



It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers

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Abstract. Environmental change is accelerating in the 21st century, but how multiple drivers may interact to alter forest resilience remains uncertain. In forests affected by large high-severity disturbances, tree regeneration is a resilience linchpin that shapes successional trajectories for decades. We modeled stands of two widespread western U.S. conifers, Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and lodgepole pine (*Pinus contorta* var. *latifolia*), in Yellowstone National Park (Wyoming, USA) to ask (1) What combinations of distance to seed source, fire return interval, and warming-drying conditions cause postfire tree-regeneration failure? (2) If postfire tree regeneration was successful, how does early tree density differ under future climate relative to historical climate? We conducted a stand-level (1 ha) factorial simulation experiment using the individual-based forest process model iLand to identify combinations of fire return interval (11–100 yr), distance to seed source (50–1,000 m), and climate (historical, mid-21st century, late-21st century) where trees failed to regenerate by 30-yr postfire. If regeneration was successful, we compared stand densities between climate periods. Simulated postfire regeneration were surprisingly resilient to changing climate and fire drivers. Douglas-fir regeneration failed more frequently (55%) than lodgepole pine (28% and 16% for non-serotinous and serotinous stands, respectively). Distance to seed source was an important driver of regeneration failure for Douglas-fir and non-serotinous lodgepole pine; regeneration never failed when stands were 50 m from a seed source and nearly always failed when stands were 1 km away. Regeneration of serotinous lodgepole pine only failed when fire return intervals were ≤ 20 yr and stands were far (1 km) from a seed source. Warming climate increased regeneration success for Douglas-fir but did not affect lodgepole pine. If regeneration was successful, postfire density varied with climate. Douglas-fir and serotinous lodgepole pine regeneration density both increased under 21st-century climate but in response to different climate variables (growing season length vs. cold limitation). Results suggest that, given a warmer future with larger and more frequent fires, a greater number of stands that fail to regenerate after fires combined with increasing density in stands where regeneration is successful could produce a more coarse-grained forest landscape.

Key words: climate change; drought; forest resilience; process-based modeling; seedling establishment; succession; wildfire; Yellowstone National Park.

INTRODUCTION

Forests will experience increased stress as environmental change accelerates in the 21st century (Millar and Stephenson 2015, Trumbore et al. 2015). It remains poorly resolved whether forests will prove resilient and recover from these perturbations (Scheffer 2009) or instead transition to alternate states (Ghazoul et al. 2015, Reyer et al. 2015). Resilience is defined as the capacity of a system to absorb disturbances while retaining function, structure, feedbacks, and thus, identity (Walker et al. 2006). It is plausible that whole forested regions, such as the Amazon and boreal forest, may prove vulnerable to environmental change (Lenton et al. 2008, Hirota et al. 2011, Scheffer et al. 2012, Gauthier et al. 2015). Yet, quantifying forest resilience is challenging because multiple drivers, like natural disturbances, drought, land use, and nitrogen deposition will act on forests simultaneously, causing compound effects that are difficult to anticipate (Paine et al. 1998, Savage and Mast 2005, Staal et al.

2014, Buma 2015, Littell et al. 2016). Further, heterogeneity in abiotic conditions (e.g., substrate, elevation, aspect) and variation in tree functional traits (among and within species) can amplify or dampen driver effects (Lamont and Enright 2000, Chmura et al. 2011, Hoffmann et al. 2012, Johnstone et al. 2016). Thus, studies identifying interactions among multiple drivers that influence forest resilience could yield substantial insight into how and why 21st-century forests may change.

Regional forest change will likely emerge from the effects of environmental drivers on local- and landscape-scale processes (e.g., dispersal, seedling establishment, tree growth, competition, and mortality; Peters et al. 2004, 2007, Turner 2010). In forests where large wildfires kill most trees (i.e., stand-replacing fire), tree regeneration is a resilience linchpin (Turner et al. 1998, Johnstone and Chapin 2006, Johnstone et al. 2010, Savage et al. 2013) because seedling establishment in the first few years after disturbance dictates species composition and stand structure for decades to centuries (Kashian et al. 2005, Martínez-Vilalta and Lloret 2016). Robust postfire tree regeneration requires sufficient seed supply and delivery. Fire activity is projected to increase globally (Pechony and Shindell 2010, Seidl et al. 2014, 2017, Abatzoglou and Williams 2016) and postfire

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seedling densities may be reduced if burned patch sizes exceed effective dispersal distances or if multiple fires reoccur before trees reach reproductive maturity (Keeley et al. 1999, Enright et al. 2014, 2015, Chambers et al. 2016, Harvey et al. 2016a, Johnstone et al. 2016, Kemp et al. 2016, Stevens-Rumann and Morgan 2016). When seed is available, changing climate can also shape regeneration outcomes because tree seedlings are very sensitive to environmental conditions (Walck et al. 2011). Warming could reduce establishment if severe droughts follow fires (Clark et al. 2016, Harvey et al. 2016a) or warming could enhance establishment by reducing frost damage (Inouye 2000) and lengthening the growing season.

