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Looking beyond the mean: Drivers of variability in postfire stand development of conifers in Greater Yellowstone

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ABSTRACT

High-severity, infrequent fires in forests shape landscape mosaics of stand age and structure for decades to centuries, and forest structure can vary substantially even among same-aged stands. This variability among stand structures can affect landscape-scale carbon and nitrogen cycling, wildlife habitat availability, and vulnerability to subsequent disturbances. We used an individual-based forest process model (iLand) to ask: Over 300 years of postfire stand development, how does variation in early regeneration densities versus abiotic conditions influence among-stand structural variability for four conifer species widespread in western North America? We parameterized iLand for lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) in Greater Yellowstone (USA). Simulations were initialized with field data on regeneration following stand-replacing fires, and stand development was simulated under historical climatic conditions without further disturbance. Stand structure was characterized by stand density and basal area. Stands became more similar in structure as time since fire increased. Basal area converged more rapidly among stands than tree density for Douglas-fir and lodgepole pine, but not for subalpine fir and Engelmann spruce. For all species, regeneration-driven variation in stand density persisted for at least 99 years postfire, and for lodgepole pine, early regeneration densities dictated among-stand variation for 217 years. Over time, stands shifted from competition-driven convergence to environment-driven divergence, in which variability among stands was maintained or increased. The relative importance of drivers of stand structural variability differed between density and basal area and among species due to differential species traits, growth rates, and sensitivity to intraspecific competition versus abiotic conditions. Understanding dynamics of postfire stand development is increasingly important for anticipating future landscape patterns as fire activity increases.

1. Introduction

Large, high-severity, infrequent disturbances such as fires can shape landscape patterns of forest age, structure, and species composition for decades to centuries (Foster et al., 1998). Warming climate and concomitant increases in fire activity will likely reset forest succession across larger expanses of the western United States (Westerling et al., 2006; Abatzoglou and Williams, 2016; Westerling, 2016). Therefore, understanding how stands develop after fire is critical for anticipating future forest landscapes. This is particularly important in the Northern Rocky Mountains (USA), where decadal area burned increased 889% from the 1970s to the early 2000s (Westerling, 2016) and 34% of area burned across all forest types is stand-replacing fire (41% in subalpine and 25% in mid-montane forests; Harvey et al., 2016a). During large fire years, stand-replacing fire can exceed 50% of area burned (Turner et al., 1994). In the Greater Yellowstone Ecosystem (GYE) within the Northern Rocky Mountains, successional dynamics in subalpine forests have been influenced by infrequent (100–300 year fire return interval), high-severity (i.e., stand-replacing) fires throughout the Holocene (Romme and Despain, 1989; Millspaugh et al., 2004; Schoennagel et al., 2004; Whitlock et al., 2008; Higuera et al., 2011).

Among-stand variation in forest structure over stand development has received surprisingly little attention in studies of postfire stand trajectories (but see Kashian et al., 2005a, 2005b). Structure and function can vary considerably among stands of the same age (e.g., Turner, 2010), with substantial implications for carbon pools and fluxes (Litton et al., 2004; Turner et al., 2004; Bradford et al., 2008; Kashian et al., 2013), nitrogen pools and fluxes (Smithwick et al., 2009a, 2009b;

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Turner et al., 2009), wildlife habitat (Tews et al., 2004), and vulnerability to subsequent disturbances (Bebi et al., 2003; Seidl et al., 2016a). Due to high variation in stand structure following fire, simple descriptions of mean conditions within these forests might overlook important information about the ecological dynamics of a landscape (Fraterrigo and Rusak, 2008).

Initially distinct post-disturbance stands may converge over time due to competition and environmental constraints or follow distinct trajectories if the effects of initial post-disturbance regeneration and environmental heterogeneity persist over time (Glenn-Lewin and van der Maarel, 1992; Walker and del Moral, 2003; Tepley et al., 2013; Meigs et al., 2017). Postfire stand development pathways differ among species based on their fire adaptations, tolerances, and growth rates (Baker, 2009; Knight et al., 2014). For example, species that exhibit serotiny depend on a canopy seedbank that must be released by an environmental trigger such as fire (Crossley, 1956). Serotinous species [e.g., lodgepole pine (*Pinus contorta* var. *latifolia*), jack pine (*Pinus banksiana*)] can recruit in abundance following stand-replacing fire (Turner et al., 2004; Buma et al., 2013; Pinno et al., 2013; Edwards et al., 2015). In the Northern Rocky Mountains, postfire lodgepole pine densities vary widely as a result of broad-scale gradients in prefire serotiny (Tinker et al., 1994; Turner et al., 1997; Schoennagel et al., 2003). In contrast, other species must disperse into recently burned areas (Baker, 2009). Following severe stand-replacing fire, which kills all trees and consumes the shallow litter layer, tree seedling establishment occurs on mineral soil (Turner et al., 1997, 1999), and early seedling survival varies with climate (Harvey et al., 2016b; Stevens-Rumann et al., 2018).

