Forest Ecology and Management 430 (2018) 460–471

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

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ARTICLE INFO

Keywords:
Stand structure
Variability
Forest development
Process-based modeling
Greater Yellowstone Ecosystem
Wildfire

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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https://doi.org/10.1016/j.foreco.2018.08.034
Received 19 June 2018; Received in revised form 16 August 2018; Accepted 18 August 2018
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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

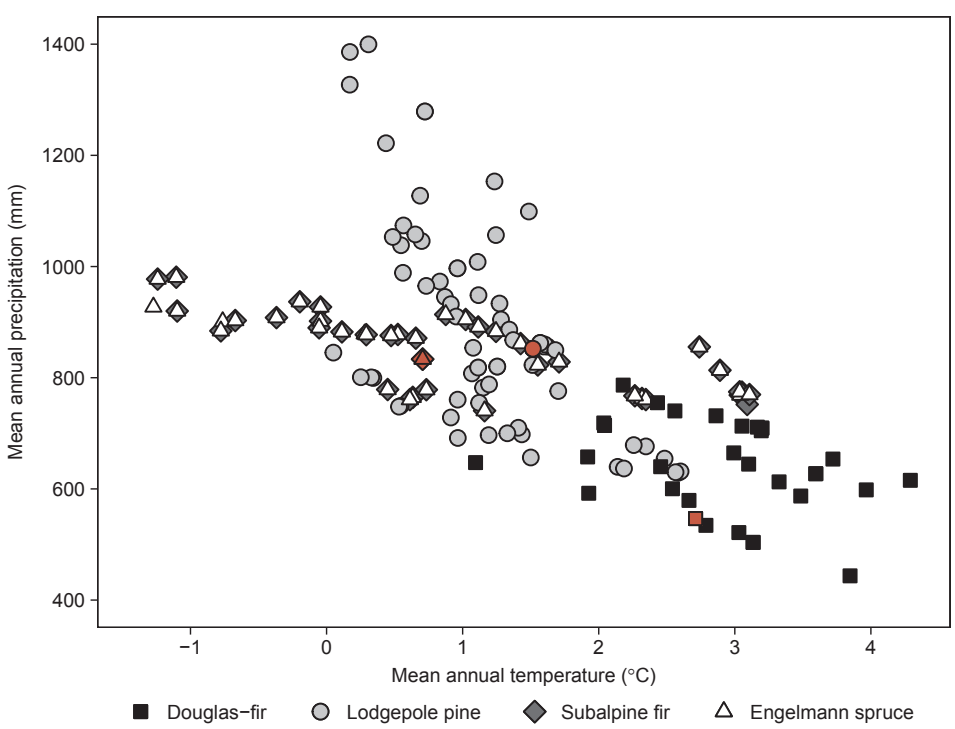

Fig. 1. Climate envelope for evaluation and simulation experiments, characterized by mean annual precipitation and mean annual temperature (derived from 1980 to 2015 daily climate data; Thornton et al., 2017) for each species. Each simulated stand is represented by one point within this climate space. 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.

further expected early regeneration densities to influence stand structural variability of lodgepole pine for a longer period of time than other conifers, due to its wider range of initial stem densities resulting from variation in prefire serotiny.

2. Methods

2.1. Study area

The Greater Yellowstone Ecosystem in the Northern Rocky Mountains of the United States comprises 89,000 km^2 (YNP, 2017) primarily in northwest Wyoming, and also in southeast Idaho and southwest Montana. The majority of the GYE is federally managed land, anchored by Yellowstone and Grand Teton National Parks and adjacent national forests, and natural processes such as disturbance and regeneration occur with minimal intervention across large areas within this relatively intact forested landscape. Forests in the GYE span a broad elevation gradient (1800 to 3050 m) and include mid-montane forests at lower elevations dominated by interior Douglas-fir, mid-elevation subalpine forests dominated by lodgepole pine, and higher-elevation subalpine forests dominated by Engelmann spruce and subalpine fir (Despain, 1990; Knight et al., 2014). Climate is warmer and drier at lower elevations, and cooler and wetter at higher elevations (mean annual temperatures range from −1.3 to 4.3 °C and mean annual precipitation from 444 to 1400 mm; Fig. 1). Soils in the central area of Greater Yellowstone are nutrient poor and largely derived from underlying rhyolitic or andesitic bedrock (Despain, 1990; Rodman et al., 1996). Soil inorganic nitrogen availability is very low, even following disturbance (Turner et al., 2007), and postfire tree nitrogen uptake is facilitated by associations with ectomycorrhizal communities (Douglas et al., 2005; Smithwick et al., 2009a). Rhyolite-derived soils, which cover most of Yellowstone's lodgepole pine-dominated central plateau, are coarser and less fertile than andesite-derived soils (Despain, 1990; Whitlock, 1993).

Forests in the GYE have been shaped by historical fire regimes (Romme, 1982). Fire return intervals are longer and percent serotiny of lodgepole pine is lower at higher elevations (Schoennagel et al., 2003). Of the four focal species, only mature Douglas-fir with its very thick bark is adapted to survive fire, and fire regimes in lower-elevation Douglas-fir forests are typically characterized as mixed severity (Baker, 2009). However, stand-replacing fires can occur in all forest types (Baker et al., 2007; Harvey et al., 2016a). Postfire regeneration densities following stand-replacing fire are extremely variable (Table 1) based on prefire stand conditions, local burn severity, and the spatial pattern of fires, which determine distances to seed sources (Turner et al., 1997, 1999). For example, regenerating lodgepole pine stands ranged from 0 to > 500,000 stems ha^{-1} 11 years following stand-replacing fire (Turner et al., 2004). High-severity fire behavior in this region is primarily weather-driven (e.g., drought, wind; Schoennagel et al., 2004; Higuera et al., 2011).

2.2. Simulation model

2.2.1. Model overview

We simulated stand (1 ha) development using the individual-based forest landscape and disturbance model iLand (Seidl et al., 2012),

Table 1
Initial conditions and drivers for simulated stands. Median values indicate the no among-stand variation condition.

Variable (units)	Douglas-fir (n = 34) Min-Max	Mean (SE) Median	Lodgepole pine (n = 70) Min-Max	Mean (SE) Median	Subalpine fir (n = 38) Min-Max	Mean (SE) Median	Engelmann spruce (n = 39) Min-Max	Mean (SE) Median
Time since fire (years)*	–	24 (–) 24	–	24 (–) 24	10–19	14 (0.4) 13	10–19	14 (0.5) 13
*Postfire regeneration**								
Density of trees, saplings, and seedlings (stems ha^{-1})	14–13,653	2224 (490) 1370	33–344,075	21,446 (6546) 4050	14–3154	268 (90) 83	14–11,997	610 (327) 83
Climate†								
Mean annual temperature (°C)	1.1–4.3	2.9 (0.1) 3.0	0.0–2.6	1.2 (0.1) 1.1	−1.2–3.1	1.0 (0.2) 0.7	−1.3–3.1	0.8 (0.2) 0.6
Annual precipitation (mm)	444–787	637 (14) 642	629–1400	888 (22) 853	741–981	847 (11) 866	741–981	855 (11) 877
Daily global radiation (MJ m^{-2})	15.3–18.4	16.4 (0.1) 16.2	16.8–19.8	18.5 (0.1) 18.5	16.7–20.3	18.6 (0.2) 18.6	16.7–20.3	18.7 (0.2) 18.8
Daily vapor pressure deficit (kPa)	0.42–0.51	0.45 (0.00) 0.44	0.40–0.43	0.42 (0.00) 0.42	0.38–0.46	0.42 (0.00) 0.41	0.38–0.46	0.42 (0.00) 0.41
Soils								
Effective depth (cm)‡	83–152	102 (3) 106	83–137	114 (3) 106	83–152	111 (5) 86	83–152	106 (4) 86
Sand (%)‡	30–71	50 (1) 48	52–56	54 (0) 54	30–56	48 (1) 53	30–56	48 (1) 53
Silt (%)‡	21–49	33 (1) 33	30–33	32 (0) 33	30–49	35 (1) 32	30–49	35 (1) 32
Clay (%)‡	8–22	17 (1) 19	13–15	14 (0) 14	13–21	17 (1) 15	13–21	17 (1) 15
Substrate§	–	Andesite	–	Rhyolite	–	Andesite	–	Andesite

* Postfire regeneration densities and time since fire from field data (Donato et al., 2016; Harvey et al., 2016b; Turner et al., 2016).
† Climate data from Daymet Version 3 (Thornton et al., 2017), extracted using geographic coordinates of field data* or field-verified forest type (Simard et al., 2012).
‡ Soil depth and texture from CONUS-SOIL (Miller and White, 1998), extracted using geographic coordinates of field data* or field-verified forest type (Simard et al., 2012).
§ Soil substrate assigned based on parent material associated with each forest type (Despain, 1990; Knight et al., 2014). Substrate was used to derive relative fertility.

which integrates species-specific responses to environmental drivers such as light availability, temperature, precipitation, soil moisture, and nutrient levels. These environmental drivers limit seedling cohort establishment and modify sapling cohort growth and survival. Trees > 4 m in height are represented as individuals (2-m spatial resolution) in their responses to resource availability. Limitations to physiological processes (e.g., temperature and water limitation) are considered at a daily time step, and stand structure is updated annually. Nutrient levels (i.e., soil relative fertility) are expressed as plant available nitrogen and modify tree growth according to a species-specific nitrogen response class. Processes such as seed dispersal and competition for light are spatially explicit. Light availability for an individual tree is attenuated based on the heights and crown characteristics of neighboring trees. The growth allocation of individual trees to height and diameter responds dynamically to light competition within a species-specific range. In the absence of disturbance, variation in tree sizes and forest structure within stands (i.e., 100 × 100 m grid cells of homogeneous climate and soil conditions) emerges from these fine-scale tree-level dynamics,

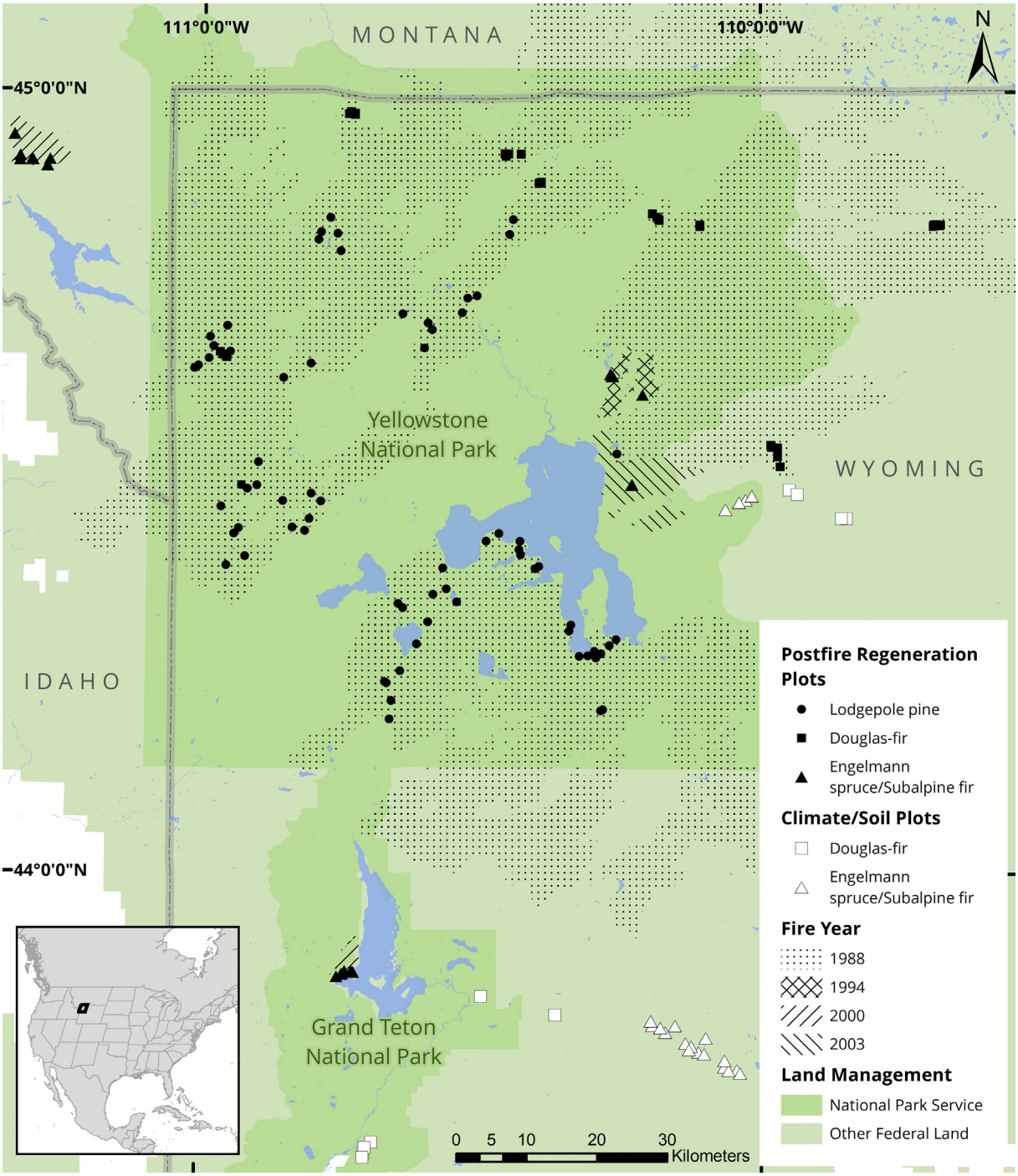

Fig. 2. (Inset) Location of our study area within North America. (Main) Plot locations (Simard et al., 2012; Donato et al., 2016; Harvey et al., 2016b; Turner et al., 2016) within the Greater Yellowstone Ecosystem used for data on postfire regeneration, climate, and soils to simulate stand development in iLand. Fire years for postfire regeneration plots are indicated with differential shading, and additional climate and soil plots were identified to better encompass the expected range of variability in abiotic conditions for each species. Data sources: ESRI, Tele Atlas, National Atlas of the United States, YNP Spatial Analysis Center, and Monitoring Trends in Burn Severity (MTBS).

while among-stand variability is also driven by differences in environmental conditions between stands (Seidl et al., 2012). iLand has been demonstrated to work well in forested ecosystems in the Pacific Northwest (Seidl et al., 2012, 2014b) and in Europe (Seidl et al., 2014a; Silva Pedro et al., 2015; Thom et al., 2017), and Hansen et al. (2018) evaluated iLand's representation of early postfire regeneration dynamics in lodgepole pine and Douglas-fir forests in Yellowstone. Extensive model documentation is available at http://iland.boku.ac.at/ (Seidl and Rammer, 2018).

2.2.2. Model parameterization

We parameterized iLand for the four dominant conifer species in the Greater Yellowstone Ecosystem (Appendix A). Most species-specific traits and parameters were sourced from peer-reviewed literature and government reports, and a few parameters (e.g., height-to-diameter ratios, aging) were fit or iteratively derived by simulating stand development of initial conditions (see Seidl et al., 2012; Seidl and Rammer, 2018).

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.08.034.

2.2.3. Model evaluation

Because iLand had not previously been used for our focal species in the Greater Yellowstone Ecosystem, we undertook a three-stage evaluation of iLand to assess the model's ability to simulate stand structural development in the region, including single-species, mixed-species, and model comparison assessments (Appendix B). The model appropriately characterized monospecific stand structural trajectories and variability, encompassing a majority of independent field observations over 300 years of stand development (Figs. B.1 and B.2); reproduced expected successional trajectories from bare ground to Douglas-fir, lodgepole pine, and spruce-fir forest types given appropriate seed source species composition and abiotic conditions (Fig. B.5); and responded consistently to variation in initial stem densities and environmental conditions with the forest growth model Forest Vegetation Simulator (FVS; Dixon, 2002; Crookston and Dixon, 2005) for at least 50 years of simulation (Figs. B.9–B.11). Overall, iLand performed well across multiple evaluations, supporting its use in studying the relative importance of factors influencing among-stand structural variability over hundreds of years of stand development in the Greater Yellowstone Ecosystem.

2.3. Initial conditions and drivers

We initialized model simulations using species-specific field data recorded in previously published studies of postfire regeneration following stand-replacing fires in the GYE (Table 1, Fig. 2; Donato et al., 2016; Harvey et al., 2016b; Turner et al., 2016). Individual trees (densities, diameters, and heights) and the number and height of sapling and seedling cohorts were initialized for each simulated 1-ha stand. Because our interest here was in long-term stand development once early postfire establishment had occurred, we began simulations with stands that were 10–25 years postfire (but see Hansen et al., 2018 for simulations of early postfire establishment).

For each postfire stand from the same published studies, we extracted daily historical (1980–2015) climate drivers (temperature, vapor pressure deficit, precipitation, and radiation) from Daymet Version 3 (Thornton et al., 2017) and soil depth and texture from CONUS-SOIL (Miller and White, 1998) using geographic coordinates of plot centers (Fig. 2). Available field plots for lodgepole pine regeneration were widely distributed across Yellowstone National Park. However, some field plots for Douglas-fir, Engelmann spruce, and subalpine fir stands were in close proximity, resulting in replicated climate conditions, and higher-elevation Engelmann spruce-subalpine fir climates were underrepresented. To adequately simulate expected ranges of abiotic variability for each species, we extracted additional climate and soil conditions in the GYE based on field-verified forest type (see Figs. 1 and 2; Simard et al., 2012). Soil relative fertility was held constant by species to control for inconsistent field data on soil substrate, and simulated stands were assigned a fertility value based on associations between species and soil parent material in this region (i.e., rhyolite parent material for lodgepole pine and andesite parent material for Douglas-fir, Engelmann spruce, and subalpine fir; Despain, 1990; Knight et al., 2014).

Initial conditions and drivers represented a wide range of early regeneration densities and abiotic conditions for each species (Table 1, Fig. 1). Initial stem densities varied by at least two and up to four orders of magnitude. All species spanned a range of at least 2.5 °C mean annual temperature, 240 mm mean annual precipitation, and 50 cm effective soil depth. Mean annual temperature and precipitation ranges in our climate data were also representative of the longer-term (starting as early as 1881 through 2012) historical climate record from weather stations throughout the GYE (WRCC, 2018).

2.4. Simulation experiment

We conducted a 2-by-2 factorial simulation experiment to assess the influence of two distinct drivers of among-stand structural variability, early regeneration densities or abiotic (climate plus soil depth and texture) conditions. All stands were either simulated with observed variation in postfire regeneration and abiotic conditions or with no among-stand variation, resulting in four scenarios (*Both vary, Abiotic varies, Regeneration varies, Neither varies*). A representative abiotic and early regeneration stand was derived for each species based on the central tendency of observed drivers (i.e., median soil depth and texture, climate period with median vapor pressure deficit, stand with median postfire regeneration stem density; Table 1, Fig. 1). For scenarios with no among-stand variation in abiotic conditions or in early regeneration, the respective representative stand conditions were assigned to all simulated stands for a given species. Abiotic conditions were randomly assigned to early postfire regeneration densities by species in the *Both vary* scenario.