It is challenging to disentangle the effects of multiple drivers on postfire regeneration, but process-based models offer a promising approach when empirical studies cannot capture the full range of potential conditions. Large, short-interval fires and severe postfire droughts may become more prevalent in the western United States (Westerling 2016, Westerling et al. 2006) but still occur infrequently in subalpine forests. Thus, opportunities to observe in the field how combinations of changing fire and drought affect tree regeneration across heterogeneous landscapes are scant. Further, the magnitude of projected 21st-century environmental changes, their complex interactions, and the potential for emergent feedbacks suggest that future ecosystem dynamics may be difficult to predict solely based on current observation (Gustafson 2013, Bowman et al. 2015). However, process-based models allow exploration of a more complete set of conditions than found in the field and should provide robust projections under novel conditions because they are based on ecological first principles rather than empirical relationships (Seidl et al. 2011, Gustafson 2013, Keane et al. 2015). Models also can help distill complex phenomena down to essential components and highlight gaps in ecological understanding (Grimm and Berger 2016, Dietze 2017, Seidl 2017).

Yellowstone National Park (Wyoming, USA) is an excellent place to study how changing climate and fire regimes may alter postfire tree regeneration. Subalpine forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) experienced large stand-replacing fires at 100 to 300 yr intervals during the Holocene (Millsbaugh et al. 2000, Power et al. 2011). Postfire tree regeneration has generally been robust following fires (Turner et al. 1997, 2004, 2016). Some lodgepole pine trees in Yellowstone develop serotinous cones that remain closed and accumulate for many years; when heated

by fire, they open and drop large quantities of seed. Other lodgepole pines produce only non-serotinous cones that open as they mature. (Tinker et al. 1994). Lower montane forests are dominated by more drought-tolerant Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Warming and increased drought during the 21st century are projected to cause marked increases in the size, severity, and frequency of wildfires (Westerling et al. 2011) and alter the environmental context in which trees reestablish. The magnitude of expected change may be inconsistent with current forest structure and tree-species composition, meaning that forests could change profoundly (Hansen and Phillips 2015, Clark et al. 2017).

We conducted a factorial simulation experiment to evaluate effects of changing fire regimes and postfire climate conditions in Yellowstone on regeneration of two widespread Rocky Mountain conifer tree species: lodgepole pine and Douglas-fir. We asked two questions. (1) What combinations of distance to seed source, fire return interval (FRI) and warming-drying conditions cause postfire tree-regeneration failure? We hypothesized that postfire regeneration failure would be more likely if seed delivery was reduced by increasing distance to seed source (i.e., a proxy of increasing fire size or changing perimeter shape), if seed supply decreased with shortened FRI because trees burned before reaching maturity, or if postfire drought reduced seedling establishment (Table 1). We also expected that lodgepole pine and Douglas-fir would differ in their responses. We hypothesized Douglas-fir regeneration would be most sensitive to distance to seed source because Douglas-fir produce fewer relatively heavy seeds and rely on adjacent unburned forests for seed delivery; non-serotinous lodgepole pine regeneration would show intermediate sensitivity because they produce a greater number of lighter seeds; and serotinous lodgepole pine regeneration would be least sensitive due to the canopy seedbank. However, we expected serotinous lodgepole pine to be very sensitive to shortened FRIs that burn stands before the canopy seedbank develops. (2) If postfire tree regeneration was successful, how does early postfire tree density differ under future climate relative to historical climate? We hypothesized that, once trees established, their postfire densities would be sensitive to variation in climate such that increasing drought frequency and severity would be associated with reduced tree density. We also expected that early postfire Douglas-fir densities would be less affected by future drought than lodgepole pine because Douglas-fir are physiologically adapted to drier conditions.

