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Tree mortality in western U.S. forests forecasted using forest inventory and Random Forest classification

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Citation: McNellis, B. E., A. M. S. Smith, A. T. Hudak, and E. K. Strand. 2021. Tree mortality in western U.S. forests forecasted using forest inventory and Random Forest classification. Ecosphere 12(3):e03419. 10.1002/ecs2.3419

Abstract. Climate change is projected to significantly affect the vulnerability of forests across the western United States to wildfires, insects, disease, and droughts. Here, we provide recent mortality estimates for large trees for 53 species across 48 ecological sections using an analysis of 23,215 Forest Inventory plots and a Random Forest classification model. Models were also used to predict mortality in future FIA inventories under the RCP 4.5 emissions scenario. Model performance indicated species identity as the most important predictor of mortality under both current and future scenarios, with contributions from climate and soil variables. Our results show relatively high levels of recent mortality in the Middle and Southern Rocky Mountains driven by high mortality in *Populus tremuloides*, *Pinus contorta*, *Pinus albicaulis*, and *Abies lasiocarpa*. Low levels of mortality were observed in several species, with <1% annual mortality observed throughout all other sections. Future mortality was predicted to increase significantly for most species and correlated well with recent mortality at the species level, but not at the plot level. These results suggest that future attempts to model or predict widespread forest mortality would benefit from more research on vulnerable species and that significant mortality events in some species may not be important for dynamics across all systems.

Key words: bark beetles; drought mortality; dynamic vegetation model; forest dieback; forest disease; Forest Inventory Analysis; Random Forest; recent mortality; tree mortality; western USA.

Received 11 January 2020; revised 23 September 2020; accepted 7 October 2020; final version received 11 January 2021. Corresponding Editor: Charles D. Canham.

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INTRODUCTION

Tree mortality is one of the most sudden and significant demographic processes within forested ecosystems (Waring 1987, Allen et al. 2010, Kosiba et al. 2018). Changes to future climate regimes are projected to increase the vulnerability of forested ecosystems to external stressors and exacerbate tree death, especially in the western USA (McDowell et al. 2008, McDowell et al. 2015, Romero-Lankao et al. 2014, Smith et al. 2014, Kolb 2015). The degree to which these climatic changes affect ecosystem structure and function will depend partly on what factors are driving current tree mortality and what systems or species are most vulnerable. Previous work on forest mortality has largely been done in a small number of well-studied model systems (Allen and Breshears 1998, Geils et al. 2010, Hicke and Zeppel 2013). However,

regional and continental studies are needed in order to accurately predict future impacts on ecosystem processes such as carbon cycling and community succession (Hartmann et al. 2018).

Extensive work in plant physiological ecology suggests that future forests will be threatened by a hotter, drier climate that causes death by water stress or increases mortality risk from insects and fire (Jiang et al. 2013, McDowell et al. 2015, Kolb et al. 2016). Less work has attempted to answer the challenging question of where and how severe these threats will manifest, although modeling work generally supports these predictions. For example, one recent study assessed drought and fire risk across the western USA through 2049 using a simulation model and predicted that forests in the low- and middle-elevation desert southwest and southern Rocky Mountains (36% of the study area) will face serious threats from drought and fire (Buotte et al. 2019). Longer term predictions also exist; in one such study, forest mortality in the Sierra Nevada was predicted up to the 2090s but predicted future mortality rates varied strongly depending on what environmental variables were used in the model (Das et al. 2013). Although models have provided novel and valuable insight, few studies have attempted to predict mortality risk using empirical data on observed tree mortality despite the utility in this approach in a broader framework for generating new hypotheses and advancing the general understanding of forest mortality (Meir et al. 2015).

Causes of tree mortality in the western USA commonly include drought, disease, insect attack, windthrow, and competition (Lutz and Halpern 2006, Geils et al. 2010, Long and Lawrence 2016, Choat et al. 2018). Many of these causal agents are co-occurring and coupled (McDowell et al. 2011, van Mantgem et al. 2018). Few studies to date have attempted to assess multiple co-occurring mortality agents at regional or larger extents in addition to predicting future mortality (Berner et al. 2017, Buotte et al. 2019). For example, Berner et al. determined mortality rates across the western United States from 2003 to 2012 for harvest, fire, and insect attack under the influence of water stress but did not attempt to predict future mortality (Berner et al. 2017). Nonetheless, the cause of tree death is important for understanding their interactions and their relationship to overall forest mortality as well as how forests will respond to climate change in the future (McDowell et al. 2011).

The Forest Inventory and Analysis (FIA) program is a national inventory program conducted regularly by the United States Forest Service (USFS) that provides a regular re-measurement inventory of individual trees. Previous research has utilized FIA demography data to answer questions related to several mortality agents including fire, bark beetles and other insects, hurricanes, and drought (Klos et al. 2009, Thompson 2009, Negrón-Juárez et al. 2010, Pugh et al. 2011, Shaw et al. 2017). Therefore, FIA data are well suited to examine recent and future tree mortality across the western United States. Tinkham et al. (2018) provide a thorough overview of FIA data, sampling procedures, and applications.

In this study, we used FIA tree inventory data to assess the following broad research questions and associated hypotheses about forest mortality across the western USA:

1. What environmental and biological factors are significantly related to recently observed forest mortality rates? We hypothesize that precipitation and temperature variables are most important to recent mortality rates due to their relationship to drought, disease, and insect mortality.
2. What explains the cause of tree death for recent data? We hypothesize that cause of tree death is also driven by precipitation and temperature variables due to their relationship to drought and insect mortality.
3. How do mortality rates change under future emissions scenarios? Future mortality rates are expected to increase under future climates in accordance with previous work on mortality in western U.S. forests.
4. How does cause of tree death change under future climates? We hypothesize insect mortality will increase through the previously documented direct influence of increased temperature on insect life cycles.

Materials and Methods

Experimental design, climate, and soil data

FIA established a systematic grid of inventory plots to monitor U.S. forests in 2000 (Smith 2002).

This population of plots is censused every 5 (eastern USA) to 10 (western USA) years using a rolling inventory that remeasures 10% (western USA) or 20% (eastern USA) of the plots per year. The first such set of rolling inventories in the western USA was conducted from 2000 to 2005, with re-measurements beginning in 2010. Here, we define a census interval as two sets of rolling inventories that include an initial inventory and a re-measurement inventory. With at least two sets of inventories (one census interval), we are able to calculate demographic rates, including mortality. We used the first such census interval in FIA data to calculate our recent mortality rates using all plots that have been remeasured at least once. Assuming the inventories proceed as scheduled, the next set of rolling inventories will begin in 2020 and will involve a second re-measurement of trees originally measured in 2000. This third rolling inventory will complete a second census interval and allow for another calculation of demographic rates across the FIA study design. Here, our predicted future mortality represents a forecast of demographics in this second census interval.

Tree- and stand-level explanatory variables were taken directly from individual tree (TREE) and inventory (PLOT) data tables. We limited consideration to the 53 most common tree species due to restrictions imposed by our analysis software. This reduced our total sample size by <0.9% of all available trees. Condition tables in FIA data contain spatially referenced plot information at the within-plot level such as slope and aspect in order to better characterize within-plot heterogeneity; here, we reference these condition tables to assign condition variables to individual trees. Aspect was transformed to topographic solar-radiation index to avoid data circularity (Roberts and Cooper 1989, Cremers and Klugkist 2018).

In order to assess tree mortality over many disparate ecosystems and tree communities, we included coded information on the physio-geographic identity of plot locations in the form of ecological section codes assigned by the USFS (Cleland et al. 2007). Ecological sections are unique qualitative spatial delineations designed to group land area by similar structural, eco-physiological, and ecological attributes and provide a setting to interpret tree demographic processes (Cleland et al. 2007, McNab et al. 2007). Sections are further nested within provinces. Here, ecological sections were excluded if they were represented by less than 60 plots to improve model performance and statistical reliability. This eliminated 301 plots and 9 ecological sections from our analysis.

Tree-level analysis was conducted on all plot trees >12.7 cm diameter at breast height (1.37 m) at the time of the first inventory. Mortality was calculated according to the following equation:

$$\text{Mortality rate} = ((N_{\text{dead}}/N_{\text{total}}) \times 100)/\text{time}$$

where N_{dead} is the number of dead trees for a given species or plot, N_{total} is the total number of trees, and time is the interval between censuses (to the nearest 0.1 year) according to the value of the FIA re-measurement period variable (Burril et al. 2018). To be counted toward a plot-level mortality rate, an individual tree was required to be observed alive at the initial inventory and observed dead at the subsequent re-measurement inventory. Trees with unknown status at the second inventory or trees observed dead at both inventories were excluded from both dead and total tree tallies. Trees observed dead but subsequently observed alive were assumed alive. Finally, we excluded dead trees missing a field-assigned cause of death. Overall, irregularly reported stems represented <0.04% of total sample trees, and we assumed their exclusion did not bias our results. Partially forested plots were included if at least 1 candidate tree was present on the plot. Mean and median tree count per plot was 28.48 and 25, respectively. We further quantified the growing environment of each tree by including measures of plot-level live stem density at the time of the first inventory and total tree basal area aggregated to the plot level. We also attempt to quantify relative tree maturity by calculating a maturity index defined as the ratio of tree diameter to the 95th diameter percentile for its species across the entire experiment.

Tree-level mortality agent codes assigned by FIA field crews include insect, disease, animal, weather (includes windthrow and lightning strike), vegetation (apparent suppression or competition), and other (includes unknown and not sure). Trees killed by stand-replacing disturbances (i.e., harvest and fire) were excluded from live and dead tree tallies. Animal includes attack or damage from non-insect macroscopic animals such as bears and beavers.

Due to very low rates of occurrence, animal mortality was grouped with other for this study. The mortality agent codes presented here are taken directly from FIA metadata, and their definitions are specific to this dataset (Burrill et al. 2018). Of special importance is the distinction between weather as a mortality agent code defined by FIA and our other climate variables. The former is used in our analysis here as a response variable, while the latter are used as explanatory variables. Further details on FIA methodology, variable metadata, and species taxonomy are available in version 8.0 of the FIA field guide (Burrill et al. 2018).

Downscaled (4 km) climate data for six variables (precipitation, maximum temperature, minimum temperature, specific humidity, wind speed, and downward surface shortwave radiation) for 2000–2019 were sourced from the gridMET dataset (Abatzoglou 2013). For predictions of future mortality, similarly downscaled (4 km) Community Earth System Model climate variables were sourced from coarse-resolution Global Climate Model outputs using a Multivariate Adaptive Constructed Analogs approach (Gent et al. 2011, Abatzoglou and Brown 2012, Kay et al. 2015). Downscaled variables were further used to derive 17 additional climate variables related to plant eco-physiology (Rehfeldt 2006, Rehfeldt et al. 2006). Derivation procedures were taken directly from Rehfeldt (2006) except for the calculation of day of year of last freezing date of spring (SDAY) and day of year of the first freezing date of fall (FDAY) which was modified to the following procedure:

If M_{7i} or $M_{8i} \geq 5.5$ then

$$\mathrm{SDAY}_i = -1.08 + 0.93 S_{5i} + 2.08 M_{2i} + 1.9 M_{11i} - 3.85 M_{12i}$$

and

$$\mathrm{FDAY}_i = 30.28 + 0.92 F_{5i} - 1.80 M_{6i} + 1.84 M_{9i}$$

else if M_{7i} or $M_{8i} < 5.5$ then

$$\mathrm{SDAY}_i = 213.11 - 0.08 M_{10i}^2 - 2.65 M_{9i} - 0.04 S_{-2i} M_{7i}$$

and

$$\mathrm{FDAY}_i = 211.97 + 5.75 M_{8i} - 9.23 M_{6i} + 0.05 F_{-2i} M_{6i}$$

where M_{ni} is the mean temperature for the nth (1–12) month and ith plot, S_{xi} is the interpolated day of year that mean daily temperature first reached x°C for the ith plot, and F_{yi} is the interpolated day of year that mean daily temperature last remained above y°C for the ith plot. If M_{1i} was above 6.8°C, then SDAY_i was set to 0, while if M_{12i} was above 7.5°C, then FDAY_i was set to 365. This modification corrects for unreasonably late spring freezing and unreasonably early fall freezing at low to mid-elevations across the study area.

Climate variables were calculated for each plot based on the mean value for the 10 yr previous to the re-measurement inventory year. Soil variables were taken from 250-m resolution SoilGrids maps and weighted profile averages from 0 to 30 cm depth (Hengl et al. 2017). Additionally, standard deviation of each climate variable over this 10-yr interval was included in each model to help account for variability in climate at each plot location.