For each scenario, we simulated postfire development of monospecific 1-ha stands for 300 years with no additional disturbance under historical climate conditions ($n = 20$ replicates per scenario). Climate year was randomly drawn with replacement from 1980 to 2015. Initial trees and saplings within a stand were the only seed source for subsequent tree recruitment.

2.5. Model outputs and analysis

Stand structure for each species was characterized using two metrics, stand density and stand basal area. Both metrics were calculated each year for trees > 4 m in height. The coefficient of variation (CV) was used to quantify variation in structure among stands of the same species and age (as in Kashian et al., 2005a, 2005b). As a relative estimate of variance, the CV enables comparisons among datasets with different means (Fraterrigo and Rusak, 2008). Because the coefficient of variation can be sensitive to low mean values, CVs were only calculated when mean stand density was ≥ 50 trees ha^{-1} and mean basal area was ≥ 2 m^2 ha^{-1} (5% of approximate stand density and basal area of a mature stand).

For each species and scenario, mean stand density, mean stand basal area, and mean CV (among the $n = 20$ replicates) were calculated for each year. We first assessed differences in stand structure convergence among species in the *Both vary* scenarios, in which both abiotic conditions and early regeneration densities varied among stands, based on when CV declined below 50% and when mean stand density peaked. Past studies in this region have documented convergence at CVs slightly below 50% (Kashian et al., 2005b). We next assessed similarities and differences among the four scenarios for each species. For *Abiotic varies* and *Regeneration varies* scenarios, we characterized time periods at

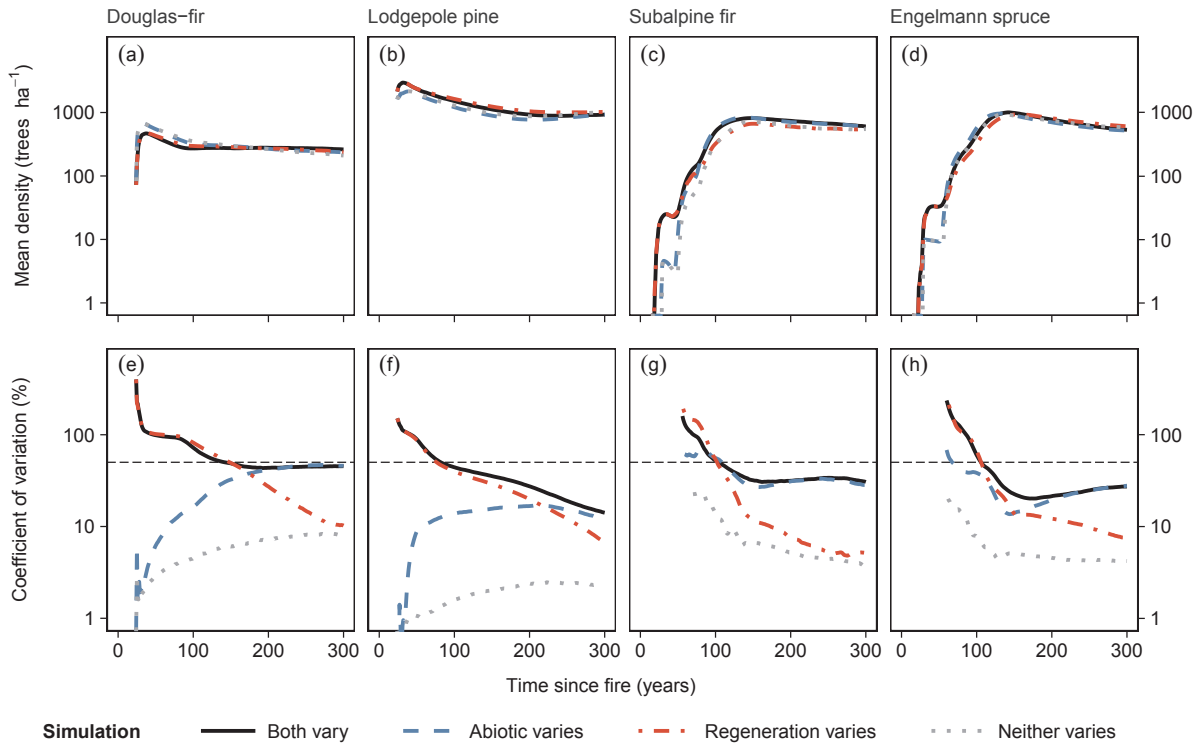

Fig. 3. (a-h) Mean stand density and mean among-stand density CV for the four simulation scenarios over 300 years of postfire stand development (n = 20 replicates of each). All metrics are for trees > 4 m in height. All vertical axes are on a log10 scale to facilitate comparison over time and among simulations. Convergence to CV = 50% is indicated by a dashed black line.

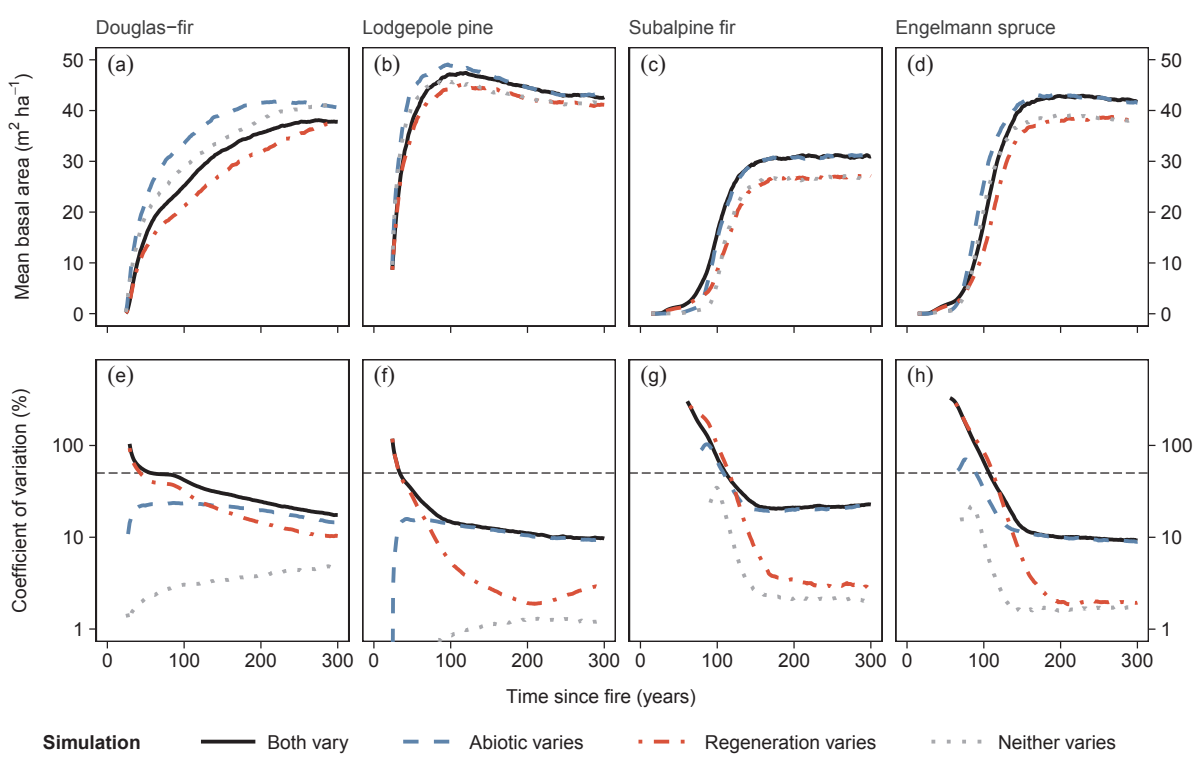

Fig. 4. (a–h) Mean stand basal area and mean among-stand basal area CV for the four simulation scenarios over 300 years of postfire stand development (n = 20 replicates of each). All metrics are for trees > 4 m in height. The vertical axis for CVs (e–h) is on a log10 scale to facilitate comparison over time and among simulations. Convergence to CV = 50% is indicated by a dashed black line.

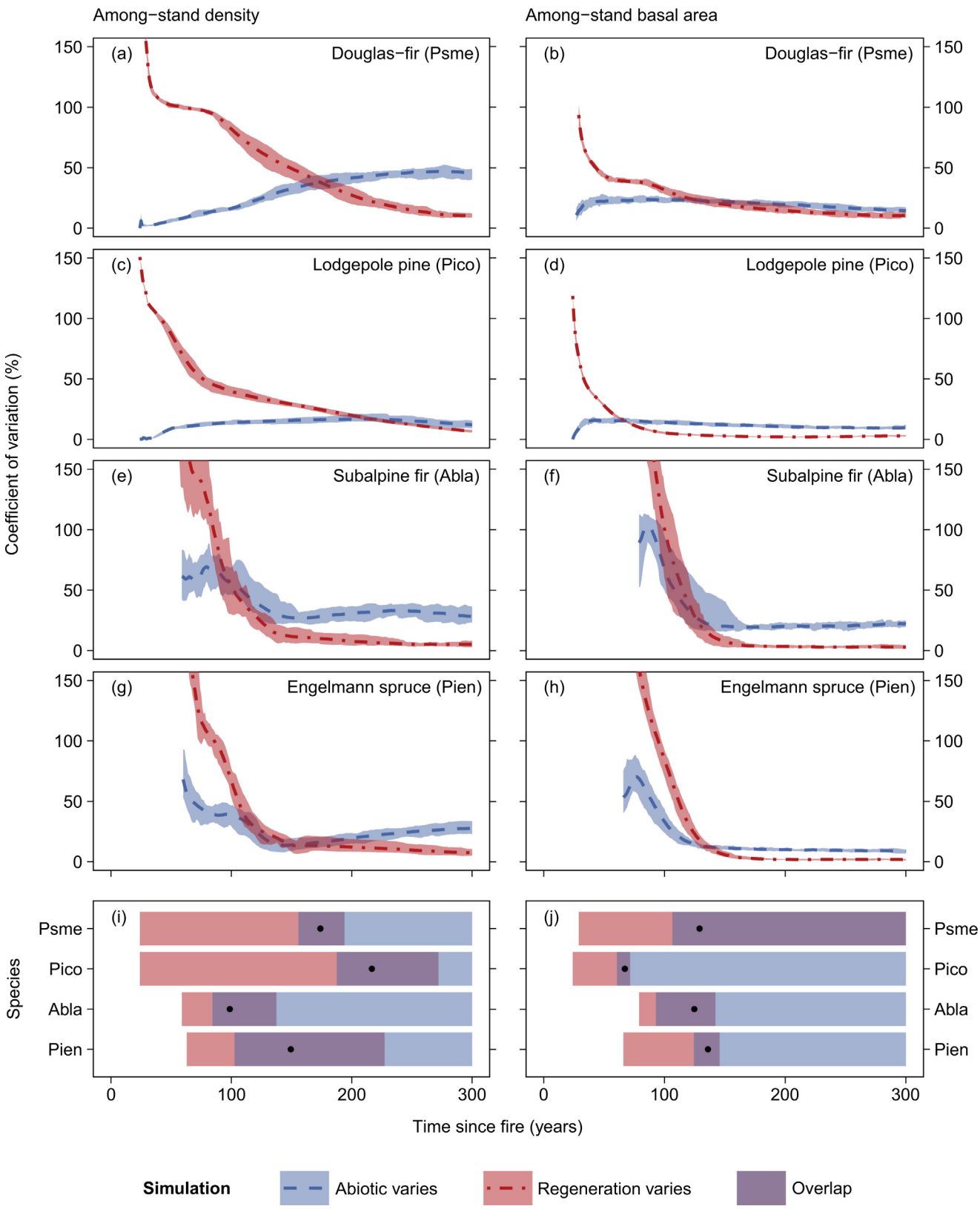

Fig. 5. (a–h) Ranges of CVs (min to max) across $n = 20$ replicates each of *Abiotic varies* and *Regeneration varies* scenarios. (i–j) Timeline plot for all four species, showing time since fire years when *Regeneration* CVs > *Abiotic* CVs (red), years when *Regeneration* and *Abiotic* CV ranges overlapped (purple), and years when *Abiotic* CVs > *Regeneration* CVs (blue). The range of *Regeneration varies* and *Abiotic varies* overlap encompasses the first to last point of overlap, and in some cases includes non-overlapping years. Points indicate the point of intersection of the mean trajectories for each species. Psme = Douglas-fir, Pico = lodgepole pine, Abla = subalpine fir, and Pien = Engelmann spruce.

which abiotic drivers versus early regeneration densities were more important in influencing among-stand variation using the point of intersection of mean CVs and the overlap of CV ranges (minimum to maximum CV across the 20 replicates). Trends among species were compared based on time since fire in years. R statistical software (R Core Team, 2017) was used for all analyses of model outputs.

3. Results

3.1. Variation and convergence in among-stand structural trajectories (Both vary scenario)

When stands varied both in their early postfire densities and their abiotic conditions (*Both vary* scenario), among-stand CVs for stand density and basal area were highest at or near the beginning of the simulation. Stands eventually converged in density (Fig. 3) and in basal area (Fig. 4), but the timing of convergence differed among species. Stand density converged most rapidly for lodgepole pine (mean among-stand density CV declined below 50% by 83 years postfire), followed by subalpine fir (105 years), Engelmann spruce (106 years), and Douglas-fir (143 years; Fig. 3). Mean stand density (trees > 4 m height) peaked earlier in stand development for both Douglas-fir (468 trees ha^{-1} at 37 years postfire) and lodgepole pine (2960 trees ha^{-1} at 31 years postfire) compared to subalpine fir and Engelmann spruce (817 trees ha^{-1} and 1005 trees ha^{-1} at 149 and 143 years postfire, respectively). At peak stand density, among-stand variation was greater for Douglas-fir and lodgepole pine (mean CV = 108% for Douglas-fir and 112% for lodgepole pine) than for subalpine fir (mean CV = 32%) or Engelmann spruce (mean CV = 24%). By 300 years postfire, among-stand variability in density had declined to ≤ 45% mean CV for all species.

Basal area converged more rapidly than stand density for Douglas-fir and lodgepole pine, with mean among-stand basal area CV falling below 50% by 58 and 34 years postfire, respectively (Fig. 4). However, basal area and stand density converged at similar times for subalpine fir and Engelmann spruce (mean CV declined below 50% by 111 and 107 years postfire, respectively). By 300 years postfire, among-stand variability in basal area had declined to a mean CV of ≤ 23% for all species.

3.2. Influence of early regeneration densities versus abiotic conditions on stand structural variability (among-scenario comparisons)

Trajectories of mean tree density were similar over time across the four scenarios (Fig. 3a-d), but trajectories of among-stand variation in density differed among scenarios and species (Fig. 3e-h). Early in stand development, mean CVs for stand density were similar when early regeneration densities and abiotic conditions both varied (*Both vary*) and when only regeneration densities varied (*Regeneration varies*), but mean CVs were much lower when only abiotic conditions varied (*Abiotic varies*). When only early regeneration densities varied, mean CVs declined over time as stand density converged, eventually reaching a value lower than the *Both vary* scenario. In contrast, when only abiotic conditions varied, mean CVs were initially lower but declined less rapidly and in some cases increased over time. By 300 years postfire, *Abiotic varies* and *Both vary* scenarios had similar mean CVs, both of which were greater than mean CVs for *Regeneration varies*.

For all species, early regeneration densities were the most important driver of among-stand variation in density early in stand development (when *Regeneration varies* scenarios had the highest mean CV), and abiotic drivers were most important later in stand development (when *Abiotic varies* scenarios had the highest mean CV). However, species differed in both the postfire year at which the most important driver switched from early regeneration densities to abiotic conditions (point of intersection between *Regeneration varies* and *Abiotic varies* scenarios in Fig. 5i-j) and in the time period during which both drivers similarly influenced among-stand variation (overlap in CV ranges across all $n = 20$ replicates per scenario; Fig. 5).

Variation in early postfire regeneration influenced among-stand variability in lodgepole pine density for a longer period of time than other species. Lodgepole pine *Abiotic* and *Regeneration varies* scenarios intersected at 217 years postfire (Fig. 5c). The point of intersection was earliest for subalpine fir stands (99 years postfire; Fig. 5e), followed by Engelmann spruce (149 years postfire; Fig. 5g) and Douglas-fir (174 years postfire; Fig. 5a).

Mean basal area also followed similar trajectories among all four scenarios (Fig. 4a-d), whereas among-stand variation in basal area differed among scenarios and species (Fig. 4e-h). In general, mean among-stand basal area variability behaved similarly to mean among-stand density variability over time for each of the four scenarios. Among-stand variation was initially high when only early regeneration densities varied (*Regeneration varies*) or when both regeneration and abiotic conditions varied (*Both vary*), but mean CV declined over time. When only abiotic conditions varied (*Abiotic varies*), among-stand variation was initially lower. However, the *Abiotic varies* mean CV equaled (point of intersection) and then surpassed the *Regeneration varies* mean CV over time.

The relative importance of abiotic conditions versus early regeneration densities as drivers of among-stand structural variability differed between basal area and density for a given species. For example, the point of intersection of mean CVs in *Abiotic* and *Regeneration varies* scenarios was earlier for basal area compared to stand density for all species except subalpine fir (Fig. 5i-j). Lodgepole pine had the earliest point of intersection (67 years postfire; Fig. 5d), and mean CVs for subalpine fir (Fig. 5f), Douglas-fir (Fig. 5b), and Engelmann spruce (Fig. 5h) intersected at similar times in stand development (125, 129, and 136 years postfire, respectively). For all species other than Douglas-fir, the overlap in CV ranges between *Abiotic* and *Regeneration varies* scenarios ended earlier compared to density (Fig. 5i-j). The ranges of Douglas-fir basal area CVs overlapped until the end of the simulation (300 years postfire).

4. Discussion

Here we show that variation in early postfire regeneration densities affects stand structural trajectories for decades to centuries for four widespread conifer species. Variation in early regeneration densities was particularly important in shaping long-term patterns of lodgepole pine stand densities. Among-stand structural variability was highest in young stands for all species, and stand structures converged with time since fire. Basal area converged more rapidly than stand density for Douglas-fir and lodgepole pine, but not for subalpine fir and Engelmann spruce. Differential responses among species correspond to variation in life history traits, growth rates, and sensitivity to intraspecific competition versus abiotic conditions. This study highlights the importance of understanding variability in early postfire regeneration and in young stand structures to anticipate future landscape patterns in ecosystems characterized by high-severity, infrequent disturbance regimes.

4.1. Variation and convergence in among-stand structural trajectories

Convergence of simulated stand density when both abiotic conditions and early regeneration varied (*Both vary* scenarios) is consistent with postfire chronosequence studies in this region (Kashian et al., 2005a, 2005b). Convergence occurs when initially dense stands undergo self-thinning as individual trees outcompete their neighbors (Peet, 1992), while establishment continues in sparser stands where light is available at the forest floor (Kashian et al., 2005b; Turner et al., 2016). Simultaneous self-thinning in some stands and infilling in others was evident early in simulations of both lodgepole pine and Douglas-fir. In field chronosequences, rapid declines in stand density (until 50 or 100 years postfire) and convergence have also been documented

(Kashian et al., 2005b). In contrast, prolonged time to convergence and self-thinning in simulated subalpine fir and Engelmann spruce stands may be related to slower initial growth of these species during seedling and sapling stages, as well as alleviated light competition due to smaller initial stem numbers and narrower crowns (Oosting and Reed, 1952; LeBarron and Jemison, 1953; Alexander, 1987; Purves et al., 2007).