TABLE 1. Hypotheses of how changing climate and fire regimes will interact to cause postfire regeneration failure in subalpine forest types found throughout western North America (adapted from Johnstone et al. 2016).

| Process | Driver | Hypothesized mechanism | Citations |
|------------------------|-------------------------|---|---|
| Seed supply | fire return interval | If fires become more frequent and sequential fires occur before trees mature, then postfire regeneration will be constrained. Serotinous lodgepole pine may be particularly vulnerable due to reliance on an in situ seedbank. | Buma et al. (2013) |
| Seed delivery | distance to seed source | If patches of stand-replacing fire exceed seed dispersal distances, postfire regeneration may be constrained, especially in the middle of large burned patches. Non-serotinous lodgepole and Douglas-fir may be particularly vulnerable due to their reliance on unburned trees as a seed source. | Harvey et al. (2016a), Turner et al. (1999, 2004, 2016) |
| Seedling establishment | postfire drought | If drought occurs in the first few years postfire, seedling establishment may be reduced even if seed is abundant. Lower montane sites, which are already warmer and drier, may be especially vulnerable to drought. | Harvey et al. (2016a) |

STUDY AREA AND METHODS

Study area

Yellowstone National Park encompasses approximately 9,000 km² in northwestern Wyoming, USA. Elevation ranges from 1,600 m to 3,400 m, with lower tree line at 1,800 m and upper tree line at 3,050 m (Despain 1990). Climate is relatively warm and dry in the lower montane zone where Douglas-fir is common, with a mean July temperature of 17.5°C and 390 mm of annual precipitation (Western Regional Climate Center 2017a,b). Climate is cooler and wetter in the higher-elevation subalpine zone, with a mean July temperature of 14°C and annual precipitation of 584 mm. Forest soils are generally derived from volcanic parent material, typically rhyolite or andesite. Rhyolite-derived soils have less mineral nitrogen (Whitlock 1993) and poor water holding capacity (Simard et al. 2012) compared to soils derived from andesite (Despain 1990), but both are considered infertile. Douglas-fir and lodgepole pine are obligate seeders and, in Yellowstone, both experience stand-replacing fire. Seeds are wind dispersed and most seeds fall within 100 m of the source (Burns and Honkala 1990). Following the iconic 1988 Yellowstone fires, which burned two-thirds of the park, Douglas-fir and lodgepole pine both reestablished successfully, albeit with substantial variability across the landscape. Early (24 yr) post-1988 fire Douglas-fir stand densities ranged from 0 to 19,667 stems/ha with a median of 1,250 stems/ha (Donato et al. 2016); postfire (24 yr) lodgepole pine densities ranged widely, from 0 to >340,000 stems/ha with a median density of 4,050 stems/ha (Turner et al. 2016). Stands where prefire serotiny was high account for the denser postfire regeneration. Stands where prefire serotiny was low had postfire densities ranging from 600 to 2,300 stems/ha (Turner et al. 1997, 2004).

Model overview and simulation experiment

We simulated stand-level (1-ha) dynamics using an individual-based forest process model, iLand (Seidl et al. 2012, 2014). iLand simulates trees within a stand and uses a hierarchical framework wherein broader-scale processes emerge dynamically from interactions among individual trees (Seidl et al. 2012). iLand represents tree growth, mortality, and competition in response to canopy light interception, radiation, thermal conditions, soil water, and nutrient limitation. While climate and soil conditions are assumed to be spatially homogeneous within a stand (1 ha), variation in light is simulated at 2 × 2 m horizontal resolution based on overstory structure and composition. Climate variability is considered at a daily temporal grain. iLand also simulates disturbances. Extensive model documentation is *available online*.⁴ The model has been well tested and extensively used in the western United States (Seidl et al. 2012, 2014) and Europe (Pedro et al. 2015, Thom et al. 2017a,b), and has recently been parameterized and evaluated for Yellowstone.

The model explicitly simulates tree regeneration based on seed production, seed dispersal, and effects of temperature, light, and soil-moisture conditions on seedling establishment

and survival (Seidl et al. 2012; Appendix S1). We extended the regeneration module of iLand in two ways. First, we added serotiny as a functional trait for lodgepole pine. Serotinous lodgepole pine only drop seeds in the year following a fire. When trees are serotinous, the amount of seed released is a multiple of the seeds produced by a non-serotinous tree, representing the accumulation of cones over multiple years. We further incorporated an effect of soil moisture on rates of seedling establishment in addition to the already existing temperature limitation. The probability of seedling establishment at a 2-m cell is linearly scaled between a species-specific minimum soil water potential, where establishment does not occur, and field capacity, where establishment is not constrained by soil moisture. We evaluated the improved regeneration module of iLand and simulated tree establishment agreed well with independent field observations (Appendix S2).