Study area and initial plot composition

Data were analyzed from 588,012 and 486,122 trees for recent and future mortality, respectively, tallied on 23,215 and 22,477 plots located in California, Colorado, Idaho, Montana, New Mexico, Nevada, Oregon, Utah, and Washington states. Plots were distributed through 12 ecological provinces and 48 ecological sections (Cleland et al. 2007). Large provinces included the Cascade Mixed Forest, Sierra Steppe, and Middle Rocky Mountain Steppe provinces which contained 31.91%, 16.73%, and 14.35% of all trees, respectively, for a combined 62.99% of all trees. Mean plot count by section was 967, with a maximum of 4956 (Western Cascades) and minimum of 60 (Owyhee Uplands). Species composition included 35 conifer species in 11 genera. Douglas-fir (*Pseudotsuga menzeisii*) was by far the most common species, representing 23% of all trees and twice that of the next most abundant *Pinus contorta* represented by 11% of all trees.

Random Forest model building

Random Forest classification models were constructed on tree-level mortality data (Breiman 2001, Cutler et al. 2007, Birch et al. 2015). Two models were built to predict (1) which trees would die during the next FIA census interval and (2) what mortality agent would kill the trees that were predicted dead. The response variable was a binary dead/not dead (TRUE/FALSE) condition observed at the second inventory for the

first model and mortality agent code (AGENTCD) for the second model. Mortality agent models predicted mortality on only the trees that were observed dead or predicted dead by the primary mortality model.

With imbalanced data, Random Forest models favor predictions of the dominant class at expense of the subdominant classes to reduce overall model error (Chen et al. 2004). In this study, live trees were randomly under-sampled to equal the number of trees in the smallest mortality class. Class imbalance sampling was not stratified by tree size or species, but diameter and species distributions in the final training dataset were very similar to the overall dataset. Under-sampling resulted in 206,568 trees (35.13% of total trees) used for training of the first mortality model and 23,215 (44.20% of total dead trees) trees used for training of the second model.

Models were cross-validated against out-of-bag samples for individual trees. Preliminary analysis suggested this was similar in robustness to cross-validation using a random subset of the training data, while model predictive performance improved slightly with the inclusion of all available data in the training dataset. We evaluated model performance using the overall percent of out-of-bag observations correctly classified, classification accuracy for each class group, user's and producer's accuracy as well as using the area under the receiver operating characteristic (ROC) curve (Breiman 2001, Fawcett 2006).

Variable importance in reducing model error was assessed as the mean difference in out-of-bag error rate before and after predictor variable permutation (Liaw and Wiener 2002). While variable importance measures can be a useful assessment of overall variable performance, they can be biased toward certain classes of variables and do not examine how variables influence predicted values (Strobl et al. 2008). To help quantify the relationship between explanatory variables and their influence on predicting mortality, median feature contributions were calculated for important variables (Palczewska et al. 2013). A positive feature contribution for a given explanatory variable indicates that the value of the variable directs the forest to assign a positive predicted value. In our models, the positive predicted value was set as "tree predicted dead" for the overall mortality model and "tree killed by a given mortality agent" for the mortality agent model. A negative feature contribution directs the model toward other levels of the predicted value—"tree predicted alive" and "tree killed by any other mortality agent."

Variables used to train the model and their units are given in Appendix S1: Table S1. We utilized the R packages randomForest, rfFC, and rfUtilities during model building and evaluation (Liaw and Wiener 2002, Murphy et al. 2010, Evans et al. 2011, Palczewska and Robinson 2015).

Future mortality was calculated by running updated climate and stand data through trained Random Forest models. Tree diameter at the re-measurement census was used for tree diameter in future calculations, and tree maturity index was re-calculated using this updated tree diameter value. Stand density and plot basal area were also re-calculated using updated re-measurement census data. Soils data were not updated for future calculations.

Other comparisons between groups

Mann-Whitney U-tests were performed on pairs of provinces and sections, as well as between predicted and recent mortality rates, to test for statistically significant differences (Hollander and Wolfe 1973). Provinces are reported with significant differences from province means, while sections are reported with significant differences relative to other sections within their province. Significant differences between recent and future mortality for species were assessed using Fisher's chi-squared test of independence on the proportion of trees dead within a species (Newcombe 1998). Significance values from multiple comparisons were adjusted to reduce false discovery rate (Benjamini and Hochberg 1995). All statistics were evaluated in R version 3.6.3 (R Core Team 2020).

Results

Recent mortality rates and model performance

Overall mortality varied widely across ecosystems and between species (Fig. 1, Tables 1, 2). Relatively high (>1% yr^{-1}) mortality rates were observed in the Southern, Middle, and Northern

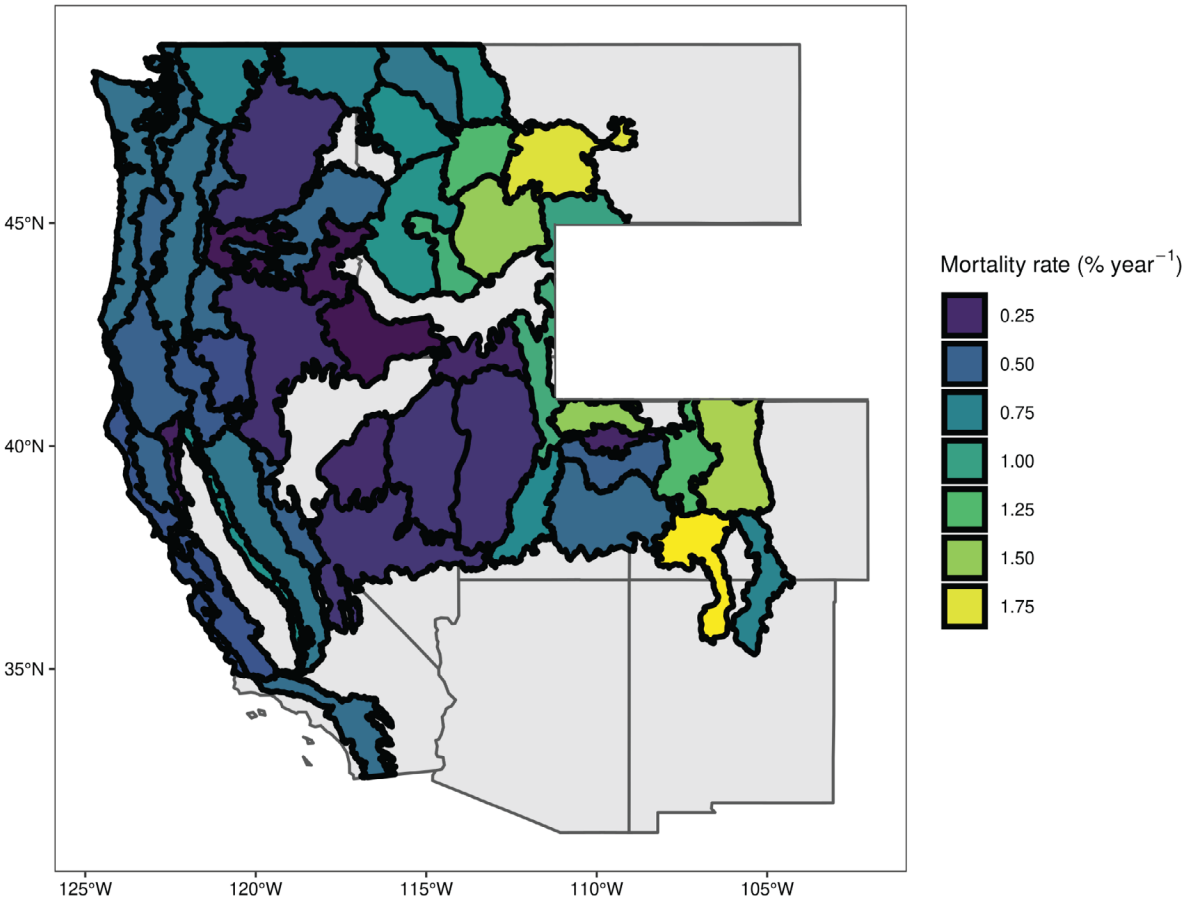


Fig. 1. Map of recent mortality calculated from FIA census data. Mortality rates are calculated over one FIA census interval and annualized to yearly rates. Polygons outline ecological sections and are colored by mean recent mortality rate aggregated over all plots within a section ($n \geq 60$).

Rocky Mountains and were generally significantly higher than in other regions (Table 1). Species in these sections with elevated mortality included *Abies lasiocarpa, Populus tremuloides, P. contorta, and Pinus albicaulis*, the last of which had the highest mortality rate of any species at 2.2% yr^{-1} (Table 2). All sections with >1% mortality occurred in the Middle and Southern Rocky Mountains (Table 1). Sections in the Cascade Mixed Forest Province, generally contiguous with the productive wet temperate forests of the Pacific Northwest, had intermediate mortality rates of between 0.58% and 0.78%. These rates were principally driven by the moderate mortality rates for the dominant conifers *Tsuga heterophylla* and *P. menzeisii* at 0.44% and 0.47%, respectively. The lowest recent mortality rates occurred in the semi-arid sections of the Great Basin and Colorado Plateau and in some sections within California. Low mortality rates in the Sierra and Klamath Mountains were driven by low species rates and large sample sizes for *Pinus ponderosa* and *Abies concolor*, with a smaller contribution from species in the genus *Quercus*. Notably, some elevated-mortality species occur in regions that did not show high overall forest mortality, such as *Abies magnifica* and *Quercus gambelii*.

Mortality model prediction accuracy (PCC) during training was 71.3% with class error rates for alive and dead trees of 27.8% and 29.5%, respectively. Cohen's Kappa and the area under the receiver operating characteristic (AUC) curve were 0.43 and 0.71, respectively. User's and

Table 1. Recent and future mortality rates (% year^{-1}) for ecological provinces and sections across the western USA.

Province†	Section‡	Recent§	Future¶	Difference#
California Coastal Chaparral Forest and Shrub[a]	Central California Coast	0.42	1.01	+0.60*
California Coastal Range Open Woodland[a]	Central California Coast Ranges[a]	0.41	0.84	+0.44^{NS}
California Coastal Range Open Woodland	Southern California Mountain and[b] Valley	0.61	1.73	+1.12**
California Coastal Steppe[b]	Northern California Coast	0.41	0.95	+0.54***
Cascade Mixed Forest[c]	Eastern Cascades[a]	0.58	1.54	+0.96***
Cascade Mixed Forest	Northern Cascades[b]	0.78	2.77	+1.99***
Cascade Mixed Forest	Oregon and Washington Coast Ranges[b]	0.63	2.07	+1.43***
Cascade Mixed Forest	Western Cascades[b]	0.63	2.28	+1.65***
Intermountain Semi-Desert[d]	Blue Mountain Foothills[a]	0.17	0.61	+0.44***
Intermountain Semi-Desert	Columbia Basin[b]	0.28	0.82	+0.53^{NS}
Intermountain Semi-Desert	Eastern Basin and Range[ab]	0.24	1.05	+0.80*
Intermountain Semi-Desert	Northwestern Basin and Range[ab]	0.27	0.95	+0.68**
Intermountain Semi-Desert	Owyhee Uplands[ab]	0.15	1.20	+1.05*
Intermountain Semi-Desert and Desert[a]	Bonneville Basin[a]	0.28	1.23	+0.95***
Intermountain Semi-Desert and Desert	Mono[a]	0.52	1.36	+0.84***
Intermountain Semi-Desert and Desert	Northern Canyonlands[b]	0.58	2.73	+2.15***
Intermountain Semi-Desert and Desert	Southeastern Great Basin[a]	0.29	1.01	+0.72***
Intermountain Semi-Desert and Desert	Uinta Basin[ab]	0.22	0.57	+0.34^{NS}
Middle Rocky Mountain Steppe[ce]	Beaverhead Mountains[a]	1.51	3.80	+2.29***
Middle Rocky Mountain Steppe	Belt Mountains[a]	1.74	3.74	+1.99***
Middle Rocky Mountain Steppe	Blue Mountains[b]	0.56	2.26	+1.71***
Middle Rocky Mountain Steppe	Challis Volcanics[cd]	1.15	4.72	+3.57***
Middle Rocky Mountain Steppe	Idaho Batholith[c]	0.90	3.56	+2.66***
Middle Rocky Mountain Steppe	Northern Rockies and Bitterroot Valley[d]	1.24	3.52	+2.29***
Nevada-Utah Mountains Semi-Desert[a]	East Great Basin and Mountains[a]	0.29	1.52	+1.23***
Nevada-Utah Mountains Semi-Desert	Tavaputs Plateau[a]	0.49	1.8	+1.31***
Nevada-Utah Mountains Semi-Desert	Utah High Plateau[b]	0.81	2.76	+1.95***
Nevada-Utah Mountains Semi-Desert	West Great Basin and Mountains[a]	0.26	1.34	+1.08***
Northern Rocky Mountain Forest-Steppe[e]	Bitterroot Mountains[a]	0.87	2.56	+1.69***
Northern Rocky Mountain Forest-Steppe	Flathead Valley[a]	0.68	2.32	+1.64***
Northern Rocky Mountain Forest-Steppe	Northern Rockies[a]	0.89	3.48	+2.59***
Northern Rocky Mountain Forest-Steppe	Okanogan Highland[a]	0.75	2.29	+1.54***
Pacific Lowland Mixed Forest[b]	Puget Trough[a]	0.63	1.69	+1.06***
Pacific Lowland Mixed Forest	Willamette Valley[b]	0.55	0.97	+0.42**
Sierran Steppe[b]	Klamath Mountains[ab]	0.51	2.04	+1.53***
Sierran Steppe	Modoc Plateau[c]	0.37	1.21	+0.83***
Sierran Steppe	Northern California Coast Ranges[ad]	0.53	1.52	+0.99***
Sierran Steppe	Northern California Interior Coast Ranges[e]	0.20	0.52	+0.32^{NS}
Sierran Steppe	Sierra Nevada[d]	0.68	2.08	+1.40***
Sierran Steppe	Sierra Nevada Foothills[b]	0.89	1.50	+0.61**
Sierran Steppe	Southern Cascades[b]	0.45	1.04	+0.58***
Southern Rocky Mountain Steppe[f]	North Central Highlands and Rocky Mountains[abc]	1.25	3.31	+2.06***

