlus (https://www.frames.gov/behaveplus/home). Of the 69 models evaluated, ~75% of models tested had excellent or good predictive ability, while 17 had poor performance. The FOFEM5 model consistently over-predicted angiosperms mortality. For conifers, FOFEM5 over-predicted mortality for thick-barked species, but under-predicted mortality at low levels of crown scorch levels with moderate bark thickness. The species-specific models had higher AUCs than FOFEM5 models for 15 of the 22 models. Poorly performing models were primarily angiosperms or thin-barked conifers. This suggests that other approaches, such as different model forms, better bark thickness estimates, and additional predictors, may be warranted for these taxa.

The project also investigated the addition of climate data to improve model accuracy in predicting tree death from fire. We evaluated the effect of climatic water deficit (CMD), summarized over three temporal windows (3-years pre-fire, fire year, and 3-years post-fire) as a predictor to 11 of the FOFEM models. These models were selected because they had excellent data quality and model performance. In all cases, CMD significantly improved model performance, but this did not always translate in a significant improvement in classification accuracy, based on statistical comparisons of the ACUs.

We suggest a two-pronged approach to future research: (1) continued improvements and evaluations of empirical models to quantify uncertainty and incorporate new regions and species and (2) acceleration of basic physiological research on the proximate and ultimate causes of fire-induced tree mortality to incorporate processes of tree death into models. Advances in both empirical and process fire-induced tree modelling will allow creation of hybrid models that could advance understanding of how fire injures and kills trees, while improving prediction accuracy of fire-driven feedbacks on ecosystems and landscapes, particularly under novel future conditions.

Objectives

Our two primary objectives of this research were to:

- 1. Assemble available, existing fire-induced tree mortality data into a unified database, using these data to validate existing predictive mortality models across a wide range of species at a continental scale.
- 2. Determine the influence of pre-fire climate on tree mortality within the current logistic modeling framework of FOFEM, FFE-FVS, and BehavePlus and compare the accuracy of these newly developed models with the current models in FOFEM, FFE-FVS, and BehavePlus to quantify improvement to existing models.

We capitalized on the large number of existing independent datasets to validate current models of fire-caused tree mortality embedded in FOFEM, BehavePlus, and FFE-FVS. By combining these observations into a single database spanning observations from across the U.S., we were able to estimate patterns of fire-caused tree mortality and describe variability in responses.

We hypothesized that patterns in post-fire tree mortality would be sensitive to pre-fire climatic conditions and that accounting for these factors would improve predictions of mortality. Our large database allowed us to test how these relationships extend beyond limited conditions. This is especially imperative as climate change may cause additional chronic stress that interacts with fire-caused injuries to increase mortality (van Mantgem et al. 2013). The warming experienced across much of North America is subtle compared to expected future climatic conditions (Collins et al. 2013), so even small contributions of climate on post-fire tree mortality has potentially profound consequences for fire severity and forest carbon emissions.

In performing the actions described above, our proposal related to the *Task Statement Research Questions* by addressing JFSP's primary interests for this task statement:

- Using existing datasets from prescribed fire and wildfire to validate existing tree mortality models
- Incorporating climate data on fire-induced tree mortality into existing models so that they can be used over a wider range of conditions
- Improving our understanding of how direct and indirect influences determine post-fire tree mortality

We developed a national dataset of Fire-Induced Tree Mortality (FITM) observations, and this has been submitted as an open access database in the Forest Service Research Data Archive. Our submission is under review and should be available to the public by early 2020.

The first portion of Objective 2, which is to evaluate the predictive accuracy of the models in FOFEM, FFE-FVS, and BehavePlus using the FITM database, is complete. A manuscript describing the database and the accuracy of the software systems will be submitted in October 2019. The analysis to determine if adding climate to the models increases predictive accuracy of tree death is nearing completion, with manuscript submission expected in early 2020. This final portion of the project was delayed due to the overwhelming response of data contributions received for the FITM database, which increased the complexity of the database creation. In our proposal we estimated approximately 87,000 trees representing 24 species would be available to create the FITM database. However, our final FITM database includes 173,120 tree-level observations for 160 species – *double* the size of our original estimate.

Background

Millions of forested hectares burn annually, causing both positive and negative impacts on carbon storage, biodiversity conservation, hydrologic processes, and economic and social services (Bowman et al. 2009). Tree mortality is a critical mechanism through which fire limits ecosystem productivity, influences resource availability, and changes the structure and composition of vegetation (Bond and Keeley 2005, Dantas et al. 2016). In fire-prone ecosystems, fire controls tree density and species dominance, creating habitat that supports diverse plant and animal species that cannot persist in the absence of fire. Fire-prone ecosystems may be vulnerable to emergent climate-driven alterations to fire regimes via increasing fire size, frequency, and severity (Flannigan et al. 2009, Pechony and Shindall 2010, Seidl et al. 2016). Climate-mediated increases in fire severity and frequency are projected to cause large changes in forest structure and composition (Bowman et al. 2014, Liang et al. 2017) Trees may be more sensitive to fire-caused injury following episodes of drought-stress (van Mantgem et al. 2013), which may become more frequent with continued warming (Cook et al. 2015).

The global pervasiveness of fire highlights the importance of understanding how fire injures and kills trees in order to accurately model those impacts for a wide range of applications and conditions. Yet the underlying mechanisms of fire-induced tree death remain poorly understood. This gap in understanding limits our ability to accurately predict mortality from fire, estimate fire-driven feedbacks to the global carbon cycle, extrapolate to novel future conditions, and implement appropriate management actions to increase forest resilience to wildfire.

Post-fire tree mortality has been traditionally modeled as a function of tree defenses (bark thickness) and fire injury (crown scorch, stem char). The same empirical models are all used to predict fire effects, from the fine-scale software tools for fire management planning in FOFEM, FFE-FVS, and BehavePlus (Reinhardt et al. 1997, Reinhardt et al. 2009, Andrews 2014) to process-based succession models (Keane et al. 2011) and DGVMs of the terrestrial carbon cycle (Thonicke et al. 2010). Though numerous attempts have been made to improve model performance by including additional variables, such as species identity, pre-fire climate, season of fire, tree vigor, insects and pathogens, or other local conditions (Varner et al. 2007, Hood 2010, Woolley et al. 2012, van Mantgem et al. 2013), most alternative models were developed from smaller, regionally specific data and vary widely in inputs. Attempts at model validation have been nearly non-existent or restricted to a few species and geographic locations (Hood et al. 2007, Ganio and Progar 2017, Grayson et al. 2017, Kane et al. 2017a), making confidence in the general applicability of these models limited. New models with inconsistent input requirements for model parameters also create challenges to incorporating into widely used software programs such as FOFEM.

Materials and Methods

Fire-induced Tree Mortality Review

We reviewed the mechanisms causing fire-induced tree mortality, developed standardized terminology, and summarized key knowledge gaps from the review. While the focus of the review describes tree mortality where the main stem dies (i.e., top-kill) and how that is modelled, we also addressed fire-induced tree injury and recovery via resprouting.

Fire-induced Tree Mortality (FITM) Database

To construct our FITM database, we conducted a literature search for publications reporting post-fire tree mortality data and contacted corresponding authors to inquire if they were willing to contribute to data. Many of these included prior JFSP funded projects. To collect additional data, we also posted data requests on the Ecolog-L listserv hosted by the Ecological Society of America and each of the JFSP Fire Science Exchanges' newsletters and websites. We spoke at the US and Canada Bark Beetle Technical Work Group Meeting, which includes many of the people involved in collecting forest health data after fire. Lastly, we coordinated with the National Park Service to receive the agency's fire ecology program fire effects monitoring data.

We developed the FITM database with standardized field observations from 40 contributed databases from researchers, managers, and archived datasets. At a minimum, datasets had to contain measurements of individual trees, species identity, stem diameter, fire injury, and post-fire survival. We included any trees where post-fire status was measured within 10 years of the fire. Only trees that were alive before the fire were included in the database. All data contributors were provided with the reformatted data, and given an opportunity to check and provide corrections following the data standardization process.

Model Evaluation

We assessed accuracy of all models—at the scale of individual species—included in FOFEM for which there were at least 50 observations with measurements of the variables used in the model, and at least 10 live and 10 dead trees. We were able to assess the FOFEM5 model for 45 species (**Table 1**). For this model evaluation analysis, any second observations (e.g., a tree was burned in a second known fire), was an independent record, which mirrors how managers would use FOFEM for a second-entry fire. FOFEM also includes 29 species-specific tree mortality models, with unique predictors and coefficients. We assessed 24 species-specific models: 15 models intended to be applied before the fire (hereafter "pre-fire models") and 9 models intended for use after the fire (hereafter "post-fire models"). Note that "pre-fire models" still predict post-fire mortality, but are meant to be used before the fire occurs, such as for prescribed burn planning.

For each model we created a one-page summary that shows and summarizes information on the quality of the data used to evaluate model performance, the performance statistics of the model, and a simple qualitative summary of data quality and model performance (**Appendix D**). We then tabulated model performance across species to explore general trends.

