**Tree survival scales to community-level effects following mixed severity fire in a mixed-
conifer forest**

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Abstract

Identifying the drivers of tree mortality and survival is critical to developing conceptual and predictive models of fire effects on forest communities and landscapes. Individual tree characteristics (a function of species traits and tree size) govern tree- and community-scale mortality following fire, but mortality can also depend on tree density and effects arising from instantaneous extreme fire behavior. However, the relative importance and interaction of these factors are not well understood, especially for mixed-severity fire regimes. We sampled burned mixed-conifer forests dominated by western larch (*Larix occidentalis*) in the Bob Marshall Wilderness of Montana, U.S.A. We combined these field measurements with a remotely-sensed estimate of initial burn severity (dNBR) to test predictions about drivers of fire effects that produce heterogeneous post-fire tree and stand-level mortality. Tree survival 8 to 13 years after fire depended on complex interactions between species, size, and initial burn severity. Western larch experienced much higher survival than other tree species across tree sizes. Predictably, less fire-tolerant species experienced much lower survival than western larch. These tree-level probabilities in survival scale up to govern community-level mortality through variability in species composition. Greater relative abundance of fire-tolerant larch was associated with reduced levels of mortality at community scales. Interestingly, higher tree densities were either uncorrelated with community-level mortality or associated with lower community-level mortality. Our results show that traits of individuals can govern fire effects from trees to communities, and give rise to highly variable fire effects characteristic of mixed-severity fire.

Keywords: fire severity, *Larix occidentalis*, mixed-conifer, mixed-severity fire, wildfire

Highlights:

Trees vary in their fire tolerance which influences forest community fire effects.
We studied fire effects in unharvested western larch-mixed conifer forests.
Community responses to fire were influenced by survival of individual western larch.
Pre-fire stand density did not influence community-scale mortality.

Introduction

Fire governs species and landscape composition of many ecosystems globally, especially in coniferous forests. Most wildfires burn in spatially heterogeneous mixtures of high, moderate, and low severity, with embedded unburned patches (Kolden et al. 2012), and the predominant fire regime in the western U.S. is classified as mixed-severity (Schoennagel and Nelson 2011). While the ecological consequences of mixed-severity fires are increasingly well understood (e.g., Schoennagel et al. 2011, Perry et al. 2011, Halofsky et al. 2011, Tepley et al. 2013, Harvey et al. 2013), the cross-scale mechanisms that produce mixed-severity fires are not yet fully resolved (McKenzie et al. 2011, Larson and Churchill 2012). Ecological effects of fire can be characterized by mechanisms that operate across spatial scales that range from <0.0001 to $>10,000$ hectares (McKenzie et al. 2011). Mixed-severity fires emerge from heterogeneity in patterns of individual tree mortality (Woolley et al. 2012) and large-scale drivers of burn severity, such as topography and climatic variation (Cansler and McKenzie 2014).

The complexity of mixed-severity fires and fire regimes peaks at intermediate scales (see Figure 1.5 in McKenzie et al. 2011), and is mediated by the functional traits of individual trees that make up the forest community (Agee 1993). Numerous previous studies have investigated individual tree survival (or mortality) following both wildfire and prescribed fire (Woolley et al.

2012). However, such tree-level studies rarely consider controls on, or effects of, fires at larger spatial extents, making this body of work difficult to integrate with community and landscape fire ecology theory (McKenzie et al. 2011).

The purpose of this study is to identify drivers of wildfire effects on forest community composition and structure within the spatial domain of maximum complexity of landscape fire regimes (McKenzie et al. 2011). Previous studies have provided insights into how individual species influence community- and ecosystem-level patterns following disturbance across diverse ecosystems, including grassland responses to drought (Tilman and Downing 1994), savannah plant communities responses to fire and altered grazing regimes (Sankaran and McNaughton 1999), and coral reef responses to bleaching events (Côté and Darling 2010). Scaling of conceptual models from species to communities and ecosystems is thus an important research agenda for predicting responses of ecosystems to disturbance (Suding et al. 2008) including understanding mechanisms governing mixed-severity fire effects in mixed-conifer forests (McKenzie et al. 2011).

At the tree scale, we predicted that smaller trees will experience lower post-fire survival than larger trees because larger trees typically have thicker bark and taller crown-base heights, but that size-dependent mortality may vary among species of different fire tolerance. Because individual trees are embedded in communities that experience variable fire intensity and behavior, we also included a remotely-sensed measure of short-term (i.e., first year) burn severity to investigate if long-term survival occurred even in patches of initial high burn severity. A secondary objective was to investigate post-fire tree survival in western larch/mixed-conifer forests has been identified in a recent literature review as a high priority for research (Woolley et al. 2012).