Initial stand structure.—Simulations were initialized with a representative monospecific stand for each forest type using median stem density and tree heights for each forest type as recorded 11 yr after the 1988 Yellowstone fires (Turner et al. 1999, 2004, 2016, Donato et al. 2016). We chose not to vary initial stand structure within each forest type because we were interested in experimentally testing climate–fire interactions and therefore we minimized other sources of variation.

Topoedaphic conditions.—Our simulations did include variation in substrate and elevation, because both influence tree establishment, and thus, are important for addressing our questions. We simulated soils derived from two volcanic parent materials, rhyolite and andesite, which account for most of Yellowstone's subalpine landscape (Despain 1990). Relative fertility rating (calibrated within iLand to 45 and 55 for rhyolite and andesite, respectively, on a [0–100] scale) and soil texture (62% sand, 30% silt, 8% clay for rhyolite, 51% sand, 37% silt, 12% clay for andesite) were set according to representative soil surveys conducted throughout Yellowstone (Turner et al. 1999, Simard et al. 2012). For all soils, effective depth was set to 95 cm. Elevation was included by simulating stands at lower treeline (2,000 m), as well as the mid (2,300 m), and high elevation (2,600 m) of the subalpine zone. These span the elevational range in which Douglas-fir and lodgepole pine are found regionally.

Factorial simulation experiment.—We conducted a factorial experiment using iLand to evaluate how combinations of climate and fire conditions affected early (30 yr) postfire tree regeneration of Douglas-fir, non-serotinous lodgepole pine, and serotinous lodgepole pine. Thirty years was selected as a benchmark for assessing regeneration because it accommodates the more protracted establishment window of conifers that lack a canopy seedbank (Turner et al. 1999, Donato et al. 2016), captures longer-term effects of climate on young trees, and largely avoids the self-thinning that occurs in dense stands during later periods of stand development. The factors considered in the experiment for all forest types were FRI, distance to seed source, and variation in climate and they were applied to every combination of the two substrates and three elevations.

⁴ <http://iland.boku.ac.at>

Return interval for high-severity fire.—Effects of FRI were simulated by burning stands at age 11, 20, 50, or 100 yr. Simulated FRI spanned the range from short-interval fires projected by the end of the 21st century (Westerling et al. 2011) and observed in Yellowstone (e.g., the 2000 Boundary Fire burned 12-yr old lodgepole pine that regenerated from the 1988 fires) to the lower end of FRIs observed during the Holocene (Mills et al. 2000). Stand development was simulated until the specified FRI was reached, at which time stand-replacing fire killed all prefire trees, saplings, and seedlings.

Distance to seed source.—We simulated stands at distances of 50 m, 500 m, and 1 km from the nearest unburned seed source, which could either represent forest at the fire edge or islands of unburned forest in the middle of burned patches. In actual fires, distance to seed source is primarily a function of the size and shape of high-severity burned patches. Seed supply and dispersal were modeled with species-specific negative exponential dispersal kernels and compared with field surveys (Appendices S1 and S2).

Variation in climate.—Effects of climate were simulated by driving the model with climate from three 30-yr periods. We used a historical period (1950–1980) and two levels of climate change that represented a temperature increase of 3.0° and 5.5°C, indicative of mid-century (2029–2059) and late-century (2069–2099) warming under the Representative Concentration Pathway (RCP) 8.5. The RCP 8.5 scenario represents a substantial increase in CO₂ over the next 100 yr, although current trends suggest this emissions scenario is already being exceeded (Smith et al. 2016). We used the CNRM-CM5 global circulation model (GCM; Voltaire et al. 2013), which reproduces historical conditions in the northern Rockies well (Westerling et al. 2011). Climate variables that drive iLand simulations include maximum and minimum daily temperature, daily precipitation, radiation, and vapor pressure deficit. Climate data were statistically downscaled to a 4-km resolution using the Multivariate Adaptive Constructed Analogs approach (Abatzoglou and Brown 2012; see data *available online*).⁵ Data were extracted for one grid cell per elevation that corresponded to a median density field plot. We chose only one grid cell per elevation because we were not attempting to characterize effects of climate variation within elevation bands, but rather across the elevational range of the species' current distributions.

Replication.—Simulations were each run 20 times and years were drawn randomly with replacement from the appropriate 30-yr climate record to ensure the order of the climate record did not influence simulation results. This led to 20 replicates of each forest type (three levels), substrate (two levels), elevation (three levels), FRI (four levels), distance to seed source (three levels), and climate (three levels) combination.