Past studies of lodgepole pine stand development in the GYE indicate that basal area increment converges more rapidly than stem density (Kashian et al., 2005b), but this was not observed for all species in our simulations. Lodgepole pine trees in sparser stands can exhibit a compensatory growth response to lower densities (e.g., Copenhaver and Tinker, 2014) and therefore tend toward similar basal area as denser stands. However, continued establishment and growth of the more shade-tolerant subalpine fir and Engelmann spruce under low light conditions may enable convergence in stand density and basal area simultaneously.

4.2. Influence of early regeneration densities versus abiotic conditions on stand structural variability

Variation in early postfire regeneration densities was the most important driver of stand structural variability for at least 99 and up to 217 years, depending on the species. Over time, stands shifted from competition-driven convergence to environment-driven divergence, in which variability among stands was maintained or increased. This supports our expectation that variation in regeneration densities would drive variability among young stands, with variation in abiotic drivers becoming increasingly important as stands aged. As stands continue to age, it is also possible that processes such as mortality of trees from the first wave of postfire regeneration and continued infilling will contribute to homogenization of stand structures across different abiotic conditions later in stand development (as may be the case with subalpine fir and lodgepole pine in Fig. 3f,g). However, the long-lasting influence of early postfire regeneration is striking given the wide range of abiotic conditions. As fire frequency is likely to increase in the future (Westerling et al., 2011), the influence of variation in tree regeneration is also likely to increase relative to the effect of abiotic variation.

Our expectation that regeneration would influence stand structural variability of lodgepole pine for a longer period of time than other conifers was supported for density, highlighting the importance of species life history traits. Traits that favor abundant and rapid initial regeneration after fire, such as high prefire serotiny in lodgepole pine and rapid abscission schedule (e.g., jack pine; Greene et al., 2013), can have long-lasting effects on stand densities (Mason, 1915; Kashian et al., 2005b). Lodgepole pine also regenerates non-serotinously, but shading from an initial cohort may suppress subsequent regeneration and seedling growth (Lotan and Perry, 1983; Knight et al., 2014). Given smaller ranges of early postfire densities and prolonged periods of establishment and growth in the understory, species such as subalpine fir and Engelmann spruce may more rapidly overcome initial variation in regeneration. Of the three solely wind-dispersed species, subalpine fir is generally characterized as the most shade-tolerant and as a relatively prolific and regular seeder (Oosting and Reed, 1952; Alexander, 1987). Consistent with these traits, variation in early regeneration densities had the shortest influence on subalpine fir stand densities compared to Douglas-fir and Engelmann spruce.

In contrast, our expectation that regeneration would have a prolonged influence on lodgepole pine compared to other species was not supported for among-stand basal area. Differential growth rates and their sensitivity to environmental drivers and competition may explain differences among species. Lodgepole pine is relatively faster growing at young ages and radial growth increment is highly sensitive to crowding (Wykoff, 1990; Veblen et al., 1991; Buechling et al., 2017), resulting in accelerated growth of individual trees in sparser stands (Copenhaver and Tinker, 2014). Tree growth may also be enhanced given moderate annual precipitation (in the range of 600 to 900 mm yr^{-1}; Buechling et al., 2017), and growing conditions are more limited at the upper (shorter growing season) and lower (drier) treeline (Knight et al., 2014). Among the four species, Douglas-fir radial growth increment is least sensitive to crowding (Buechling et al., 2017), potentially maintaining variability in stand basal area due to early regeneration densities for a longer period of time than in other species.

4.3. Implications and limitations of our model-based approach

Modeling studies can inform management decisions by serving as a benchmark of the historical range of ecosystem responses to drivers that are expected to change in the future (Seidl et al., 2016b). For example, the results of this study could be used to evaluate whether the relative importance of the abiotic template in influencing stand structural variability increases in scenarios of future interannual climate variability. This, in turn, may indicate whether forests are likely to be characterized by divergent stand structural trajectories under changing climate as well as changing fire regimes. Process-based models that integrate emergent, fine-scale responses to environmental drivers are particularly well suited to explore long-term landscape trajectories under no-analog conditions (Cuddington et al., 2013; Gustafson, 2013; Grimm et al., 2017). These models are powerful tools for characterizing ecosystem patterns and processes, generating new or improved understanding of underlying mechanisms, and facilitating a synthetic approach with field-based experiments to understanding complex systems (Jenerette and Shen, 2012; Bowman et al., 2015; Cottingham et al., 2017; Grimm et al., 2017; Rastetter, 2017; Seidl, 2017). Future studies could employ process-based models to disentangle the relative influence of individual abiotic drivers.

For simulating variability in ecosystems, it must be noted that models are still likely to underestimate real-world environmental variation. Stand structural variability is probably higher among real stands compared to our simulations, which did not include covariation between high regeneration densities and favorable abiotic conditions (Schoennagel et al., 2003; Turner et al., 2004; Donato et al., 2016; Harvey et al., 2016b; Stevens-Rumann et al., 2018), subsequent disturbances (e.g., insect outbreaks; Antos and Parish, 2002), interspecific interactions, and seed supply from neighboring stands. In addition, stands may reburn prior to the 300 years of stand development simulated in this study. Historically, extensive portions of reburned forest in Yellowstone were at least 300 years old (Romme and Despain, 1989), and higher-elevation (> 2400 m) forests were characterized by approximately 300-year fire return intervals (Schoennagel et al., 2003). However, as warming climate continues to drive increasing fire activity (Westerling et al., 2006, 2011; Abatzoglou and Williams, 2016; Westerling, 2016), it is increasingly likely that younger stands will reburn.

4.4. Variability is important for anticipating forest landscape structure and function

Variability characterizes many post-disturbance systems (e.g., Kashian et al., 2005b; Suzuki et al., 2009) and has substantial implications for future forests, but remains understudied (Fraterrigo and Rusak, 2008). Assumptions that all stands have the same value of aboveground carbon storage may be inappropriate with increasing fire activity and therefore increasing extent of young, structurally variable forest (Kashian et al., 2006, 2013). When variability is high, mean estimates of stand structure may be increasingly inaccurate predictors of ecosystem patterns and processes (Cottingham et al., 2000; Fraterrigo and Rusak, 2008), particularly if relationships between drivers and responses are nonlinear and interact across scales (Lovett et al., 2005; Peters et al., 2007). Increased forest landscape heterogeneity could also dampen the spread or severity of future disturbances (Bebi et al., 2003; Kulakowski and Veblen, 2007; Seidl et al., 2016a).

For forests adapted to high-severity, infrequent fire regimes,

understanding causes and patterns of variation in early postfire regeneration appears critically important for anticipating long-term landscape variability. Early postfire regeneration (within the first two decades) affected structural trajectories of four widespread conifer species for decades to centuries in stands across a wide gradient of environmental conditions. Regeneration processes, such as seed supply, dispersal, establishment, and early seedling survival, are often highly sensitive to changes in disturbance regimes and environmental fluctuations (Kipfmueller and Kupfer, 2005; Larson and Kipfmueller, 2010; Harvey et al., 2016b; Kemp et al., 2016; Hansen et al., 2018; Stevens-Rumann et al., 2018). Early regeneration densities may forecast long-term trajectories in ecosystems that experience periodic high-severity disturbances (Turner et al., 1998), although it may be necessary to consider more than just the first few years of establishment (e.g., Peterson and Pickett, 1995; Gill et al., 2017). Ongoing research on the effects of changing climate, disturbance regimes, and other drivers of variation in early postfire regeneration is needed to anticipate future forest landscape patterns.

Acknowledgements

KHB, RS, and MGT designed the study; KHB parameterized and evaluated the model in consultation with RS, WR, WDH, and MGT; RS and WR provided model code and ongoing development; KHB performed simulations and analyzed data; KHB and MGT wrote manuscript, and all authors contributed. We thank Anthony Ives, Chris Kucharik, Zak Ratajczak, and two anonymous reviewers for providing constructive feedback that greatly improved this paper. This research was funded by the Joint Fire Science Program (Project No. 16-3-01-4) and the University of Wisconsin-Madison Vilas Trust. KHB also acknowledges support from a University of Wisconsin-Madison Integrative Biology Department first-year fellowship. RS and WR acknowledge support from the Austrian Science Fund through START grant Y895-B25.

Data availability statement

The model output data that support the findings of this study and files to recreate model simulations are openly available in the Environmental Data Initiative (EDI) at DOI https://doi.org/10.6073/pasta/152ed98663904892d9d11903949cadb7.

References

Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. 113, 11770–11775. https://doi.org/10.1073/pnas.1607171113.

Alexander, R.R., 1987. Ecology, silviculture, and management of the Engelmann spruce - subalpine fir type in the central and southern Rocky Mountains. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Agriculture Handbook No. 659, Fort Collins, CO.

Antos, J.A., Parish, R., 2002. Dynamics of an old-growth, fire-initiated, subalpine forest in southern interior British Columbia: Tree size, age, and spatial structure. Can. J. For. Res. 32, 1935–1946. https://doi.org/10.1139/x02-116.

Aplet, G.H., Laven, R.D., Smith, F.W., 1988. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. Ecology 69, 312–319. https://doi.org/10.2307/1940429.

Baker, W.L., 2009. Fire ecology in Rocky Mountain landscapes. Island Press, Washington, DC.

Baker, W.L., Veblen, T.T., Sherriff, R.L., 2007. Fire, fuels and restoration of ponderosa pine-Douglas fir forests in the Rocky Mountains USA. J. Biogeogr. 34, 251–269. https://doi.org/10.1111/j.1365-2699.2006.01592.x.

Bebi, P., Kulakowski, D., Veblen, T.T., 2003. Interactions between fire and spruce beetles in a subalpine rocky mountain forest landscape. Ecology 84, 362–371. https://doi.org/10.1890/0012-9658(2003) 084[0362:IBFASB]2.0.CO;2.

Bowman, D.M.J.S., Perry, G.L.W., Marston, J.B., 2015. Feedbacks and landscape-level vegetation dynamics. Trends Ecol. Evol. 30, 255–260. https://doi.org/10.1016/j.tree.2015.03.005.

Bradford, J.B., Birdsey, R.A., Joyce, L.A., Ryan, M.G., 2008. Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests. Glob. Chang. Biol. 14, 2882–2897. https://doi.org/10.1111/j.1365-2486.2008.01686.x.

Buechling, A., Martin, P.H., Canham, C.D., 2017. Climate and competition effects on tree growth in Rocky Mountain forests. J. Ecol. 105, 1636–1647. https://doi.org/10.1111/1365-2745.12782.

Buma, B., Brown, C.D., Donato, D.C., Fontaine, J.B., Johnstone, J.F., 2013. The impacts of changing disturbance regimes on serotinous plant populations and communities. Bioscience 63, 866–876. https://doi.org/10.1525/bio.2013.63.11.5.

Copenhaver, P.E., Tinker, D.B., 2014. Stand density and age affect tree-level structural and functional characteristics of young, postfire lodgepole pine in Yellowstone National Park. For. Ecol. Manage. 320, 138–148. https://doi.org/10.1016/j.foreco.2014.03.024.

Cottingham, K.L., Rusak, J.A., Leavitt, P.R., 2000. Increased ecosystem variability and reduced predictability following fertilisation: Evidence from palaeolimnology. Ecol. Lett. 3, 340–348. https://doi.org/10.1046/j.1461-0248.2000.00158.x.

Cottingham, K.L., Fey, S.B., Fritschie, K.J., Trout-Haney, J.V., 2017. Advancing ecosystem science by promoting greater use of theory and multiple research approaches in graduate education. Ecosystems 20, 267–273. https://doi.org/10.1007/s10021-016-0070-3.

Crookston, N.L., Dixon, G.E., 2005. The forest vegetation simulator: A review of its structure, content, and applications. Comput. Electron. Agric. 49, 60–80. https://doi.org/10.1016/j.compag.2005.02.003.

Crossley, D.I., 1956. Fruiting habits of lodgepole pine. Canada Department of Northern Affairs and National Resources, Forestry Branch, Forest Research Division, Technical Note No. 35, Ottawa, Ont.

Cuddington, K., Fortin, M.J., Gerber, L.R., Hastings, A., Liebhold, A., O'Connor, M., Ray, C., 2013. Process-based models are required to manage ecological systems in a changing world. Ecosphere 4, 20. https://doi.org/10.1890/ES12-00178.1.

Despain, D.G., 1990. Yellowstone vegetation: Consequences of environment and history in a natural setting. Roberts Rinehart, Boulder, CO.

Dixon, G.E., 2002. Essential FVS: A user's guide to the Forest Vegetation Simulator. USDA Forest Service, Forest Management Service Center, Fort Collins, CO.

Donato, D.C., Harvey, B.J., Turner, M.G., 2016. Regeneration of montane forests a quarter-century after the 1988 Yellowstone Fires: A fire-catalyzed shift in lower treelines? Ecosphere 7, e01410. https://doi.org/10.1002/ecs2.1410.

Douglas, R.B., Parker, V.T., Cullings, K.W., 2005. Belowground ectomycorrhizal community structure of mature lodgepole pine and mixed conifer stands in Yellowstone National Park. For. Ecol. Manage. 208, 303–317. https://doi.org/10.1016/j.foreco.2004.12.011.

Edwards, M., Krawchuk, M.A., Burton, P.J., 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire. For. Ecol. Manage. 338, 163–175. https://doi.org/10.1016/j.foreco.2014.11.011.

Foster, D.R., Knight, D.H., Franklin, J.F., 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems 1, 497–510. https://doi.org/10.1007/s100219900046.

Fraterrigo, J.M., Rusak, J.A., 2008. Disturbance-driven changes in the variability of ecological patterns and processes. Ecol. Lett. 11, 756–770. https://doi.org/10.1111/j.1461-0248.2008.01191.x.

Gill, N.S., Jarvis, D., Veblen, T.T., Pickett, S.T.A., Kulakowski, D., 2017. Is initial post-disturbance regeneration indicative of longer-term trajectories? Ecosphere 8, e01924. https://doi.org/10.1002/ecs2.1924.

Glenn-Lewin, D.C., van der Maarel, E., 1992. Patterns and processes of vegetation dynamics. In: Glenn-Lewin, D.C., Peet, R.K., Veblen, T.T. (Eds.), Plant Succession: Theory and Prediction. Chapman & Hall, London, UK, pp. 11–59.

Greene, D.F., Splawinski, T.B., Gauthier, S., Bergeron, Y., 2013. Seed abscission schedules and the timing of post-fire salvage of Picea mariana and Pinus banksiana. For. Ecol. Manage. 303, 20–24. https://doi.org/10.1016/j.foreco.2013.03.049.

Grimm, V., Ayllón, D., Railsback, S.F., 2017. Next-generation individual-based models integrate biodiversity and ecosystems: Yes we can, and yes we must. Ecosystems 20, 229–236. https://doi.org/10.1007/s10021-016-0071-2.

Gustafson, E.J., 2013. When relationships estimated in the past cannot be used to predict the future: Using mechanistic models to predict landscape ecological dynamics in a changing world. Landsc. Ecol. 28, 1429–1437. https://doi.org/10.1007/s10980-013-9927-4.

Hansen, W.D., Braziunas, K.H., Rammer, W., Seidl, R., Turner, M.G., 2018. It takes a few to tango: Changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99, 966–977. https://doi.org/10.1002/ecy.2181.

Harvey, B.J., Donato, D.C., Turner, M.G., 2016a. Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984–2010). Landsc. Ecol. 31, 2367–2383. https://doi.org/10.1007/s10980-016-0408-4.

Harvey, B.J., Donato, D.C., Turner, M.G., 2016b. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob. Ecol. Biogeogr. 25, 655–669. https://doi.org/10.1111/geb.12443.

Higuera, P.E., Whitlock, C., Gage, J.A., 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. Holocene 21, 327–341. https://doi.org/10.1177/0959683610374882.

Jenerette, G.D., Shen, W., 2012. Experimental landscape ecology. Landsc. Ecol. 27, 1237–1248. https://doi.org/10.1007/s10980-012-9797-1.

Kashian, D.M., Turner, M.G., Romme, W.H., 2005a. Variability in leaf area and stemwood increment along a 300-year lodgepole pine chronosequence. Ecosystems 8, 48–61. https://doi.org/10.1007/s10021-004-0067-1.

Kashian, D.M., Turner, M.G., Romme, W.H., Lorimer, C.G., 2005b. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. Ecology 86, 643–654. https://doi.org/10.1890/03-0828.

Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., Ryan, M.G., 2006. Carbon storage on landscapes with stand-replacing fires. Bioscience 56, 598. https://doi.org/

10.1641/0006-3568(2006) 56[598:CSOLWS]2.0.CO;2.
Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta-dominated forests. Ecol. Monogr. 83, 49–66. https://doi.org/10.1890/11-1454.1.
Kemp, K.B., Higuera, P.E., Morgan, P., 2016. Fire legacies impact conifer regeneration across environmental gradients in the US Northern Rockies. Landsc. Ecol. 31, 619–636. https://doi.org/10.1007/s10980-015-0268-3.
Kipfmueller, K.F., Kupfer, J.A., 2005. Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area. Ann. Assoc. Am. Geogr. 95, 495–510. https://doi.org/10.1111/j.1467-8306.2005.00471.x.
Knight, D.H., Jones, G.P., Reiners, W.A., Romme, W.H., 2014. Mountains and plains: The ecology of Wyoming landscapes, Second edition. Yale University Press, New Haven, CT.
Korzukhin, M.D., Ter-Mikaelian, M.T., Wagner, R.G., 1996. Process versus empirical models: Which approach for forest ecosystem management? Can. J. For. Res. 26, 879–887.
Kulakowski, D., Veblen, T.T., 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88, 759–769. https://doi.org/10.1890/06-0124.
Larson, E.R., Kipfmueller, K.F., 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon USA. Can. J. For. Res. 40, 476–487. https://doi.org/10.1139/X10-005.
LeBarron, R.K., Jemison, G.M., 1953. Ecology and silviculture of the Engelmann spruce-alpine fir type. J. For. 51, 349–352.
Litton, C.M., Ryan, M.G., Knight, D.H., 2004. Effects of tree density and stand age on carbon allocation patters in postfire lodgepole pine. Ecol. Appl. 14, 460–516. https://doi.org/10.1890/02-5291.
Lotan, J., Perry, D., 1983. Ecology and regeneration of lodgepole pine. USDA Forest Service Agriculture Handbook 606, Washington, DC.
Lovett, G.M., Jones, C.G., Turner, M.G., Weathers, K.C., 2005. Conceptual frameworks: Plan for a half-built house. In: Lovett, G.M., Jones, C.G., Turner, M.G., Weathers, K.C. (Eds.), Ecosystem Function in Heterogeneous Landscapes. Springer, New York, NY, pp. 463–470.
Mason, D.T., 1915. The life history of lodgepole pine in the Rocky Mountains. USDA Bulletin 154, Washington, DC.
Meigs, G.W., Morrissey, R.C., Bače, R., Chaskovskyy, O., Čada, V., Després, T., Donato, D.C., Janda, P., Lábusová, J., Seedre, M., Mikoláš, M., Nagel, T.A., Schurman, J.S., Synek, M., Teodosiu, M., Trotsiuk, V., Vítková, L., Svoboda, M., 2017. More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. For. Ecol. Manage. 406, 410–426. https://doi.org/10.1016/j.foreco.2017.07.051.
Miller, D.A., White, R.A., 1998. A conterminous United States multilayer soil characteristics dataset for regional climate and hydrology modeling. Earth Interact. 2, 1–26. https://doi.org/10.1175/1087-3562(1998) 002<0001:ACUSMS>2.3.CO;2.
Millspaugh, S.H., Whitlock, C., Bartlein, P.J., Wallace, L.L., 2004. Postglacial fire, vegetation, and climate history of the Yellowstone-Lamar and Central Plateau provinces, Yellowstone National Park. In: Wallace, L.L. (Ed.), After the Fires: The Ecology of Change in Yellowstone National Park. Yale University Press, New Haven, Connecticut, USA, pp. 10–28.
Oosting, H.J., Reed, J.F., 1952. Virgin spruce-fir of the Medicine Bow Mountains Wyoming. Ecol. Monogr. 22, 69–91.
Peet, R.K., 1992. Community structure and ecosystem function. In: Glenn-Lewin, D.C., Peet, R.K., Veblen, T.T. (Eds.), Plant Succession: Theory and Prediction. Chapman & Hall, London, UK, pp. 103–151.
Peters, D.P.C., Bestelmeyer, B.T., Turner, M.G., 2007. Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. Ecosystems 10, 790–796. https://doi.org/10.1007/s10021-007-9055-6.
Peterson, C.J., Pickett, S.T.A., 1995. Forest reorganization: A case study in an old-growth forest catastrophic blowdown. Ecology 76, 763–774. https://doi.org/10.2307/1939342.
Pinno, B.D., Errington, R.C., Thompson, D.K., 2013. Young jack pine and high severity fire combine to create potentially expansive areas of understocked forest. For. Ecol. Manage. 310, 517–522. https://doi.org/10.1016/j.foreco.2013.08.055.
Purves, D.W., Lichstein, J.W., Pacala, S.W., 2007. Crown plasticity and competition for canopy space: A new spatially implicit model parameterized for 250 North American tree species. PLoS One 2, e870. https://doi.org/10.1371/journal.pone.0000870.
Core Team, R., 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rastetter, E.B., 2017. Modeling for understanding v. modeling for numbers. Ecosystems 20, 215–221. https://doi.org/10.1007/s10021-016-0067-y.
Reyer, C.P.O., Rammig, A., Brouwers, N., Langerwisch, F., 2015. Forest resilience, tipping points and global change processes. J. Ecol. 103, 1–4. https://doi.org/10.1111/1365-2745.12342.
Rodman, A., Shovic, H.F., Thoma, D.P., 1996. Soils of Yellowstone National Park. Yellowstone Center for Resources, YCR-NRSR-96-2, Yellowstone National Park, WY.
Romme, W., 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monogr. 52, 199–221. https://doi.org/10.2307/1942611.
Romme, W.H., Despain, D.G., 1989. Historical perspective on the yellowstone fires of 1988. Bioscience 39, 695–699. https://doi.org/10.2307/1311000.
Schoennagel, T., Turner, M.G., Romme, W.H., 2003. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. Ecology 84, 2967–2978. https://doi.org/10.1890/02-0277.
Schoennagel, T., Veblen, T.T., Romme, W.H., 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. Bioscience 54, 661. https://doi.org/10.1641/0006-3568(2004) 054[0661:TIOFFA]2.0.CO;2.
Scholes, R.J., 2017. Taking the mumbo out of the jumbo: Progress towards a robust basis for ecological scaling. Ecosystems 20, 4–13. https://doi.org/10.1007/s10021-016-0047-2.
Seidl, R., 2017. To model or not to model, that is no longer the question for ecologists. Ecosystems 20, 222–228. https://doi.org/10.1007/s10021-016-0068-x.
Seidl, R., Rammer, W., 2018. iLand online model documentation [WWW Document]. URL http://iland.boku.ac.at (accessed 12.29.17).
Seidl, R., Rammer, W., Scheller, R.M., Spies, T.A., 2012. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. Ecol. Modell. 231, 87–100. https://doi.org/10.1016/j.ecolmodel.2012.02.015.
Seidl, R., Rammer, W., Blennow, K., 2014a. Simulating wind disturbance impacts on forest landscapes: Tree-level heterogeneity matters. Environ. Model. Softw. 51, 1–11. https://doi.org/10.1016/j.envsoft.2013.09.018.
Seidl, R., Rammer, W., Spies, T.A., 2014b. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecol. Appl. 24, 2063–2077. https://doi.org/10.1890/14-0255.1.
Seidl, R., Donato, D.C., Raffa, K.F., Turner, M.G., 2016a. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. Proc. Natl. Acad. Sci. 113, 13075–13080. https://doi.org/10.1073/pnas.1615263113.
Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hicke, J.A., 2016b. Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. J. Appl. Ecol. 53, 120–129. https://doi.org/10.1111/1365-2664.12511.
Silva Pedro, M., Rammer, W., Seidl, R., 2015. Tree species diversity mitigates disturbance impacts on the forest carbon cycle. Oecologia 177, 619–630. https://doi.org/10.1007/s00442-014-3150-0.
Simard, M., Powell, E.N., Raffa, K.F., Turner, M.G., 2012. What explains landscape patterns of tree mortality caused by bark beetle outbreaks in Greater Yellowstone? Glob. Ecol. Biogeogr. 21, 556–567. https://doi.org/10.1111/j.1466-8238.2011.00710.x.
Smithwick, E.A.H., Kashian, D.M., Ryan, M.G., Turner, M.G., 2009a. Long-term nitrogen storage and soil nitrogen availability in post-fire lodgepole pine ecosystems. Ecosystems 12, 792–806. https://doi.org/10.1007/s10021-009-9257-1.
Smithwick, E.A.H., Ryan, M.G., Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., 2009b. Modeling the effects of fire and climate change on carbon and nitrogen storage in lodgepole pine (Pinus contorta) stands. Glob. Chang. Biol. 15, 535–548. https://doi.org/10.1111/j.1365-2486.2008.01659.x.
Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D.C., Morgan, P., Veblen, T.T., 2018. Evidence for declining forest resilience to wildfires under climate change. Ecol. Lett. 21, 243–252. https://doi.org/10.1111/ele.12889.
Suzuki, S.N., Kachi, N., Suzuki, J.I., 2009. Changes in variance components of forest structure along a chronosequence in a wave-regenerated forest. Ecol. Res. 24, 1371–1379. https://doi.org/10.1007/s11284-009-0621-6.
Tepley, A.J., Swanson, F.J., Spies, T.A., 2013. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. Ecology 94, 1729–1743. https://doi.org/10.1890/12-1506.1.
Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. J. Biogeogr. 31, 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x.
Thom, D., Rammer, W., Dirnböck, T., Müller, J., Kobler, J., Katzensteiner, K., Helm, N., Seidl, R., 2017. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. J. Appl. Ecol. 54, 28–38. https://doi.org/10.1111/1365-2664.12644.
Thornton, P.E., Thornton, M.M., Mayer, B.W., Wei, Y., Devarakonda, R., Vose, R.S., Cook, R.B., 2017. Daymet: Daily surface weather data on a 1-km grid for North America, Version 3. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ORNLDAAC/1328.
Tinker, D.B., Romme, W.H., Hargrove, W.W., Gardner, R.H., Turner, M.G., 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Can. J. For. Res. 24, 897–903. https://doi.org/10.1139/x94-118.
Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833–2849. https://doi.org/10.1890/10-0097.1.
Turner, M.G., Romme, W.H., 1994. Landscape dynamics in crown fires ecosystems. Landsc. Ecol. 9, 59–77. https://doi.org/10.1007/BF00135079.
Turner, M.G., Hargrove, W.W., Gardner, R.H., Romme, W.H., 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park. Wyoming. J. Veg. Sci. 5, 731–742. https://doi.org/10.2307/3235886.
Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, W.W., 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol. Monogr. 67, 411–433. https://doi.org/10.1890/0012-9615(1997) 067[0411:EOFSAP]2.0.CO;2.
Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems 1, 511–523. https://doi.org/10.1007/s100219900047.
Turner, M.G., Romme, W.H., Gardner, R.H., 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park Wyoming. Int. J. Wildl. Fire 9, 21–36. https://doi.org/10.1071/WF99003.
Turner, M.G., Tinker, D.B., Romme, W.H., Kashian, D.M., Litton, C.M., 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7, 751–775. https://doi.org/10.1007/s10021-004-0011-4.
Turner, M.G., Smithwick, E.A., Metzger, K.L., Tinker, D.B., Romme, W.H., 2007. Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. Proc. Natl. Acad. Sci. USA 104, 4782–4789. https://doi.org/10.1073/pnas.0700180104.
Turner, M.G., Smithwick, E.A.H., Tinker, D.B., Romme, W.H., 2009. Variation in foliar nitrogen and aboveground net primary production in young postfire lodgepole pine.

Can. J. For. Res. 39, 1024–1035. https://doi.org/10.1139/X09-029.
Turner, M.G., Whitby, T.G., Tinker, D.B., Romme, W.H., 2016. Twenty-four years after the Yellowstone fires: Are postfire lodgepole pine stands converging in structure and function? Ecology 97, 1260–1273. https://doi.org/10.1890/15-1585.1.
Veblen, T.T., 1986. Age and size structure of subalpine forests in the Colorado Front Range. Bull. Torrey Bot. Club 113, 225. https://doi.org/10.2307/2996361.
Veblen, T.T., Hadley, K.S., Reid, M.S., 1991. Disturbance and stand development of a Colorado subalpine forest. J. Biogeogr. 18, 707–716. https://doi.org/10.2307/2845552.
Walker, L.R., del Moral, R., 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press, New York, NY.
Westerling, A.L., 2016. Increasing western US forest wildfire activity: Sensitivity to changes in the timing of spring. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150178. https://doi.org/10.1098/rstb.2015.0178.
Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase Western U.S. forest wildfire activity. Science 313, 940–943. https://doi.org/10.1126/science.1128834.
Westerling, A.L., Turner, M.G., Smithwick, E.A.H., Romme, W.H., Ryan, M.G., 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proc. Natl. Acad. Sci. 108, 13165–13170. https://doi.org/10.1073/pnas.1110199108.
Western Regional Climate Center (WRCC), 2018. Cooperative climatological data summaries: NOAA cooperative stations - temperature and precipitation. Stations 482375, 485115, 485345, 485355, 486440, 486845, 488315, 489025, and 489905. [WWW Document]. URL https://wrcc.dri.edu/Climate/west_coop_summaries.php (accessed 8.14.18).
Whitlock, C., 1993. Postglacial vegetation and climate of Grand Teton and southern Yellowstone National Parks. Ecol. Monogr. 63, 173–198. https://doi.org/10.2307/2937179.
Whitlock, C., Marlon, J., Briles, C., Brunelle, A., Long, C., Bartlein, P., 2008. Long-term relations among fire, fuel, and climate in the north-western US based on lake-sediment studies. Int. J. Wildl. Fire 17, 72–83. https://doi.org/10.1071/WF07025.
Wykoff, W.R., 1990. A basal area increment model for individual conifers in the Northern Rocky Mountains. For. Sci. 36, 1077–1104.
Yellowstone National Park (YNP), 2017. Yellowstone resources and issues handbook: 2017. Yellowstone National Park, WY.

Appendices

Looking beyond the mean:

Drivers of variability in postfire stand development of conifers in Greater Yellowstone

Kristin H. Braziunas, Winslow D. Hansen, Rupert Seidl, Werner Rammer, and Monica G. Turner

Appendix A. Parameters

We parameterized iLand for four widespread conifer species in the Greater Yellowstone Ecosystem (GYE): Lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). The majority of species-specific parameters were sourced from peer-reviewed literature and government reports. A few parameters (e.g., height-to-diameter ratios, aging) were fit or iteratively derived by simulating stand development of initial conditions (see Seidl et al., 2012 and Seidl and Rammer, 2018). Species parameters are reported in Table A.1. Regional, non-species-specific model parameters for the GYE, such as atmospheric CO_2 concentration, are reported in Table A.2. Extensive model documentation and parameter descriptions are available at http://iland.boku.ac.at/, and a sensitivity analysis of species parameters was performed by Seidl et al. (2012).

Some lodgepole pine trees produce serotinous cones (closed cones that retain seeds and only open in response to elevated temperatures, such as those experienced during fire), while others only produce cones that are non-serotinous and open at maturity (Tinker et al., 1994). To capture the resulting differences in postfire regeneration, serotinous and non-serotinous

lodgepole pine were simulated as two separate "species," and parameters for serotinous lodgepole pine were derived by Hansen et al. (2018).

References Appendix A

Hansen, W.D., Braziunas, K.H., Rammer, W., Seidl, R., Turner, M.G., 2018. It takes a few to tango: Changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99, 966–977. https://doi.org/10.1002/ecy.2181

Seidl, R., Rammer, W., 2018. iLand online model documentation [WWW Document]. URL http://iland.boku.ac.at (accessed 12.29.17).

Seidl, R., Rammer, W., Scheller, R.M., Spies, T.A., 2012. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. Ecol. Modell. 231, 87–100. https://doi.org/10.1016/j.ecolmodel.2012.02.015

Tinker, D.B., Romme, W.H., Hargrove, W.W., Gardner, R.H., Turner, M.G., 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Can. J. For. Res. 24, 897–903. https://doi.org/10.1139/x94-118

Table A.1. Species-specific parameters for conifers in the Greater Yellowstone Ecosystem. Abla = *Abies lasiocarpa*, Pico = *Pinus contorta* var. *latifolia* (non-serotinous), PicS = *Pinus contorta* var. *latifolia* (serotinous), Pien = *Picea engelmannii*, and Psme = *Pseudotsuga menziesii* var. *glauca*, dim = dimensionless, exp = expression, sdlings = seedlings. Parameters are fully described in Seidl and Rammer (2018).

Parameter	Unit	Source	Abla	Pico	PicS	Pien	Psme
Tree growth							
Specific leaf area	$m^2\ kg^{-1}$	1–4	4.4	4.6	4.6	5.0	5.8
Leaf turnover	$year^{-1}$	5,6	0.14	0.33	0.33	0.17	0.20
Root turnover	$year^{-1}$	3	0.33	0.33	0.33	0.33	0.33
Height to diameter low a	dim	6–12,71	33.80	38.51	38.51	29.79	44.37
Height to diameter low b	dim	6–12,71	-0.101	-0.126	-0.126	-0.0752	-0.131
Height to diameter high a	dim	6–12,71	169.39	287.99	287.99	188.96	439.47
Height to diameter high b	dim	6–12,71	-0.249	-0.288	-0.288	-0.245	-0.476
Wood density	$kg\ m^{-3}$	6	309	380	380	330	450
Form factor	dim[0,1]	13–16	0.466	0.470	0.470	0.469	0.453
Biomass allocation							
Stem wood biomass a	*	17–21	0.04687	0.1401	0.1401	0.2462	0.04510
Stem wood biomass b	*	17–21	2.527	2.136	2.136	2.049	2.634
Stem foliage biomass a	*	19,21–23	0.3894	0.02723	0.02723	0.02860	0.3021
Stem foliage biomass b	*	19,21–23	1.231	1.882	1.882	2.010	1.308
Root biomass a	*	10,24	0.02327	0.021	0.021	0.01135	0.02002
Root biomass b	*	10,24	2.313	2.281	2.281	2.522	2.450
Branch biomass a	*	19,21–23	0.1926	0.01903	0.01903	0.05266	0.2624
Branch biomass b	*	19,21–23	1.571	2.120	2.120	2.060	1.546
Mortality							
Probability of survival to max age (intrinsic mortality)	dim[0,1]	25,71	0.10	0.10	0.10	0.10	0.20
Stress-related mortality	dim	3,71	1.0	1.0	1.0	1.0	1.0
Aging							
Max age	years	26–28,71	300	500	500	600	400
Max height	m	26,27,29	42	41	41	55	57
Aging a	dim	30,71	0.75	0.50	0.50	0.75	0.60
Aging b	dim	30,71	2.50	2.50	2.50	2.50	4.50
Environmental responses							
Vapor pressure deficit response	dim	3	-0.65	-0.65	-0.65	-0.65	-0.65
Min temperature	°C	3,31–34,71	-4.0	-6.0	-6.0	-6.0	-6.0

Table A.1, cont.

Parameter	Unit	Source	Abla	Pico	PicS	Pien	Psme
Environmental responses (cont.)							
Optimum temperature	°C	3,31–34,71	19.0	17.0	17.0	17.0	17.0
Nitrogen class	dim[1,3]	35,36,71	2.5	1.0	1.0	2.5	1.5
Phenology	int[0,2]	29	0	0	0	0	0
Max canopy conductance	m s^{-1}	3	0.017	0.017	0.017	0.017	0.017
Min soil water potential	MPa	27,37,38, 71	-1.91	-2.0	-2.0	-1.78	-2.40
Light response	dim[1,5]	27,71	4.5	2.0	2.0	4.0	2.5
Fine root to foliage ratio	dim[0,1]	39,71	0.75	0.75	0.75	0.75	0.75
Seed production and dispersal							
Cone bearing age	years	26,27,29, 40,71	25	15	15	25	55
Seed year interval	years	26,29, 41–47,71	4	1	1	5	5
Non-seed year fraction	dim[0,1]	26,29, 41–47,71	0.25	0	0	0.1	0.24
Seed mass	mg	29,33,42	13.03	4.1	4.1	3.37	11.31
Germination rate	dim[0,1]	47–52,71	0.229	0.36	0.36	0.114	0.30
Fecundity	sdlings m^{-2}	51,53,71	30.0	115.9	115.9	42.8	43.9
Seed kernel a	m	29,54–58	19	6	6	19	30
Seed kernel b	m	29,54–58	110	160	160	110	200
Seed kernel c	dim[0,1]	29,54–58	0.2	0.05	0.05	0.2	0.2
Establishment							
Min temperature	°C	59	-67	-85	-85	-45	-37
Chill requirement	days	59	60	63	63	49	56
Min growing degree days	degree days	59	198	186	186	74	340
Max growing degree days	degree days	59	5444	3374	3374	1911	3261
Growing degree days base temperature	°C	59	2.6	2.9	2.9	3.1	3.4
Growing degree days before bud burst	degree days	59	119	116	116	145	255
Frost free days	days	59	95	80	80	30	100
Frost tolerance	dim[0,1]	59	0.9	0.9	0.9	0.9	0.5
Min soil water potential	MPa	55,60,61, 71	-2.5	-2.3	-2.3	-2	-7
Sapling growth							
Sapling growth a	dim	6–12, 62–69	0.029	0.05	0.05	0.020	0.036
Sapling growth b	m	6–12,27, 62–69	38	24	24	55	47
Max stress years	years	39,71	2	2	2	2	3
Stress threshold	dim[0,1]	39,71	0.2	0.2	0.2	0.1	0.05
Height to diameter ratio	dim	6,8,11,12	75	72	72	72	88
Reineke's R	saplings ha^{-1}	6,8,11,12, 39,55,71	350	14.33	550	400	500
Reference ratio	dim[0,1]	71	0.345	0.457	0.457	0.409	0.451

Table A.1, cont.