Finally, we investigated patterns and potential mechanisms at the community-level when aggregating data to tree neighborhood scales. Specifically, we predicted that effects of tree-level mechanisms “scale up” to community patterns of mortality through differences in species composition. In other words, we predicted that the abundance of fire-tolerant species would generate lower community-level mortality. At community scales, we also expected that variability in tree densities would influence community mortality, where denser stands would have higher fuel loads, and more interlocking crowns with higher crown bulk density resulting in greater mortality.

Methods

Study area

The study area includes the lower slopes and valley floor of the South Fork (SF) Flathead River valley in the Bob Marshall Wilderness of northwestern Montana, U.S.A. To control for known large-scale drivers of fire severity (McKenzie et al. 2011, Dillon et al. 2011, Cansler and McKenzie 2014) we sampled at sites within the SF Flathead Valley with similar recent fire histories, forest types, and topographic settings. Through aerial photo interpretation and ground reconnaissance, we selected three study sites of 41, 48, and 149 hectares (Fig. 1A) that represent an upland montane mixed-conifer forest type composed of old-growth (i.e., un-harvested stands) western larch, Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*), with minor amounts of ponderosa pine (*Pinus ponderosa*) and quaking aspen (*Populus tremuloides*). We excluded riparian areas, meadows, monotypic lodgepole pine stands, and ponderosa pine savannas from the three sites of our study area.

The study area historically experienced a mixed-severity fire regime, with mean fire-return intervals ranging from approximately 20 to 80 years (Hopkins et al. 2014). Many fires were suppressed during the middle 20th century (Steele 1960), but since the early 1980s managers have allowed many lightning-ignited fires to burn (Smith 1986), and the study area now supports an active fire regime (Larson et al. 2013). The three study sites (Fig. 1A) include portions of the Helen Creek and Little Salmon Creek fires, which burned in 2000 and 2003 (Keane et al. 2006), respectively—years when annual area burned exceeded the 90th percentile for the region (Morgan et al. 2008). We did not sample areas where the Little Salmon Creek fire burned into the Helen Creek fire perimeter. Prior to the most recent fires, these sites had not burned since at least 1910 (Steele 1960).

Data collection and reduction

In 2011 and 2012 we established 30 circular 0.10 ha sample plots, with 10 plots in each of the three study sites (Fig. 1A) using the spatially-balanced randomized sampling technique of Stevens and Olson (2004). This design ensured random points were spatially-balanced within each of our three sites. We identified coordinates of these points prior to field work using the spsurvey package in R. Within these plots all live and dead trees taller than breast height (1.4 meters) were measured and identified to species. For each tree ≥ 20 cm dbh in both plot sizes, we recorded if it was a live standing tree, a dead standing tree, or a tree that was uprooted or snapped below breast height, but inferred to have been standing at the time of the most recent fire. In 2013, to collect a more representative sample of large-diameter trees, we randomly established 18 additional 0.60 hectare plots where we measured only trees ≥ 80 cm dbh. We used the methods of Larson and Franklin (2005) to determine if trees died before (e.g., via evidence of charring under bark) or after (e.g., no evidence of charring under bark) the fire allowing us to

reconstruct forest composition and structure prior to the fires of 2000 and 2003 for trees ≥ 20 cm. For this reason, most analyses focus on trees ≥ 20 cm, though we include smaller trees in some analyses to test predictions about pre-fire density and community-level mortality (see below).

We obtained remotely-sensed burn severity data from the Monitoring Trends in Burn Severity (MTBS) program. MTBS data are produced from Landsat imagery resulting in 30-m $\times$ 30-m pixels quantifying short-term (typically one year post-fire) fire effects (Eidenshink et al. 2007). Differenced normalized burn ratio (dNBR) data are a measure of pre- to post-fire spectral change calculated using near-infrared and shortwave infrared ranges (Eidenshink et al. 2007) and are related to changes in biomass (both living and non-living), level of scorch, char, ash, and soil exposure (Cansler and McKenzie 2012). Thus, dNBR data could be a reasonable proxy of pixel-scale fire intensity, and associated fire-caused injuries (e.g., bole char, crown volume killed) that are typically measured the first year after fire in logistic regression modeling studies of post-fire tree survival (Peterson and Arbaugh 1986, Woolley et al. 2012).

dNBR data were extracted for the entirety of our three study sites to assess landscape-scale composition of burn severity (Figure 1B), and for our specific plot locations using the bilinear interpolation function in ArcGIS to relate burn severity to tree- and plot-level fire effects. Bilinear interpolation provides a neighborhood weighted average of dNBR values for each plot location using four nearest cell values. Based on dNBR data across our 3 study sites, 57.8%, 28.7%, and 5.8% of the landscape burned at low, moderate, and high severity, respectively, with the remaining area being classified as unburned or increasing in greenness (Fig. 1B). We investigated potential influences of topography on dNBR within our study areas and found no relationships (Appendix A).