producer's accuracy for predicting dead trees was 71.7% and 70.5%, indicating similar errors of omission and co-omission, that is, balanced models. Contrary to expectations, model accuracy was most improved by the inclusion of species identity and ecological section rather than soil or climate variables (Fig. 2). Diameter of the tree at the previous inventory, tree maturity index and total plot basal area at the previous inventory were more important than all but two climate variables, although less critical than species identity and ecological section. Climate variables of

(Table 1. *Continued*.)

Province†	Section‡	Recent§	Future¶	Difference#
Southern Rocky Mountain Steppe	Northern Parks and Ranges[ad]	1.57	3.51	+1.93***
Southern Rocky Mountain Steppe	Overthrust Mountains[be]	1.10	3.03	+1.92***
Southern Rocky Mountain Steppe	South Central Highlands[d]	1.85	3.82	+1.97***
Southern Rocky Mountain Steppe	Southern Parks and Rocky Mountain Range[e]	0.77	2.37	+1.60***
Southern Rocky Mountain Steppe	Uinta Mountains[acd]	1.49	3.52	+2.03***
Southern Rocky Mountain Steppe	Yellowstone Highlands[bc]	1.02	3.55	+2.52***

† Superscripts for provinces show significant differences between province mean mortality rates, where provinces that share letter groups are not significantly different from one another (Mann–Whitney *U*-test, $\alpha = 0.05$). Province names are described in McNab et al. (2007) and mapped in Cleland et al. (2007).

‡ Superscripts for sections show significant differences in mean mortality rate between sections within a province, where sections that share letter groups are not significantly different from one another (Mann–Whitney *U*-test, $\alpha = 0.05$). Section names are described in McNab et al. (2007) and mapped in Cleland et al. (2007).

§ Recent mortality is calculated as plot-level percent mortality over a 10-yr FIA census interval and annualized for yearly rates.

¶ Future mortality is calculated as plot-level percent mortality from predicted individual tree mortality over a 10-yr FIA census interval immediately following the 10-yr recent census interval and annualized for yearly rates.

Difference in percent mortality between future predicted mortality and recent mortality. Asterisks show statistical significance (Mann-Whitney *U*-test) of with $\alpha = 0.05$, 0.01, and 0.001 for *, **, and *** respectively. Comparisons with $P > 0.05$ are indicated by NS.

importance were largely related to temperature, especially variables describing the timing and severity of frosts (Fig. 2, Appendix S1: Table S1). Variables related to water availability were second to temperature variables, with the most important climate variable (summer moisture index) being strongly related to temperature. Standard deviations of climate variables were much less important than mean values, although variables with important means had generally more important standard deviations. Soil variables were generally unimportant.

Important variables contributed unequally to the probability of assigning a tree as either alive or dead (Fig. 3). Species was the strongest contributor in predicting dead trees, with the contribution to predicting live trees supported mostly by climate variables related to winter frost and low temperatures as well as tree size. Contributions were also unequal among species, with contributions to predicting dead trees larger in the genus *Pinus; P. contorta*, *P. albicaulis*, and *Pinus monticola* especially (Fig. 4). The only other conifers with significant contribution to predicting dead trees were in *Abies*: *A. lasiocarpa*, *A. lasiocarpa* var. *arizonica*, and *A. magnifica*. Among hardwoods, *P. tremuloides* was the third-strongest contributor to predicting dead trees after the less common *Betula papyrifera* and *Chrysolepsis chrysophylla*. The most important species for predicting live trees were principally slow-growing conifers in the genus *Juniperus* along with *P. menzeisii* and *Thuja plicata*. *Juniperus* had low overall mortality rates, while *P. menzeisii* had very large sample sizes and are most frequently encountered in regions with low overall mortality (Table 2). In contrast to congenerics, *P. ponderosa* and *Pinus jeffreyi* were significantly related to predicting live trees.

Agent mortality and model performance

Recent mortality rates caused by individual agents averaged from 0.04% yr^{-1} to 0.28% yr^{-1}, with the highest rates coming from disease (0.19% yr^{-1}) and insects (0.28% yr^{-1}) as hypothesized. Agent model prediction accuracy during training was 62.8% with class error rates of 31.4% (disease), 19.3% (insect), 33.6% (other), 27.3% (vegetation), and 36.3 % (weather). Cohen's Kappa was 0.62. User's accuracy ranged from 65.9% (weather) to 76.4% (insect) and was similar to producer's accuracy, which ranged from 63.7% (weather) to 80.3% (insect). Insects and disease accounted for 48.7% and 27.3% of total deaths, respectively. Other and vegetation accounted for 9.2% and 8.0% of total mortality, while weather was the least prevalent agent with 6.8% of total deaths. Variable importance in the agent mortality model was similar to the overall mortality model, with species identity (encapsulating genetic factors) and ecological section being the two most important variables to improving model accuracy (Fig. 5). Climate variables of importance were also similar and generally featured temperature- and frost-related

Table 2. Recent and future mortality rates (% year^{-1}) for tree species across the western USA.

Species†	Recent‡	Future§	Difference¶
Abies amabilis	0.63	2.34	+1.72***
Abies concolor	0.73	2.56	+1.84***
Abies grandis	0.72	2.51	+1.79***
Abies lasiocarpa	0.93	4.38	+3.46***
Abies lasiocarpa var. *arizonica*	2.72	5.89	+3.18***
Abies magnifica	0.90	3.67	+2.77***
Abies procera	0.43	1.51	+1.08^{NS}
Abies shastensis	0.75	2.91	+2.16***
Acer grandidentatum	0.41	1.17	+0.77***
Acer macrophyllum	0.45	0.71	+0.27^{NS}
Alnus rubra	1.15	1.67	+0.52***
Arbutus menziesii	0.77	1.91	+1.14***
Betula papyrifera	2.17	5.59	+3.42***
Calocedrus decurrens	0.42	1.55	+1.13***
Cercocarpus ledifolius	0.36	2.98	+2.62***
Chamaecyparis lawsoniana	0.30	4.25	+3.95***
Chamaecyparis nootkatensis	0.11	2.60	+2.49***
Chrysolepis chrysophylla var. *chrysophylla*	0.97	3.11	+2.14***
Juniperus monosperma	0.08	1.77	+1.69***
Juniperus occidentalis	0.04	0.29	+0.25^{NS}
Juniperus osteosperma	0.03	1.03	+1.00***
Juniperus scopulorum	0.06	0.99	+0.93***
Larix occidentalis	0.60	2.93	+2.33***
Lithocarpus densiflorus	0.39	0.43	+0.04**
Picea engelmannii	1.44	2.84	+1.40***
Picea pungens	0.43	1.43	+1.00***
Picea sitchensis	0.59	2.69	+2.10***
Pinus albicaulis	2.20	5.84	+3.63**
Pinus aristata	0.40	3.96	+3.56***
Pinus contorta	2.03	3.64	+1.61***
Pinus edulis	0.36	1.61	+1.24***
Pinus flexilis	1.29	4.54	+3.25***
Pinus jeffreyi	0.24	0.70	+0.47^{NS}
Pinus lambertiana	0.87	2.81	+1.94***
Pinus monophylla	0.37	0.98	+0.61***
Pinus monticola	1.28	4.57	+3.29***
Pinus ponderosa	0.43	0.91	+0.48***
Pinus sabiniana	0.57	0.48	-0.09^{NS}
Populus balsamifera ssp. *trichocarpa*	0.65	1.76	+1.11**
Populus tremuloides	1.86	4.16	+2.29***
Pseudotsuga menziesii	0.47	1.96	+1.49***
Quercus agrifolia	0.73	1.09	+0.37*
Quercus chrysolepis	0.2	0.44	+0.24*
Quercus douglasii	0.34	0.55	+0.21^{NS}
Quercus gambelii	0.82	2.12	+1.30***
Quercus garryana	0.41	0.92	+0.51*
Quercus kelloggii	0.62	1.45	+0.83***
Quercus wislizeni	0.8	1.49	+0.69***
Sequoia sempervirens	0.09	0.96	+0.87*
Thuja plicata	0.12	1.43	+1.30***
Tsuga heterophylla	0.44	1.61	+1.17***
Tsuga mertensiana	0.38	1.74	+1.36***
Umbellularia californica	0.22	0.39	+0.17^{NS}

† Species identity and taxonomic information are found in Burril et al. (2018), Appendix F.

‡ Recent mortality is calculated as species-level percent mortality over a 10-yr FIA census interval and annualized to yearly rates.

§ Future mortality is calculated as species-level percent mortality from predicted individual tree mortality and annualized to yearly rates.

¶ Difference in percent mortality between future predicted mortality and recent mortality. Asterisks show statistical significance (Mann–Whitney U-test) with $\alpha = 0.05$, 0.01, and 0.001 for *, **, and *** respectively. Comparisons with $P > 0.05$ are indicated by NS.

variables. Notably, minimum zero-degree-days was an important feature for reducing model error in the agent mortality model (7th most important) but not important for reducing model error in the overall mortality model (25th most important). Additionally, the standard deviation of zero-degree-days was very important for agent mortality and was the only climate variability feature to be one of the 15 most-valuable features in either model (Figs. 2, 5).

Variables did not contribute equally to the probability of predicting dead or live trees across all mortality agents (Fig. 5, Table 3). Variables that contributed strongly to predicting trees killed by insect were total zero-degree-days based on minimum temperatures (+0.93%), minimum temperature of the coldest month (+1.13%), and specific humidity (+0.66%; Table 3). Specific humidity also contributed to predicting disease deaths (+0.26%), but so did owner group code (+0.22%). Interestingly, no precipitation variables contributed to predicting dead trees of any mortality agent (Table 3). Mortality from weather was only predicted by the length of the frost-free period (+0.17%) and local physiographic class (+0.25%). The only variable with a greater than 0.05% contribution to predicting vegetation mortality was species (+0.18%).