Model outputs

We focused on two model outputs: frequency of regeneration failure at 30 yr postfire (Question 1) and, if regeneration was successful during the historical climate period, the

difference in mean tree density between historical and projected 21st-century climate (Question 2). Regeneration failure was defined as stands that had <50 stems/ha (including seedlings, saplings, and young trees) at postfire-year 30, which would indicate potential transition to a non-forest condition. The United Nations Food and Agricultural Organization (FAO) defines forest as any area > 0.5 ha that has > 10% canopy cover (Chazdon et al. 2016). Our threshold of 50 stems/ha in Yellowstone would fall well below the FAO definition, and such densities are considerably lower than those commonly observed following recent fires in Yellowstone. For example, only 1.4% of early postfire (24 yr) stands had densities <50 stems/ha after the 1988 Yellowstone fires (Turner et al. 2016). We then calculated the frequency of regeneration failure across the 20 replicates of each simulation. If regeneration was successful (i.e., ≥50 trees/ha) during the historical climate period, we calculated the difference in mean 30-yr postfire stem density between the historical and each projected 21st-century climate period.

Data analysis

To address Question 1 (regeneration frequency), we first used ANOVA to explain factors influencing the frequency of regeneration failure based on the levels of each treatment in the simulation experiment. We conducted analyses separately by forest type. We then explored the influences of climate in more detail, applying linear mixed-effects models (LMMs). We included mean growing-season temperature, mean annual precipitation, mean growing season soil water potential, and number of growing season frost events as fixed effects. Random effects included non-climate related treatment-level variables (i.e., distance to seed source and fire return interval). This approach allowed us to ask, controlling for non-climate related factors, what specific climate variables explained variation in response variables? We used the lme4 package in R (Bates et al. 2015) and all explanatory variables were assessed for collinearity. Variables were not included in the same model if they had a pairwise correlation of >0.7. The dependent variable was transformed using a logit transformation. In regressions, all continuous variables were standardized prior to analysis. Exhaustive model selection (Burnham and Anderson 2002) was conducted in all analyses (ANOVA and LMM) to determine the most important variables using the R package MuMIn (Barton 2016). Top models (Akaike's information criterion corrected for sample size, AIC_c < 2) are presented for ANOVA and model averages are presented for LMMs. Analyses were conducted in R statistical software (R Core Team 2016).

To address Question 2 (density differences), we first used ANOVA to explain differences in stand densities between the 21st century and historical periods, when regeneration was successful, for each forest type. We then used LMMs to identify climate variables that explained treatment level effects (as described above). A $\sqrt{}$ transformation was applied to the dependent variable for serotinous lodgepole pine so that residuals were approximately normally distributed. All statistical analyses were conducted to efficiently find patterns in the simulated data as opposed to determine statistical significance. Thus, in results the magnitudes of difference between treatments are emphasized. In the text, means ± SE are presented.

⁵<http://maca.northwestknowledge.net/index.php>

RESULTS

Across all simulations, Douglas-fir densities at postfire year 30 ranged from 0 to 21,186 stems/ha ($2,677 \pm 327$ stems/ha, median = 132 stems/ha). Non-serotinous lodgepole pine densities ranged from 3 to 3,197 stems/ha (815 ± 62 stems/ha, median = 412 stems/ha). Serotinous lodgepole pine densities were between 7 and 93,972 stems/ha ($23,120 \pm 1,730$ stems/ha, median = 4,569 stems/ha). Simulated stand densities of these forest types closely matched field observations of postfire densities in Yellowstone (Donato et al. 2016, Turner et al. 2016; Appendix S2). In general, simulated densities decreased with distance to seed source and increased or stayed the same under 21st century climate, compared with historical conditions.

Frequency of regeneration failure (Question 1)

Douglas-fir.—Douglas-fir failed to regenerate by postfire year 30 in 55% of the simulations (Fig. 1), primarily due to distance from seed source (Table 2A, Fig. 2A). Regeneration was always successful if stands were 50 m from a seed source and nearly always failed when stands were 1 km away (Fig. 3A). Climate period was also an important driver, with regeneration failure declining from $64\% \pm 6\%$ under historical climate to $41\% \pm 5\%$ under late-21st-century climate. When direct measures of climate were substituted for categorical variables, LMMs revealed that reduced failure of Douglas-fir regeneration in 21st-century climate periods was driven by fewer growing season frost events (Table 3A).