Data analysis

To investigate general patterns of tree-mortality across tree sizes and species, we calculated the percent of trees (≥ 20 cm dbh) within plots that died during or following the fire by species, by size class, and by species and size classes. After plotting the mean and range of these data, we investigated probabilities of survival among tree sizes and species groups using a generalized linear mixed model with the binomial family, using the lme4 package in R v3.0 (Bates et al. 2013). We used this package to parameterize logistic regression models where probability of tree survival was modeled as a function of species group (categorical), diameter at breast height (continuous), and their interaction. We included dNBR (continuous) in this model to test our prediction that initial burn severity mediates long-term tree survival probabilities of trees. Including this term in the model allowed us to evaluate whether initial burn severity of surrounding pixels in which each tree was located altered the main and interactive effects of species and size on long-term individual tree survival. In these models we combined subalpine fir, Engelmann spruce, and lodgepole pine into one “fire-sensitive” functional group, as these species are considered more fire intolerant (Fischer and Bradley 1987), and because of their relatively low abundance in our sample.

The resulting analysis of covariance using logistic regression investigated whether the probability of survival of trees varied with diameter at breast height among the three species groups (western larch, Douglas-fir, and the group of fire-sensitive species), as well as whether the effects of tree-level factors varied across gradients of burn severity (dNBR). Before data analysis, four trees of unknown species were removed from the data set, as were three ponderosa pines and one quaking aspen, due to low sample size, leaving 695 total trees for the analysis. The interaction terms between diameter, species, and burn severity were used to test whether the influence of diameter on the probability of survival varied among species and burn severity. We

accounted for variance explained by plot and sites by including these terms as random-effects factors in the model following Zuur et al. (2009). We evaluated models comprising various combinations and entries of both fixed (species group, diameter, and fire severity) and random effects (plot and site). We compared different candidate models using Akaike information criterion (AIC) values.

A second data set collected in 2013 and 2014 was used to validate parameterized logistic regression models. The validation data comprises 2234 trees ≥ 20 cm dbh, of which 794 are western larch, 843 are Douglas-fir, and 597 belong to the fire-sensitive functional group (fire-sensitive trees are $n = 45$ subalpine fir, $n = 226$ Engelmann spruce, and $n = 326$ lodgepole pine). The validation data were obtained within two, 4.41 ha stem map plots located within the original study area (one plot each in the northwestern and southern polygons shown in Figure 1A), both of which burned in the 2003 Little Salmon Fire. Field assessment of pre-fire tree status (i.e., was each tree alive or dead prior to the 2003 fire) used exactly the same protocol as in the original data collection (described above).

We used the area under the receiver-operator characteristic curve and classification tables to validate parameterized logistic regression models of tree survival. A receiver-operator characteristic (ROC) curve graphs the performance of a binary classifier in sensitivity (the proportion of correctly classified positive observations) and specificity (the proportion of correctly classified negative observations) space as the classification threshold is moved across the range of possible values (Robin et al. 2011, Hosmer et al. 2013). The area under the ROC curve (AUC) is a measure of the model's ability to discriminate between subjects that experience alternative outcomes (Hosmer et al. 2013): in this case, the model's ability to discriminate between trees in the validation data set that survived and those that died. ROC AUC values

range from 0.5 to 1, where 0.5 indicates no discrimination. Hosmer et al. (2013) recommends that AUC values < 0.7 indicate poor discrimination; $0.7 \leq \text{AUC} < 0.8$ is acceptable discrimination; $0.8 \leq \text{AUC} < 0.9$ is excellent discrimination; and $\text{AUC} \leq 0.9$ is outstanding discrimination. We used the R package pROC to calculate and statistically compare ROC curves (Robin et al. 2011). Classification tables summarize the observed outcome (tree survival or mortality) compared to the predicted outcome (Hosmer et al. 2013). We constructed classification tables for threshold (cutpoint) survival probabilities between 0.1 and 0.9. A tree is predicted to survive if the predicted survival probability is equal to or greater than the classification threshold probability; it is predicted to die if the predicted survival probability is less than the threshold probability.

At community-scales to test our prediction concerning how species composition within plots was related to plot-level mortality of trees, we calculated the relative density (i.e., number of stems of a species / total number of stems $\times 100$) for trees ≥ 20 cm of western larch, Douglas-fir, and the fire-sensitive species. Then to investigate whether relative abundance of these different species groups before fire explained total mortality by regressing mortality against percent composition of each species. We accounted for spatial autocorrelation by including coordinates of plots in the models as first entry terms.