Information on data quality is summarized by number of tree observations, mapped to the number and locations of fires sampled. We created two bi-plots for each model, which show where the observations used to evaluate models fall within the species' bioclimatic niche space: one plot shows temperature and precipitation, the other shows climatic moisture deficit (potential evapotranspiration minus precipitation) and reference evapotranspiration. Annual climate data were sampled at locations and associated elevations with the ClimateNA v5.10 software package (available at http://tinyurl.com/ClimateNA), based on methodology described in Wang et al. (2016). We calculated 30-year normals using the annual climate data, and used those normals for plotting bioclimatic niche space. We created violin plots showing observation frequencies of the primary defense and injury variables used in each model. We show live and dead trees ranges separately, and the maximum, median, minimum, and number of live and dead observations.

Table 1. Sample sizes and distributional statistics for assessment of FOFEM5 model accuracy.Dead and live tree status is for three years post-fire, unless otherwise noted.

Scientific name	Dead	Live	n	Scorch	DBH
Abies amabilis	64	47	111	0-95	17.5 - 113
Abies concolor	6,820	5,688	12,508	0-100	0.1 - 228.5
Abies grandis	1,377	587	1,964	0-100	0.4 - 115.6
Abies lasiocarpa	405	116	521	0-100	2.5 - 99.1
Abies magnifica	191	333	524	0-100	0.3 - 155.9
Acer rubrum	16	72	88	0-100	10 - 65.9
Calocedrus decurrens	1,727	1,385	3,112	0-100	0.1 - 182.2
Chamaecyparis lawsoniana	11	58	69	0-98	12.7 - 152.4
Cornus nuttallii	55	62	117	0-100	10.3 - 25.1
Juniperus deppeana	50	71	121	0-100	0.4 - 192
Juniperus occidentalis	23	31	54	0-100	12.4 - 104
Juniperus osteosperma	47	159	206	0-100	15.4 - 96.4
Juniperus scopulorum	37	86	123	0-100	8.9 - 59.5
Larix occidentalis	216	952	1,168	0-100	0.8 - 119.4
Notholithocarpus densiflorus	46	13	59	0-100	0.3 - 96.3
Oxydendrum arboreum	26	164	190	0-100	10 - 32.8
Picea engelmannii	462	205	667	0-100	2.2 - 94
Pinus albicaulis	121	79	200	0-100	5.9 - 100.8
Pinus attenuata	138	99	237	0-100	15.1 - 72
Pinus contorta	4,131	1,875	6,006	0-100	0.3 - 102.9
Pinus coulteri ^b	124	58	182	0-100	16.5 - 110
Pinus echinata	82	62	144	0-100	9.6 - 41.5
Pinus edulis	79	203	282	0-100	14.5 - 61
Pinus elliottii	58	258	316	0-100	5 - 18.5
Pinus flexilis	55	27	82	0-100	3.9 - 79
Pinus jeffreyi	270	400	670	0-100	6.5 - 248.9
Pinus lambertiana	1,405	1,012	2,417	0-100	0.1 - 205.8
Pinus monticola	110	99	209	0-100	15.2 - 84.1
Pinus palustris	78	125	203	0-100	4.5 - 58.9
Pinus ponderosa	15,160	29,154	44,314	0-100	0.1 - 208.3
Pinus strobiformis	26	33	59	0-100	0.5 - 60.4
Pinus taeda	101	224	325	0-100	10.1 - 43.3
Pinus virginiana	24	26	50	0-91	10.8 - 42.4
Populus deltoides ssp. wislizeni ^b	110	24	134	0-100	4 - 38
Populus tremuloides	507	597	1,104	0-100	0.3 - 59.9
Pseudotsuga menziesii	5,934	9,266	15,200	0-100	0.2 - 226.2
Quercus alba	12	88	100	0-100	10.3 - 55
Quercus gambelii	157	430	587	0-100	2.3 - 80
Quercus garryana	26	102	128	0-100	11.4 - 41.9
Quercus kelloggii	182	224	406	0-100	0.3 - 97.2
Quercus montana	12	95	107	0-100	10 - 63.2
Sequoiadendron giganteum	10	145	155	0-100	2.2 - 711.2
Thuja plicata	313	113	426	0-100	12.7 - 135.6
Tsuga heterophylla	1,164	337	1,501	0-100	12.7 - 199.5
Tsuga mertensiana ^a	223	337	560	0-100	5 - 89

We calculated model performance statistics for each species-model combination using classification tables (**Table 2**). We created ROC curves and calculated the AUC for the ROC curve for each species-model combination using the package pROC in the statistical program R (R Development Core Team 2017). We also produced confidence intervals around the AUC, using 10,000 bootstraps of our sample using the pROC package (Robin et al. 2011). AUC values ≤ 0.5 suggest that the model does not perform better than random chance, values between 0.5-0.6 are poor, between 0.7-8.0 are acceptable, 0.8-0.9 are excellent, and >0.9 are outstanding.

Table 2. Classification table of model predictions and model performance statistics calculated based on predicted and true conditions. Managers may wish to use models that perform optimally for different scenarios.

			True co		
			Positive (P)	Negative (N)	Model performance statistics
			Dead	Live	
condition	Positive (P)	Dead	True Positive (TP) Dead trees that were predicted to be dead	False Positive (FP) Live trees that were predicted to be dead	Positive predictive value (PPV) $PPV = \frac{TP}{TP + FP}$ Dead trees that were predicted to be dead / predicted dead Example use: Prescribed fire planning where there is a need to kill small shade-tolerant trees to reduce future
Predicted	Negative (N)	Live	False Negative (FN) Dead trees that were predicted to be live	True Negative (TN) Live trees that were predicted to be live	Negative predictive value (NPV) $NPV = \frac{TN}{TN + FN}$ Live trees that were predicted to be live / predicted live Example use: Prescribed fire planning where there is a need to avoid killing large/old trees.
Model performance statistics			Sensitivity (Sens) $Sens = \frac{TP}{TP + FN}$ Dead trees that were predicted to be dead / total dead Example use: Post-fire salvage in campground, where there is a need to remove any trees that may die and pose a risk.	Specificity (Spec) $Spec = \frac{TN}{TN + FP}$ Live trees that were predicted to be live / total live Example use: Post-fire salvage where there is a need to avoid harvesting large trees that may survive (e.g., potential seed trees or large wildlife trees.)	Accuracy (ACC) $ACC = \frac{TP + TN}{TP + TN + FP + TN}$ Correctly classified live and dead trees / total trees Example use: Need to optimize multiple objectives.

We provide a table of model performance over a range of probability thresholds to aid in the

selection of probability thresholds for a given purpose. For 9 thresholds from every 0.1 distance from 0.1 to 0.9 we calculated the specificity, sensitivity, the true positive rate, true negative rate, and overall accuracy. Typically a threshold of 0.5 is used: i.e. trees that have a \geq 50% probability of mortality are classified as dead. Additionally, we used the pROC package to identified probability thresholds for which the model performed "best" (optimizing both specificity and sensitivity), and the "best" thresholds with either \geq 80% sensitivity or \geq 80% specificity.

We assessed population-level error for each species in relation to the primary crown injury variable (i.e. CVS, CLS, CLK, and BCH, see abbreviation/acronym list) used in each model. For each model we graphically compared the predicated probability of mortality (P_m) and the observed proportion of trees that were killed within binned observations of the primary injury variable. The number of dead trees were assessed by assigning live or dead status based on a 0.5 threshold. For CVS, CLS, and CLK, we tabulated proportional mortality using 10% bins, with additional bins for 0% and 100% injury (e.g., $0, \ge 1$ and $< 10, \ge 10$ and < 20, etc.). For BCH we used 2 m bins, with an additional bin for BCH=0. We calculated the population-level error rate in relation to the primary canopy damage variable used in each model as: ((N_model-N_obs))/N_bin. Where N_model is the number of predicted deaths based on a 0.5 threshold, N_obs is the number of observed deaths, and N_bin is the number of total observations in each injury variable bin.

For each model, we provide ratings of the quality of data used to evaluate the models, model performance, and the direction or error in model predictions. The logical decision framework used to determine the qualitative ratings is provided in **Table 3**. The data quality assessment is meant to help both managers and researchers determine if more data would allow for a more thorough assessment of the model. We based our data quality rating in part on the amount of data, including the number of total observations, number of observations in both the live and dead classes, and number of fires sampled. By definition, if the data quality was "poor" we did not assess the model. In order for the data to be ranked "excellent" or "outstanding", the model evaluation would have to use observations across the full range of the primary canopy injury variable. To be ranked "outstanding" the trees sampled have to cover much of the species DBH range, and the sites sampled have to provide reasonable coverage of the species bioclimatic niche. We based our model quality standards on the AUC, as well as the positive predicted values (PPV) and negative predictive values (NPV). Finally, we describe how often the model over-predicts or under-predicts mortality by assessing the population-level error rate.