Parameter	Unit	Source	Abla	Pico	PicS	Pien	Psme
Serotiny							
Serotiny formula	exp	8			(x,20,0, 80,1)		
Serotiny fecundity	dim	8			30		
Crown parameters for light influence patterns							
Crown shape coefficient	dim	70	0.2530	0.2700	0.2700	0.2615	0.3015
Max crown radius a	m	70	0.9778	1.1194	1.1194	1.0486	1.3817
Max crown radius b	m	70	2.2195	2.7325	2.7325	2.4760	3.6825
Relative crown height	dim[0,1]	27,39,70	0.5450	0.3065	0.3065	0.4190	0.4356

* Used in allometric equation to calculate biomass (kg) from diameter at breast height (cm).

References Table A.1

1. Kaufmann, M.R., Troendle, C.A., 1981. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. For. Sci. 27, 477–482.
2. Kloeppel, B.D., Gower, S.T., Treichel, I.W., Kharuk, S., 1998. Foliar carbon isotope discrimination in Larix species and sympatric evergreen conifers: A global comparison. Oecologia 114, 153–159. https://doi.org/10.1007/s004420050431
3. Seidl, R., Rammer, W., Scheller, R.M., Spies, T.A., 2012. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. Ecol. Modell. 231, 87–100. https://doi.org/10.1016/j.ecolmodel.2012.02.015
4. White, M.A., Thornton, P.E., Running, S.W., Nemani, R.R., 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: Net primary production controls. Earth Interact. 4, 1–85. https://doi.org/10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2
5. Keane, R.E., Arno, S.F., Brown, J.K., 1989. FIRESUM - an ecological process model for fire succession in western conifer forests. USDA Forest Service Intermountain Research Station General Technical Report INT-266, Ogden, UT.

6. Rebain, S., 2010. The fire and fuels extension to the forest vegetation simulator: Updated model documentation. USDA Forest Service Forest Management Service Center, Fort Collins, CO.

7. Donato, D.C., Harvey, B.J., Romme, W.H., Simard, M., Turner, M.G., 2013. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecol. Appl. 23, 3–20. https://doi.org/10.1890/12-0772.1

8. Donato, D.C., Harvey, B.J., Turner, M.G., 2016. Regeneration of montane forests a quarter-century after the 1988 Yellowstone Fires: A fire-catalyzed shift in lower treelines? Ecosphere 7, e01410. https://doi.org/10.1002/ecs2.1410

9. Kashian, D.M., Turner, M.G., Romme, W.H., 2005. Variability in leaf area and stemwood increment along a 300-year lodgepole pine chronosequence. Ecosystems 8, 48–61. https://doi.org/10.1007/s10021-004-0067-1

10. Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta-dominated forests. Ecol. Monogr. 83, 49–66. https://doi.org/10.1890/11-1454.1

11. Turner, M.G., Whitby, T.G., Tinker, D.B., Romme, W.H., 2016. Twenty-four years after the Yellowstone fires: Are postfire lodgepole pine stands converging in structure and function? Ecology 97, 1260–1273. https://doi.org/10.1890/15-1585.1

12. USDA Forest Service, 2016. Forest inventory and analysis national program - data and tools, Phase 2, Version 6.0.2. FIA Data Mart. [WWW Document]. URL http://apps.fs.fed.us/fiadb-downloads/datamart.html (accessed 3.11.16).

13. Adekunle, V.A.J., Nair, K.N., Srivastava, A.K., Singh, N.K., 2013. Models and form factors for stand volume estimation in natural forest ecosystems: A case study of

Katarniaghat Wildlife Sanctuary (KGWS), Bahraich District, India. J. For. Res. 24, 217–226. https://doi.org/10.1007/s11676-013-0347-8

14. Cole, D.M., 1971. A cubic-foot stand volume equation for lodgepole pine in Montana and Idaho. USDA Forest Service Intermountain Forest and Range Experiment Station Research Note INT-150, Ogden, UT.

15. Harmon, M.E., Franklin, J.F., 2015. Dendrometer studies for stand volume and height measurements of trees of the western US, 1976 to 1993, Version 9. Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR. https://doi.org/10.6073/pasta/7285268c91826498ef60bb6bd2f823c1

16. Rustagi, K.P., Loveless, R.S., 1991. Improved cubic volume prediction using a new measure of form factor. For. Ecol. Manage. 40, 1–11. https://doi.org/10.1016/0378-1127(91)90087-C

17. Harmon, M.E., Means, J., 2015. Pacific Northwest plant biomass component equation library, Version 7. Long-Term Ecological Research. Forest Science Data Bank. [WWW Document]. URL http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP072 (accessed 9.1.16).

18. Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2004. Comprehensive database of diameter-based biomass regressions for North American tree species. USDA Forest Service Northeastern Research Station General Technical Report NE-319, Newtown Square, PA. https://doi.org/10.2737/NE-GTR-319

19. Landis, T.D., Mogren, E.W., 1975. Tree strata biomass of subalpine spruce-fir stands in southwestern Colorado. For. Sci. 21, 9–12.

20. Marshall, P.L., Wang, Y., 1995. Above ground tree biomass of interior uneven-aged

Douglas-fir stands. University of British Columbia Working Paper WP-1.5-003, Vancouver, BC.

21. Pearson, J.A., Fahey, T.J., Knight, D.H., 1984. Biomass and leaf area in contrasting lodgepole pine forests. Can. J. For. Res. 14, 259–265. https://doi.org/10.1139/x84-050

22. Brown, J.K., 1978. Weight and density of crowns of Rocky Mountain conifers. USDA Forest Service Intermountain Forest and Range Experiment Station Research Paper INT-197, Ogden, UT.

23. Ter-Mikaelian, M.T., Korzukhin, M.D., 1997. Biomass equations for sixty-five North American tree species. For. Ecol. Manage. 97, 1–24. https://doi.org/10.1016/S0378-1127(97)00019-4

24. Chojnacky, D.C., Heath, L.S., Jenkins, J.C., 2014. Updated generalized biomass equations for North American tree species. Forestry 87, 129–151. https://doi.org/10.1093/forestry/cpt053

25. Keane, R.E., Austin, M., Field, C., Huth, A., Lexer, M.J., Peters, D., Solomon, A., Wyckoff, P., 2001. Tree mortality in gap models: Application to climate change. Clim. Change 51, 509–540. https://doi.org/10.1023/A:1012539409854

26. Alexander, R.R., 1987. Ecology, silviculture, and management of the Engelmann spruce - subalpine fir type in the central and southern Rocky Mountains. USDA Forest Service Rocky Mountain Forest and Range Experiment Station Agriculture Handbook No. 659, Fort Collins, CO.

27. Keane, R.E., Loehman, R.A., Holsinger, L.M., 2011. The FireBGCv2 landscape fire and succession model: A research simulation platform for exploring fire and vegetation dynamics. USDA Forest Service Rocky Mountain Research Station General Technical

Report RMRS-GTR-255, Fort Collins, CO.

28. Romme, W.H., 2016. Personal communication.

29. Burns, R.M., Honkala, B.H., 1990. Silvics of North America. Volume 1: Conifers. USDA Forest Service Agriculture Handbook 654, Washington, DC.

30. Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manage. 95, 209–228. https://doi.org/10.1016/S0378-1127(97)00026-1

31. DeLucia, E.H., Smith, W.K., 1987. Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer. Can. J. For. Res. 17, 527–533. https://doi.org/10.1139/x87-088

32. Edmonds, R.L., 1982. Analysis of coniferous forest ecosystems in the western United States. US/IPB Synthesis Series 14. Hutchinson Ross Publishing Co., Stroudsburg, PA.

33. Koch, P., 1996. Lodgepole pine in North America. Volumes I, II, and III. Forest Products Society, Madison, WI.

34. Krueger, K.W., Ferrell, W.K., 1965. Comparative photosynthetic and respiratory responses to temperature and light by Pseudotsuga menziesii var. menziesii and var. glauca seedlings. Ecology 46, 794–801. https://doi.org/10.2307/1934011

35. Busing, R.T., Solomon, A.M., 2006. Modeling the effects of fire frequency and severity on forests in the northwestern United States. US Geological Survey Scientific Investigations Report 2006-5061, Reston, VA.

36. Foster, A.C., Shugart, H.H., Shuman, J.K., 2016. Model-based evidence for cyclic phenomena in a high-elevation, two-species forest. Ecosystems 19, 437–449. https://doi.org/10.1007/s10021-015-9945-y

37. Bradford, J.B., Schlaepfer, D.R., Lauenroth, W.K., 2014. Ecohydrology of adjacent sagebrush and lodgepole pine ecosystems: The consequences of climate change and disturbance. Ecosystems 17, 590–605. https://doi.org/10.1007/s10021-013-9745-1

38. Lassoie, J.P., Salo, D.J., 1981. Physiological response of large Douglas-fir to natural and induced soil water deficits. Can. J. For. Res. 11, 139–144. https://doi.org/10.1139/x81-019

39. Seidl, R., Rammer, W., 2018. iLand online model documentation [WWW Document]. URL http://iland.boku.ac.at (accessed 12.29.17).

40. Alexander, R.R., Shearer, R.C., Shepperd, W.D., 1984. Silvical characteristics of subalpine fir. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report RM-115, Fort Collins, CO.

41. Boe, K.N., 1954. Periodicity of cone crops for five Montana conifers. Mont. Acad. Sci. Proc. 14, 5–9.

42. Bonner, F.T., Karrfalt, R.P., 2008. The woody plant seed manual. USDA Forest Service Agriculture Handbook 727, Washington, DC.

43. Haig, I., Davis, K., Weidman, R., 1941. Natural regeneration of the western white pine type. USDA Technical Bulletin 767, Washington, DC.

44. LeBarron, R.K., Jemison, G.M., 1953. Ecology and silviculture of the Engelmann spruce-alpine fir type. J. For. 51, 349–352.

45. Noble, D.L., Ronco, F.J., 1978. Seedfall and establishment of Engelmann spruce and subalpine fir in clearcut openings in Colorado. USDA Forest Service Rocky Mountain Forest and Range Experiment Station Research Paper RM-200, Fort Collins, CO.

46. Shearer, R.C., 1981. Silviculture, in: DeByle, N. V. (Ed.), Clearcutting and fire in the larch/Douglas-fir forests of western Montana: A multifaceted research summary. USDA

Forest Service Intermountain Forest and Range Experiment Station General Technical Report INT-99, Ogden, UT, pp. 27–32.

47. Shearer, R.C., Schmidt, W.C., 1970. Natural regeneration in ponderosa pine forests of western Montana. USDA Forest Service Intermountain Forest and Range Experiment Station Research Paper INT-86, Ogden, UT.

48. Boyce, R.B., Neuenschwander, L.F., 1989. Douglas-fir germination and seedling establishment on burned and unburned seedbeds, in: Baumgartner, D.M. (Ed.), Proceedings of prescribed fire in the intermountain region: Forest site preparation and range improvement. Washington State University Extension, Pullman, WA, pp. 69–74.

49. Farmer, R.E., 1997. Seed ecophysiology of temperate and boreal zone forest trees. St. Lucie Press, Delray Beach, FL.

50. Lotan, J., Perry, D., 1983. Ecology and regeneration of lodgepole pine. USDA Forest Service Agriculture Handbook 606, Washington, DC.

51. Moles, A.T., Westoby, M., 2004. Seedling survival and seed size: A synthesis of the literature. J. Ecol. 92, 372–383. https://doi.org/10.1111/j.0022-0477.2004.00884.x

52. Noble, D.L., Alexander, R.R., 1977. Environmental factors affecting natural regeneration of Engelmann spruce in the central Rocky Mountains. For. Sci. 23, 420–429.

53. Moles, A.T., Falster, D.S., Leishman, M.R., Westoby, M., 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. J. Ecol. 92, 384–396. https://doi.org/10.1111/j.0022-0477.2004.00880.x

54. Garman, S.L., 2003. LandMod 2.0 - Documentation. Oregon State University, Corvallis, OR.

55. Hansen, W.D., Braziunas, K.H., Rammer, W., Seidl, R., Turner, M.G., 2018. It takes a

few to tango: Changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99, 966–977. https://doi.org/10.1002/ecy.2181

56. Harvey, B.J., Donato, D.C., Turner, M.G., 2016. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob. Ecol. Biogeogr. 25, 655–669. https://doi.org/10.1111/geb.12443

57. McCaughey, W.W., Schmidt, W.C., 1987. Seed dispersal of Engelmann spruce in the intermountain west. Northwest Sci. 61, 1–6.

58. McCaughey, W.W., Schmidt, W.C., Shearer, R.C., 1986. Seed-dispersal characteristics of conifers in the inland mountain west, in: Shearer, R.C. (Ed.), Proceedings – Conifer Tree Seed in the Inland Mountain West Symposium. USDA Forest Service Intermountain Research Station General Technical Report INT-203, Ogden, UT, pp. 50–62.

59. Nitschke, C.R., Innes, J.L., 2008. A tree and climate assessment tool for modelling ecosystem response to climate change. Ecol. Modell. 210, 263–277. https://doi.org/10.1016/j.ecolmodel.2007.07.026

60. Gill, R.A., Campbell, C.S., Karlinsey, S.M., 2015. Soil moisture controls Engelmann spruce (Picea engelmannii) seedling carbon balance and survivorship at timberline in Utah, USA. Can. J. For. Res. 45, 1845–1852. https://doi.org/10.1139/cjfr-2015-0239

61. Kavanagh, K.L., Bond, B.J., Aitken, S.N., Gartner, B.L., Knowe, S., 1999. Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. Tree Physiol. 19, 31–37. https://doi.org/10.1093/treephys/19.1.31

62. Alexander, R.R., 1967. Site indexes for Engelmann spruce in the central Rocky Mountains, Research Paper RM-32. USDA Forest Service, Rocky Mountain Forest and

Range Experiment Station, Fort Collins, CO.

63. Brickell, J.E., 1966. Site index curves for Engelmann spruce in the Northern and Central Rocky Mountains. USDA Forest Service Intermountain Forest and Range Experiment Station Research Note INT-42, Ogden, UT.

64. Chen, H.Y.H., Klinka, K., 2000. Height growth models for high-elevation subalpine fir, Engelmann spruce, and lodgepole pine in British Columbia. West. J. Appl. For. 15, 62–69.

65. Klinka, K., Chen, H.Y.H., Wang, Q., Chourmouzis, C., 1998. Height growth curves and site index tables for subalpine fir, Engelmann spruce, and lodgepole pine in the ESSF zone of BC. Scientia Silvica Extension Series 15, Forest Sciences Department, University of British Columbia, Vancouver, BC.

66. Milner, K.S., 1987. The development of site specific height growth curves for four conifers in western Montana. PhD Thesis. University of Montana, Missoula, MT.

67. Milner, K.S., 1992. Site index and height growth curves for ponderosa pine, western larch, lodgepole pine, and Douglas-fir in western Montana. West. J. Appl. For. 7, 9–14.

68. Rammig, A., Fahse, L., Bugmann, H., Bebi, P., 2006. Forest regeneration after disturbance: A modelling study for the Swiss Alps. For. Ecol. Manage. 222, 123–136. https://doi.org/10.1016/j.foreco.2005.10.042

69. Rammig, A., Bebi, P., Bugmann, H., Fahse, L., 2007. Adapting a growth equation to model tree regeneration in mountain forests. Eur. J. For. Res. 126, 49–57. https://doi.org/10.1007/s10342-005-0088-0

70. Purves, D.W., Lichstein, J.W., Pacala, S.W., 2007. Crown plasticity and competition for canopy space: A new spatially implicit model parameterized for 250 North American tree species. PLoS One 2, e870. https://doi.org/10.1371/journal.pone.0000870

71. This study.

Table A.2. Regional model parameters for the Greater Yellowstone Ecosystem, which apply to all stands in the simulation. Parameters from Seidl et al. (2012) were used or modified for this study. Additional regional parameters were set to default values per Seidl and Rammer (2018).

Parameter	Units	Value
Light extinction coefficient	dim	0.5
Potential light utilization efficiency	g C MJ^{-1}	2.9
Boundary layer conductance	mm s^{-1}	0.15
Temperature delay time constant	days	6.0
Base CO_2 concentration	ppm	330
Latitude	°N	44.5

Appendix B. Model evaluation

We evaluated iLand's ability to simulate stand structural development under historical climatic conditions in the Greater Yellowstone Ecosystem (GYE) in three stages: Evaluation of monospecific stands, evaluation of succession in mixed-species stands, and comparison with the forest growth model Forest Vegetation Simulator (FVS; Dixon, 2002). Evaluations were designed to assess how well iLand characterized (1) single-species stand structural trajectories and variability over time, (2) successional trajectories, species composition, and stand structure in late-seral stages in different forest types, and (3) responses to variation in initial stem densities and environmental conditions. Comparison of stand development with FVS allowed us to evaluate iLand against the simulator used most widely by federal forest managers in the western United States.

1. Single-species evaluation

We first evaluated monospecific stand structural trajectories and variability over time for each of the four dominant conifer species. Derivation of initial conditions and drivers followed the methods described in the main body of the paper, except that we varied soil fertility among stands when field data was available (i.e., for Douglas-fir and lodgepole pine; Donato et al., 2016; Turner et al., 2016). For these stands, relative soil fertility was assigned based on the recorded parent material (andesite, rhyolite, or lacustrine sediments; Despain, 1990; Knight et al., 2014). We simulated development of monospecific 1-ha stands for 300 years with no additional disturbance under historical climate conditions. Climate year was randomly drawn with replacement from 1980 to 2015.

We evaluated how well the model simulated variation in stand development by comparing stand-level live tree densities, basal areas, quadratic mean diameters (QMDs), and mean heights with independent field observations (Kashian et al., 2005a; Simard et al., 2011; Donato et al., 2013a; Griffin et al., 2013; Kashian et al., 2013) and data from the Forest Inventory and Analysis (FIA) Database (USDA Forest Service, 2016). Field observations included stands dominated by lodgepole pine or Douglas-fir that were either undisturbed or had recently experienced bark beetle disturbance (red stage). In the latter, standing dead trees were treated as live trees for the purpose of comparison. The FIA stands for Douglas-fir, Engelmann spruce, and subalpine fir were selected from unreplicated (inventory year 2000) stands on federally owned land and dominated (> 75% of tree density) by the focal species. All stand ages in comparison data were plotted as time since stand-replacing fire. For consistency with field data, metrics of stand structure were calculated for trees > 4 cm diameter at breast height (DBH).