Tree mortality across the western USA under future climates

Forest mortality across the study area was predicted to increase in most regions with the largest magnitude increases in the Southern and Middle

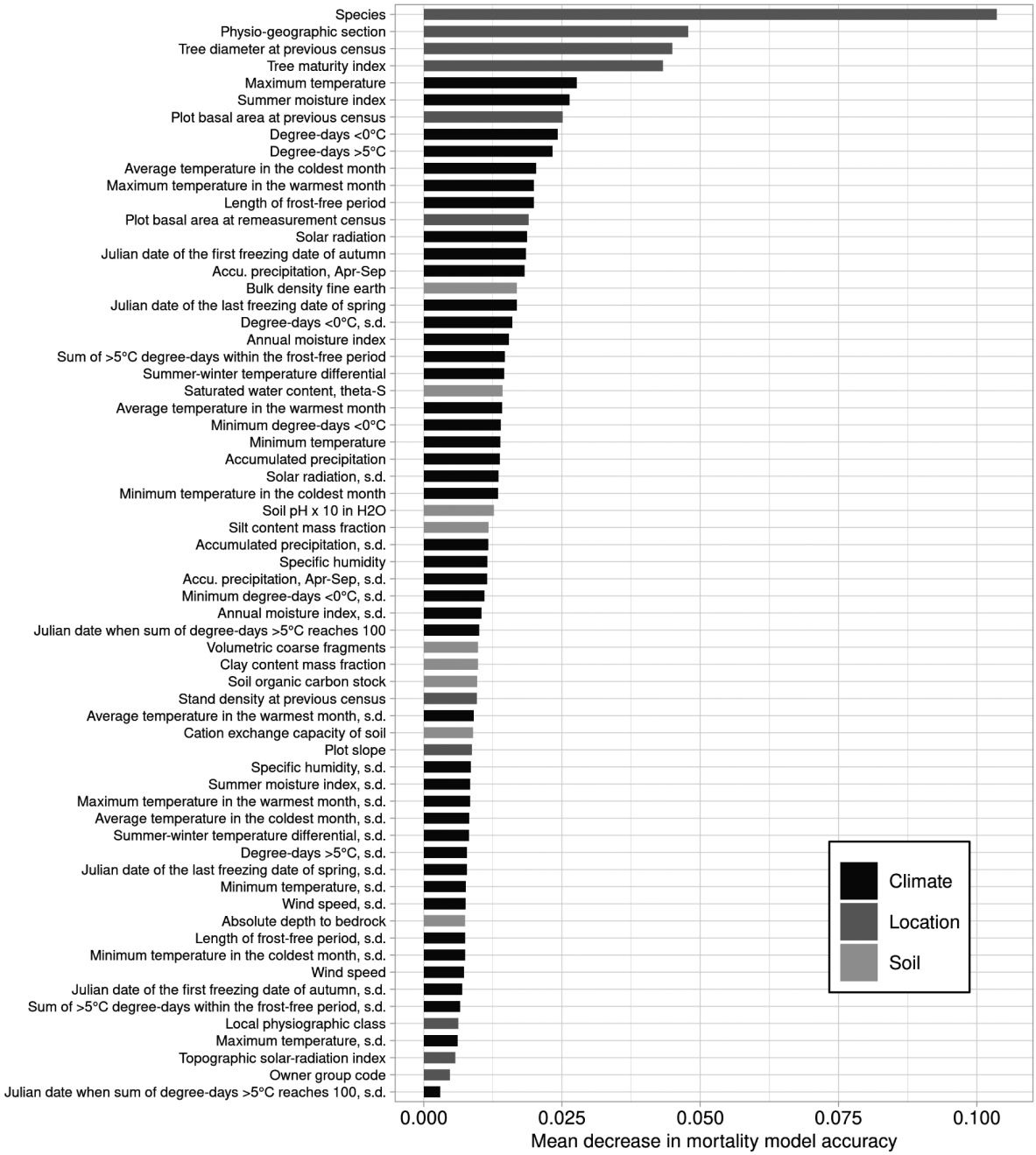


Fig. 2. Feature importance for the overall mortality model. Units for each feature are given in Appendix S1: Table S1. Variables are sorted according to their contribution to the decrease in overall model accuracy when they are excluded from mortality predictions. Variables are colored according to their source: Dark gray location variables are sourced or derived from plot- or tree-level FIA data, light gray soil variables are sourced from 250 m SoilGrids soils data, and black climate variables are sourced or derived from gridMET and MACA gridded climate data sets.

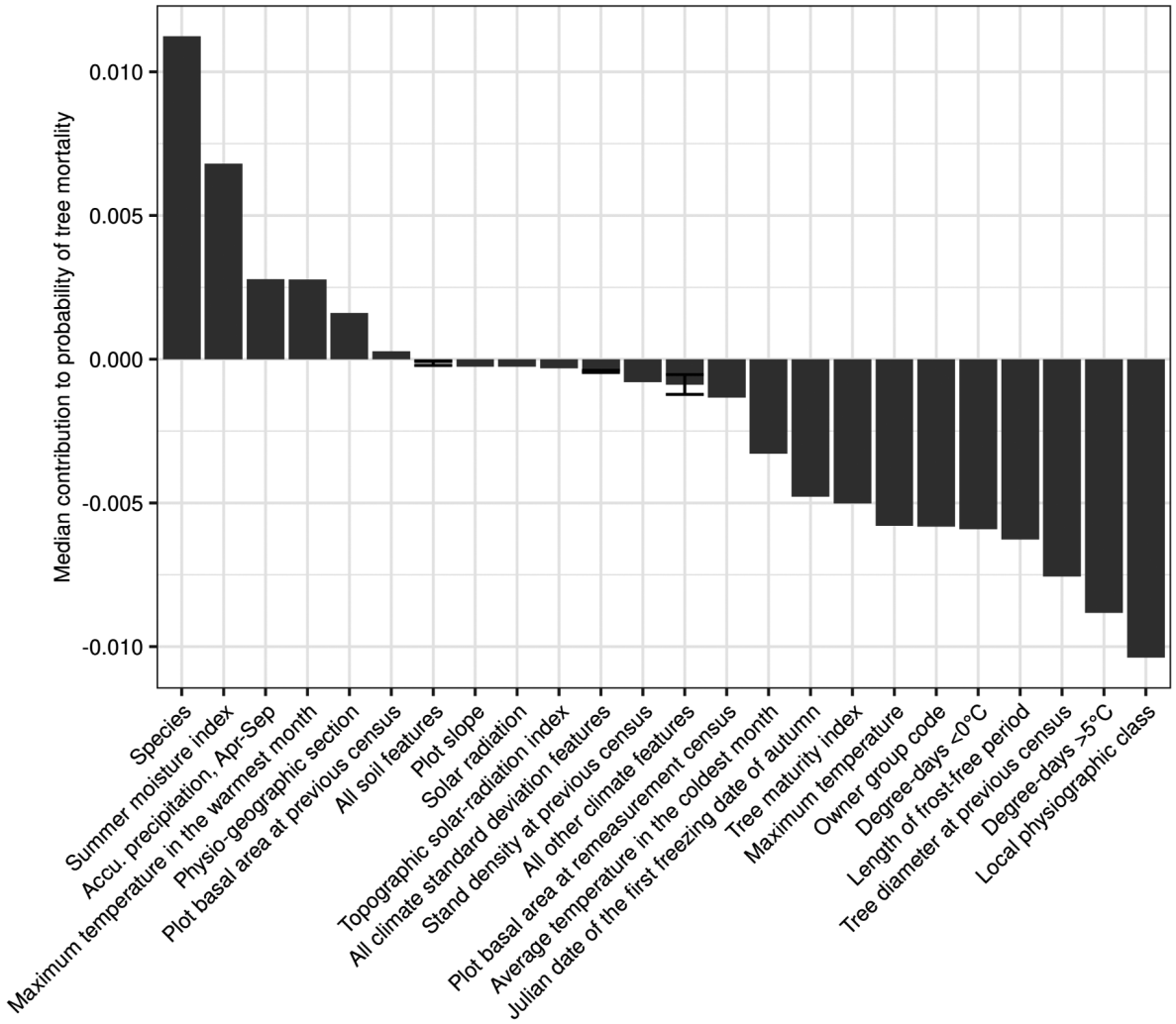


Fig. 3. Median contribution of each Random Forest feature to the probability of positively identifying a tree that died during the census interval ($y > 0$) when assessed over the entire forest of classification trees. Units on the y-axis are decimal probability.

Rocky Mountains (+2.02–2.52% yr^{-1}, Fig. 6, Table 1). Species-specific effects (including genetic effects) were most important to future mortality rates and were inflated by increases in mortality for some species of up to 3.63% yr^{-1}, including *P. albicaulis* (+3.63%), *P. contorta* (+1.61%), *A. lasiocarpa* (+3.46%), *A. lasiocarpa* var. *arizonica* (+3.18%), and *P. tremuloides* (+2.29%, Table 2). Only one species, *Pinus sabiana*, had a non-statistically significant decrease in mortality rates under future climates. Recent mortality at the plot level was not correlated with future mortality but showed a strong correlation by species ($r^2 = 0.59$; Fig. 7). Broader patterns in future rates for genera were visible, including low future rates for *Juniperus* and *Quercus* and high future rates for *Pinus* (Table 2). However, no genus represented by multiple species was significantly more or less vulnerable overall than another. *Pinus ponderosa* and *Pinus jeffreyi* were notable outliers within *Pinus*, with a less than 0.5% predicted increase (Table 2). Mortality rates increased substantially under future climates for all agents up to more than 0.6% yr^{-1} for disease and Insect (Fig. 8). The proportion of trees killed by insect dropped from 48.6% to 27.6% and was

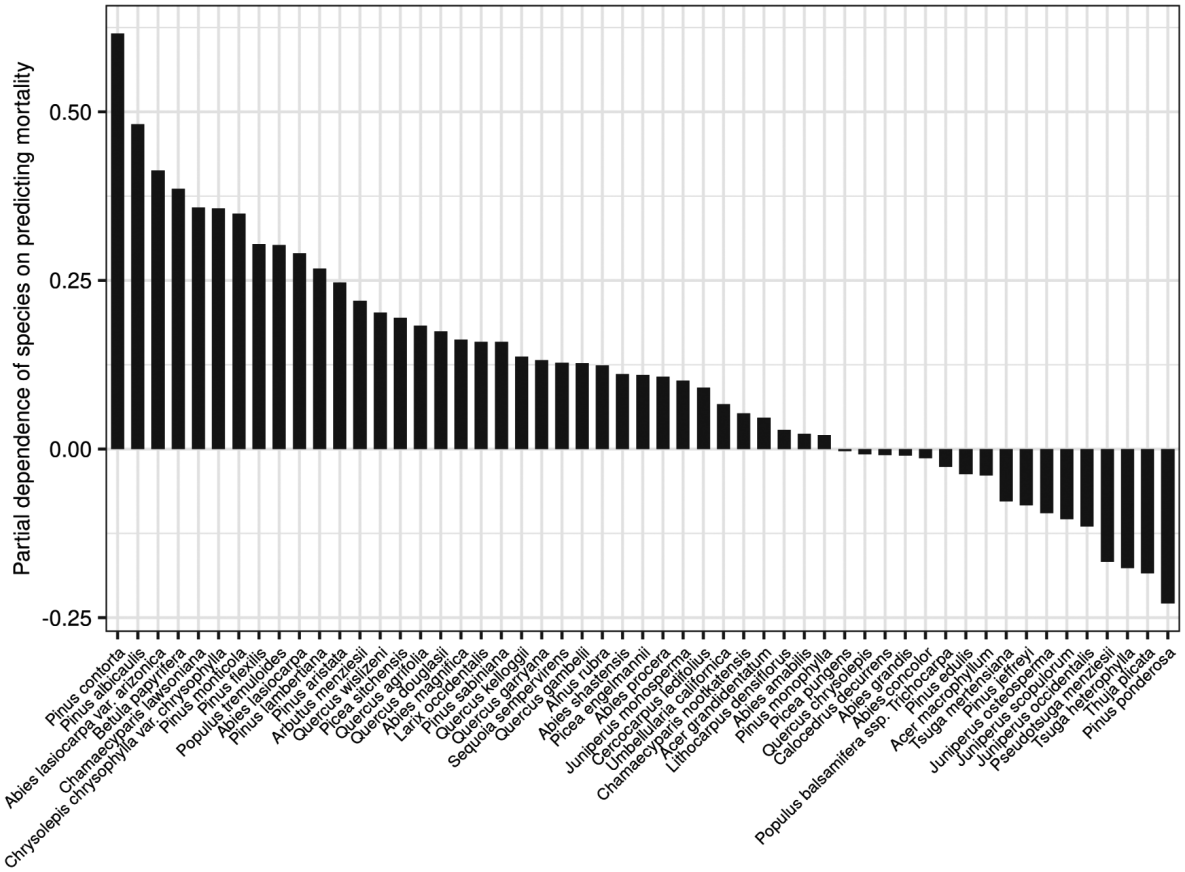


Fig. 4. Partial dependence of dead tree predictions on the species of the individual tree, when all other variables are controlled for. Units on the *y*-axis are expressed as the logit of the probability of predicting a dead tree, with 0 representing an equal contribution to predicting alive and dead trees.

accompanied by increases in all other categories (Fig. 8).