For model evaluations for which the available data was considered excellent or outstanding, and the existing model was well-specified (i.e., also performed to excellent or outstanding standards), we assessed whether drought stress increased the probability of mortality, for a given level of fire injury. Eleven models total were assessed: the FOFEM5 models for *Abies concolor, Calocedrus decurrens, Pinus lambertiana,* and *Pinus jeffrey*; the pre-fire models for *A. concolor, C. decurrens, Larix occidentalis,* and *Pinus ponderosa (2 pre-fire models)*; and the post-fire model for *Pinus contorta.* As a proxy for drought stress, we used climatic water deficit (CWD) data from ClimateNA, sampled at the location of the fire (Wang et al. 2016). Because location data varied in scale within the database, we summarized all climate observations at the scale of the fire. For datasets without plot-level location data, we downloaded fire perimeters from the Monitoring Trends in Burn Severity project (Eidenshink et al. 2007), or acquired fire perimeter shape files from National Park Service units, and used the fire centroid as the location. For

datasets with plot-level location data, we took the average of all plot locations. We then sampled a 30-m Digital Elevation model at the fire location, and used latitude, longitude, and location data to query climate observations from the ClimateNA program, for individual years from 1980-2017. Drought is a derivation from the normal water availability at a given locations. Therefore we converted annual observation into z-scores, by subtracting the 30 year climate normals (1981-2010) from the annual climate, and dividing by the standard deviation. We then summarized these climate z-scores over the following time windows: average 3-years before the fire, the year of the fire, and average 3-years after the fire.

In order to compare models with, and without climate predictors, we re-parametrized the models in FOFEM with the same injury and defense variables (hereafter "basic model"), and then parameterized new models that included climate predictors (hereafter "climate model"). With the climate models, we went through normal model reduction steps, dropping un-significant climate predictors. We compared the two models statistically using a χ^2 test, which is appropriate for comparing nested logistic regression models. We summarize model predictive accuracy, using a 0.5 threshold for classifying live and dead observations, in terms of the overall accuracy and AUC. We statistically compare AUCs using DeLong's test for correlated ROC curves (DeLong et al. 1988). Significance was determined at $\alpha = 0.05$ level.

model pre	alettons.		
Туре	Rating		Criteria
Data quality	Poor ^a		< 50 observations total
		or	< 10 live observations
		or	< 10 dead observations
	Acceptable		\geq 50 observations total
		and	≥ 10 live observations
		and	≥ 10 dead observations
	Excellent		Meets "Acceptable" standards
		and	\geq 5 fires were sampled
		and	\geq 50 live observations
		and	\geq 50 live observations
		and	at least 10 observations for every damage level bin (for models with
			CVS, CLS, CVK, only.)
		and	minimum damage variable (CVS, CLS, CVK, BCH) = 0
		and	maximum damage variable (CVS, CLS, CVK) = 100
	Outstanding		Meets "Excellent" standards
	-	and	maximum $DBH \ge 100 \text{ cm}$
		and	maximum DBH \geq "large" DBH for species (Table X)
		and	observations are from sites ≥ 1 S.D. of the AET range for the species
		and	observations are from sites ≤ 1 S.D. of the AET range for the species
		and	observations are from sites ≥ 1 S.D. of the deficit range for the species
		and	observations are from sites ≤ 1 S.D. of the deficit range for the species
Model	Poor		AUC < 0.7
quality		and	PPV < 0.6
- - -		and	NPV < 0.6
	Acceptable		$AUC \ge 0.7$
	-	and either	$PPV \ge 0.6$
		or	$NPV \ge 0.6$
	Excellent	and	$AUC \ge 0.8$
		and	$PPV \ge 0.7$
		and	$NPV \ge 0.7$
	Outstanding		Meets "Excellent" standards
		and	$AUC \ge 0.9$
Over-	Rarely		Population-level error rate >0.25 across < 30% of the range of primary
predicts			damage variable
	Sometimes		Population-level error rate > 0.25 across $> 30\%$ of the range of
			primary damage variable
	Often		Population-level error rate > 0.25 over 70% of the range of primary
			damage variable population-level error rate > 0.5 over 30% of the
		or	range of primary damage variable
	Always		Population-level error rate > 0.5 over 50% of the range of primary
			damage variable
Under-	Rarely		Population-level error rate < -0.25 over 70% of the range of primary
predicts			damage variable
produces	Sometimes		Population-level error rate > 0.25 across $> 30\%$ of the range of
	2011100		primary damage variable
	Often		Population-level error rate < -0.25 over 70% of the range of primary
	- 10011		damage variable population-level error rate < -0.5 over 30% of the
		~	range of primary damage variable
	Almong	OF	Deputation lovel array rate < 0.5 even $500/$ of the range of minutes
	Always		r opulation-level error rate < -0.5 over 50% of the range of primary
			uamage variable

Table 3. Criteria for qualitative ratings of data quality, model quality, and direction or error in model predictions.

Results and Discussion

Fire-induced Tree Mortality Review

We refer readers to our published review in Hood et al. (2018) for a full explanation of fireinduced tree mortality and modeling applications. Our key points are included here.

Plant and ecosystem responses to fire are categorized into either direct or indirect fire effects (Reinhardt et al. 2001). The assumed mechanism of tree death from fire is cambium necrosis via heat transfer to one or more of the crown, stem, and root tissues (**Figure 1**) (Dickinson and Johnson 2001, Michaletz and Johnson 2007, O'Brien et al. 2018). Although partial injuries to multiple parts of the trees can also lead to mortality, these interactions and indirect effects are not currently incorporated into any process models. While most tree mortality is from direct effects, mortality from proximal, indirect effects often occurs in large trees and may account for a large proportion of forest biomass loss from fire (Van Mantgem et al. 2011). Indirect mortality may be influenced by pre-fire stress from competition, drought, and disease, or by post-fire conditions such as elevated bark beetle populations. Because of these multiple interactions, predicting delayed tree mortality is less straightforward than predicting immediate, fire-caused tree mortality (Kane et al. 2017b).



Figure 1. Top panel - Heat during a fire injuries and kills tree tissue. Bottom panel – After a fire, injuries occur to the crown, stem, and roots. Reprinted from Hood et al. (2018).

Most research into fire-induced tree mortality is empirical and uses logistic distribution models

where the binary outcome is tree status, either alive or dead. These empirical logistic regression models are used in fine-scale software tools for fire management planning (Reinhardt et al. 1997, Reinhardt and Crookston 2003, Reinhardt and Dickinson 2010, Andrews 2014), process-based landscape succession models (Sturtevant et al. 2009, Keane et al. 2011), and DGVMs of the terrestrial carbon cycle (Thonicke et al. 2010, Kelley et al. 2014). Empirical models are applied to predict mortality at one of two scales: the probability of individual tree mortality or the proportion of tree mortality by size class and species (or functional type) (Hood et al. 2007).

The current structure of empirical models relies on simple, external measures of observable tree injuries that are proxies for the fire's actual effect on tree physiology. This structure makes it possible to predict fire-caused tree death for a range of flame lengths (the most common metric of fire behavior, but also a proxy for actual heat flux; O'Brien et al. 2018) as long as species and tree diameter and height are known. For non-resprouting species and those where crown scorch and bud kill are equal, the current framework seems to work reasonably well if the bark thickness coefficient (i.e. predicted relationship of bark thickness based on species and diameter) is correct and delayed mortality due to insects is not a factor (Hood et al. 2007, Grayson et al. 2017, Kane et al. 2017a). When the above conditions are not met, model performance is reduced due to over-simplification of species responses, extrapolation beyond the models' underlying data, the inability to quantify long-term effects on tree-to-ecosystem productivity, and difficulty correctly incorporating indirect effects on mortality.

Empirical models are inherently limited to the underlying data distributions, creating uncertainty in accuracy when extrapolating beyond initial data ranges and for novel conditions. The data used to develop current empirical models have limited scope in terms of species, sizes, and life history strategies. Furthermore, the data were collected primarily from fires occurring in the 1980s to the early 2000s, and therefore performance hasn't been evaluated under the hotter climate experienced since and anticipated in the near future. Because increased temperatures exacerbate plant moisture stress via increased vapor pressure deficits (Breshears et al. 2013), it is critical that we further our understanding of fire-drought interactions on tree death. The overwhelming focus of tree mortality research has been on moderate-sized trees, with very few studies including small trees (i.e., ≤ 10 cm DBH), but fuels treatments and prescribed burning objectives often involve killing small trees. It would be useful to know how effective such prescribed burns are for killing small trees and if models need re-parameterization for predicting small tree mortality. Limited evidence suggests that higher levels of damage may be needed to cause mortality in smaller trees (Engber and Varner 2012). While crown injuries are still influential for small trees, basal scorch and ground char can be more important because of thin juvenile bark (van Mantgem and Schwartz 2004, Battaglia et al. 2009). Likewise, large, old conifers often experience elevated mortality after fire, through a combination of factors: damage to roots from smoldering combustion in fuel accumulations near the tree base, fire burning in existing fire scars, low leaf area relative to carbon demands, and decreased hydraulic conductance (Kolb et al. 2007, Hood 2010). In addition, some bark beetle species preferentially attack larger-diameter trees, thereby increasing post-fire mortality of these trees that likely would have survived based solely on fire-injuries (Hood and Bentz 2007, Kolb et al. 2016). To accurately predict mortality of small or very large trees, different or additional predictor variables may need to be incorporated into models.