Simulated stand densities in iLand for all four species fell within observed ranges of field data over 300 years of stand development, and variation in stand density and basal area corresponded well to observations over time since fire (Fig. B.1). At 300 years postfire, Douglas-fir densities (trees > 4 cm DBH) ranged from 97-521 trees ha^{-1} (mean 242 trees ha^{-1}), lodgepole pine from 695-1713 trees ha^{-1} (mean 894 trees ha^{-1}), subalpine fir from 224-988 trees ha^{-1} (mean 566 trees ha^{-1}), and Engelmann spruce from 385-988 trees ha^{-1} (mean 601 trees ha^{-1}). Simulated basal areas also were within observed ranges for Douglas-fir, lodgepole pine, and Engelmann spruce throughout stand development; however, field observations for older (> 150-year-old) subalpine fir stands showed a decline in basal area that was not captured in simulated stands (Fig. B.1f). Simulated stands did not always achieve maximum or minimum values observed in the field. Across all species, the range of iLand simulations encompassed 69% of field

observations of stand density (n = 186) and 67% of field observations of basal area (n = 186). Simulated QMDs and heights also fell within observed ranges of field data (Kashian et al., 2005a; Simard et al., 2011; Donato et al., 2013a; Griffin et al., 2013; Kashian et al., 2013; USDA Forest Service, 2016), and variation among stands was maintained over time (Fig. B.2).

2. Succession experiment

We next evaluated iLand's ability to achieve expected late-seral stand structure and species composition after 300 years of succession in three distinct, widespread forest types in the GYE: (1) Low-elevation Douglas-fir, (2) mid-elevation lodgepole pine, and (3) high-elevation spruce-fir. Geographic locations for each forest type were determined by extracting random points > 1 km apart from a map of Yellowstone National Park (YNP) pre-1988 cover types (Despain, 1990; provided by YNP Spatial Analysis Center). To minimize overlap between climatic conditions of the three forest types, high-elevation Douglas-fir, low-elevation spruce-fir, and extreme high- and low-elevation lodgepole pine points were removed (elevations from 10-m Digital Elevation Model provided by YNP Spatial Analysis Center). From this dataset, 10 points were randomly sampled from each forest type (Table B.1) and used to derive historical climatic (Daymet Version 3; Thornton et al., 2017) and edaphic (CONUS-SOIL; Miller and White, 1998) conditions for simulated stands (see Fig. B.3 for climate envelope). Relative soil fertility was assigned based on soil parent material associated with each forest type (andesite for Douglas-fir and spruce-fir, rhyolite for lodgepole pine; Despain, 1990; Knight et al., 2014).

For each forest type, 10 1-ha stands were simulated for 300 years (climate year drawn randomly with replacement, no disturbance) along an elevation transect, starting from bare ground and allowing seed inputs from two, opposite sides (Fig. B.4). Seed availability differed

by forest type based on tree species composition (Table B.1), and once mature trees had established, simulated stands could also serve as seed sources for each other. Because seed inputs were affected by stochastic processes (e.g., probability of mast year) and we were interested in capturing a wide range of stand structures, simulations were replicated three times for a total of n = 30 per forest type.

Simulated stand trajectories of tree density, basal area, and importance value (IV, species proportion of density + species proportion of basal area, potential range from zero to two) were consistent with expectations of succession over time for the studied forest types (Fig. B.5). Early pulses of lodgepole pine regeneration occurred in both Douglas-fir and spruce-fir forests (Fig. B.5a,c), but after 300 years of stand development, forest types were dominated by expected species (Fig. B.5g,i). Additionally, subalpine fir basal area and IV declined in older high-elevation spruce-fir stands (Fig. B.5i), which is consistent with expected increasing dominance of longer-lived spruce (Aplet et al., 1988, 1989; Baker, 2009).

Simulated mature (300-year-old) stand structure and dominant species composition overlapped with observed ranges in field data (Figs. B.6-B.8; Binkley et al., 2003; Kashian et al., 2005b; Donato et al., 2016). However, simulated stem densities did not reach the highest values recorded in field data, and median simulated densities were lower than median observed densities (Figs. B.6-B.8a). These discrepancies likely reflect the subsetting of simulated forest types by elevation (e.g., low-elevation Douglas-fir stands are more dry than mesic) and the lack of fire-induced regeneration of serotinous lodgepole pine. Basal areas and dominance of species were mostly consistent with field observations (Figs. B.6-B.8b-c).

3. Model comparison with FVS

We evaluated iLand's ability to respond appropriately to variation in initial stem densities and environmental conditions by comparison with the Forest Vegetation Simulator, a widely used semi-distance-independent individual-tree growth and yield model parameterized for the GYE (Teton Variant; Keyser and Dixon, 2008). In FVS, stand level variables such as elevation, slope, and aspect incorporate environmental variation among sites and affect tree growth. We simulated single-species stand development of the same lodgepole pine (n = 70) and Douglas-fir (n = 34) stands (starting at 24 years postfire) in both iLand and FVS for 300 years without disturbance under historical climate conditions. Initial conditions and simulation in iLand followed the methods for (1) single-species evaluation, and initial conditions for FVS (densities, tree sizes, stand environmental variables) were derived from the same field data. We used empirically-derived parameters from two studies that successfully evaluated and applied FVS for these two species in the GYE (Donato et al., 2013b; Seidl et al., 2016) to adjust tree growth, mortality, and infilling in FVS.

Stand densities and basal areas for the same stands simulated in iLand versus FVS were compared at three time periods during stand development (74, 124, and 224 years postfire; Figs. B.9 and B.10). Spearman's rank order correlation was used to compare stands modeled with iLand and FVS because assumptions of normality and linearity were not met. After 50 years of simulation (74 years postfire), iLand and FVS represented lodgepole pine stand densities and Douglas-fir stand densities and basal areas similarly across a wide range of initial densities and environmental conditions (r_s = 0.70, 0.94, and 0.55, respectively, all $p < 0.001$), but iLand and FVS-simulated lodgepole pine basal areas were only weakly correlated (r_s = 0.24, $p < 0.05$). In

both cases the strength of correlation between iLand and FVS for the same stands decreased with stand age (Figs. B.9 and B.10).

Simulated iLand and FVS stand trajectories for density and basal area were compared over 300 years with each other and with field observations (combined research publication and FIA data from single-species evaluation; Fig. B.11). Although the ranges overlapped for much of earlier (< 150 years) stand development, development trajectories differed over time. FVS median stand densities were mostly higher and median basal areas appeared to more closely follow a logistic (Douglas-fir) or logarithmic (lodgepole pine) growth curve than in iLand. During the first 150 years of simulation, both models maintained variation in stand density and basal area and encompassed many of the field observations. Later in stand development, FVS simulations converged, particularly for basal area, which is consistent with intended model behavior to approach a maximum stand density index in the absence of disturbance (Crookston and Dixon, 2005). However, iLand simulations continued to capture the variability observed in field data for late-seral stands.

References Appendix B

Aplet, G.H., Laven, R.D., Smith, F.W., 1988. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. Ecology 69, 312–319. https://doi.org/10.2307/1940429

Aplet, G.H., Smith, F.W., Laven, R.D., 1989. Stemwood biomass and production during spruce-fir stand development. J. Ecol. 77, 70–77. https://doi.org/10.2307/2260917

Baker, W.L., 2009. Fire ecology in Rocky Mountain landscapes. Island Press, Washington, DC.

Binkley, D., Olsson, U., Rochelle, R., Stohlgren, T., Nikolov, N., 2003. Structure, production

and resource use in some old-growth spruce/fir forests in the front range of the Rocky Mountains, USA. For. Ecol. Manage. 172, 271–279. https://doi.org/10.1016/S0378-1127(01)00794-0

Crookston, N.L., Dixon, G.E., 2005. The forest vegetation simulator: A review of its structure, content, and applications. Comput. Electron. Agric. 49, 60–80. https://doi.org/10.1016/j.compag.2005.02.003

Despain, D.G., 1990. Yellowstone vegetation: Consequences of environment and history in a natural setting. Roberts Rinehart, Boulder, Colorado.

Dixon, G.E., 2002. Essential FVS: A user's guide to the Forest Vegetation Simulator. USDA Forest Service, Forest Management Service Center, Fort Collins, CO.

Donato, D.C., Harvey, B.J., Romme, W.H., Simard, M., Turner, M.G., 2013a. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecol. Appl. 23, 3–20. https://doi.org/10.1890/12-0772.1

Donato, D.C., Simard, M., Romme, W.H., Harvey, B.J., Turner, M.G., 2013b. Evaluating post-outbreak management effects on future fuel profiles and stand structure in bark beetle-impacted forests of Greater Yellowstone. For. Ecol. Manage. 303, 160–174. https://doi.org/10.1016/j.foreco.2013.04.022

Donato, D.C., Harvey, B.J., Turner, M.G., 2016. Regeneration of montane forests a quarter-century after the 1988 Yellowstone Fires: A fire-catalyzed shift in lower treelines? Ecosphere 7, e01410. https://doi.org/10.1002/ecs2.1410

Griffin, J.M., Simard, M., Turner, M.G., 2013. Salvage harvest effects on advance tree regeneration, soil nitrogen, and fuels following mountain pine beetle outbreak in lodgepole pine. For. Ecol. Manage. 291, 228–239. https://doi.org/10.1016/j.foreco.2012.11.029

Kashian, D.M., Turner, M.G., Romme, W.H., 2005a. Variability in leaf area and stemwood increment along a 300-year lodgepole pine chronosequence. Ecosystems 8, 48–61. https://doi.org/10.1007/s10021-004-0067-1

Kashian, D.M., Turner, M.G., Romme, W.H., Lorimer, C.G., 2005b. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. Ecology 86, 643–654. https://doi.org/10.1890/03-0828

Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta-dominated forests. Ecol. Monogr. 83, 49–66. https://doi.org/10.1890/11-1454.1

Keyser, C.E., Dixon, G.E., 2008. Tetons (TT) variant overview: Forest Vegetation Simulator. USDA Forest Service, Forest Management Service Center, Fort Collins, CO.

Knight, D.H., Jones, G.P., Reiners, W.A., Romme, W.H., 2014. Mountains and plains: The ecology of Wyoming landscapes. Second edition. Yale University Press, New Haven, CT.

Miller, D.A., White, R.A., 1998. A conterminous United States multilayer soil characteristics dataset for regional climate and hydrology modeling. Earth Interact. 2, 1–26. https://doi.org/10.1175/1087-3562(1998)002<0001:ACUSMS>2.3.CO;2

Seidl, R., Donato, D.C., Raffa, K.F., Turner, M.G., 2016. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. Proc. Natl. Acad. Sci. 113, 13075–13080. https://doi.org/10.1073/pnas.1615263113

Simard, M., Romme, W.H., Griffin, J.M., Turner, M.G., 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol. Monogr. 81, 3–24. https://doi.org/10.1890/10-1176.1

Thornton, P.E., Thornton, M.M., Mayer, B.W., Wei, Y., Devarakonda, R., Vose, R.S., Cook,

R.B., 2017. Daymet: Daily surface weather data on a 1-km grid for North America, Version 3. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ORNLDAAC/1328

Turner, M.G., Whitby, T.G., Tinker, D.B., Romme, W.H., 2016. Twenty-four years after the Yellowstone fires: Are postfire lodgepole pine stands converging in structure and function? Ecology 97, 1260–1273. https://doi.org/10.1890/15-1585.1

USDA Forest Service, 2016. Forest inventory and analysis national program - data and tools, Phase 2, Version 6.0.2. FIA Data Mart. [WWW Document]. URL http://apps.fs.fed.us/fiadb-downloads/datamart.html (accessed 3.11.16).

Table B.1. Elevation ranges and seed source species composition for each forest type. All species were included as potential seed sources in all forest types (minimum value = 0.01). Species composition was calculated from trees greater than breast height in reference field data. Abla = *Abies lasiocarpa* (subalpine fir), Pico = *Pinus contorta* var. *latifolia* (lodgepole pine), Pien = *Picea engelmannii* (Engelmann spruce), and Psme = *Pseudotsuga menziesii* var. *glauca* (Douglas-fir).

Forest type	Elevation range (m)	Seed source species composition				Reference for seed source species composition
		Abla	Pico	Pien	Psme	
Douglas-fir	1993-2275	0.06	0.16	0.02	0.76	Donato et al. 2013a, 150-200-year-old Douglas-fir forest
Lodgepole pine	2196-2573	0.03	0.90	0.03	0.04	Kashian et al. 2005b, 250-358-year-old stands in a lodgepole pine chronosequence
Spruce-fir	2427-2774	0.52	0.03	0.44	0.01	Binkley et al. 2003, 200-450-year-old spruce-fir forest

Figure Legends

Fig. B.1. (a-h) Trajectories of stand density and basal area over time. All values are for trees > 4 cm diameter at breast height (DBH) to be consistent with the measurements reported in available field data. Density is on a log10 scale. Lines show simulated stand trajectories, and points show field observations, differentiated by data source [research publications (Kashian et al., 2005a; Simard et al., 2011; Donato et al., 2013a; Griffin et al., 2013) or FIA Database (USDA Forest Service, 2016)].

Fig. B.2. (a-h) Trajectories of quadratic mean diameter (QMD) and mean stand height over time. All values are for trees > 4 m in height. Lines show simulated stand trajectories, and field observation points are differentiated by data source [research publications (Kashian et al., 2005a; Simard et al., 2011; Donato et al., 2013a; Griffin et al., 2013) or FIA Database (USDA Forest Service, 2016)].

Fig. B.3. Climate envelope for succession experiment, characterized by mean annual precipitation and mean annual temperature for each forest type. Each simulated stand is represented by one point within this climate space.

Fig. B.4. Simulation layout for a single forest type. Each forest type was simulated separately. Stands (1-ha, n = 10 per simulation) were arranged from low to high elevation, with seed inputs from both adjacent sides. Seed availability differed by forest type (Table B.1), and once mature trees had established, simulated stands could also serve as seed sources for each other.

Fig. B.5. Mean (*n* = 30) stand structural trajectories (based on trees > breast height) for three forest type transects [Douglas-fir (a, d, g), lodgepole pine (b, e, h), and spruce-fir (c, f, i)], starting from bare ground with multispecies seed inputs. Importance values (g-i) were calculated for each species (maximum value = 2).

Fig. B.6. Boxplot comparison of forest structure and species composition in simulated mature Douglas-fir stands (300 years old, *n* = 30) with lower-montane, mature Douglas-fir dominated stands in the GYE on mesic (*n* = 23) and dry (*n* = 32) topographic positions (Donato et al., 2016). Total (all species) stand densities (a), total basal areas (b), and Douglas-fir dominance as proportion of tree density (c) were calculated for trees > 15 cm DBH to be consistent with field observations. Bold lines show the median value, boxes show the interquartile range (IQR), and whiskers extend 1.5 x IQR or to the most extreme data point (whichever is closest to the median). Prop = proportion.

Fig. B.7. Boxplot comparison of forest structure and species composition in simulated mature lodgepole pine stands (300 years old, *n* = 30) with mature stands in a lodgepole pine chronosequence in the GYE (250-358-year-old stands, *n* = 12; Kashian et al., 2005b). Total (all species) stand densities (a), total basal areas (b), and lodgepole pine dominance as proportion of tree density (c) were calculated for trees > 4 cm DBH to be consistent with field observations. Bold lines show the median value, boxes show the interquartile range (IQR), and whiskers extend 1.5 x IQR or to the most extreme data point (whichever is closest to the median). Prop = proportion.

Fig. B.8. Boxplot comparison of forest structure and species composition in simulated mature spruce-fir stands (300 years old, $n = 30$) with old growth spruce-fir stands in Colorado (200-450-year-old stands, $n = 18$; Binkley et al., 2003). Total (all species) stand densities (a), total basal areas (b), and subalpine fir (c) and Engelmann spruce (d) dominance as proportion of tree density were calculated for trees > breast height to be consistent with field observations. Bold lines show the median value, boxes show the interquartile range (IQR), and whiskers extend 1.5 x IQR or to the most extreme data point (whichever is closest to the median). Prop = proportion.

Fig. B.9. Comparison of densities (a-c) and basal areas (d-f) for the same Douglas-fir stands ($n = 34$, each stand = 1 point) simulated in iLand and FVS at three time periods: 74, 124, and 224 years postfire. Stand structure was calculated from trees > 4 m in height. Stand density is on a log10 scale, and a 1:1 line is shown for comparison on each plot. Spearman's rank correlation coefficient and two-tailed p-values are noted on each plot. * $0.01 < p < 0.05$, ** $0.001 < p < 0.01$, *** $p < 0.001$, ns = not significant at $\alpha = 0.05$.

Fig. B.10. Comparison of densities (a-c) and basal areas (d-f) for the same lodgepole pine stands ($n = 70$, each stand = 1 point) simulated in iLand versus FVS at three time periods: 74, 124, and 224 years postfire. Stand structure was calculated from trees > 4 m in height. Stand density is on a log10 scale, and a 1:1 line is shown for comparison on each plot. Spearman's rank correlation coefficient and two-tailed p-values are noted on each plot. * $0.01 < p < 0.05$, ** $0.001 < p < 0.01$, *** $p < 0.001$, ns = not significant at $\alpha = 0.05$.

Fig. B.11. Stand trajectories in density (a, c) and basal area (b, d) for lodgepole pine (n = 70) and Douglas-fir (n = 34) stands simulated with iLand (red shading, solid line) and FVS (blue shading, dashed line) over time, compared to field observations. All values are for trees > 4 cm diameter at breast height (DBH) to be consistent with the measurements reported in available field data. Density is on a log10 scale. Simulated medians (lines), interquartile ranges (IQR, intermediate shading), and ranges (minimum to maximum values, light shading) are shown.