Discussion

Factors most important to recent and future forest mortality

Our results report on recent mortality rates for many western U.S. forests and attempt to elucidate the important drivers of mortality in these systems. Previous work on forest mortality has largely focused on catastrophic mortality from drought, fire, and insects, and we therefore hypothesized that the most important predictors of both recent and future mortality would be environmental variables associated with precipitation and temperature (Berner et al. 2017, Fettig et al. 2019). Rather than climate or soil, species identity was overwhelmingly our most important predictor variable, which demonstrates the important influence of genetics on tree mortality (Rehfeldt et al. 2006). Although beyond the scope of this study, the significant contribution of species identity to our mortality predictions warrants more careful consideration of the influence that genetics may have on overall tree mortality as well as how cause of death may vary between species subpopulations (Rehfeldt et al. 2006).

We found that large tree mortality in the western USA is likely to accelerate under future climate regimes, in general agreement with other studies (Dale et al. 2001, Allen et al. 2010). This result supports our hypothesis of increased mortality under future climates, but drivers of these increases may be nuanced. Specifically, the importance of species identity in model

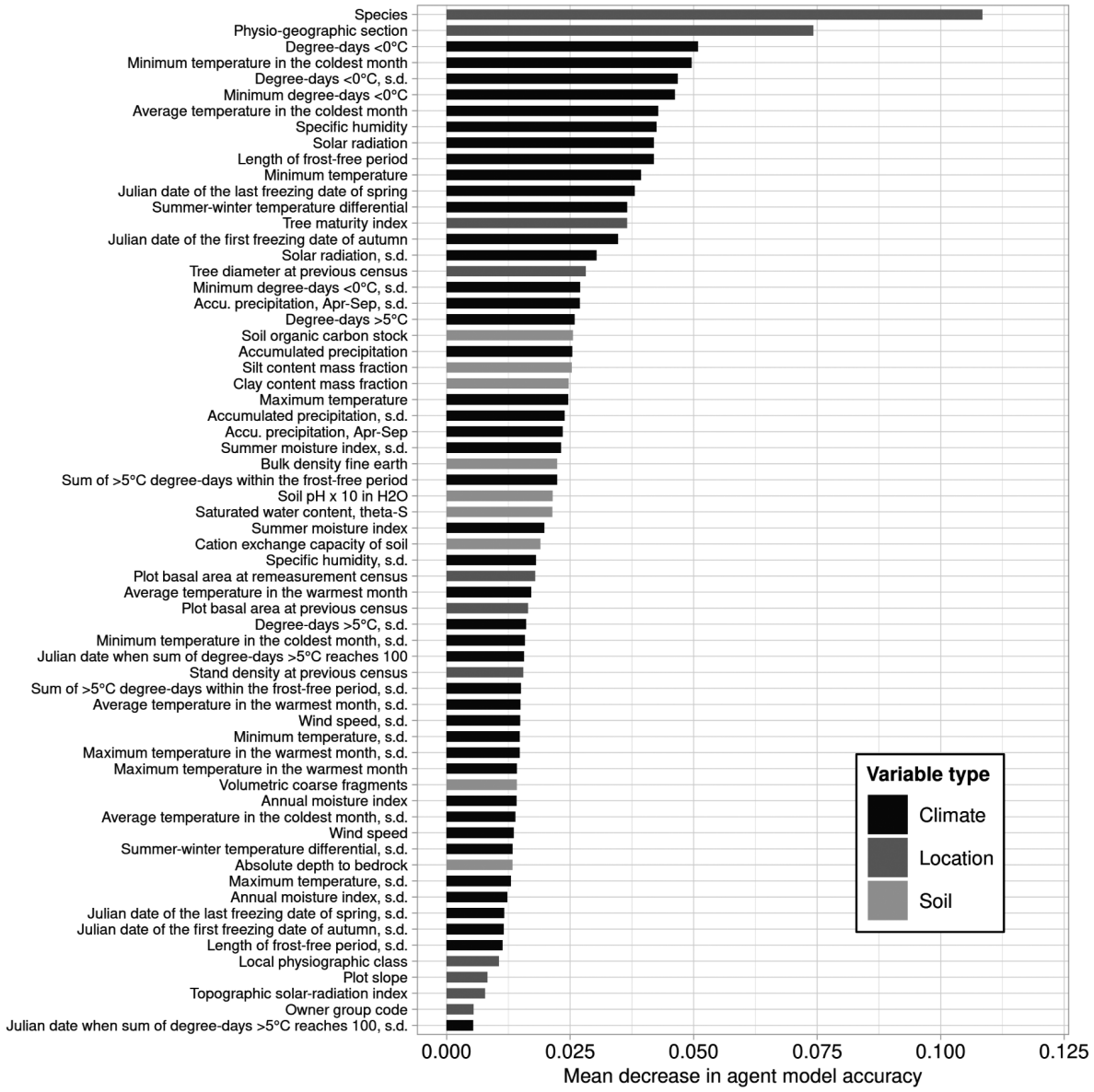


Fig. 5. Feature importance for the agent mortality model. Units for each feature are given in Appendix S1: Table S1. Variables are sorted according to their contribution to the decrease in overall model accuracy when they are excluded from predictions. Variables are colored according to their source: Dark gray location variables are sourced or derived from plot- or tree-level FIA data, light gray soil variables are sourced from 250 m SoilGrids soils data, and black climate variables are sourced or derived from gridMET and MACA gridded climate data sets.

performance suggests that these changes will be heavily dependent on species and ecosystem. In support of this, future mortality was not correlated with past mortality at the plot level but showed a strong dependence on species. Large variability in future mortality rates suggests that predicting how these forests change in the future will require detailed knowledge of how vulnerable species respond to environmental drivers. Perhaps more importantly, detailed empirical

Table 3. Median contribution of each feature to the probability of positively identifying a tree killed by insects, disease, weather, vegetation, or other when assessed over the entire forest of classification trees.

Feature	Insect	Disease	Weather	Vegetation	Other
Absolute depth to bedrock	−0.02	−0.07	−0.06	−0.04	−0.07
Accu. precipitation, April–September	−0.04	−0.06	−0.12	−0.03	−0.05
Accu. precipitation, April–September, SD	−0.1	−0.07	−0.08	−0.06	−0.03
Accumulated precipitation	−0.14	−0.07	−0.14	−0.12	−0.06
Accumulated precipitation, SD	−0.23	−0.09	−0.08	−0.1	−0.08
Annual moisture index	−0.01	−0.04	−0.09	−0.03	−0.06
Annual moisture index, SD	−0.01	−0.05	−0.08	−0.03	−0.07
Average temperature in the coldest month	−0.78	−0.04	0.06	−0.36	0.03
Average temperature in the coldest month, SD	−0.01	−0.06	−0.07	−0.03	−0.08
Average temperature in the warmest month	−0.04	−0.04	−0.05	−0.02	−0.11
Average temperature in the warmest month, SD	−0.04	−0.05	−0.04	−0.03	−0.05
Bulk density fine earth	−0.02	−0.06	−0.12	−0.11	−0.07
Cation exchange capacity of soil	−0.03	−0.03	−0.11	−0.09	−0.05
Clay content mass fraction	0.02	−0.18	−0.03	−0.05	−0.11
Degree-days <0°C	−0.7	0	−0.04	−0.73	0.05
Degree-days <0°C, SD	0.09	0.07	−0.33	−0.85	−0.04
Degree-days >5°C	−0.34	−0.07	−0.06	−0.09	−0.09
Degree-days >5°C, SD	−0.05	−0.06	−0.06	−0.05	−0.06
Day of year of the first freezing date of autumn	−0.6	−0.16	0.07	−0.11	−0.03
Day of year of the first freezing date of autumn, SD	−0.02	−0.07	−0.06	−0.04	−0.08
Day of year of the last freezing date of spring	−0.64	−0.13	0.06	−0.05	−0.04
Day of year of the last freezing date of spring, SD	−0.03	−0.06	−0.03	−0.02	−0.07
Day of year when sum of degree-days >5°C reaches 100	−0.24	−0.05	−0.02	−0.06	−0.02
Day of year when sum of degree-days >5°C reaches 100, SD	−0.02	−0.03	−0.02	−0.02	−0.02
Length of frost-free period	−0.95	−0.13	0.17	−0.12	−0.03
Length of frost-free period, SD	−0.03	−0.07	−0.04	−0.03	−0.06
Local physiographic class	−0.02	−0.05	0.25	−0.03	0.14
Maximum temperature	−0.14	−0.07	−0.03	−0.03	−0.11
Maximum temperature in the warmest month	−0.02	−0.04	−0.06	−0.03	−0.08
Maximum temperature in the warmest month, SD	−0.03	−0.05	−0.04	−0.02	−0.1
Maximum temperature, SD	−0.02	−0.04	−0.08	−0.01	−0.04
Minimum degree-days <0°C	0.93	0.34	−0.52	−1.25	−0.07
Minimum degree-days <0°C, SD	−0.2	−0.05	−0.08	−0.08	−0.07
Minimum temperature	0.03	0.08	−0.16	−0.72	−0.04
Minimum temperature in the coldest month	1.13	0.48	−0.69	−1.49	−0.04
Minimum temperature in the coldest month, SD	−0.02	−0.05	−0.09	−0.03	−0.1
Minimum temperature, SD	−0.02	−0.06	−0.05	−0.02	−0.06
Owner group code	−0.13	0.22	−0.08	0.09	−0.04
Physio-geographic section	−0.09	−0.18	−0.02	−0.05	−0.27
Plot basal area at previous census	−0.01	−0.1	−0.06	−0.03	−0.1
Plot basal area at re-measurement census	−0.03	−0.08	−0.07	−0.04	−0.08
Plot slope	−0.01	−0.04	−0.05	−0.04	−0.07
Saturated water content, theta-S	−0.01	−0.05	−0.14	−0.1	−0.08
Silt content mass fraction	−0.02	−0.14	−0.12	−0.02	−0.05
Soil organic carbon stock	0.06	−0.1	−0.15	−0.17	0.02
Soil pH × 10 in H2O	−0.02	−0.05	−0.04	−0.03	−0.17
Solar radiation	−0.04	−0.24	−0.02	0.03	−0.43
Solar radiation, SD	0.09	−0.07	−0.14	−0.22	−0.17
Species	−0.53	0.17	0.35	0.18	0.9
Specific humidity	0.66	0.26	−0.35	−1.05	−0.02
Specific humidity, SD	−0.01	−0.03	−0.01	−0.06	−0.19
Stand density at previous census	−0.01	0.01	−0.03	−0.08	−0.04
Sum of >5°C degree-days within the frost-free period	−0.16	−0.06	−0.06	−0.05	−0.13

(Table 3. *Continued.*)

Feature	Insect	Disease	Weather	Vegetation	Other
Sum of >5°C degree-days within the frost-free period, SD	−0.03	−0.05	−0.05	−0.04	−0.06
Summer moisture index	−0.03	−0.06	−0.08	−0.03	−0.08
Summer moisture index, SD	0	−0.13	0	0.02	−0.21
Summer–winter temperature differential	0.23	0.05	−0.23	−0.47	0.01
Summer–winter temperature differential, SD	−0.02	−0.06	−0.05	−0.03	−0.05
Topographic solar-radiation index	−0.01	−0.04	−0.05	−0.03	−0.08
Tree diameter at previous census	−0.05	−0.18	−0.19	0	−0.17
Tree maturity index	−0.01	0.12	−0.07	−0.37	0.02
Volumetric coarse fragments	−0.03	−0.08	−0.08	−0.04	−0.05
Wind speed	−0.03	−0.03	−0.07	−0.03	−0.08
Wind speed, SD	−0.01	−0.03	−0.06	−0.01	−0.16

Notes: Units are decimal probability × 10^2. Standard deviation of climate variables is indicated with an SD.

data on demographic changes to U.S. forests will be needed across large geographic areas and over decadal time periods.