Perhaps the most limiting aspect of current empirical models is that predictions are binary -

either the tree survives or dies from fire. This approach is appropriate for predicting individual tree mortality, but constrains modeling how sub-lethal fire-caused injuries affect tree growth and recovery from stress. Fire-driven changes in stand structure through loss of photosynthetic biomass and reductions in hydraulic conductivity due to injury that further constrains photosynthesis can alter stand and ecosystem-scale gas exchange and productivity patterns for years (Nolan et al. 2014, Smith et al. 2016). Although spatially explicit ecosystem process models already include algorithms of fire-induced tree mortality and factor changes in the competitive environment on subsequent projections of tree growth, additional research could allow inclusion of fire injury on post-fire growth and vulnerability of surviving trees. In summary, empirical models can effectively predict binary mortality outcomes, but due to the lack of widespread model evaluation and uses that often extrapolate far beyond models' scopes, we do not know how well empirical models work for numerous species, tree sizes, and geographic regions, nor can we predict fire-caused changes in productivity.

Fire-induced Tree Mortality (FITM) Database

The FITM database we assembled includes 159,660 individual trees and 173,120 total tree observations of fire injury and survival (some trees were tracked through multiple fires; **Figure 2**). Our FITM data represent 143 tree species across 61 genera. 97.1% of the trees are identified to species level, and 99.7% identified to genus level. The dataset includes data from 435 prescribed fires and wildfires occurring over 35 years from 1981 to 2016 (no fires were present in the database from 1985). The data archive's metadata describe all data fields (including many fields not used in this analysis but of use to others), as well as standardization and quality control methods.





Model Evaluation

We assessed accuracy of the FOFEM5 model for 45 tree species and assessed 24 species-specific models for 13 species, using data from 96,278 trees, 96,433 tree-level injury records (**Figure 3**; 2.2% of tress had records from a second fire), 366 fires, and 34 datasets. Approximately 75% of models tested had either excellent or good predictive ability. The models that performed poorly were primarily angiosperms or thin-barked conifers.





Figure 3. Locations of fires by data density of individual tree data used to evaluate models in this study.

The 69 model summaries are provided in Appendix D, available on the "other products" tab of the JFSP project's website. Here we summarize results for the FOFEM5 model for individual species, and provide a few illustrative examples of the model evaluation figures that are included Appendix D. We encourage readers to examine the figures in Appendix D to understand the detailed results. The summaries show the species geographic range, fire locations that include the species, sample location with the species climate range, distribution of live and dead trees by DBH and CVS, model accuracy statistics, and stand-level predicted and observed values over a range of CVS. The summaries also provide a qualitative assessment of data quality and model quality. **Figure 4** is the summary of ponderosa pine.

Tree species in **Figure 5** are ordered from thin-barked to thick-barked. The model performed very well for thick-barked (e.g., $BT_{coef} \leq 0.55$) species and the top half shows a consistent pattern of high sensitivities and low specificities, and low PPVs and high NPVs. There were a few exceptions to this pattern, as seen in *Pinus attenuata*, *Pinus albicaulis*, and *Pinus contorta*. Gymnosperms with bark-thickness in the mid-ranges (e.g., $0.35 \leq BT_{coef} \leq 0.52$) generally had reasonable AUC values, but sometimes had un-balanced errors, continuing the pattern of high sensitivities and low specificities. *Abies magnifica Tsuga mertensiana* fall into this group. The FOFEM5 model consistently over-predicted mortally for thin-barked western conifers.

Pinus ponderosa - ponderosa pine - Model: FOFEM5

Region: Western - Leaf habit: Evergreen - Division: Gymnosperm - Family: Pinaceae







200	max-192	max-208		Model accura AUC: 0.888 (CI: 0	cy statisti 885 - 0.892	cs				1.00-
-			_	Threshold	Accuracy	Sens.	Spec.	PPV	NPV	14月1日日日日日 日日
50-			-	Best: 0.84	0.84	0.78	0.87	0.75	0.89	0.75-
	1.5		DBH	Sens>0.8: 0.8	0.83	0.80	0.85	0.73	0.89	morte
00-	10	100	(cm)	Spec>0.8: 0.84	0.84	0.78	0.87	0.75	0.89	0.50-
50	0.740	25 24	-	0.1	0.45	0.98	0.18	0.38	0.94	Page 1
~	med-31			0.2	0.57	0.96	0.36	0.44	0.94	2
0		med-18		0.3	0.65	0.94	0.50	0.49	0.94	
L	min-0	min-0		0.4	0.71	0.91	0.60	0.54	0.93	10 0-0 0-0
Γ	max=100	max-100		0.5	0.76	0.88	0.69	0.60	0.92	0.00-
	100 E.C.	mediano		0.6	0.79	0.86	0.75	0.64	0.91	0 25 50 75 Crown volume scorch (%)
30	104 114	and the		0.7	0.81	0.83	0.80	0.69	0.90	
			SCO	0.8	0.83	0.80	0.85	0.73	0.89	Trees (n) + 1 + 10 + 100 1000 1000
	and the	100	win v	0.9	0.84	0.74	0.89	0.78	0.87	Predicted - Observed
40-	AND CONTRACTOR		olume od (%)							
0	med-10			Data quality: Excellent		Mod Acce	el quality: eptable		Over- Some	r-predicts: Under-predicts: etimes Rarely
	min-0	min-0		-						

Figure 4. Data quality and evaluation statistics of predictive accuracy of FOFEM mortality model. See Appendix D for all species.

Species	AUC	Acc.	Sens.	Spec.	PPV	NPV
Juniperus occidentalis	0.96	0.54	1.00	0.19	0.48	1.00
Juniperus osteosperma	0.74	0.41	0.87	0.27	0.26	0.88
Juniperus scopulorum	0.92	0.33	1.00	0.03	0.31	1.00
Pinus contorta	0.78	0.69	0.99	0.05	0.70	0.66
Pinus albicaulis	0.83	0.64	0.98	0.14	0.63	0.79
Pinus attenuata	0.67	0.59	0.74	0.37	0.62	0.51
Pinus edulis	0.73	0.32	0.96	0.07	0.29	0.82
Pinus flexilis	0.91	0.67	1.00	0.00	0.67	
Pinus strobiformis	0.93	0.47	0.92	0.12	0.45	0.67
Juniperus deppeana	0.95	0.59	1.00	0.30	0.50	1.00
Pinus virginiana	0.71	0.40	0.79	0.04	0.43	0.17
Pinus monticola	0.72	0.72	0.62	0.84	0.81	0.66
Thuja plicata	0.88	0.83	0.84	0.81	0.92	0.64
Picea engelmannii	0.67	0.62	0.60	0.68	0.81	0.43
Pinus echinata	0.55	0.59	0.85	0.24	0.60	0.56
Abies magnifica	0.81	0.59	0.91	0.41	0.47	0.89
Tsuga heterophylla	0.80	0.68	0.64	0.81	0.92	0.39
Tsuga mertensiana	0.76	0.61	0.89	0.42	0.51	0.86
Abies lasiocarpa	0.88	0.78	0.94	0.20	0.80	0.50
Abies grandis	0.78	0.71	0.70	0.73	0.86	0.51
Abies amabilis	0.57	0.46	0.11	0.94	0.70	0.44
Abies concolor	0.89	0.77	0.90	0.62	0.74	0.83
Pinus palustris	0.53	0.27	0.59	0.07	0.28	0.22
Pinus taeda	0.68	0.67	0.52	0.74	0.48	0.78
Pinus elliottii	0.76	0.18	0.98	0.00	0.18	0.50
Calocedrus decurrens	0.97	0.84	0.97	0.69	0.79	0.94
Larix occidentalis	0.82	0.81	0.69	0.83	0.49	0.92
Pinus ponderosa	0.89	0.76	0.88	0.69	0.60	0.92
Pseudotsuga menziesii	0.89	0.79	0.85	0.76	0.69	0.89
Pinus coulteri	0.61	0.61	0.66	0.50	0.74	0.41
Pinus jeffreyi	0.91	0.84	0.86	0.83	0.77	0.90
Pinus lambertiana	0.90	0.80	0.72	0.91	0.91	0.70
Chamaecyparis lawsoniana	0.63	0.87	0.36	0.97	0.67	0.89
Sequoiadendron giganteum	0.93	0.89	0.60	0.91	0.32	0.97

Figure 5. Model evaluation summary statistics and qualitative ratings for the FOFEM 5 model for gymnosperms. Species are ordered from thin bark to thick barked species.