To test our prediction concerning pre-fire density of trees and total plot mortality, we calculated the density of trees alive before fire within our thirty 0.10 ha plots using two estimates of density: one included all trees ≥ 5 cm dbh and the other included all trees ≥ 20 cm dbh. We then used Pearson correlations to investigate relationships between both pre-fire estimates of tree density and 6 measures of plot-level mortality (3 based on basal area and 3 based on tree density). Specifically, we calculated percent mortality based on: (1) all trees ≥ 20 cm dbh that

died in or after the fire; (2) trees between 55 and 95 cm dbh that died; and (3) for all trees ≥ 20 cm dbh that died except for large (≥ 70 cm dbh) dead Douglas-firs. The largest trees (>95 cm dbh) were excluded from the second mortality measure because they were only adequately sampled within our 0.60 ha plots, and we could not directly relate small tree density to the largest tree mortality in these plots. We excluded Douglas-fir from the third measure of mortality because of their potential for delayed mortality from post-fire bark beetle attack (Hood and Bentz 2007), i.e., community-level mortality may not have been a direct result of tree density and ladder fuels increasing fire energy release.

Results

Across thirty 0.10-hectare plots and eighteen 0.60-hectare plots, we measured 735 trees ≥ 20 cm, of which 13% had fallen since the fire. About 5% of dead trees measured were inferred to have been snags before the fire. Of the remaining 695 trees inferred to have been living at the time of the fire, 54% of trees died following the fire. The range of post-fire mortality across the plots varied from 0 to 100%. Mortality based on density measurements and mortality based on basal area measurements were strongly correlated ($r = 0.96$, $p < 0.001$; Appendix B).

Across size classes, we observed a full range of mortality levels among plots (Appendix C-E) resulting in high levels of heterogeneity in residual live tree composition and structure (Fig. 1C). At the plot scale, the mean mortality for each size class ranged from 75% for the 125 cm bin (120-130 cm), which was the largest diameter size class, to 39% for the 105 cm bin. Across species, subalpine fir experienced the highest mean plot-level mortality with 100% of individuals dying in the fire in all plots where it occurred, compared to 92% mean plot-level mortality of lodgepole pine, 79% of Engelmann spruce, 75% of Douglas-fir, and 34% of western larch

(Appendix D). At the tree scale across all plots and size classes, 116 of 136 fire-sensitive individuals (85%), 207 of 305 Douglas-fir (68%), and 71 of 253 western larch (28%) died in or after the fire.

The logistic regression using the generalized linear mixed-effects model that minimized AIC (AIC = 545.8) included a significant three-way diameter $\times$ species $\times$ dNBR interaction while accounting for random effects of plot (Table 1, Fig. 2.). Coefficients of parameters for the overall three-way interaction model were all significant ($p \leq 0.04$). Site was removed as a random effect, as the model including it did not improve model fit (AIC = 545.9, compared to AIC value of 545.8 for model with just plot). Including plot in the model improved the fit substantially (AIC without plot = 608.6). Including the diameter $\times$ species $\times$ dNBR interaction improved the model compared to a model with only diameter (AIC = 770.7), species (AIC = 649.0), or dNBR (AIC = 760.5). The model with just a diameter $\times$ species interaction resulted in AIC = 590.8, compared to the model with the three-way diameter $\times$ species $\times$ dNBR interaction of AIC = 545.8. Based on these results we report the full models with the three-way interaction (Table 1, Fig. 2), as well as the two-way diameter $\times$ species interaction (Table 2, Fig. 3). Residuals of both models approximated a normal distribution (Shapiro-Wilk W -statistic = 0.99 for both models).

These logistic regression models provide an estimate of survival probability across diameters and a gradient of remotely-sensed burn severity for Douglas-fir, western larch, and the other more fire-sensitive species (subalpine fir, Engelmann spruce, and lodgepole pine). The 3-way diameter $\times$ species $\times$ dNBR interaction in the model suggested that different probabilities of survival depended on the size and species of the individual, but that these patterns differed across burn severities (Fig. 2). When not accounting for variability in pixel-level dNBR, the probability

of survival of western larch was higher than other species and slightly increased with size (Fig. 3). In contrast, Douglas-fir survival decreased with size and other species survival probability was low but variable across tree sizes (Fig. 3). When accounting for variability in dNBR in the models (Fig. 2), the probability of western larch was higher than other species under low-severity fire, but decreased with size under high-severity fire. The relatively high probability of survival for small western larch may have been partially due to small sample sizes of small trees. Douglas-fir survival probability was consistently low across tree diameters under high burn severity and decreased with diameter under low burn severity. The probability of survival was consistently low for fire-sensitive species and decreased with size for both low and high burn severity (dNBR), though more steeply under high severity.

Model validation with ROC AUC indicated that both the three-way diameter $\times$ species $\times$ dNBR model (Table 1, Figure 2), as well as the two-way diameter $\times$ species interaction model (Table 2, Figure 3) discriminated excellently (*sensu* Hosmer et al. 2013). The AUC for the three-way interaction model was 0.846 and the AUC for the two-way interaction model was 0.856. These AUCs are not statistically different (DeLong's test: $Z = 1.82$, $p = 0.068$; Robin et al. 2011), suggesting that the two models discriminate with equivalent performance. Overall classification accuracy peaked at a threshold survival probability between 0.5 and 0.6 for the three-way interaction model (Table 3) and between 0.2 and 0.3 for the two-way interaction model (Table 4).