Species-specific life-history traits, especially tree age, likely contributed heavily to mortality predictions. This was supported by unequal species contributions to predicting mortality as well as significant variability in observed and predicted mortality rates (Fig. 4, Table 2). While tree age itself may not be directly impacting mortality through age-related senescence, low stem turnover in long-lived trees complicates interpretation between some of our species. For example, relatively high mortality rates may be normal for some short-lived (~100 yr) early successional species such as *A. rubra* or *P. tremuloides* (Harrington et al. 1994, Mitton and Grant 1996). Conversely, long-lived tree species such as *P. menzeisii* or members of *Juniperus* may live more than 1000 yr and may not die for some time after the onset of lethal environmental or biotic stress (Alexander et al. 2018). Differences in life-history traits may partly be responsible for the strong dependence of mortality predictions on species identity but seem unlikely to contribute to our predictions of mortality under future climates. In support of this, we found that our maturity index variable was the 4th most important variable for reducing model error in our first mortality model and contributed significantly to predicting live trees. Other important life-history traits may include vulnerability to host-specific pathogens —*P. monticola and P. albicaulis;* for example, both had high recent and future mortality rates and previous research implicates bark beetles and white pine blister rust as major contemporary disturbances throughout the range of these species (Geils et al. 2010, Jacobi et al. 2018). Alternatively, some species or populations may currently be in the midst of a widespread dieback due to anthropogenic climate change that is pushing them past critical environmental stress tolerance thresholds despite apparently normal mortality for the ecosystem or region (Huang et al. 2015, Kolb 2015). Our results somewhat agree with previous work that suggests future forest mortality may be a widespread phenomenon, but we emphasize that some species and regions may be disproportionately affected (Allen et al. 2010, Kane et al. 2014, McDowell and Allen 2015). Future efforts to mitigate the effects of anthropogenic climate change should focus on active management or conservation of key species or populations, and future efforts to model mortality risk in western U.S. forests should emphasize plant functional traits or physiology common to vulnerable species, such as current efforts to control white pine blister rust in *P. monticola* and *P. albicaulis* (Geils et al. 2010, Jacobi et al. 2018).

We assessed mortality rates for some well-studied tree species and many other tree species that, to our knowledge, do not have any published mortality rates. The most common focal conifer species in recent mortality work have been conifers in the genera *Abies*, *Pinus*, and *Juniperus* (Gaylord et al. 2013, Krofcheck et al. 2014, Mortenson et al. 2015, Fettig et al. 2019, Flake and Weisberg 2019, Pile et al. 2019, McDowell et al. 2019). We improve on previous

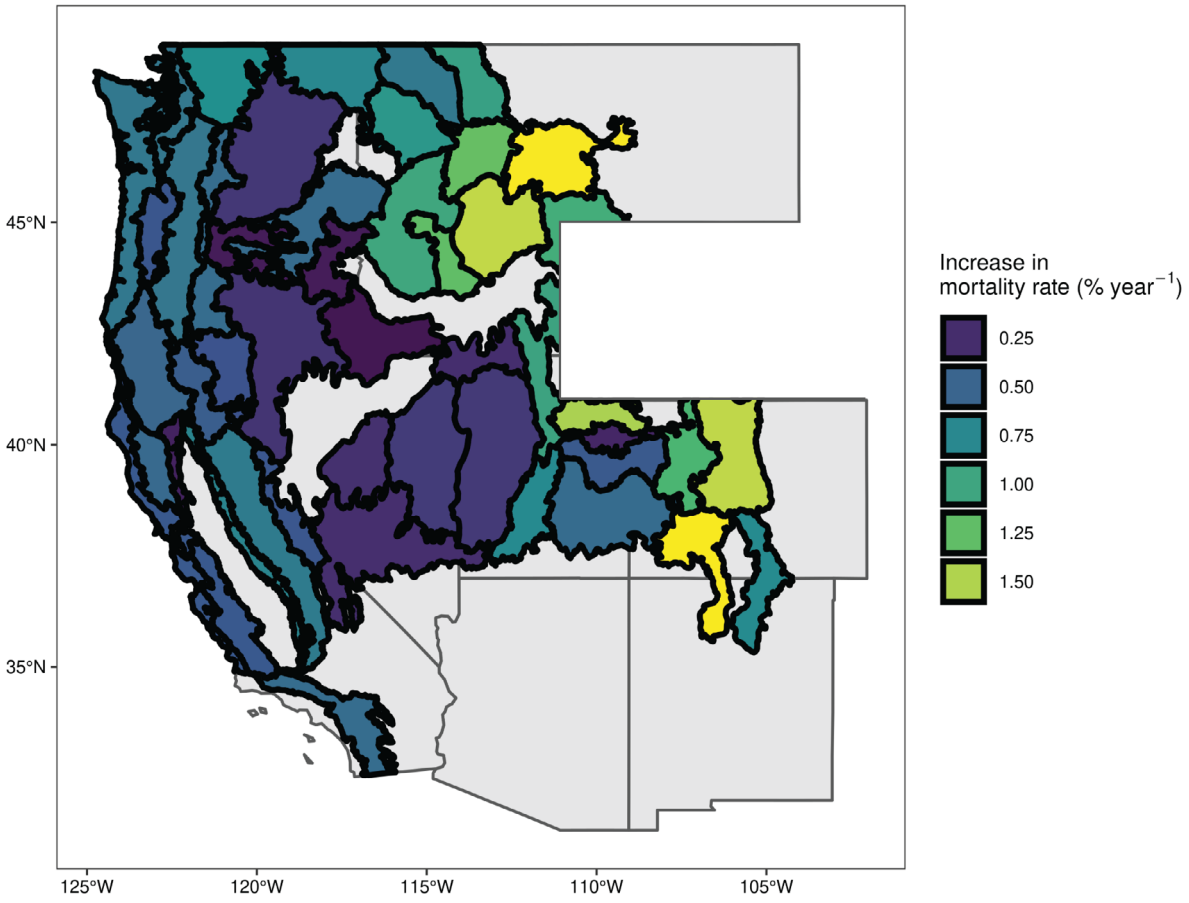


Fig. 6. Map of differences in mortality rate between recent forest mortality and mortality predicted under the RCP 4.5 emissions scenario. Polygons outline ecological sections and are colored by mean difference in mortality rate aggregated over all plots within a section.

mortality research for these species by including populations over wide areas, as well as including species closely related to common focal species that are less well studied. Future research should incorporate these species to improve modeling efforts and inform forest managers and policy-makers.

Arguably the most well-studied forest dieback is the recent widespread decline of quaking aspen, *P. tremuloides* (Rehfeldt et al. 2009, Worrall et al. 2010, Huang and Anderegg 2012, Anderegg et al. 2013, Tai et al. 2017). Despite being one of the highest recent mortality rates observed in our dataset, our mean rate of 1.86% yr^{-1} was less than mortality rates observed in other studies. Part of this may be due to the spatial extent of plots in our dataset—other studies tend to focus on specific mortality events, localized to one forest or region. For example, Worrall et al. (2008) found mortality rates of ~11% yr^{-1} in four stands of *P. tremuloides* in Colorado, but this was in an area of highly concentrated aspen mortality. Predicted future mortality rates were significantly higher than recent rates as well as some future rates predicted by other studies. For example, Rehfeldt et al. (2009) used Random Forest to predict bioclimate envelopes for *P. tremuloides* and suggested a decrease of 6–41% in available envelope area by 2030, a 0.3–2% yr^{-1} mortality rate that contrasts with our projected future rate of 4.16% yr^{-1} (Table 2). Nonetheless, *P. tremuloides* will likely be one of the most at-risk western U.S. tree species under future climates and may face significant local and regional risk of extirpation

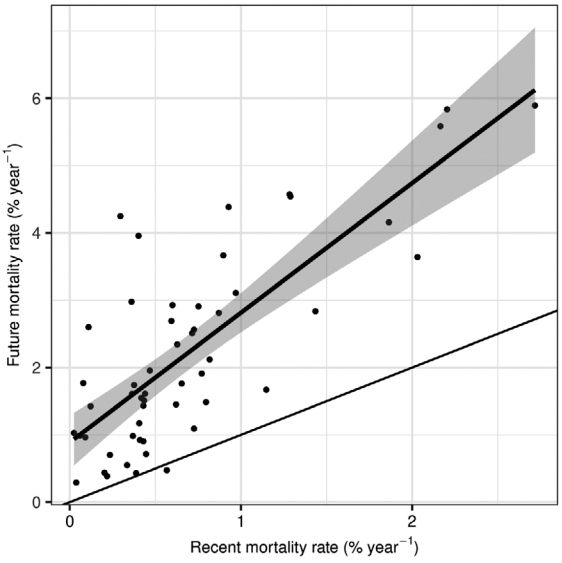


Fig. 7. Scatterplot of recent mortality rates versus future mortality for 53 large tree species across the western USA; $P < 0.01$, $r^2 = 0.59$. The thin gray line represents a 1:1 reference between recent and future mortality rates.

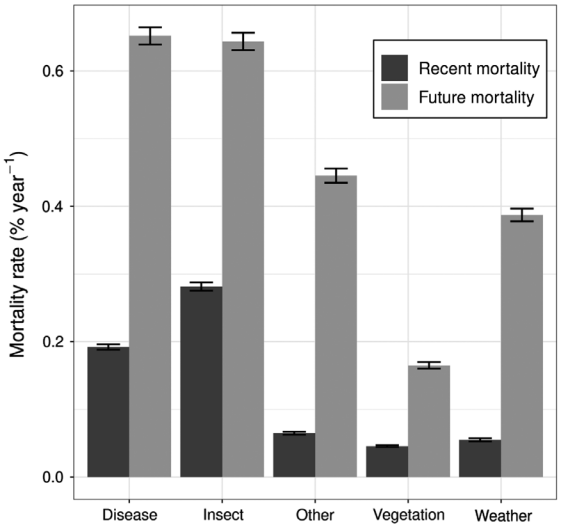


Fig. 8. Recent and future mortality rates for five mortality agent classes. Bars are mean rates across plots expressed as annualized plot mortality ± 1 SE.

(Aitken et al. 2008). To reconcile differences in the magnitude of predicted mortality for *P. tremuloides,* future research should utilize empirical predictions of future mortality as well as modeled estimates for a more robust assessment of emerging risks to western U.S. forests (Meir et al. 2015).

Our recent mortality rates are generally lower than previously published rates for other less well-studied species. For example, Mortenson et al. (2015) reported mortality rates in the Klamath range for *A. magnifica, P. jeffreyi, P. contorta,* and *A. concolor* as 1.8% yr^{-1}, 1.9% yr^{-1}, 1.1% yr^{-1}, and 3.0% yr^{-1}, respectively, compared with 0.90% yr^{-1}, 0.24% yr^{-1}, 2.03% yr^{-1}, and 0.72% yr^{-1} for the same species in this study. Our exclusion of fire as a mortality agent probably lowers our estimated and predicted rates for species in fire-prone ecosystems such as the Klamath range (Hagmann et al. 2013). However, we can extend this work by noting that mortality rates are likely to increase even further, especially for *A. magnifica* (+3.66%) and *P. contorta* (+3.64%).

The partial dependence of species on predicting live trees suggested some species that may be less vulnerable under future climates, including *P. ponderosa* and members of the genus *Juniperus* or *Quercus*. While *P. ponderosa* in this study showed a small increase in mortality rates relative to congenerics, other studies have observed dramatic *P. ponderosa* mortality from drought events at the southern end of its range (Allen and Breshears 1998). These species may serve as good models or keystone species when examining future forest dieback—diebacks at low latitudes or low elevations may portend similar events at high latitudes or high elevations (Aitken et al. 2008). Alternatively, shifts in the distribution and abundance of these species due to climate change may occur in younger cohorts or in conjunction with disturbance events such as fire (Kemp et al. 2019). Future work on forest mortality would benefit from examining whole-range demographics of these species, especially in the context of plant functional traits or population genetics measured throughout a species range (Rehfeldt et al. 2006).

Juniper mortality increased only moderately under future climates in this study, confirming previous work that suggests that juniper is robust to die-off events (Table 2; Floyd et al. 2009). A significant body of work suggests that in these systems, *Pinus edulis, P. monophylla,* and *P. ponderosa* may have elevated-mortality rates under future climates. Interestingly, our

predicted increases in mortality rates are much smaller in magnitude than other studies observing *Pinus* die-off events. This is probably because our rates reflect mortality dynamics aggregated throughout the species' entire range, in contrast to other studies that focus on mortality at their edges (e.g., Allen and Breshears 1998). Future work should focus on the consequences of these marginal die-off events for *Juniperus*, for example, type conversion to smaller-statured woodland or shrubland or loss of ecosystem services such as carbon storage.

Other factors driving recent tree mortality and mortality agents across the western USA

Tree diameter was the 3rd most important variable for improving model accuracy and contributed significantly to predicting alive trees. Larger, longer-lived trees may be less vulnerable to density-dependent mortality effects from competition for water or nutrients (Luo and Chen 2011, Harmon and Pabst 2015). This is supported by our finding that tree maturity and plot basal area at either inventory were important for predicting live trees, although maturity was much less important overall to reducing model error. Nonetheless, tree size alone was not enough to account for observed mortality rates and was unlikely to be responsible for increases in mortality in the future (Uriarte et al. 2004, Zhang et al. 2013, Birch et al. 2015).