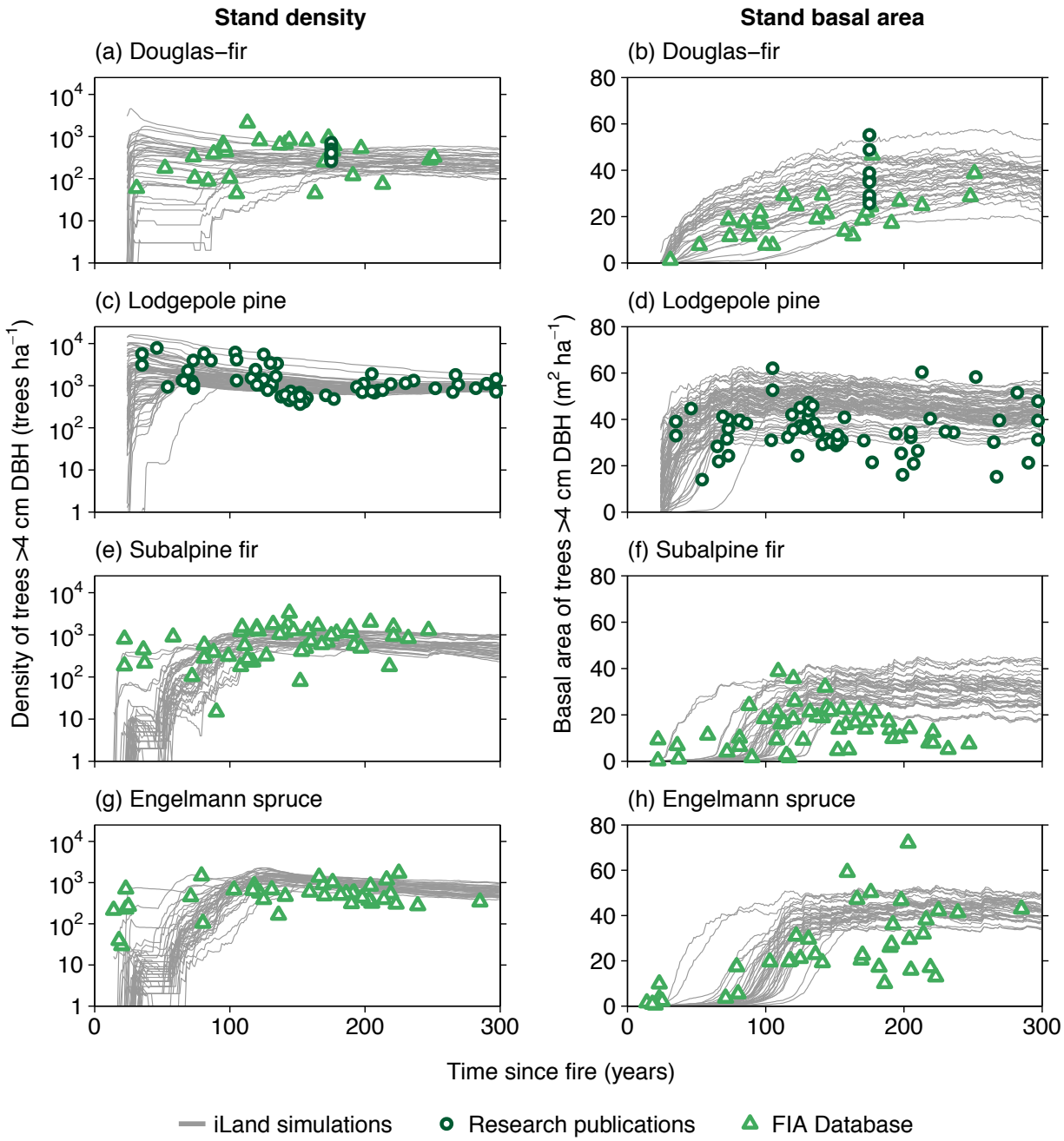
Stand density
Stand basal area
(a) Douglas–fir
(b) Douglas–fir
(c) Lodgepole pine
(d) Lodgepole pine
(e) Subalpine fir
(f) Subalpine fir
(g) Engelmann spruce
(h) Engelmann spruce
Density of trees >4 cm DBH (trees ha^{-1})
Basal area of trees >4 cm DBH (m^2 ha^{-1})
Time since fire (years)
iLand simulations
Research publications
FIA Database

Fig. B.1

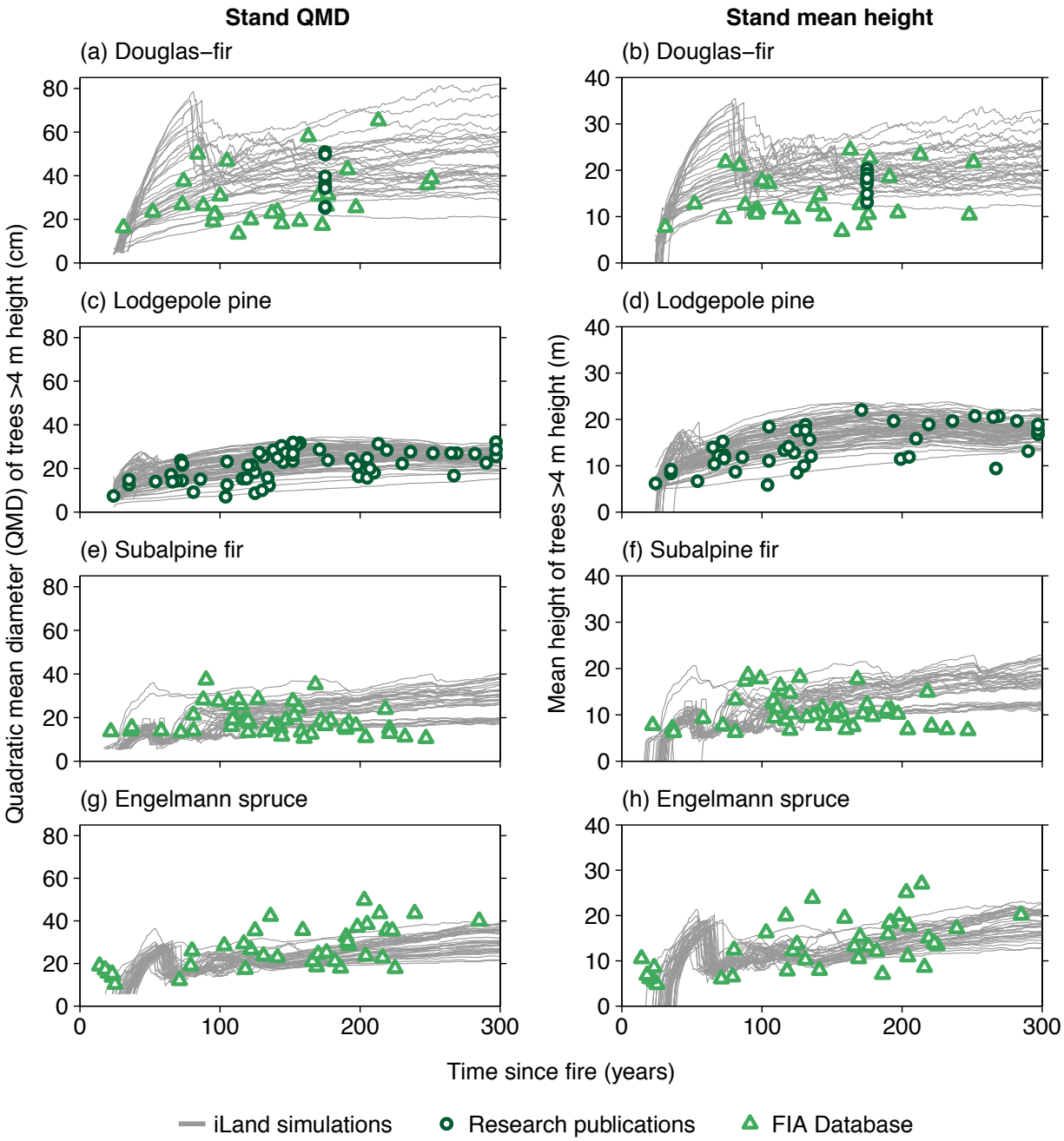
Stand QMD
Stand mean height
(a) Douglas–fir
(b) Douglas–fir
(c) Lodgepole pine
(d) Lodgepole pine
(e) Subalpine fir
(f) Subalpine fir
(g) Engelmann spruce
(h) Engelmann spruce
Quadratic mean diameter (QMD) of trees >4 m height (cm)
Mean height of trees >4 m height (m)
Time since fire (years)
iLand simulations
Research publications
FIA Database

Fig. B.2

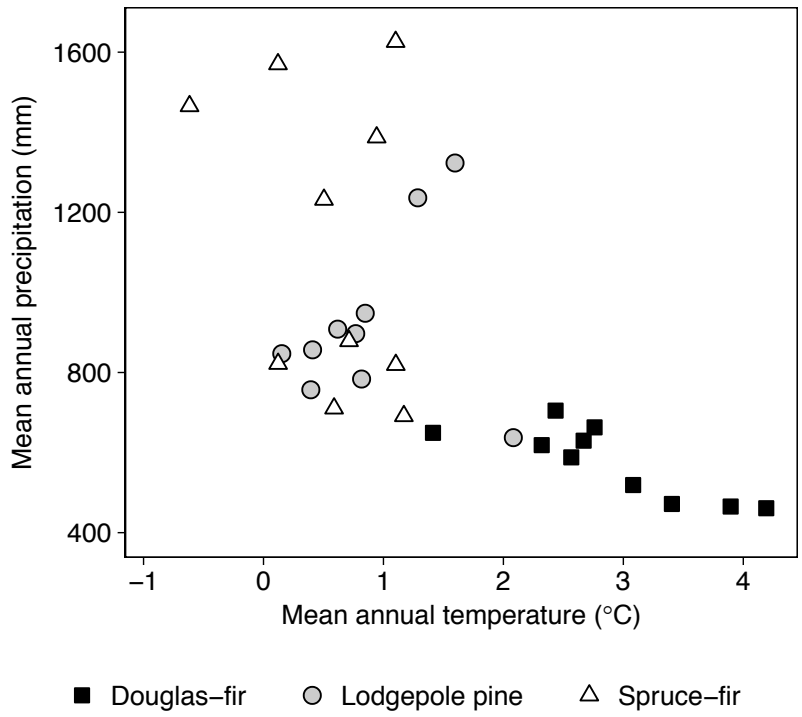
1600
1200
800
400
Mean annual precipitation (mm)
–1
0
1
2
3
4
Mean annual temperature (°C)
Douglas–fir
Lodgepole pine
Spruce–fir

Fig. B.3

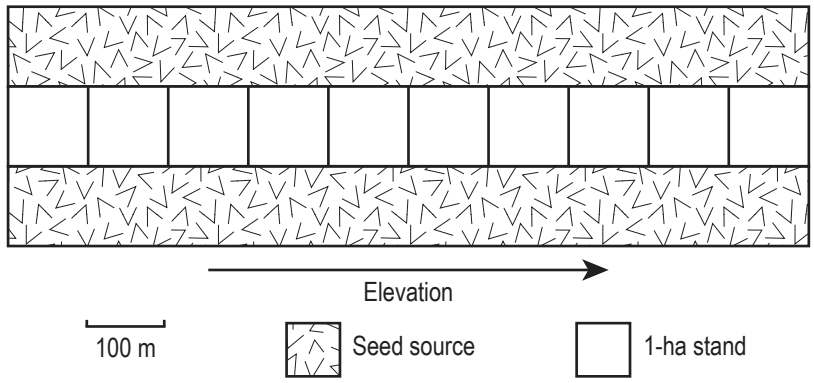

Fig. B.4

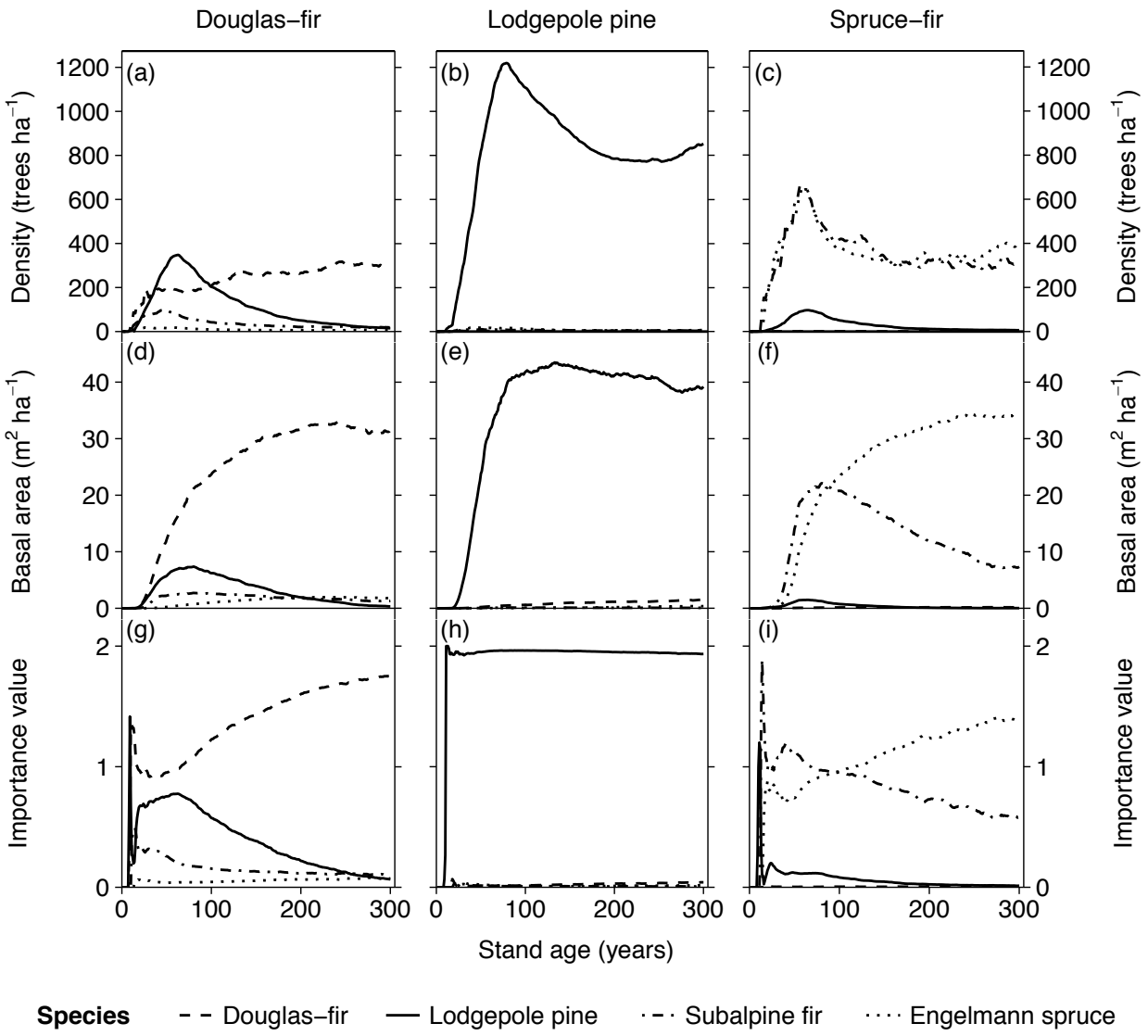
Douglas−fir
Lodgepole pine
Spruce−fir
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
Density (trees ha^{-1})
Basal area (m^2 ha^{-1})
Importance value
Stand age (years)
Species
Douglas−fir
Lodgepole pine
Subalpine fir
Engelmann spruce

Fig. B.5

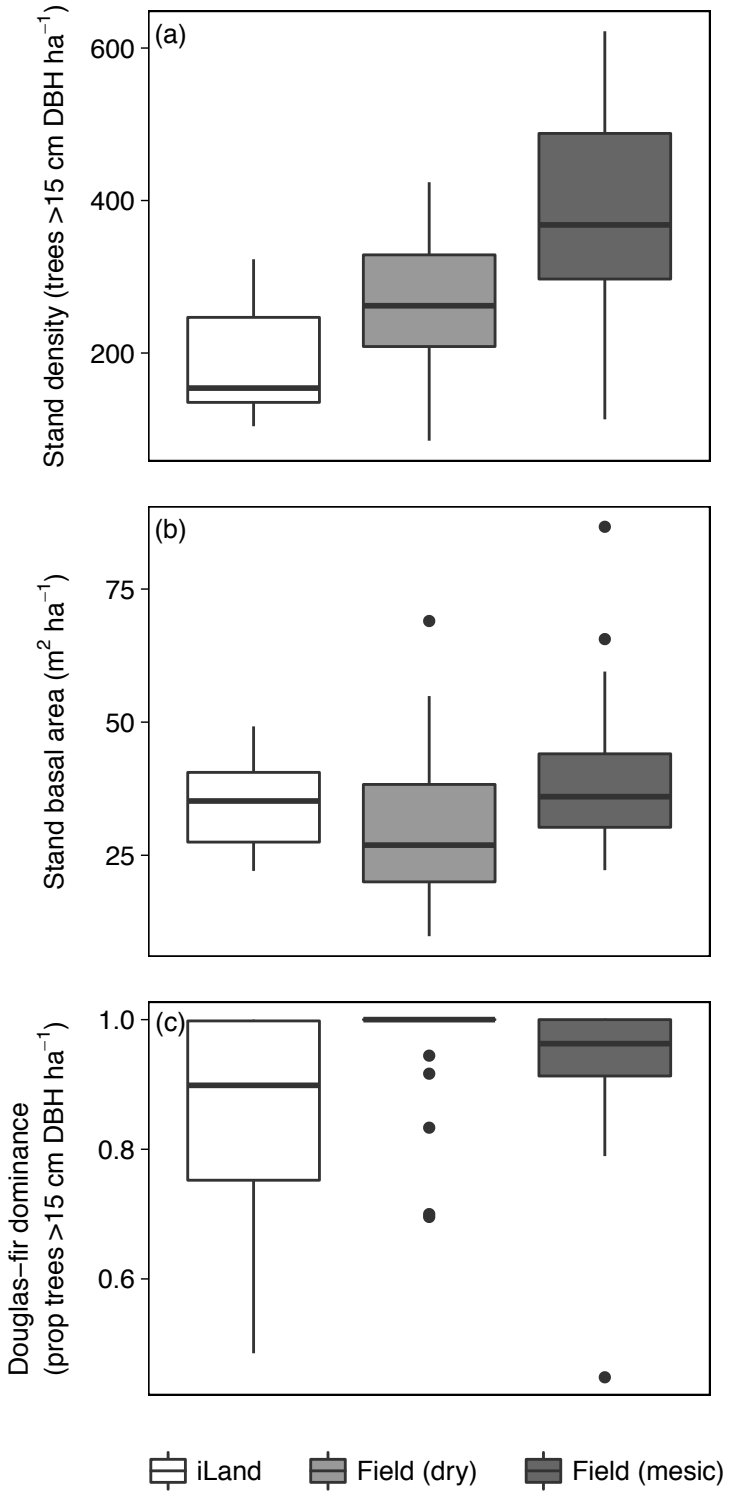
(a)
Stand density (trees >15 cm DBH ha^{-1})
600
400
200
(b)
Stand basal area (m^2 ha^{-1})
75
50
25
(c)
Douglas–fir dominance
(prop trees >15 cm DBH ha^{-1})
1.0
0.8
0.6
iLand
Field (dry)
Field (mesic)