Plot-level mortality was negatively related to the percent of pre-fire trees that were western larch ($R^2 = 0.39$, slope = -0.97 , $p < 0.001$; Fig. 4A) and positively related to the percent of other fire-sensitive species ($R^2 = 0.25$, slope = 0.63 , $p = 0.01$; Fig. 4B). In other words, as western larch increased in relative abundance in communities, total plot-level mortality

decreased, and as other fire-sensitive species increased in communities, total plot-level mortality increased. Relative abundance of Douglas-fir was not a significant predictor of total plot-level mortality ($p = 0.86$).

Relationships between pre-fire tree density and plot-level mortality were either non-significant (i.e., no correlation) or negatively correlated (i.e., plots with greater pre-fire tree densities experienced less mortality). Specifically, pre-fire density of trees >5 cm dbh was negatively correlated with total plot-level mortality based on change in live density and basal area (Table 5; Appendix F). However, pre-fire density of trees ≥ 20 cm dbh was unrelated to plot-level mortality. Pre-fire density was not correlated with mortality of larger trees (55-95 cm in diameter) regardless of the measure of density or mortality. After excluding large dead Douglas-fir, mortality based on percent change in density was negatively correlated to pre-fire density of trees >5 cm dbh, but not pre-fire density of trees ≥ 20 cm dbh. Neither measure of pre-fire density was related to basal area mortality after excluding Douglas-fir.

Discussion

Our results suggest that individual tree resistance to fire scales up to influence community-level mortality via variability in species composition among plots. Greater proportions of fire-resistant individuals resulted in lower community-level mortality following fire compared to plots with greater relative numbers of fire-sensitive species. From a management perspective, these results underscore the need to maintain fire-tolerant species (e.g., western larch or ponderosa pine in other forest types) in order to maintain and sustain live tree cover in fire-prone ecosystems. Put simply, fire-tolerant species give rise to fire-resilient forests.

Tree species composition influences post-fire tree survival more than pre-fire tree density does, at least for stems ≥ 20 cm dbh, in the mixed-conifer forests we studied. In general, a higher proportion of larch before fire confers fire resistance at community-scales. In other mixed-conifer forests where western larch is not present, other fire-resistant species may similarly function to buffer community-scale patterns of post-fire mortality (e.g., Tepley et al. 2013). Responses of species that scale to communities and ecosystem properties are likely important mechanisms governing fire effects in other mixed-conifer forests following mixed severity fire (McKenzie et al. 2011).

The higher post-fire survival probability for western larch compared to other species was not surprising. Western larch is widely recognized as the most fire-resistant tree species in the northern Rocky Mountains (Fischer and Bradley 1987, Harrington 2013 Hopkins et al. 2014). This fire resistance is attributed to very thick bark, self-pruning of lower branches, its ability to produce epicormic branches following fire damage, and possibly due to its deciduous habit. These traits allow western larch to survive many fires when fire-sensitive species perish, which at least partially explains the association of western larch with historically mixed-severity fire regimes (Hopkins et al. 2014, Marcoux et al. 2015). The relatively consistent low survivorship of subalpine fir, Engelmann spruce, and lodgepole pine was also not surprising because of their thin bark, and for spruce and fir, low crown base heights and combustible foliage. No individuals from these fire-sensitive species were represented by the largest size classes of trees, which is likely due to their establishment occurring since the last fire at these sites, probably around the early 1900s (Steele 1960). Larger individuals of western larch, many of which were field-aged to over 500 years old, have survived several past fires, as evidenced by fire-scarred trees and multiple larch cohorts within plots (Hopkins et al. 2014).

Probability of Douglas-fir survival depended on tree dbh and burn severity, but did not follow our initial expectations. The modeled probability of survival decreased across diameter size such that mortality of trees above 70 cm was near one hundred percent. We expected that thicker bark of mature Douglas-fir would confer some fire resistance, especially in larger trees compared to smaller trees (Ryan and Reinhardt 1988). However, our data indicate the opposite trend. The most likely explanation for this result is delayed post-fire mortality caused by the bark beetle *Dendroctonus pseudotsugae* (Furniss 1965). Level of post-fire bark beetle attack is a strong predictor of long-term post-fire Douglas-fir survival in the northern US Rockies (Peterson and Arbaugh 1986). Hood and Bentz (2007) found that 50% of Douglas-firs with dbh $\geq$ 23 cm were attacked in the first two years after fire in the northern Rocky Mountains, including in mixed-conifer forests in northwest Montana that burned in 2001. They further found that probability of mortality for beetle-attacked Douglas-fir trees increased with dbh (Hood and Bentz 2006), consistent with our results (Fig. 4).