Ecological section was very important for improving model accuracy but did not contribute to dead tree predictions more than live trees. This suggests that recent mortality rates in the absence of catastrophic disturbance may be further dependent on spatially correlated variables that were not included in this dataset. Sections are defined as an aggregate of geologic, soil, and vegetative properties and may include qualitative descriptors that do not continuously vary along grids (McNab et al. 2007). While major improvements to modeling forest mortality may involve species-specific parameterizations, variation in demographic rates across space and between tree populations may present an additional challenge that may require detailed knowledge of tree eco-physiology (Bohner and Diez 2020).

The most important climate variables were related to temperature, especially variables describing the timing and severity of winter temperatures (Figs. 2, 5). Changes to winter temperatures as a result of anthropogenic climate change may influence tree mortality rates, especially at high latitudes or at high elevations such as those in the Rocky Mountains. Furthermore, increases in warm-season temperature may increase tree mortality through increased vapor-pressure deficit and mortality from drought stress (Park Williams et al. 2013). Interestingly, water availability variables were much less influential in predicting mortality despite the strong influence of precipitation on forest structure throughout the western USA. Some previous research suggests that temperature has a strong relationship with tree drought stress due to its contribution to vapor-pressure deficit (Adams et al. 2017), indicating that increased air temperature may have a direct influence on tree mortality independent of future changes to precipitation regimes. Combined with our results here, this may indicate that Rocky Mountain forests may be disproportionately affected by drier, warmer temperatures, even when compared to other regions in the western USA.

One potential explanation for the connection between winter frosts and forest mortality is the influence of snowpack. While we did not include measures of snowpack in our analysis, significant previous research has suggested that changes to snowpack volume may be critical in determining drought stress in montane environments (Anderegg et al. 2013). Alternatively, winter frosts may be influencing forest mortality by mediating the relationship between insect outbreak and tree death (Weed et al. 2013). Previous research suggests mild winter temperatures and moderate rainfall contribute most to insect outbreak risk (Sidder et al. 2016). Currently, the effect of insects on tree mortality is difficult to model and many ecosystem and earth system models do not explicitly include insect effects. The relationship between temperature and tree death may be greatly enhanced in models of mortality if the more immediate effects on snowpack and insect populations are more carefully considered (Ayres and Lombardero 2000).

Soil variables were relatively unimportant for predicting mortality across this dataset and contributed little to predicting alive or dead trees

(Figs. 2, 3). The two most important variables were bulk density of the fine earth element and available water-holding capacity. Both may be related to drought tolerance, water, or nutrient availability through competition for belowground resources, although root competition is generally less important for trees than for grasses or forbs (Casper and Jackson 1997, Sperry et al. 1998, Kiaer et al. 2013). Our results suggest little influence of soil variability on tree mortality, although soils may exert indirect control on tree demographics through other mechanisms such as habitat filtering (Kraft et al. 2015).

Implications for future work examining forest mortality

The strong influence of species identity on reducing error in the predictive model indicates that current attempts to model forest mortality will likely require extensive parameterization at the species or functional group level, even if general plant eco-physiology is faithfully represented in model processes (Adams et al. 2013, Meir et al. 2015). Buotte et al. (2019) recently accomplished this by expanding the single evergreen functional type utilized in a large earth system model to 13 functional types that represent more distinct forest ecosystems. Consequently, they reported significant improvements in model performance. While parameterizing an earth system model for 53 species is no doubt challenging in some studies, careful selection of species to include may put upper and lower bounds on the impact that climate change will have on western forests. Alternatively, new advances in earth system models could more explicitly link models to trait databases, allowing rapid evaluation of many species simultaneously (Kattge et al. 2011).

Methodological caveats and considerations

We deliberately chose to use FIA data collected since 2000. Specifically, we restricted our analysis to trees measured under the National Plot Design to improve the reliability and accuracy of our mortality estimates. While tree records before 2000 are available from FIA, mortality as a demographic process is most robustly assessed using individual tree tracking that did not begin until the National Plot Design (Smith 2002). Additionally, previous work has suggested that the irregular inventory data prior to 2000 may be significantly less reliable in assessing forest dynamics (Goeking 2015).

A potential source of error in our analysis comes from the fuzzing and swapping of plot coordinates on tribal and privately owned lands (Tinkham et al. 2018). Plot coordinates in publicly available FIA data are reported up to 1 km away from their true locations in order to prevent vandalism and to preserve the confidentiality of private landowner data (Tinkham et al. 2018). Additionally, 20% of plot coordinates located on private land are swapped with other plot coordinates within the same county (Burrill et al. 2018). While this process may significantly influence some spatial analyses, the high spatial autocorrelation of our gridded independent variables (both climate and soil variables), smaller contribution from plots on private land, and nonparametric analysis likely reduced error from plot perturbation well below other sources of variability within the dataset (Coulston et al. 2006).

Our analysis of mortality agents in FIA has significant limitations. Specifically, the limited resolution on causes of mortality in our dataset precludes strong conclusions about future mortality for some species and regions. This issue is made worse by the subjectivity often associated with assigning a causal agent in the field up to several years after a tree has died (e.g., Bigler et al. 2007). Some causal agents such as drought stress may not be immediately visible to field technicians as a proximate cause of death, and without detailed physiological measurements we cannot know for certain what killed a tree that we observed dead. Future work utilizing FIA data would benefit from a more robust understanding of the limitations imposed by FIA mortality agent methodology, including limits posed by on-the-ground accuracy that are independent of field technician training.

In this study, we specifically excluded harvest and fire mortality because of their disconnect with ultimate causes of mortality at the tree level. Nonetheless, both are major sources of mortality within all forested systems in our study area (Berner et al. 2017). Commercial tree harvest is a primary cause of mortality in sections within the Cascade Mixed Forest and likely disrupts climate-driven demographic

processes that would otherwise kill large mature trees (Berner et al. 2017). Ownership code importance provides some context on the interaction between logging and other tree mortality, although in this study was relatively unimportant. Fire was also excluded from this study due to its stochastic nature and localized area of effect, but much previous work has identified fire as a major driver of tree mortality and ecosystem change in the Sierra Nevada, Klamath Mountains, and other parts of California. Our low mortality rates in these regions may be the result of fire masking tree death from other mortality agents due to the complex interactions between fire, drought, and temperature as well as the long interval between FIA inventories (van Mantgem et al. 2018, Buotte et al. 2019). Future work on tree mortality would benefit from a better understanding of how fire interacts with other mortality agents as well as finer resolution of the relationship between local fire severity and individual tree death.

Conclusions

Recent tree mortality in the western USA, excluding mortality from logging and fire, has been largely driven by insects and generalized forest disease, but interspecific differences are significant. This is probably due to differences in how each species respond to each causal agent, although genetics considerations were beyond the scope of this study. Near-future mortality will increase for some species, especially at middle and high altitudes in the Middle and Southern Rocky Mountains, but we predict less significant increases in mortality from these agents across the Cascades, Klamath Mountains, and Sierra Nevada. Future research on other mortality agents (e.g., fire) would likely improve future mortality estimates, especially for the Sierra Nevada. Despite increases in future mortality for some species, climate and soil variables were comparatively unimportant in predicting mortality across the entire dataset. This suggests that predictions of future forest mortality will likely be species- or system-specific. Modeling efforts will likely benefit from the inclusion of vulnerable species identified here, rather than blanket parameterization of plant functional types. This study especially highlights the need for more long-term censuses of forest dynamics and further evaluation of the utility of FIA mortality estimates.

Acknowledgments

The authors thank M. Phillips for detailed feedback throughout the research and manuscript preparation. We also thank T. Bohner and P. Ibsen for helpful suggestions and commentary in earlier drafts of the manuscript. We also thank two anonymous reviewers and Dr. C. Canham for detailed feedback that significantly improved the overall quality of the work. The authors thank the Forest Inventory Analysis management team for their extensive continued work toward collecting and maintaining the FIA database.

Literature Cited

Abatzoglou, J. T. 2013. Development of gridded surface meteorological data for ecological applications and modelling. International Journal of Climatology 33:121–131.

Abatzoglou, J. T., and T. J. Brown. 2012. A comparison of statistical downscaling methods suited for wildfire applications. International Journal of Climatology 32:772–780.

Adams, H. D., G. A. Barron-Gafford, R. L. Minor, A. A. Gardea, L. P. Bentley, D. J. Law, D. D. Breshears, N. G. McDowell, and T. E. Huxman. 2017. Temperature response surfaces for mortality risk of tree species with future drought. Environmental Research Letters 12:115014.

Adams, H. D., A. P. Williams, C. Xu, S. A. Rauscher, X. Jiang, and N. G. McDowell. 2013. Empirical and process-based approaches to climate-induced forest mortality models. Frontiers in Plant Science 4:1–5.

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1:95–111.

Alexander, J. M., et al. 2018. Lags in the response of mountain plant communities to climate change. Global Change Biology 24:563–579.

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences of the United States of America 95:14839–14842.

Anderegg, W. R. L., L. Plavcová, L. D. L. Anderegg, U. G. Hacke, J. A. Berry, and C. B. Field. 2013. Drought's legacy: Multiyear hydraulic

deterioration underlies widespread aspen forest die-off and portends increased future risk. Global Change Biology 19:1188–1196.

Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of the Total Environment 262:263–286.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B 57:289–300.

Berner, L. T., B. E. Law, A. J. H. Meddens, and J. A. Hicke. 2017. Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States (2003–2012). Environmental Research Letters 12:065005.

Bigler, C., D. G. Gavin, C. Gunning, and T. T. Veblen. 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. Oikos 116:1983–1994.

Birch, D. S., P. Morgan, C. A. Kolden, J. T. Abatzoglou, G. K. Dillon, A. T. Hudak, and A. M. S. Smith. 2015. Vegetation, topography and daily weather influenced burn severity in central Idaho and western Montana forests. Ecosphere 6:art17.

Bohner, T., and J. Diez. 2020. Extensive mismatches between species distributions and performance and their relationship to functional traits. Ecology Letters 23:33–44.

Breiman, L. 2001. Random forests. Machine Learning 45:5–32.

Buotte, P. C., S. Levis, B. E. Law, T. W. Hudiburg, D. E. Rupp, and J. J. Kent. 2019. Near-future forest vulnerability to drought and fire varies across the western United States. Global Change Biology 25:290–303.

Burrill, E. A., A. M. Wilson, J. A. Turner, S. A. Pugh, J. Menlove, G. Christiansen, Conkling, B. L., and W. David. 2018. The Forest Inventory and Analysis Database: database description and user guide version 8.0 for Phase 2. U.S. Department of Agriculture, Forest Service, Washington D.C., USA. https://www.fia.fs.fed.us/library/database-documentation/

Casper, B. B., and R. B. Jackson. 1997. Plant competition underground. Annual Review of Ecology and Systematics 28:545–570.

Chen, C., A. Liaw, and L. Breiman. 2004. Using random forest to learn imbalanced data. Department of Statistics technical report number 666, University of California, Berkeley, California, USA.

Choat, B., T. J. Brodribb, C. R. Brodersen, R. A. Duursma, R. López, and B. E. Medlyn. 2018. Triggers of tree mortality under drought. Nature 558:531–539.

Cleland, D. T., J. A. Freeouf, J. E. Keys, G. J. Nowacki, C. A. Carpenter, and W. H. McNab. 2007. Ecological Subregions: sections and Subsections for the conterminous United States. General Technical Report WO-76D 76D. USDA Forest Service, Washington D.C., USA.

Coulston, J. W., K. H. Riitters, R. E. McRoberts, G. A. Reams, and W. D. Smith. 2006. True versus perturbed forest inventory plot locations for modeling: a simulation study. Canadian Journal of Forest Research 36:801–807.

Cremers, J., and I. Klugkist. 2018. One direction? A tutorial for circular data analysis using R with examples in cognitive psychology. Frontiers in Psychology 9:2040.

Cutler, D. R., T. C. Edwards, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. Ecology 88:2783–2792.

Dale, V. H., et al. 2001. Climate change and forest disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. BioScience 51:723–734.

Das, A. J., N. L. Stephenson, A. Flint, T. Das, and P. J. van Mantgem. 2013. Climatic correlates of tree mortality in water- and energy-limited forests. PLOS ONE 8:e69917.

Evans, J. S., M. A. Murphy, Z. A. Holden, and S. A. Cushman. 2011. Modeling species distribution and change using Random Forests. Pages 139–159 *in* C. A. Drew, Y. F. Wiersma, and F. Huettmann, editors. Predictive species and habitat modeling in landscape ecology: concepts and applications. Springer, New York, New York, USA.

Fawcett, T. 2006. An introduction to ROC analysis. Pattern Recognition Letters 27:861–874.

Fettig, C. J., L. A. Mortenson, B. M. Bulaon, and P. B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. Forest Ecology and Management 432:164–178.