Tsuga heterophylla, Abies lasiocarpa, and *Abies grandis* had relatively balanced errors, and acceptable performance overall. The models for *Picea engelmannii* and *Abies amabilis* performed poorly, and both of those models flipped the typical trend with higher specificity and PPV than sensitivity and NPV. Results from *Abies amabilis* should be interpreted cautiously due to a small sample size coming from only one fire. Likewise, the model for *Pinus echinata*, the one eastern gymnosperm with moderate bark-thickness, performed poorly (AUC = 0.55).

The FOFEM5 model generally performed best for gymnosperms with thick bark: AUC values exceeded 0.8 for most western conifers, including *Abies concolor, Calocedrus decurrens, Larix occidentalis, Pinus ponderosa, Pseudotsuga menziesii, Pinus jeffreyi, Pinus lambertiana, Chamaecyparis lawsoniana, and Sequoiadendron giganteum.* Included in this group are the only FOFEM5 models that met our criteria for "Outstanding" models—AUC values ≥ 0.90 , and both PPV and NPV ≥ 0.7 : *Calocedrus decurrens,* and *Pinus jeffreyi* (**Table 4**). The exceptions were for *Chamaecyparis lawsoniana* (AUC = 0.633) and *Pinus coulteri* (AUC = 0.611). These two species are demonstrative of why the amount, quality, and representativeness of the data should be considered when interpreting model results. The FOFEM5 models did not perform as well for eastern thick-barked gymnosperms, such as *Pinus palustris, Pinus elliottii,* and *Pinus taeda*.

FOFEM5 performed relatively well for some angiosperms, including *Populus deltoides* spp. *wislizeni, Notholithocarpus densiflorus*, and moderately well for *Populus tremuloides* and *Cornus nuttallii*. In contrast, the model performed poorly for many southwestern species and southeastern species, including species for which a decrease in density is a target of many prescribed fire programs (e.g., *Quercus gambelii)*. Nevertheless, 6 of the 11 angiosperms had AUCs <0.7. No angiosperm species had outstanding model quality.

Climate Analysis

Of the eleven models for which we compared re-parameterized basic models, and models that included CMD, the climate models performed significantly better than the basic models in all cases, but this only translated into significantly better AUC values for one of the FOFEM5 models (**Table 5**) and five of the species-specific models (**Table 6**). Model classification accuracy, assessed using a 0.5 threshold to assign live or dead status, was of negligible difference between most models. We are still finalizing model parameters and assessing the sensitivity of different climate windows for the manuscript.

Data quality	Model quality							
	Poor	Acceptable	Excellent	Outstanding				
Acceptable	ABAM -	ABLA - FOFEM5	LAOC - Post-	NODE3 -				
	FOFEM5	ABLA - Pre-fire	fire	FOFEM5				
	ACRU -	ABLA - Post-fire	PILA - Post-fire	PIAL - Pre-fire				
	FOFEM5	ABMA - Pre-fire	PODEW -	PILA - Pre-fire				
	CHLA - FOFEM5	CONU4 - FOFEM5	FOFEM5	PIPO - Post-fire				
	OXAR -	JUDE2 - FOFEM5		Scorch				
	FOFEM5	JUOC - FOFEM5		PIPO - Post-fire				
	PIAT - FOFEM5	JUOS - FOFEM5		Kill				
	PICO3 -	JUSC2 - FOFEM5		PSME - Post-fire				
	FOFEM5	PIAL - FOFEM5						
	PIEC2 - FOFEM5	PIED - FOFEM5						
	PIEL - FOFEM5	PIEN - Pre-fire						
	PIPA2 - FOFEM5	PIEN - Post-fire						
	PIPA2 - Pre-fire	PIFL2 - FOFEM5						
	PITA - FOFEM5	PIMO3 - FOFEM5						
	PIVI2 - FOFEM5	PIST3 - FOFEM5						
	QUAL -	POTR5 - Pre-fire						
	FOFEM5	Low						
	QUGA -	POTR5 - Pre-fire						
	FOFEM5	Moderate						
	QUGA4 -	QUKE - FOFEM5						
	FOFEM5	SEGI2 - FOFEM5						
	QUMO4 -	THPL - FOFEM5						
	FOFEM5	TSME - FOFEM5						
Ewoollow4	DIEN EOEEM5	ADCO Dest fine	ARCO	CADE27				
Excellent	PIEN - FOFEMIJ	ADCO - Post-Ille	ADCO - FOFEM5	CADE27 -				
		ADUR - FOFEMS	APCO Pro fire	CADE27 Dro fire				
		ADMA - FOFEMIJ	ABCO - Fie-life	DICO Dost fire				
		PICO Pre fire		DSME Dra fire				
		DIDO FOFEM5	FILA -	r SME - rie-lile				
		PIFU - FUFEMIJ	PUP Dra fira					
		POIRS - FOFEMS	PIPO - Fle-life					
		TSHE - FOFEMS	Rlack Hills					
		ISHE - FOFEMIS	DIACK TIHIS					
Outstanding		LAOC - FOFEM5		PIJE - FOFEM5				
5								

Table 4. Qualitative ratings of data quality, model quality. See Table 3 for rating criteria. Species with poor data quality were not evaluated for model performance.

Table 5. Statistics to compare re-parameterize the basic FOFEM5 model and models that included additional climate variables. Models that included climate variables always had a lower AIC, and significantly better fit to the data. That did not always translate into better predictive ability using a 0.5 threshold. Accuracy was higher and the AUC was significantly different for *Abies concolor*, but not for the three other species.

Species	Model	Model version	Model AIC	χ2 test comparing basic and climate models	Accuracy	AUC	AUC C.I.	DeLong's test for two correlated ROC curves <i>P</i> - value
Abies concolor	FOFEM5	basic model	7745.11		0.817	0.898	0.892 - 0.903	
		climate model	7647.47	< 0.001	0.821	0.900	0.895 - 0.905	0.002
Calocedrus decurrens	FOFEM5	basic model	1313.55		0.903	0.959	0.952 - 0.965	
		climate model	1258.03	< 0.001	0.903	0.959	0.952 - 0.966	0.624
Pinus lambertiana	FOFEM5	basic model	1477.62		0.822	0.894	0.882 -0.906	
		climate model	1462.23	< 0.001	0.818	0.896	0.883 - 0.908	0.238
Pinus jeffreyi	FOFEM5	basic model	317.67		0.816	0.911	0.884 - 0.937	
		climate model	313.31	0.012	0.810	0.914	0.888 - 0.940	0.262

Table 6. Statistics to compare re-parameterize species-specific models, and models that included additional climate variables. Models that included climate variables always had a lower AIC, and significantly better fit to the data. That did not always translate into better predictive ability using a 0.5 threshold. Accuracy was higher and the AUC was significantly different for *Abies concolor*, but not for the three other species.

Species	Model	Model version	Model AIC	χ2 test comparing models	Accuracy	AUC	AUC C.I.	DeLong's test for two correlated ROC curves <i>P</i> - value
Abies	Pre- fire							
001100101	inc	basic model	2600.84		0.800	0.878	0.868 - 0.889	
		climate model	2567.07	<0.001	0.802	0.884	0.874 - 0.895	0.005
Calocedrus	Pre-							
uccurrens		basic model	567.66		0.916	0.946	0.934 - 0.958	
		climate model	60.16	0.003	0.916	0.954	0.943 - 0.964	0.002
Larix	Pre-							
occidentalis	iiic	basic model	344.04		0.873	0.814	0.765 - 0.864	
		climate model	337.18	0.003	0.873	0.819	0.771 - 0.866	0.781
Pinus	Pre-							
ponderosa	me	basic model	23228.47		0.848	0.867	0.862 - 0.871	
		climate model	22803.70	<0.001	0.847	0.873	0.869 - 0.877	<0.001
Pinus	Pre-							
ponderosa	Black	basic model	13200.42		0.868	0.883	0.877 - 0.888	
	Hills	climate model	12776.58	<0.001	0.868	0.893	0.888 - 0.898	<0.001
Pseudotsuga menziesii	Pre- fire							
monzioon		basic model	5769.69		0.889	0.921	0.915 - 0.926	
		climate model	5611.14	<0.001	0.887	0.934	0.929 - 0.939	<0.001
Pinus	Post-							
Joniona		basic model	687.39		0.841	0.924	0.910 - 0.937	
		climate model	646.07	<0.001	0.841	0.928	0.915 - 0.942	0.089

Science Delivery Activities

We have published seven peer-reviewed journal articles directly relating to the project, with an additional article accepted and currently in press. Two more journal articles are in review at journals. We have two articles in preparation for journal submission. We also have an extended abstract in press in a proceedings.

During the course of the project, we prepared three technical reports directly aimed at helping land managers understand how fire kills trees and the likelihood of tree survival after fire based on fire-caused injuries and bark beetle attacks.

We organized a special session of 15 talks about fire-induced tree mortality at the AFE and IAWF co-sponsored Fire Continuum Conference in 2018.

We led multiple trainings about how to identify dying trees after fire in Montana in 2018 and organized two Duff Fire Science Symposia (in Florida and North Carolina) with the Southern Fire Exchange in 2017 and 2019. We have another planned for South Carolina in 2020.