Non-serotinous lodgepole pine.—Non-serotinous lodgepole pine failed to regenerate by postfire year 30 in 28% of simulations (Fig. 1). Like Douglas-fir, regeneration failure was most strongly determined by distance to seed source (Table 2A, Fig. 2B); failure was likely when stands were 1 km from a seed source and minimal when stands were 50 or 500 m away (Fig. 3B). Elevation and substrate had small effects on regeneration failure. Regeneration failure occurred more frequently at low (32%) vs. high elevations

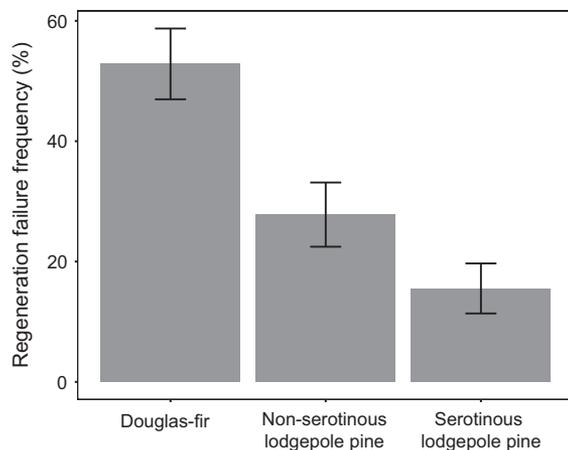


FIG. 1. Frequency of regeneration failure (%) at postfire-year 30 for Douglas-fir, non-serotinous lodgepole pine, and serotinous lodgepole pine across all simulations. Values are means \pm 2 SE.

(23%) and on rhyolite (29%) vs. andesite substrate (26%). Climate period did not affect regeneration failure. LMMs revealed that the small effects of elevation and substrate reflected tradeoffs between drying soils, which increased regeneration failure, and reduced growing season frost events, which decreased regeneration failure (Table 3A).

Serotinous lodgepole pine.—Serotinous lodgepole pine failed to regenerate by postfire year 30 in <20% of simulations (Fig. 1). Regeneration failure was driven by distance to seed source, FRI, and their interaction (Table 2A, Fig. 2C). Regeneration failure was more frequent when stands were 1 km from seed source and FRIs were ≤ 20 yr (Fig. 3C). As with non-serotinous lodgepole pine, elevation had a small effect on regeneration failure (19% at low vs. 13% at high elevation), and climate period was unimportant (Table 3B).

Density differences (Question 2)

Douglas-fir.—Where regeneration was successful under historical climate, simulated regeneration density in postfire year 30 averaged $1,205 \pm 114$ stems/ha. Postfire regeneration density increased nearly fourfold (to $4,036 \pm 411$ stems/ha) under mid-21st-century conditions and sixfold (to $7,893 \pm 776$ stems/ha) under late-21st-century conditions (Table 2B). Tree density increased only when stands were near (50 m) a seed source (Table 2B). Substrate also had a minor effect on density differences (Table 2B). LMMs revealed that stand densities increased with warming temperature and more precipitation (Table 3B, Fig. 4).

Non-serotinous lodgepole pine.—Simulated stand densities averaged 800 ± 105 stems/ha in stands where regeneration was successful under historical conditions and changed little in mid (910 ± 116 stems/ha) and late (790 ± 71 stems/ha) 21st-century periods (Table 2B). Densities were also slightly greater at low elevations close to seed source (increasing to 971 ± 32 stems/ha) (Table 2B) but did not change at mid or high elevations. LMMs suggest decreases in annual precipitation and drying soils explained variability in stand density differences (Table 3B).

Serotinous lodgepole pine.—When regeneration was successful, simulated densities of serotinous lodgepole pine at postfire year 30 averaged $19,800 \pm 1,929$ stems/ha under historical conditions. Serotinous lodgepole pine densities increased by nearly 63% (by $12,505 \pm 2,123$ stems/ha to reach $>32,000$ stems/ha) at low elevations during 21st-century periods (Table 2B). Stand densities increased with an FRI of 50 yr (to $31,247 \pm 1,298$ stems/ha) or 100 yr (to $26,013 \pm 1,566$ stems/ha) (Table 2B). Distance to seed source had a modest effect as well, with densities increasing to $27,900 \pm 1,927$ stems/ha at distances within 500 m of a seed source (Table 2B). Treatment level effects were explained by decreasing annual precipitation in the LMMs (Table 3B).