Flake, S. W., and P. J. Weisberg. 2019. Fine-scale stand structure mediates drought-induced tree mortality in pinyon–juniper woodlands. Ecological Applications 29:e01831.

Floyd, M. L., M. Clifford, N. S. Cobb, D. Hanna, R. Delph, P. Ford, and D. Turner. 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon–juniper woodlands. Ecological Applications 19:1223–1230.

Gaylord, M. L., T. E. Kolb, W. T. Pockman, J. A. Plaut, E. A. Yepez, A. K. Macalady, R. E. Pangle, and N. G. McDowell. 2013. Drought predisposes piñon-

juniper woodlands to insect attacks and mortality. New Phytologist 198:567–578.

Geils, B. W., K. E. Hummer, and R. S. Hunt. 2010. White pines, Ribes, and blister rust: a review and synthesis: Review and synthesis. Forest Pathology 40:147–185.

Gent, P. R., et al. 2011. The community climate system model version 4. Journal of Climate 24:4973–4991.

Goeking, S. A. 2015. Disentangling forest change from forest inventory change: a case study from the US Interior West. Journal of Forestry 113:475–483.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. Forest Ecology and Management 304:492–504.

Harmon, M. E., and R. J. Pabst. 2015. Testing predictions of forest succession using long-term measurements: 100 yrs of observations in the Oregon Cascades. Journal of Vegetation Science 26:722–732.

Harrington, C. A., J. C. Zasada, and E. A. Allen. 1994. Biology of red alter (*Alnus rubra* Bong.). Pages 3–22 *in* D. E. Hibbs, D. S. DeBell, and R. F. Tarrat, editors. The biology and management of red alder. Oregon State University Press, Corvallis, Oregon, USA.

Hartmann, H., et al. 2018. Research frontiers for improving our understanding of drought-induced tree and forest mortality. New Phytologist 218:15–28.

Hengl, T., et al. 2017. SoilGrids250m: global gridded soil information based on machine learning. PLOS ONE 12:e0169748.

Hicke, J. A., and M. J. Zeppel. 2013. Climate-driven tree mortality: insights from the piñon pine die-off in the United States. New Phytologist 200:301–303.

Hollander, M., and D. A. Wolfe. 1973. Nonparametric statistical methods. John Wiley & Sons, New York, New York, USA.

Huang, C.-Y., and W. R. L. Anderegg. 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. Global Change Biology 18:1016–1027.

Huang, K., C. Yi, D. Wu, T. Zhou, X. Zhao, W. J. Blanford, S. Wei, H. Wu, D. Ling, and Z. Li. 2015. Tipping point of a conifer forest ecosystem under severe drought. Environmental Research Letters 10:024011.

Jacobi, W. R., H. S. J. Kearns, C. M. Cleaver, B. A. Goodrich, and K. S. Burns. 2018. Epidemiology of white pine blister rust on limber pine in Colorado and Wyoming. Forest Pathology 48:e12465.

Jiang, X., S. A. Rauscher, T. D. Ringler, D. M. Lawrence, A. P. Williams, C. D. Allen, A. L. Steiner, D. M. Cai, and N. G. McDowell. 2013. Projected future changes in vegetation in western North America in the twenty-first century. Journal of Climate 26:3671–3687.

Kane, J. M., T. E. Kolb, and J. D. McMillin. 2014. Stand-scale tree mortality factors differ by site and species following drought in southwestern mixed conifer forests. Forest Ecology and Management 330:171–182.

Kattge, J., et al. 2011. TRY - a global database of plant traits. Global Change Biology 17:2905–2935.

Kay, J. E., et al. 2015. The community earth system model (CESM) large ensemble project: a community resource for studying climate change in the presence of internal climate variability. Bulletin of the American Meteorological Society 96:1333–1349.

Kemp, K. B., P. E. Higuera, P. Morgan, and J. T. Abatzoglou. 2019. Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, Northern Rockies, USA. Ecosphere 10: e02568.

Kiaer, L. P., A. N. Weisbach, and J. Weiner. 2013. Root and shoot competition: a meta-analysis. Journal of Ecology 101:1298–1312.

Klos, R. J., G. G. Wang, W. L. Bauerle, and J. R. Rieck. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. Ecological Applications 19:699–708.

Kolb, T. E. 2015. A new drought tipping point for conifer mortality. Environmental Research Letters 10:031002.

Kolb, T. E., C. J. Fettig, M. P. Ayres, B. J. Bentz, J. A. Hicke, R. Mathiasen, J. E. Stewart, and A. S. Weed. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. Forest Ecology and Management 380:321–334.

Kosiba, A. M., G. W. Meigs, J. A. Duncan, J. A. Pontius, W. S. Keeton, and E. R. Tait. 2018. Spatiotemporal patterns of forest damage and disturbance in the northeastern United States: 2000–2016. Forest Ecology and Management 430:94–104.

Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29:592–599.

Krofcheck, D. J., J. U. H. Eitel, L. A. Vierling, U. Schulthess, T. M. Hilton, E. Dettweiler-Robinson, R. Pendleton, and M. E. Litvak. 2014. Detecting mortality induced structural and functional changes in a piñon-juniper woodland using Landsat and RapidEye time series. Remote Sensing of Environment 151:102–113.

Liaw, A., and M. Wiener. 2002. Classification and Regression by randomForest. R News 2:18–22.

Long, J. A., and R. L. Lawrence. 2016. Mapping percent tree mortality due to mountain pine beetle damage. Forest Science 62:392–402.

Luo, Y., and H. Y. H. Chen. 2011. Competition, species interaction and ageing control tree mortality in boreal forests. Journal of Ecology 99:1470–1480.

Lutz, J. A., and C. B. Halpern. 2006. Tree Mortality during early forest development: a long-term study of rates, causes, and consequences. Ecological Monographs 76:257–275.

McDowell, N., et al. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? The New Phytologist 178:719–739.

McDowell, N. G., et al. 2015. Global satellite monitoring of climate-induced vegetation disturbances. Trends in Plant Science 20:114–123.

McDowell, N. G., et al. 2019. Mechanisms of a coniferous woodland persistence under drought and heat. Environmental Research Letters 14:045014.

McDowell, N. G., and C. D. Allen. 2015. Darcy's law predicts widespread forest mortality under climate warming. Nature Climate Change 5:669–672.

McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology & Evolution 26:523–532.

McNab, W. H., D. T. Cleland, J. A. Freeouf, J. E. Keys, G. J. Nowacki, and C. A. Carpenter. 2007. Description of ecological subregions: sections of the conterminous United States. General Technical Report WO-76B 76B:1–82. USDA Forest Service, Washington, D.C., USA.

Meir, P., M. Mencuccini, and R. C. Dewar. 2015. Drought-related tree mortality: addressing the gaps in understanding and prediction. New Phytologist 207:28–33.

Mitton, J. B., and M. C. Grant. 1996. Genetic variation and the natural history of quaking aspen. BioScience 46:25–31.

Mortenson, L. A., A. N. Gray, and D. C. Shaw. 2015. A forest health inventory assessment of red fir (*Abies magnifica*) in Upper Montane California. Ecoscience 22:47–58.

Murphy, M. A., J. S. Evans, and A. Storfer. 2010. Quantifying Bufo boreas connectivity in Yellowstone National Park with landscape genetics. Ecology 91:252–261.

Negrón-Juárez, R., D. B. Baker, H. Zeng, T. K. Henkel, and J. Q. Chambers. 2010. Assessing hurricane-induced tree mortality in U.S. Gulf Coast forest ecosystems. Journal of Geophysical Research 115: G04030.

Newcombe, R. G. 1998. Interval estimation for the difference between independent proportions: comparison of eleven methods. Statistics in Medicine 17:873–890.

Palczewska, A., J. Palczewski, R. M. Robinson, D. Neagu. 2013. Interpreting random forest models using a feature contribution method. Pages 112–119 *in* 2013 IEEE 14th International Conference on Information Reuse & Integration (IRI). IEEE, San Francisco, California, USA.

Palczewska, A., and R. M. Robinson. 2015. rfFC: random Forest Feature Contributions version 1.0/r6. Leeds Beckett University, Leeds, England, UK.

Park Williams, A., et al. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3:292–297.

Pile, L., M. Meyer, R. Rojas, O. Roe, and M. Smith. 2019. Drought impacts and compounding mortality on forest trees in the southern Sierra Nevada. Forests 10:237.

Pugh, S. A., A. M. Liebhold, and R. S. Morin. 2011. Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. Canadian Journal of Forest Research 41:2165–2175.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rehfeldt, G. E. 2006. A spline model of climate for the Western United States. RMRS-GTR-165. USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado, USA.

Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences 167:1123–1150.

Rehfeldt, G. E., D. E. Ferguson, and N. L. Crookston. 2009. Aspen, climate, and sudden decline in western USA. Forest Ecology and Management 258:2353–2364.

Roberts, D. W., and S. V. Cooper. 1989. Concepts and techniques of vegetation mapping. Pages 90–96 *in* Land classifications based on vegetation: applications for resource management. GTR-INT-257, USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Romero-Lankao, P., J. B. Smith, D. J. Davidson, N. S. Diffenbaugh, P. L. Kinney, P. Kirshen, P. Kovacs, and L. Villers-Ruiz. 2014. North America. Pages 1439–1498 *in* V. R. Barros, editor. Climate Change 2014: impacts, Adaptation, and Vulnerability. Part

B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change. Cambridge University Press, Cambridge, UK.

Shaw, J. D., S. A. Goeking, J. Menlove, and C. E. Werstak. 2017. Assessment of fire effects based on Forest Inventory and Analysis data and a long-term fire mapping data set. Journal of Forestry 115:258–269.

Sidder, A. M., S. Kumar, M. Laituri, and J. S. Sibold. 2016. Using spatiotemporal correlative niche models for evaluating the effects of climate change on mountain pine beetle. Ecosphere 7:e01396.

Smith, A. M. S., et al. 2014. Remote sensing the vulnerability of vegetation in natural terrestrial ecosystems. Remote Sensing of Environment 154:322–337.

Smith, W. B. 2002. Forest inventory and analysis: a national inventory and monitoring program. Environmental Pollution 116:S233–S242.

Sperry, J. S., F. R. Adler, G. S. Campbell, and J. P. Comstock. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. Plant, Cell and Environment 21:347–359.

Strobl, C., A.-L. Boulesteix, T. Kneib, T. Augustin, and A. Zeileis. 2008. Conditional variable importance for random forests. BMC Bioinformatics 9:307.

Tai, X., D. S. Mackay, W. R. L. Anderegg, J. S. Sperry, and P. D. Brooks. 2017. Plant hydraulics improves and topography mediates prediction of aspen mortality in southwestern USA. New Phytologist 213:113–127.

Thompson, M. T. 2009. Analysis of conifer mortality in Colorado using forest inventory and analysis's annual forest inventory. Western Journal of Applied Forestry 24:193–197.

Tinkham, W. T., P. R. Mahoney, A. T. Hudak, G. M. Domke, M. J. Falkowski, C. W. Woodall, and A. M. S. Smith. 2018. Applications of the United States Forest Inventory and Analysis dataset: a review and future directions. Canadian Journal of Forest Research 48:1251–1268.

Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004. A spatially explicit model of sapling growth in a tropical forest: Does the identity of neighbours matter? Journal of Ecology 92:348–360.

van Mantgem, P. J., D. A. Falk, E. C. Williams, A. J. Das, and N. L. Stephenson. 2018. Pre-fire drought and competition mediate post-fire conifer mortality in western US National Parks. Ecological Applications 28:1730–1739.

Waring, R. H. 1987. Characteristics of trees predisposed to die. BioScience 37:569–574.

Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs 83:441–470.

Worrall, J. J., L. Egeland, T. Eager, R. A. Mask, E. W. Johnson, P. A. Kemp, and W. D. Shepperd. 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. Forest Ecology and Management 255:686–696.

Worrall, J. J., S. B. Marchetti, L. Egeland, R. A. Mask, T. Eager, and B. Howell. 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. Forest Ecology and Management 260:638–648.

Zhang, Y., C. Peng, W. Li, X. Fang, T. Zhang, Q. Zhu, H. Chen, and P. Zhao. 2013. Monitoring and estimating drought-induced impacts on forest structure, growth, function, and ecosystem services using remote-sensing data: recent progress and future challenges. Environmental Reviews 21:103–115.

Data Availability

Data used to construct all figures and tables are available in R package format at www.github.com/bmcnellis/McNellis2021. All FIA data used in this analysis are available from the FIA data mart located at https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3419/full