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

R. Travis Belote [a,*], Andrew J. Larson [b], Matthew S. Dietz [c]

[a] The Wilderness Society, Northern Rockies Regional Office, 503 W. Mendenhall, Bozeman, MT 59715, USA
[b] Department of Forest Management, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA
[c] The Wilderness Society, California Regional Office, 250 Montgomery St., Suite 210, San Francisco, CA 94104, USA

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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 8–13 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.

1. 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 (Collins and Stephens 2010), 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 (Lutz et al., 2009; 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

* Corresponding author.
E-mail address: travis_belote@tws.org (R. Travis Belote).

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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, which 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.

2. Methods

2.1. 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., 2013). 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).

2.2. 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 m) 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 × 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 (Fig. 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).

2.3. Data analysis

To investigate general patterns of tree-mortality across tree sizes and species, we calculated the percent of trees (⩾20 cm dbh)