Variation in early regeneration densities results in differing levels of competition for light and other resources in postfire stands, which in turn may differentially affect stand development pathways depending on species traits. For example, species that are tolerant of resource-limited conditions [e.g., shade-tolerant subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*; Oosting and Reed, 1952; Alexander, 1987)] may continue to establish and survive in the understory for decades following disturbance (Veblen, 1986; Aplet et al., 1988), enabling convergence in stand density. Alternatively, species whose diameter growth rates are more sensitive to competition, such as lodgepole pine in comparison with other Rocky Mountain conifers (Buechling et al., 2017), may be likely to tend toward similar basal areas among stands of different densities. However, high-severity fire occurs in forests that span a broad range of climatic and topoedaphic conditions (Turner and Romme, 1994; Harvey et al., 2016a), and this abiotic heterogeneity may outweigh the effects of competition-driven convergence and instead maintain or increase variation among stands during postfire stand development.

Stand development unfolds over long periods of time and under changing climate, and models that can project variation in future stand structures are needed to explore these long-term trajectories and inform possible management practices. Models built on statistical relationships between environmental drivers and tree responses (i.e., empirical models) play an important role in forest management and form the basis for the development of more complex models based on mechanistic understanding of forest processes (Korzukhin et al., 1996). However, empirical models may fail to predict stand structures and forest landscapes under changing environmental drivers, whereas process-based models can improve projections of future forest conditions (Korzukhin et al., 1996; Cuddington et al., 2013; Gustafson, 2013; Reyer et al., 2015). Modeling ecological processes and variables at scales appropriate to phenomena, such as competition for resources at the individual-tree level, also allows broader-scale patterns to emerge from finer-scale interactions (Grimm et al., 2017; Scholes, 2017).

1.1. Objectives

We adapted and parameterized iLand, a process-based forest simulation model (Seidl et al., 2012) for four widespread conifer species in the Greater Yellowstone Ecosystem: Lodgepole pine, Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), Engelmann spruce, and subalpine fir. We then conducted a simulation experiment to address the question: Over 300 years of postfire stand development, how does variation in early regeneration densities versus abiotic conditions influence among-stand structural variability for four conifer species widespread in western North America? We expected variation in early regeneration densities to drive structural variability among young stands and variation in abiotic drivers to become increasingly important as stands aged. We

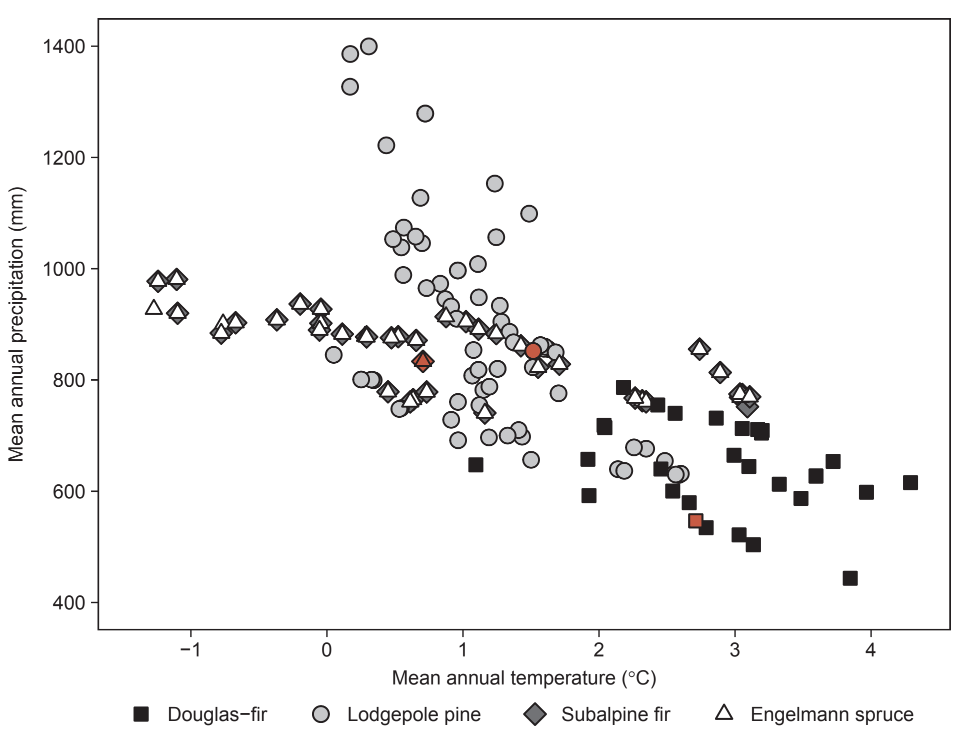

Fig. 1. Climate envelope for evaluation and simulation experiments, characterized by mean annual precipitation and mean annual temperature (derived from 1980 to 2015 daily climate data; Thornton et al., 2017) for each species. Each simulated stand is represented by one point within this climate space. Median climate conditions used in no among-stand variation scenarios (*Regeneration varies* and *Neither vary*) are shown in red. Subalpine fir and Engelmann spruce have the same median climate.

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