We have given 18 presentations relating to fire-induced tree mortality at several different conferences, workshops, and training sessions.

We have three websites about the project. These will be maintained and updated as results are finalized.

We have deliberately waited until the end of the project to schedule webinars with the Fire Science Exchanges in order to report final results. We anticipate holding webinars in Spring 2020. Invited presentations of the climate and model evaluation results will be given in November 2019 at the Association for Fire Ecology Congress and in August 2020 at the Ecological Society of America Conference. Sharon Hood will be presenting a poster and lightning talk of the project for the US Forest Service Rocky Mountain Research Station – Intermountain Region Chief's Review in November 2019.

The FITM database is in review at the Forest Service Research Data Archive and will be made publically available after our model evaluation and climate papers are accepted.

See Appendix B and "Other Products" on the JFSP project page for a full list of science delivery products.

Conclusions

Key Findings

Our state-of-the-science review highlighted a number of shortcomings in post-fire mortality research. We detailed research needs in general for better characterizing the fire behavior that causes injury, increasing representation across wide climatic variation, including competition, including the representation of small trees, for better characterizing resprouters (especially angiosperms), and the need for linking fire with other disturbances.

Predictive models of tree mortality and survival are vital for management planning and understanding fire effects in forests, woodlands, and savannas. We built a national-scale post-fire tree mortality dataset (FITM) from 40 contributed datasets. We used the FITM to formally evaluate the accuracy of fire-induced tree mortality models from the First Order Fire Effects Model (FOFEM) software system. We assessed accuracy of the FOFEM5 model for 45 tree species and assessed 24 species-specific models for 13 species. Of the 69 models evaluated, 74% (51 models) had "acceptable" or better performance (e.g., AUC values ≥ 0.70 (60%), and either PPV or NPV ≥ 0.6).

FOFEM5 model performance differed between angiosperms and gymnosperms, and across the gradient from thin-barked to thick-barked species. For conifers, the FOFEM5 model made accurate predictions of mortality across all levels of CVS for very thick barked species, over-predicted mortality at higher levels CVS for moderately thick-barked species, and under-predicted mortality at low levels of CVS for many thin-barked species. For gymnosperms with moderate bark thickness the FOFEM5 model moderately under-predicted mortality at low levels of CVS (e.g., $\leq 40\%$). For gymnosperms with thick bark the FOFEM5 model moderately over-predicted mortality at high levels of CVS (e.g., $\leq 60\%$).

Generally the models performed well for conifers species which make up the dominant canopy component of forest in western North America. For example, the only FOFEM5 models that met our criteria for "Outstanding" models—AUC values ≥ 0.90 , and both PPV and NPV ≥ 0.7 —were for *Calocedrus decurrens*, and *Pinus jeffreyi*. Model sensitivity and NPV was highest, and model sensitivity and PPV was lowest for thin-barked gymnosperms.

The trends in the performance of FOFEM5 model related to taxa and bark thickness indicate that different approaches—such as different model forms, better estimates of bark thickness, and additional predictors—may be warranted for angiosperms and thin-barked conifers. The FOFEM5 model consistently over-predicted mortality for angiosperms, resulting in high sensitivity and low specificity. For conifers, FOFEM5 slightly over-predicted mortality for thick-barked species. It also under-predicted mortality at low levels of CVS for moderately-barked conifers, perhaps indicating that injuries to the stems and roots need to be accounted for when modeling mortality of these species. The models that performed poorly were primarily angiosperms or thin-barked conifers. This patterns suggests that different approaches—such as different model forms, better estimates of bark thickness, and additional predictors—may be warranted for these taxa.

Managers who rely on these models can use the results to (1) be aware of the uncertainty and biases in model predictions, and (2) choose a threshold for assigning dead and live trees with optimizes certainty in either identifying or predicting live or dead individuals. Researchers should target data collection and modeling on data gaps and poorly performing models identified in this study. Additional variable collection for thin-barked gymnosperms and angiosperms, and thick-baked eastern conifers may be necessary for to parameterize accurate models.

Our results support that climate before, during, and after fire influences tree mortality. Nevertheless, as parametrized using logistic regression with fire-scale location data, and a relatively simple climatic water balance measure of drought, inclusion of climate data does not seem to greatly improve the prediction accuracy of the models. Thus, we are conducting further analysis to determine if the inclusion of climate predictors would improve prediction accuracy in FOFEM.

Implications for Management/Policy

The FITM database provided us with an unprecedented opportunity to evaluate the post-fire tree

mortality models in FOFEM, but the data availability for this model evaluation varied between models, and that should be considered when interpreting the results. The model evaluations where the data quality was only considered "acceptable" should be considered less conclusive than when the data quality was ranked as "excellent" or "outstanding". It is important to note that only 12 western conifers and 1 angiosperm had data quality that we considered "excellent" or "outstanding". We evaluated models for many species that have neither been included in modeling efforts nor had model evaluations conducted in the past.

The model evaluation provides managers with a standardized assessment of data quality and model performance for 69 species in the US. This greatly increases transparency of the predictive accuracy for the mortality models included in FOFEM, BehavePlus, and FFE-FVS. The model accuracy statistics allows managers to select different thresholds of Pm tiered to specific management objectives.

Future Research

Despite the limitations of empirical modeling approaches, they are useful and many of the limitations can be resolved or improved. The following research priorities should be explored simultaneously to advance our understanding of and ability to predict fire induced tree mortality. Improvement to existing empirical models and development of new empirical models should continue, so that managers who rely on these models to make decisions can do so with higher accuracy - given an understanding of model limitations and uncertainty in their predictions. Current software systems have embedded post-fire tree mortality models that predict mortality far beyond the data used to parameterize the models. Therefore, benchmark datasets are needed to allow model evaluation and quantify uncertainty across species, sizes, and geographic regions. Our results highlight species and regions where new data collection or new model development is needed. We were not able to assess the FOFEM5 models for 147 species for which FOFEM has built-in bark thickness coefficients. Sixty-three of these species have at least one observation in the FITM database, and thirty-nine have observations at 3-years post-fire. Additional data collection to evaluate and improve models of these species should be a priority. Some eastern angiosperms have already been evaluated (Keyser et al. 2018). We also were not able to evaluate 5 species-specific post-fire models.

It is important to note that we did not evaluate all steps in the FOFEM modeling process. The pre-fire models often use projected percent crown scorch (either percent of crown length or percent of crown volume), which cannot be observed prior to the fire. Instead, FOFEM allows users to either enter predicted flame length or scorch height, as well as tree height and crown ratio; percent crown volume scorch is then calculated from these inputs (Lutes et al. 2012). This sub-model to predict percent crown volume scorch has not been evaluated for accuracy. Also largely unevaluated is the sub-model to derive the bark thickness model input from DBH and a species-specific bark thickness coefficient.

Different statistical modeling approaches may be needed to make inclusion of climatic variables in predictive models of tree mortality worthwhile. It is likely that the importance of climatic stress in determining mortality is contingent on the level of injury received from the fire: severely burned trees and lightly burned trees by die, or live, respectively, regardless of climatic stress. Pre-fire and post-fire drought may be most important in determining the survival of trees with intermediate levels of injury. We will be conducting additional research in the next year to understand the role of climatic stress in fire-induced tree mortality using statistical models that are more appropriate for non-linear relationship (e.g., such as RandomForests and path analysis). Likewise, more sophistication of calculations of drought stress may improve models. For example, soil water deficit data calculated using daily times step data using method that incorporate wind and soil water holding capacity is now available (Abatzoglou et al. 2018) albeit at a much coarser spatial resolution that the ClimateNA data used here.

Research is also needed to make the connections from fire behavior, to energy release, to tissue damage of specific tissues, to the effects of the fire on whole plants-i.e., mortality, survival with reduced fitness, or survival with full recovery. The dose-dependent response approach developed for quantifying reductions in productivity associated with fire-related tree injuries rather than a binary outcome (Smith et al. 2016, Sparks et al. 2016) offer great promise. Fire behavior models based on fluid dynamics are beginning to model heat flux at scales relevant for plant tissues, but the connection between heating and physiological damage in different tissues, and how that varies with ontogeny, phenology, and morphology is not understood (O'Brien et al. 2018). Detailed knowledge of individual species response will be limiting. We suggest that grouping species based on similar traits (e.g., bark thickness, sprouting ability, morphological architecture, and hydraulic strategies) and developing functional responses to heat flux, insect attacks and disease, and competition could offer an immediate improvement to the existing empirical modeling framework. Third, we need a better understanding of the basic physiological impacts of fire on hydraulic failure and NSC maintenance and how these impacts on individual tissues scale to affect whole tree functioning and death (Venturas et al. 2017, Michaletz 2018). Also, biophysical models only account for direct fire effects, but incorporating indirect effects such as insects and competition would improve understanding of delayed tree mortality. Focusing on these lines of research will help answer some of the remaining outstanding questions about fire induced tree mortality, and improve our ability to predict fire-induced tree mortally both at immediate time scales and under novel future climates.