We assumed that dNBR would provide greater predictive accuracy in our logistic regression models of tree survival. While the AIC was minimized by the full three-way interaction model that included dNBR, model validation with ROC AUC indicated that including dNBR did not improve model performance. Our models for post-fire tree survival provide similar or better prediction accuracy compared to other models developed for western conifer species (Hood and Bentz 2007, Hood et al. 2007, Thies and Westlind 2012). The classification tables (Tables 3 and 4) for the two models do provide some evidence that including dNBR can improve model prediction accuracy for tree mortality at very low threshold survival probabilities, and for tree survival at very high threshold survival probabilities. This is likely because—in this mixed-conifer system—very low burn severities (low dNBR) are often indicative of fire behavior

and intensity so mild that some individuals of fire-intolerant species can survive (left panels in Fig. 3), while very high burn severities (high dNBR) are often indicative of fire behavior and intensity so extreme that even the most fire-resistant trees are killed (right panels in Fig. 3). In sum, the parameters from these models (Table 1 and 2) could prove useful in predicting post-fire community composition and species survival using remotely-sensed data and pre-fire forest inventories.

We found no support for our prediction that pre-fire tree density would be positively related to community-level tree mortality due to higher fuel loadings and heat production, high crown bulk densities, and lower ladder fuels. We actually observed the opposite pattern when including pre-fire density of trees >5 cm; more dense plots experienced less total mortality. No relationship between pre-fire density and mortality was observed when including only trees ≥ 20 cm living before the fire. We predicted that these results would vary depending on whether we investigated mortality based on basal area or density. We further predicted that focusing on large tree mortality or excluding large Douglas-fir from mortality estimates might yield results supporting our overall prediction. However, we found no evidence that denser plots were associated with greater community-level mortality.

The surprising negative and non-significant relationships between pre-fire tree density and total community mortality and burn severities may be explained by reduced wind speeds or higher fuel moisture in denser sites, or that other mechanisms, such as species composition, played a more influential role driving patterns of fire effects. Lydersen et al. (2014) also observed decreasing fire severity with increasing small tree density, which they attribute to cooler microsite conditions where density was higher. Higher tree densities may have decreased

the rate of fire spread and reduced wind speeds influencing torching and crowning of flames during the fire event.

In contrast to our results, Lentile et al. (2006) and Yu et al. (2009) documented density-dependent burn severity in ponderosa pine (*Pinus ponderosa*), and tree mortality in Mongolian pine (*Pinus sylvestris*) forests, respectively. Reducing tree density to mitigate fire effects is widely applied based on the hypothesis that tree density governs fire severity and tree mortality (*sensu* Martinson and Omi 2013, Stevens-Rumann et al. 2013, Kennedy and Johnson 2014, Prichard and Kennedy 2014). More research should explore how relationships between pre-fire density, fire severity, and mortality may be dependent upon interactions between weather, topography, species composition, and burn severity (Schoennagel et al. 2004). We interpret our results as an indication that fire effects were more strongly driven by species composition or stochastic factors (e.g., weather) than by pre-fire density.

Conclusions

The highly variable patterns of post-fire tree survival within and across our study sites (as illustrated in Figure 1) arose primarily from the effects of species- and size-dependent tree functional traits and plot-scale variability of pre-fire species composition. These conclusions must be interpreted in light of our study design. First, the mixed-conifer communities we studied include some of the most fire-tolerant (western larch) and fire-intolerant (subalpine fir) tree species in western North America. Second, we constrained our study area to topographically moderate valley bottom forests, thereby controlling for major topographic influences on fire effects (Appendix A), allowing for stronger expression of tree size- and species-mediated fire effects. Thus, we place our work into a broader conceptual framework (Figure 5) whereby traits

of individuals and species scale up to influence community-level (or stand) patterns, while still recognizing that trees and communities are embedded in landscapes where fuel continuity, landforms, weather, and climate influence lower-level responses to fire (McKenzie et al. 2011, Cansler and McKenzie 2014, Marcoux et al. 2015, Parks et al. 2015).

Our data were obtained from fires that burned during regional-fire years (i.e., >90th percentile of annual area burned; Morgan et al. 2008), and are thus broadly representative of the climate conditions under which most area burns in the northern US Rocky Mountains. The tree survival probabilities we identified here should have broad applicability to other western larch/mixed-conifer forests, and our approach and conclusions are relevant to the conceptual understanding of other mixed-conifer forests in which species vary greatly in their resistance to fire (e.g., Tepley et al. 2013). Ultimately, advancing the scientific understanding and science-based management of mixed severity fire regime forests will require conceptual models (e.g., Figure 5) and datasets that integrate different mechanisms operating from tree to landscape scales (McKenzie et al. 2011).

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Table 1. Coefficient estimates of parameters for the logistic regression predicting probability of survival of trees based on their species (western larch = larch; Douglas-fir; or other species), diameter at breast height (dbh), and burn severity (dNBR). Estimates shown below include Douglas-fir as the base entry into the model, therefore equations for larch and other species include estimate corrections. Resulting logistic equations plotting the three-way interaction between species, dbh, and dNBR are shown in Figure 2 for 4 levels of dNBR.