Fig. B.6

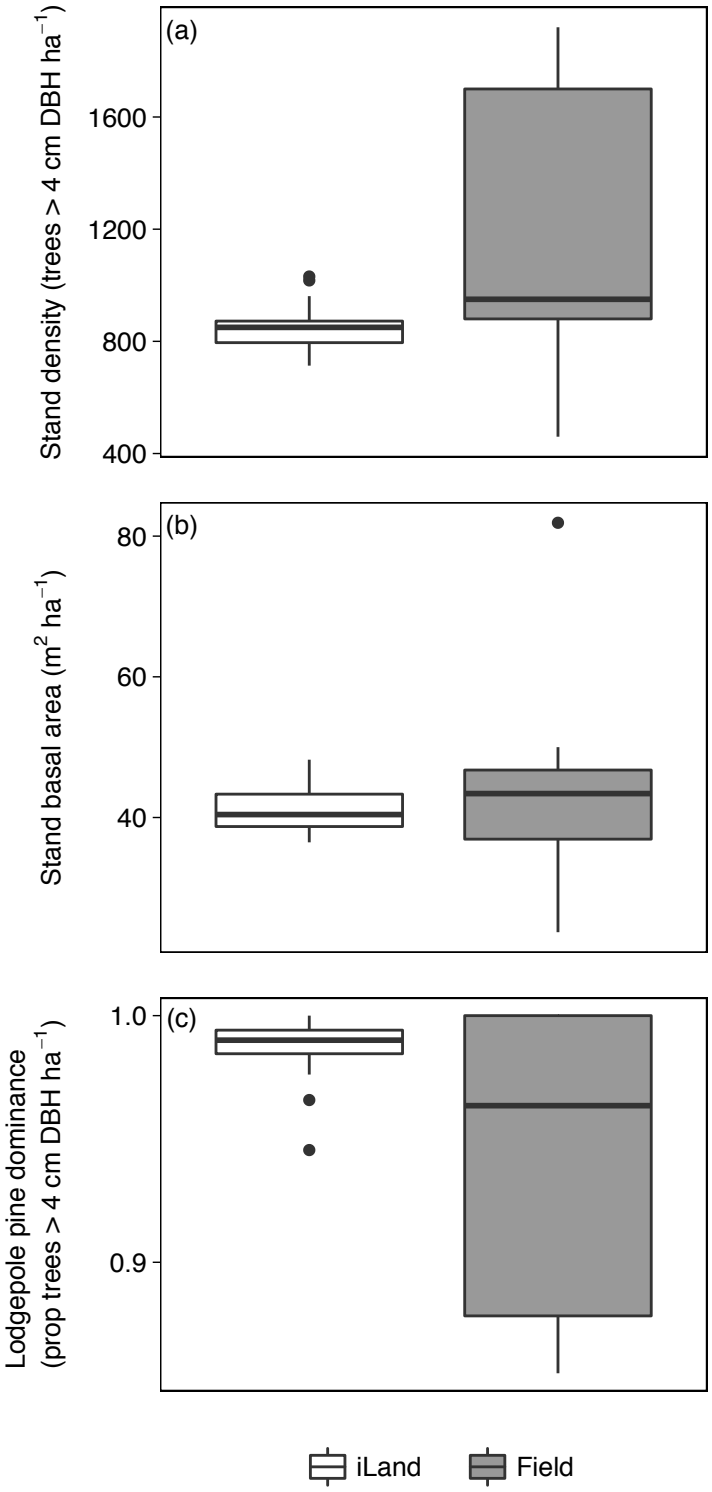
(a)
Stand density (trees > 4 cm DBH ha^{-1})
1600
1200
800
400
(b)
Stand basal area (m^2 ha^{-1})
80
60
40
(c)
Lodgepole pine dominance
(prop trees > 4 cm DBH ha^{-1})
1.0
0.9
iLand
Field

Fig. B.7

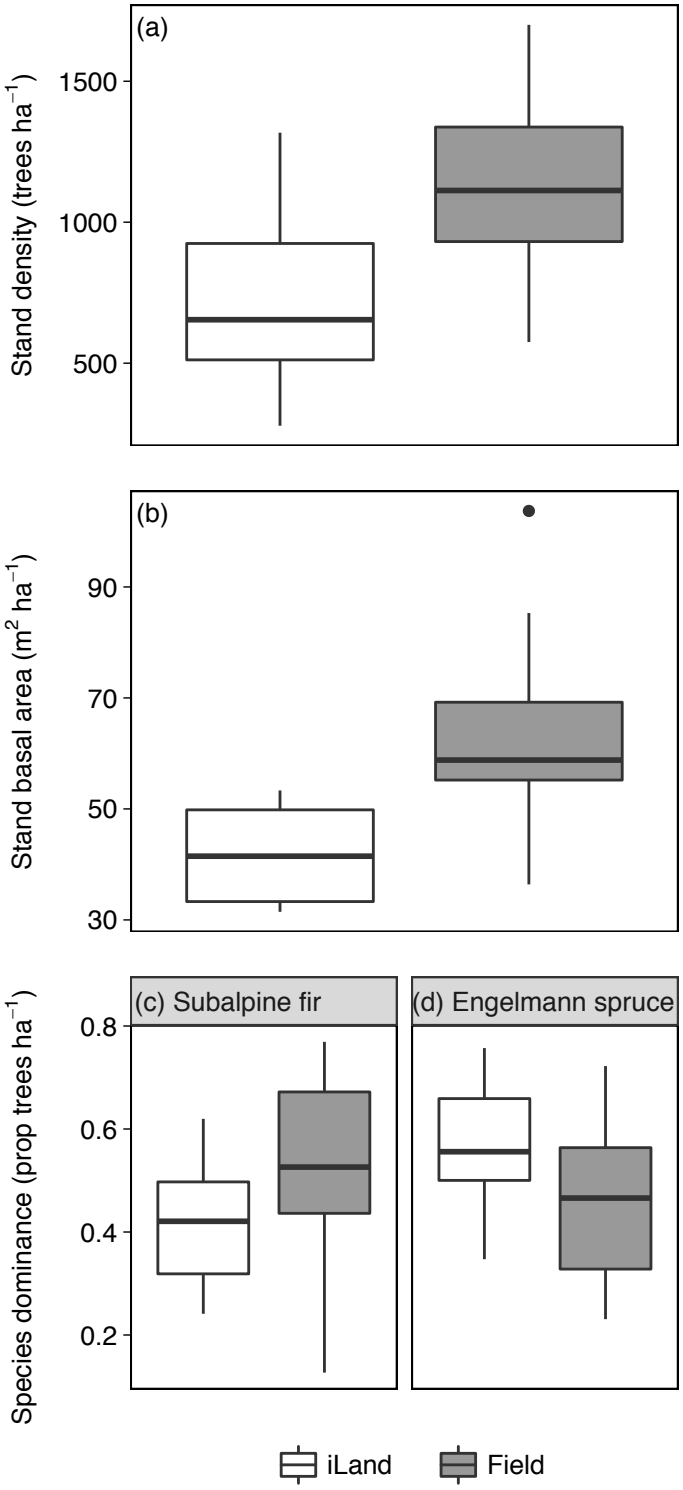
(a)
Stand density (trees ha^{-1})
1500
1000
500
(b)
Stand basal area (m^2 ha^{-1})
90
70
50
30
(c) Subalpine fir
(d) Engelmann spruce
Species dominance (prop trees ha^{-1})
0.8
0.6
0.4
0.2
iLand
Field

Fig. B.8

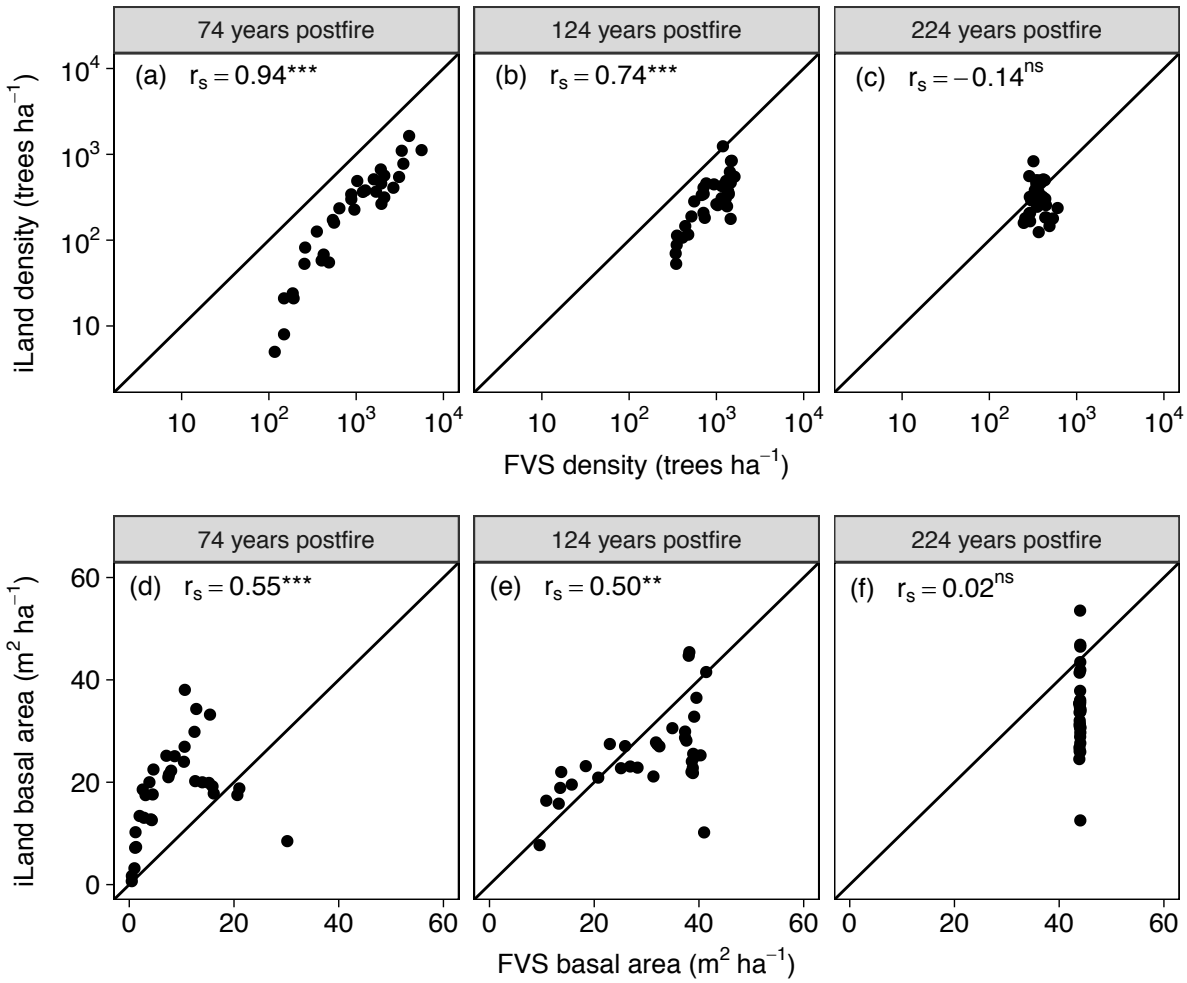
74 years postfire
124 years postfire
224 years postfire
(a) $r_s = 0.94^{***}$
(b) $r_s = 0.74^{***}$
(c) $r_s = -0.14^{ns}$
iLand density (trees ha^{-1})
FVS density (trees ha^{-1})
(d) $r_s = 0.55^{***}$
(e) $r_s = 0.50^{**}$
(f) $r_s = 0.02^{ns}$
iLand basal area (m^2 ha^{-1})
FVS basal area (m^2 ha^{-1})

Fig. B.9

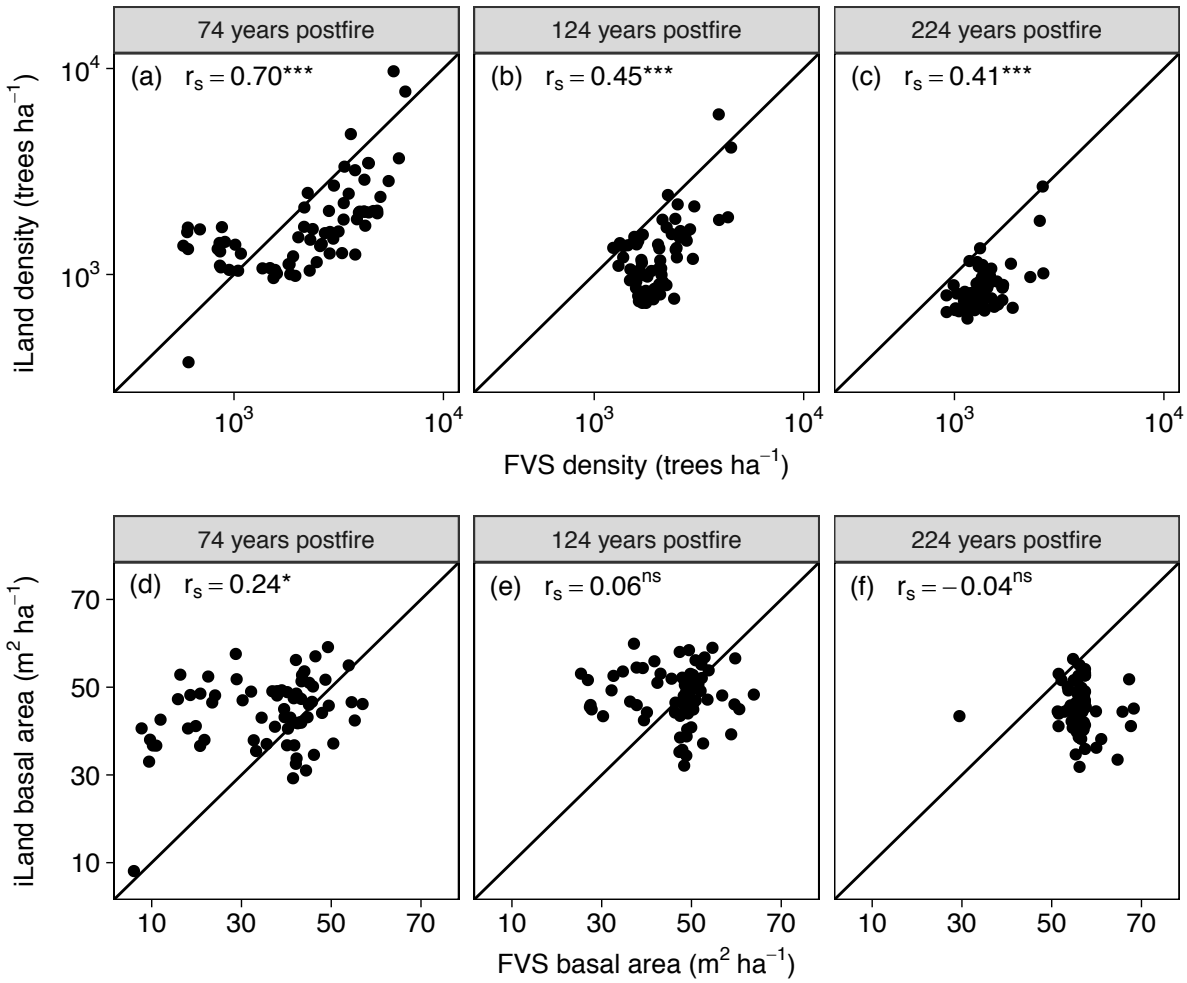
74 years postfire
124 years postfire
224 years postfire
(a) $r_s = 0.70^{***}$
(b) $r_s = 0.45^{***}$
(c) $r_s = 0.41^{***}$
iLand density (trees ha^{-1})
FVS density (trees ha^{-1})
(d) $r_s = 0.24^{*}$
(e) $r_s = 0.06^{ns}$
(f) $r_s = -0.04^{ns}$
iLand basal area (m^2 ha^{-1})
FVS basal area (m^2 ha^{-1})

Fig. B.10

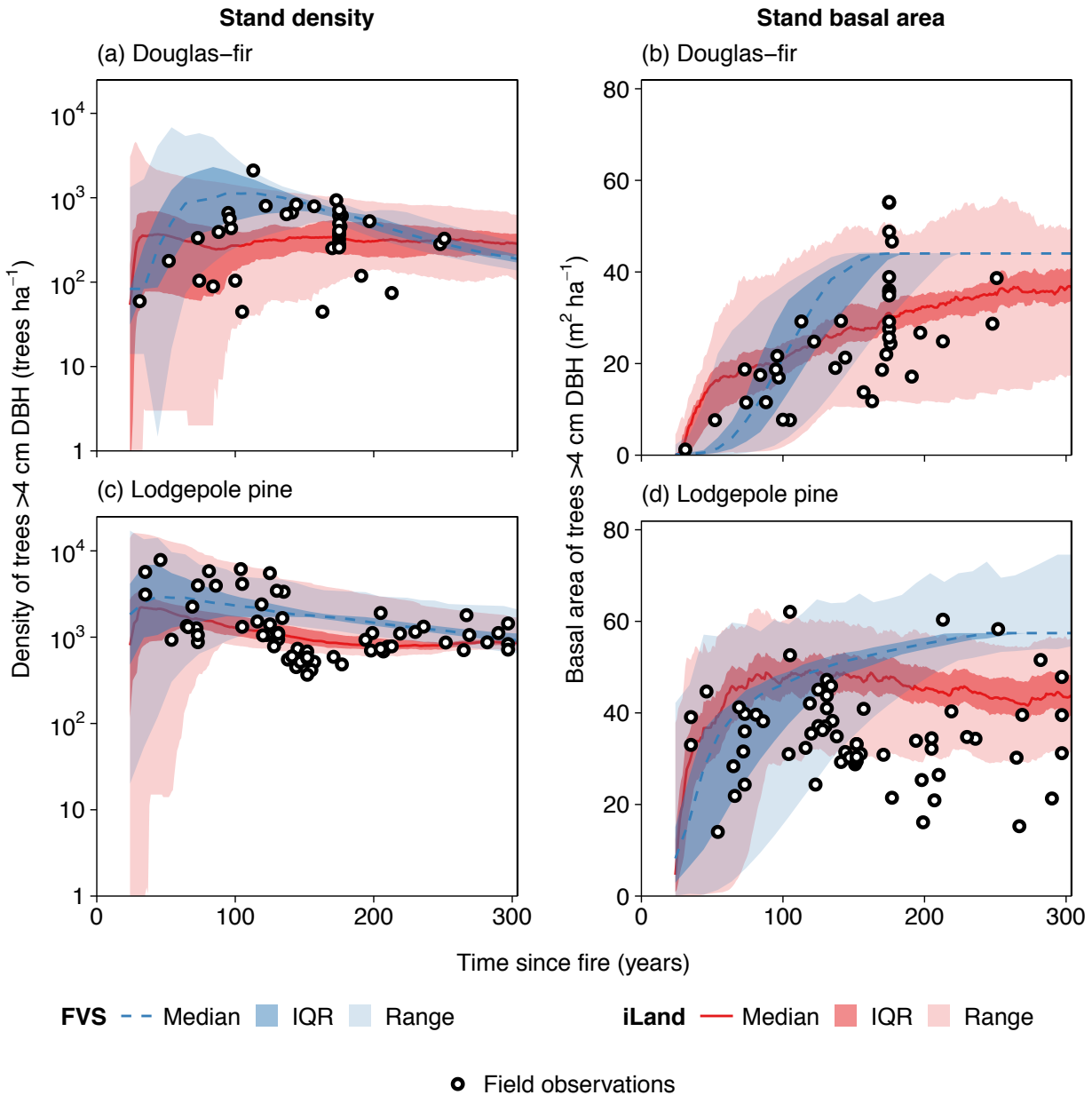
Stand density
Stand basal area
(a) Douglas–fir
(b) Douglas–fir
(c) Lodgepole pine
(d) Lodgepole pine
Density of trees >4 cm DBH (trees ha^{-1})
Basal area of trees >4 cm DBH (m^2 ha^{-1})
Time since fire (years)
FVS Median IQR Range
iLand Median IQR Range
Field observations

Fig. B.11