Although current logistic models can accurately predict mortality for some species, they are far removed from the actual physiological and ecological processes that cause immediate and delayed post-fire mortality. Other empirical analysis techniques that can detect nonlinearities and contingent relationships (e.g., classification and regression trees, path analysis) could help identify interactions and provide insight into the mechanisms of fire-induced tree mortality, laying a foundation for future advances in process-based models of fire-induced mortality. Some attempts to model fire-induced mortality with path analysis have been made (Menges and Deyrup 2001, Youngblood et al. 2009, van Mantgem et al. 2018). These models allow better accounting of the strength and direction of direct and indirect influences on post-fire tree mortality, but also require *a priori* hypotheses of effects and interactions. Applying different modeling techniques does not necessarily mean dauntingly complicated models. For example, the likelihood of death increases sharply around 70% crown scorch in some conifers, which has led to the use of piecewise regression to identify simple thresholds of mortality in predictor variables (Fowler et al. 2010, Grayson et al. 2017).

Existing research and data already provide a foundation upon which existing models and planning tools could be improved to make more accurate predictions and explicitly quantify uncertainty in predictions. Planning tools could report expected ranges of mortality (i.e., 95% C.I.) and allow for the inclusion of additional observations (e.g., bark beetle attacks, cambium

kill) where a higher degree of model accuracy is desired. Given the development of easy to acquire gridded climatic data, such as PRISM (Daly et al. 2002) or TerraClimate (Abatzoglou et al. 2018), incorporating climatic variables, such as water stress, into widely used fire effects software could provide expected mortality levels given a range of pre-fire climates. Also, older models deserve to be re-evaluated: the empirical model developed by Peterson and Ryan (1986) allows for different lethal heating thresholds in the crown due to seasonal effects and crown morphology. Though the provided temperatures are unsubstantiated, this model provides a way forward, linking fuel consumption and fire behavior to predict resulting tissue injury and tree death.

The wide-ranging applications associated with fire-induced tree mortality do not lend themselves to a one-size-fits-all approach, and it seems unlikely that empirical models will be replaced due to the need to balance model complexity with model application. Instead, empirical models should be refined for use in land management applications in the near-term, while heating and physiological process models should be developed and linked to create a hybrid-based approach to improve mechanistic understanding to predict mortality under novel scenarios.

Accurate predictions of fire-induced tree mortality with quantified uncertainty are needed for models used in planning, post-fire management, predicting future landscape dynamics, and feedback to the global carbon cycle. Fire is expected to become increasingly prevalent in many ecosystems due to climate change (Flannigan et al. 2009, Jolly et al. 2015). Direct fire effects may be exacerbated during periods of climatic stress, such as drought, where xylem function may be further compromised or more easily disrupted by heat effects of fire in stems and crown (Kavanagh et al. 2010, Michaletz et al. 2012), as well as potentially increased indirect fire-induced mortality due to bark beetles (Kolb et al. 2016). Many critical questions remain about fire-induced tree mortality. Taken together, these reasons underscore the need for increased research on the fundamental processes post-fire tree mortality coupled with the development of better management tools.

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Appendix A: Contact Information for Key Project Personnel

Sharon M. Hood (PI): Research Ecologist Rocky Mountain Research Station Fire Sciences Laboratory 5775 Highway 10 W Missoula, MT 59802 Sharon.hood@usda.gov 406-329-4818 https://www.firelab.org/profile/hood-sharon https://www.fs.fed.us/rmrs/people/shood

J. Morgan Varner (co-PI): Director of Fire Research & Senior Scientist Tall Timbers Research Station & Land Conservancy 13093 Henry Beadel Drive Tallahassee, FL 32312 mvarner@talltimbers.org Office: 850.893.4153, x224 | Cell: 707.845.1659 www.talltimbers.org

Phillip van Mangem (co-PI): Research Ecologist

U.S. Geological Survey, Western Ecological Research Center, 1655 Heindon Road, Arcata, CA 95521, USA pvanmantgem@usgs.gov 707-825-5189

C. Alina Canlser: Post-doctoral Researcher Rocky Mountain Research Station Fire Sciences Laboratory 5775 Highway 10 W Missoula, MT 59802 Courtney.cansler@usda.gov 406-329-4867

Appendix B: List of Completed/Planned Scientific/Technical Publications/Science Delivery Products

Articles in peer-reviewed journals

Cansler, C.A., S.M. Hood, P. van Mantgem, J.M. Varner. In preparation. Evaluating predictive accuracy of fire-induced tree mortality in the First Order Fire Effects Model (FOFEM). Planned submission to Fire Ecology. October 2019.

Cansler, C.A., S.M. Hood, P. van Mantgem, J.M. Varner. In preparation. Does drought increase tree mortality independent of fire intensity? Planned submission to Global Change Biology. January 2020.

Hood, S.M., J.M. Varner, P. van Mantgem, and C.A. Cansler. 2018. Fire and tree death: Understanding and improving modeling of fire-induced tree mortality. Environmental Research Letters 13:113004. DOI: https://doi.org/10.1088/1748-9326/aae934

Hood, S.M. and J.M. Varner. 2019. Post-fire tree mortality. Encyclopedia of Wildfires and Wildland-Urban Interface Fires (Springer). In press.

Grayson, L. M., R. A. Progar, and S. M. Hood. 2017. Predicting post-fire tree mortality for 14 conifers in the Pacific Northwest, USA: Model evaluation, development, and thresholds. Forest Ecology and Management **399**:213-226.

Hood, S., and D. Lutes. 2017. Predicting post-fire tree mortality for 12 western US conifers using the First-Order Fire Effects Model (FOFEM). Fire Ecology **13**:66-84.

Kane, J.M., J.M. Varner, M.R. Metz, and P. van Mantgem. 2017. Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western U.S. forests. Forest Ecology & Management 405: 188-199.

Nemens, D.G., J.M. Varner, and P. Dunwiddie. 2019. Resilience of Oregon white oak to reintroduction of fire. Fire Ecology 15: art29.

O'Brien, J.J., J.K. Hiers, J.M. Varner, C. Hoffman, M. Dickinson, and S. Michaletz, E.L. Loudermilk, and B.W. Butler. 2018. Advances in mechanistic approaches to quantifying biophysical fire effects. Current Forestry Reports DOI: 10.1007/s40725-018-0082-7.

Varner, J.M. 2018. Encroachment and persistence of trees in southeastern grasslands. Pp. 183-191 in: Southeastern Grasslands: Biodiversity, Ecology, and Management (J.G. Hill and J. Barone, Eds.), The University of Alabama Press, Tuscaloosa.

Shearman, T., J.M. Varner, S.M. Hood, C.A. Cansler, J.K. Hiers. In Review. Modelling post-fire tree mortality: Can random forest improve discrimination of imbalanced data? Submitted to Ecological Modeling.

Stevens, J., M. Kling, D. Schwilk, J.M. Varner, and J.M. Kane. In Review. Biogeography of fire regimes in western US conifer forests: a trait-based approach. Submitted to Global Ecology & Biogeography.

Technical reports

Is That Tree Dead? Quantifying Fire-Killed Trees to Inform Salvage and Forest Management. 2019. Science You Can Use Bulletin. USDA Forest Service, Rocky Mountain Research Station. Issue 36. 11 p.

https://www.fs.fed.us/rmrs/sites/default/files/documents/SYCU_issue36_firesalvagelogging_FIN AL.pdf?utm_source=Is+That+Tree+Dead%3F+Fire+Salvage+Bulletin&utm_campaign=Science +You+Can+Use+-+Is+That+Tree+Dead%3F&utm_medium=email

Hood, Sharon; Abrahamson, Ilana; and Cansler, C. Alina. 2018. Fire resistance and regeneration characteristics of Northern Rockies tree species. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory (Producer). Available: https://www.fs.fed.us/database/feis/pdfs/other/FireResistRegen.html.

USDA Forest Service Region One. 2017. Post-fire Assessment of Tree Status. Vegetation Classification, Mapping, Inventory and Analysis Report. Report 17-17 v2.0. December 21 2017. https://www.firelab.org/sites/default/files/images/downloads/Assessing_Tree_Status_Post_Fire_ WalkThrough_12.21.17.pdf

Conference or symposium proceedings scientifically recognized and referenced (other than abstracts).

Cansler, C.A., S.M. Hood, J.M. Varner, P. van Mantgem. In Press. Evaluating and optimizing the use of logistic regression for tree mortality models in the First Order Fire Effects Model (FOFEM). In: Hood, Sharon M.; Drury, Stacy; Steelman, Toddi; and Steffans, Ron, eds. In Press. Proceedings of the Fire Continuum – preparing for the future of wildland fire; 2018 May 21-24; Missoula, MT. Proceedings RMRS-P. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Online.

Workshop materials and outcome reports

Fire-induced tree mortality: Empirical modeling, physiology, and integrative approaches. 2018. Our special session at the Fire Continuum conference consisted of 15 talks in four sub-sessions: (1) predictive modeling of fire-induced tree mortality, (2) tree physiology and injury from heat flux, and (3) indirect effects and interaction with other stressors, and (4) approaches to scale-up predictions.