	Estimate	Standard Error	P-value
Intercept	8.161	1.809	<0.0001
dbh	-0.1784	0.0458	<0.0001
larch	-11.27	2.398	<0.0001
other	-12.9	2.67	<0.0001
dNBR	-0.0188	0.005717	0.001
dbh × larch	0.2831	0.05396	<0.0001
dbh × other	0.333	0.08494	<0.0001
dbh × dNBR	0.0003	0.0001454	0.039
larch × dNBR	0.02903	0.007111	<0.0001
other × dNBR	0.04181	0.01381	0.002
dbh × larch × dNBR	-0.00057	0.000162	0.0004
dbh × other × dNBR	-0.00145	0.0005625	0.009

Table 2. Coefficient estimates of parameters for the logistic regression predicting probability of survival of trees based on their species (western larch = larch; Douglas-fir; or other species) and size (diameter at breast height, dbh). Estimates shown below include Douglas-fir as the base entry into the model, therefore equations for western larch and other species include estimate corrections. Resulting logistic equations plotting the two-way interaction between species and size are shown in Figure 3.

	Estimate	Standard Error	P-value
Intercept	2.759	0.707	<0.0001
dbh	-0.097	0.016	<0.0001
larch	-1.988	0.958	0.038
other	-5.554	1.233	<0.0001
dbh × larch	0.101	0.019	<0.0001
dbh × other	0.104	0.034	0.002

Table 3. Classification table for the three-way logistic regression model predicting probability of survival of trees based on their species, size, and burn severity (Table 1, Fig. 2).

P_s	Total correct (%)	Correctly predicted survival (%)	Correctly predicted mortality (%)
0.1	61.5	57.7	92.2
0.2	74.3	68.8	87.6
0.3	76.8	72.5	84.8
0.4	78.2	74.9	83.6
0.5	79.6	78.3	81.4
0.6	79.7	80.8	78.5
0.7	77.2	82.5	72.7
0.8	72.7	85.1	65.8
0.9	60.7	85.2	55.2

677 **Table 4.** Classification table for the two-way logistic regression model predicting probability of
678 survival of trees based on their species and size (Table 2, Fig. 3).

Classification threshold (P_s)	Total correct (%)	Correctly predicted survival (%)	Correctly predicted mortality (%)
0.1	77.3	72.6	86.0
0.2	78.9	76.1	83.0
0.3	78.8	78.3	79.5
0.4	77.9	79.7	76.1
0.5	77.2	81.4	73.5
0.6	75.9	82.9	70.7
0.7	74.2	85.1	67.6
0.8	47.7	--*	47.7
0.9	47.7	--*	47.7

679 *Maximum predicted survival probability (P_s) = 0.787.
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Table 5. Pearson correlation coefficients (with p-values in parentheses) describing relationships between pre-fire density based on all trees > 5 cm or > 20 cm dbh and post-fire mortality based on percent change in density and basal area of all trees $\geq$ 20 cm dbh, tree 55-95 cm dbh, and change in density and basal area of trees after removing mortality of large ($\geq$ 70 cm) Douglas-fir. The latter analysis was conducted to determine if removing presumed delayed beetle mortality of large Douglas-fire changed our interpretation of density-influenced fire mortality. Data are shown in Appendix F.

Mortality estimate	Pre-fire density estimates based on:	
	All trees > 5 cm dbh	All trees > 20 cm dbh
Percent change in density of trees $\geq$ 20 cm dbh	-0.36 (0.05)	-0.11 (0.55)
Percent change in basal area of trees $\geq$ 20 cm dbh	-0.38 (0.04)	-0.14 (0.47)
Percent change in density of trees 55-95 cm dbh	-0.29 (0.13)	-0.04 (0.85)
Percent change in basal area of trees 55-95 cm dbh	-0.29 (0.13)	-0.05 (0.81)
Percent change in density without large Douglas-fir	-0.37 (0.04)	-0.13 (0.48)
Percent change in basal area without large Douglas-fir	0.33 (0.07)	0.09 (0.63)

Figure captions

Figure 1. A. Map of our study area along the South Fork Flathead River, Bob Marshall Wilderness in northwestern Montana (shown in inset map). Three sampling sites are outlined in black. Black circles within the three sites represent our plot locations. Fire severity from MTBS is shown (fire-severity colors are listed in B). B. Histogram of the distribution of remotely-sensed estimates of fire severity (dNBR, differenced normalized burn ratio) within the three study sites shown in A. Data are classified into fire-severity classes based on MTBS classification thresholds for the Little Salmon Creek fire. Values of dNBR extracted to forest sampling plot locations are shown as hash marks along the x-axis. C. Photos illustrating the variability of fire effects on post-fire forest structure sampled in our study sites.