DISCUSSION

Results of this study indicate that regeneration of two conifers following stand-replacing fire in subalpine forests is shaped by the complex interplay among several drivers

TABLE 2. ANOVA results of top models ($AIC_c < 2$) predicting (A) frequency of regeneration failure and (B) density differences between 21st century and historical periods, if regeneration was successful. Regeneration failure frequency was logit transformed.

| | Douglas-fir | | | Non-serotinous lodgepole pine | Serotinous Lodgepole pine |
|--------------------------------|-------------------------------------|---------------------------|---------------------------|----------------------------------|---------------------------|
| | Model 1 | Model 2 | Model 3 | Model 1 | Model 1 |
| A. Regeneration failure | | | | | |
| Distance to seed source | 3,843.8*** 2,634.9 (2) | 3,877.9*** 2,634.9 (2) | 3,846.9*** 2,634.9 (2) | 2,503.4*** 1,868.7 (2) | 519.0*** 667.7 (2) |
| Climate period | 165.8*** 113.7 (2) | 167.3*** 113.7 (2) | 165.9*** 113.7 (2) | | |
| FRI | | | | | 68.1*** 131.4 (3) |
| Elevation | | 1.9*** 1.3 (2) | | 41.4*** 30.9 (2) | 16.8*** 21.6 (2) |
| Substrate | | | 1.2*** 0.4 (1) | 16.3*** 6.1 (1) | |
| Distance × Climate period | 58.3*** 79.9 (4) | 58.8*** 79.9 (4) | 58.3*** 79.9 (4) | | |
| Distance × FRI | | | | | 61.9*** 238.9 (6) |
| Distance × Elevation | | | | 16.3*** 24.3 (4) | |
| Adj. R^2 | 0.97 | 0.97 | 0.97 | 0.96 | 0.88 |
| B. Density differences | | | | | |
| Distance to seed source | 1,225.6*** 1.7×10^9 (1) | | | 28.0*** 1.1×10^6 (2) | 30.8*** 94.5 (2) |
| Climate Period | 192.9*** 2.7×10^8 (1) | | | 27.1*** 5.1×10^5 (1) | |
| FRI | | | | | 31.1*** 142.9 (3) |
| Elevation | | | | 24.2*** 9.1×10^5 (2) | 57.3*** 175.6 (2) |
| Substrate | 22.4*** 3.2×10^7 (1) | | | | |
| Distance × Climate period | 176.8*** 2.5×10^8 (1) | | | | |
| Elevation × FRI | | | | | 14.4*** 132.9 (6) |
| Distance × Elevation | | | | 17.5*** 1.3×10^6 (4) | |
| Adj. R^2 | 0.95 | | | 0.58 | 0.71 |

Notes: Density differences for serotinous lodgepole pine was transformed to the $\sqrt{9}$. Sum of squares, F values, significance levels, and model-adjusted R^2 are presented. AIC_c , Akaike's information criterion corrected for sample size; FRI, fire return interval. *** $P < 0.001$.

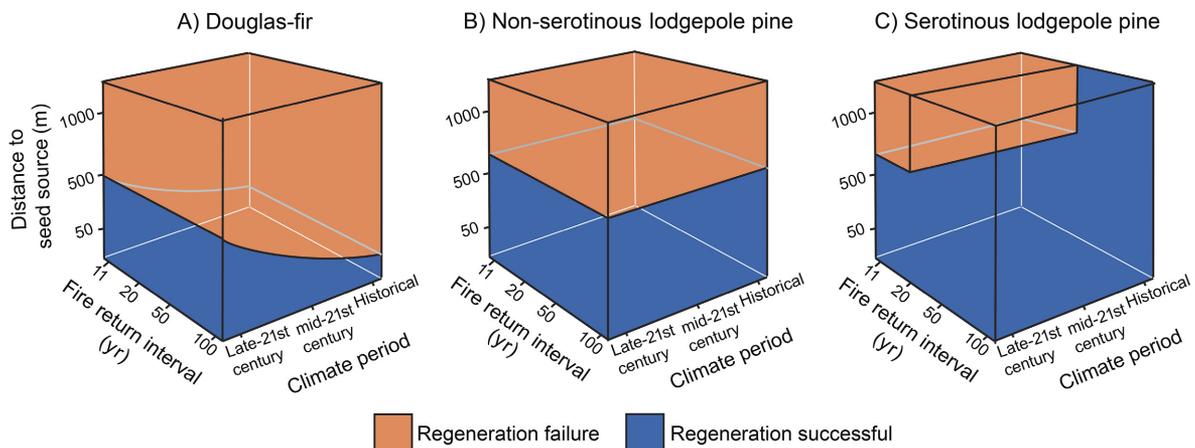


FIG. 2. State space conceptualizing conditions that led to postfire-year 30 tree regeneration failure and success as a function of distance to seed source, fire return interval, and climate period for (A) Douglas-fir, (B) non-serotinous lodgepole pine, and (C) serotinous lodgepole pine, three widespread forest types in Rocky Mountain forests.