Field demonstration/tour summaries

Duff Fire Science Symposium, Florida State University Marine Lab, Carrabelle, FL. October 2017 (36 attendees)

Multiple site visits to National Forests in the Northern Region to teach approximately 65 people about fire injury and delayed tree mortality following fire in 2017 and the R1 2018 Timber Strike Team (approximately 40 people).

Website development

ResearchGate Website: Mortality reconsidered: Testing and extending models of fire-induced tree mortality across the US. JFSP Project ID 16-1-04-8 <u>https://www.researchgate.net/project/Mortality-reconsidered-Testing-and-extending-models-of-fire-induced-tree-mortality-across-the-US-JFSP-Project-ID-16-1-04-8</u>

Firelab.org website https://www.firelab.org/project/fire-induced-tree-mortality

Rocky Mountain Research Station: <u>https://www.fs.fed.us/rmrs/science-spotlights/how-does-fire-kill-trees</u>

Presentations/webinars/other outreach/science delivery materials.

van Mantgem, P.J. Can prescribed fire promote resistance to drought? Natural Areas Conference. Davis, CA. October 20, 2016.

van Mantgem, P. and C. Farris. Prescribed fire research in the Sierra Nevada and beyond: NPS-USGS partnerships to restore a natural process to western forests. National Cohesive Wildland Fire Management Strategy Workshop. Reno, NV. April 26, 2017.

van Mantgem, P.J. Drought, fire, and tree mortality. Guest lecture, Humboldt State University, Arcata, CA. April 3, 2017.

National Advanced Silviculture Program: Disentangling post-fire tree mortality. Presentation to National Advanced Silviculture Program participants (42 FS employees), Cloquet, MN 08/02/2017

RX-310: Post-fire tree mortality. Included in a training session at RX-310 (28 participants, state and federal agency personnel) at Kentucky-TN Fire Academy, Bell Buckle, TN 01/06/2017

Varner, J.M., J.K. Hiers, J.J. O'Brien, J.M. Kane, J.K. Kreye, and L.N. Kobziar. Consequences of long-duration soil heating for tree stress and mortality. Presentation at the Fifth International Fire Congress, Orlando, FL. December 2017.

Varner, J.M. 2017. Advances in understanding duff fires in longleaf pine forests. Duff Fire Science Symposium, Florida State University Marine Lab, Carrabelle, FL. October 2017 (36 attendees).

Another look at analyzing post-fire tree mortality data. 2018. Invited presentation to Fire Continuum Conference, Missoula, MT.

Validating mortality predictions from the First Order Fire Effects Model (FOFEM) model with external. 2018. Invited presentation to Fire Continuum Conference, Missoula, MT.

van Mantgem, P.J. Tree mortality, uncertainty, and forest conservation in the West. Schatz Forestry Seminar, Humboldt State University, Arcata, CA. May 2, 2018. Invited.

van Mantgem, P.J. Drought, fire, and tree mortality -- What will the future hold? Redwood Region Forest Management and Market Trends, Eureka, CA. April 4, 2018. Invited.

van Mantgem, P.J. Drought, fire, and tree mortality. RX-310 Firefighter Training, Orick, CA. March 28, 2018.

Varner, J.M. 2018. Ecological consequences of restoring fire following prolonged fire exclusion. 2nd Biodiversity Symposium, University of Florida. Gainesville, FL, April 2018 (75 attendees)

RX-310 Introduction to Fire Effects, Murfreesboro, TN (April 2019; Coord. by Dept of Defense). 33 participants from across US. Post-fire tree mortality (1.5 hours)

National Advanced Silviculture Program- Ecological Systems Module, University of Minnesota, Cloquet Forestry Center (August 2019), Post-fire tree mortality: silvicultural implications (38 USFS personnel)

C. Alina Cansler, Sharon Hood, Phillip van Mantgem, J. Morgan Varner. 2019 Evaluating predictive accuracy of fire-induced tree mortality in the First Order Fire Effects Model (FOFEM). Contributed presentation. North American Forest Ecology Workshop. June 25, 2019, Flagstaff, Arizona, USA.

C. Alina Cansler, Sharon Hood, Phillip van Mantgem, J. Morgan Varner. 2019. Does drought increase tree mortality independent of fire intensity? Invited presentation. Special Session: Historical and contemporary pyrodiversity in fire-prone forest ecosystems: Relevance to future climate and wildfire adaptation. 8th International Fire Ecology and Management Congress. Nov. 21, 2019, Tucson, Arizona, USA.

Post-fire tree mortality, J.W. Jones Ecological Research Center at Ichauway, Newton, GA (October 2019)

C. Alina Cansler, Sharon Hood, Phillip van Mantgem, J. Morgan Varner. 2020. Understanding fire-induced tree mortality as mediated by interactions between species' traits, fire injury, water stress, and biotic agents. Proposed Special Session: Enhancing our ecological understanding of the new fire normal with large datasets, novel methods, and traditional perspectives. Ecological Society of America Annual Meeting. Aug. 2-7, 2020, Salt Lake City, Utah, USA.

Appendix C: Metadata

The Fire-Induced Tree Mortality (FITM) database has been submitted for publication to the Forest Service Research Data Archive and is under review. The submitted data product consists of five data files and the metadata describing each of the data files. The FITM.html file uploaded with the final report to the JFSP website provides the metadata to the database. The FITM database includes standardized observations of fire injury and survival or mortality for 160 tree species and 173,120 trees in the United States. These trees were burned in 435 prescribed fires and wildfires occurring in 35 years, from 1981 to 2016. The database was developed 40 contributed datasets from researchers, managers, and archived data products. The purpose of the Fire-Induced Tree Mortality database is to provide access to data on tree mortality from wildland fire. The FITM database also allows easy identification of data gaps to direct future data collection efforts. The FITM database also allows evaluation of post-fire mortality models, such as the First Order Fire Effects Model (FOFEM), BehavePlus, and FFE-FVS. At a minimum, datasets had to contain measurements of individual trees, size, fire injury, and post-fire survival, but some datasets include additional data such as bark beetle attack. Only trees that were alive before the fire were included in the database. We included any trees where post-fire status was measured within 10 years of the fire.

Data Product Citation:

C. Alina Cansler, Sharon M. Hood, J. Morgan Varner, Phillip van Mantgem, James K. Agee, Michelle C. Agne, Robert Andrus, Matthew P. Ayres, Bruce D. Ayres, Jonathan D. Bakker, Michael Battaglia, Barbara Bentz, Carolyn Breece, James Brown, Karen Clancy, Daniel Cluck, Tom W. Coleman, Greg Corace, W. Wallace Covington, Douglas Cram, James Cronan, Joseph E. Crouse, Adrian J. Das, Ryan Davis, Darci Dickinson, Brett Dickson, Andris Eglitis, Stephen A. Fitzgerald, Lisa Ganio, Lindsay M Grayson, Charles B. Halpern, Jim Hanula, Brian Harvey, Kevin Hiers, David W. Huffman, MaryBeth Keifer, Tara Keyser, Leda Kobziar, Tom Kolb, Crystal Kolden, Karen Kopper, Jason Kreitler, Jesse Kreye, Andrew M Latimer, Andrew Lerch, Maria J Lombardero, Virginia McDaniel, Charles McHugh, Joel McMillin, Connie Mehmel, Joseph J. O'Brien, Jessica J Page, Daniel D.B. Perrakis, David W. Peterson, Susan Prichard, Robert Progar, Kenneth Raffa, Elizabeth Reinhardt, Joe Restaino, John P. Roccaforte, Brendan M. Rogers, Kevin Ryan, Hugh D Safford, Alyson Santoro, Timothy Shearman, Alice M. Shumate, Carolyn Sieg, Sheri Smith, Rebecca J Smith, Nathan L Stephenson, Mary Steuver, Jens T Stevens, Michael T. Stoddard, Walter G. Thies, Nicole Vaillant, Shelby Weiss, Douglas J. Westlind, Travis J. Woolley. Fire-Induced Tree Mortality Database. In Review. Fort Collins, CO: Forest Service Research Data Archive: RMRS-FFS-2019-003.

Data product files:

- FITMdatabase.csv: data included in the FITM database
- FITM_fires.csv: The fire name, year, dataset contact, and location.
- Dataset_primary_contacts.csv: The dataset name as appears in the FITM database, primary contact, and email.
- Species_BarkThickness.csv: lists all species in the FITM database and the bark thickness information used to evaluate FOFEM model accuracy
- Dataset_citations.csv: The main citation for each contributed dataset in the FITM database for additional information about the data collected.

Appendix D: Species Model Evaluation Results

For each model evaluated in FOFEM, we created a one-page summary that summarizes information on the quality of the data used to evaluate model performance, the performance statistics of the model, and a simple qualitative summary of data quality and model performance.

For the model summaries, please see the "other products" tab on this project's JFSP webpage. There are seven parts to Appendix D, organized by species.