Figure 2. Predicted probability of survival from generalized mixed model logistic regression for western larch (top row), Douglas-fir (middle row), and other fire sensitive species (bottom row) across sampled tree sizes (dbh). The curves represent the parameterized models of a two-way interaction between species and tree size (see Table 1 for coefficients). The three-way interaction models that include dNBR are shown in Fig 3.

Figure 3. Predicted probability of survival from generalized mixed model logistic regression for western larch (top row), Douglas-fir (middle row), and other fire sensitive species (bottom row) across sampled tree sizes (dbh) under four levels of severity fire. Ninety-five percent confidence intervals are shown in grey, and coefficient estimates used to produce figures are in Table 2. Individual observations of trees surviving (1) or dying (0) in or after fire are shown as open symbols and represent trees in plots experiencing dNBR values ranging from <150 to 225 panels

with prediction curves where dNBR = 150; 226-375 for panel where dNBR = 300; 376-525 for panel where dNBR = 450; and >450 for panel where dNBR = 600.

Figure 4. Relationships between relative abundance (number of individuals of a species / total number of individuals *100) of western larch (A) and fire-sensitive conifers (B) before fires and the percentage of total individuals that died after fire. Statistics can be found in text.

Figure 5. Understanding the mechanisms determining the effects of mixed-severity fire requires cross-scale considerations from tree-based characteristics to landscape-scale determinants of fire severity. The conceptual diagram illustrates hypothesized within- (parenthetical terms) and among-scale (italicized vertically oriented terms) mechanisms that generate post-fire patterns in mixed severity fire regimes. Tree-scale mechanisms influence fire effects through the functional traits of individuals. Collectively these tree-based mechanisms can influence community (tree neighborhood or stand) fire effects via variability in species composition. Density of communities can drive fire effects independent of species composition which can influence landscape patterns of fire severity, depending on their landscape continuity and arrangement. Landscape-scale fire effects can be strongly driven by climate, topography, and weather.

Unburned

21 % mortality

63 % mortality

99 % mortality

733
734 Figure 1.

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738 Figure 2.

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742 Figure 3.

Figure 4.

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750 Figure 5.

Appendix A. We investigated whether patterns of burn severity as measured by dNBR were related to topographic position among our three study sites and plot locations. First, we used the “Area Solar Radiation” tool in spatial analyst in ArcMap 10.2 to estimate total incoming solar radiation (insolation) for the month of August using a 30-meter digital elevation model (DEM) calculated for the entire Bob Marshall Wilderness Complex. We used the same DEM to calculate slope and aspect, and transformed aspect to represent southerly exposures. We then multiplied this aspect by slope to weight the aspects by steepness of slopes. We then overlaid these values in our GIS and extracted all values within our three study sites, as well as to each of our thirty 0.10 ha plot locations. We then ran correlations between our slope-weighted aspect and total August insolation to confirm that our topographic reflected differences in estimated environmental conditions associated with solar energy inputs. We also correlated slope-weighted aspect to dNBR values. Slope-weighted aspect was strongly related to modeled insolation across pixels within our three study sites (A) and among our plot locations (B). However, slope-weighted aspect was not correlated with dNBR for the entire study sites (C) or among our plots (D). From this analysis we concluded that topography did not directly influence burn severity in our study sites.

Appendix B. Total tree percent mortality based on density (x-axis) and basal area (y-axis) across thirty 0.10 hectare plots with burned western larch-mixed conifer forests in the Bob Marshall Wilderness. The mixed-severity fire produced a full range of mortality, which we captured in our sampling design.

Appendix C. Mean percentage of trees that died within diameter classes (grey bars) and individual observations of percentage mortality within diameter classes and plots (closed circles) to show variability within classes. Some closed circles overlap with others and are hidden from view.

Appendix D. Means (grey bars) and individual plot-level sample values (closed circles) of percent mortality for dominant species observed in burned plots in the Bob Marshall Wilderness, Montana. Some closed circles overlap with others and are hidden from view. ABLA=*Abies lasiocarpa*; PICO=*Pinus ponderosa*; PIEN=*Picea engelmannii*; PSME=*Pseudotsuga menziesii*; LAOC=*Larix occidentalis*.

Appendix E. Plot-level mortality of four tree species by size class. Grey bars are mean mortality per plot and black circles represent individual plot-level mortality to illustrate the wide range of variability in mortality among plots.

831 Appendix F. Relationship between pre-fire density based on all trees > 5 cm (left column) or ≥
832 20 cm (right column) dbh and post-fire mortality based on percent change in density (A-B) and
833 basal area (C-D) of all trees ≥ 20 cm dbh, density (E-F) and basal area (G-H) trees 55-95 cm dbh,
834 and change in density (I-J) and basal area (K-L) of trees after removing mortality of large (≥ 70
835 cm) Douglas-fir. Pearson correlation coefficients and p-values are reported in Table 3.