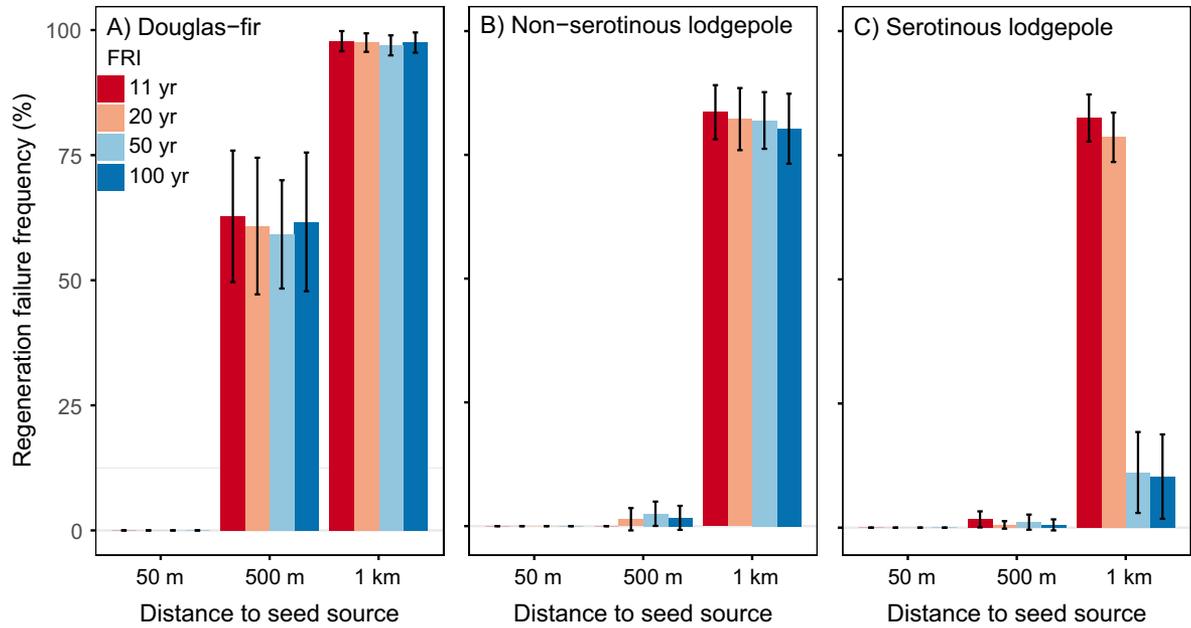


FIG. 3. Frequency of regeneration failure (%) at postfire-year 30 as a function of distance from seed source and fire return interval (FRI) for (A) Douglas-fir, (B) non-serotinous lodgepole pine, and (C) serotinous lodgepole pine. Values are means \pm 2 SE.

TABLE 3. Averaged linear mixed effects regression results of top models ($AIC_c < 2$) predicting (A) frequency of regeneration failure and (B) density differences between 21st century and historical periods, if regeneration was successful.

| | Douglas-fir | Non-serotinous lodgepole pine | Serotinous lodgepole pine |
|--|-------------|-------------------------------|---------------------------|
| (A) Regeneration failure | | | |
| Fixed effects | | | |
| Intercept | 0.02 | -0.003 | -0.004 |
| Growing season frost events | 0.16*** | 0.09** | 0.14** |
| Growing season soil water potential | | -0.11*** | -0.04 |
| Growing season temperature | -0.06** | | |
| Annual precipitation | | -0.01 | -0.04 |
| Frost events \times temperature | 0.03 | | |
| Frost events \times soil water potential | | | -0.03 |
| Frost events \times Precipitation | | -0.006 | -0.02 |
| Random effects | | | |
| FRI | | | 0.37 |
| Distance to seed source | 0.95 | 0.96 | 0.76 |
| (B) Density differences | | | |
| Fixed effects | | | |
| Intercept | -0.16 | 0.14 | 0.06 |
| Growing season frost events | | 0.14 | 0.07 |
| Growing season soil water potential | | 0.30** | -0.01 |
| Growing season temperature | 0.47*** | | |
| Annual precipitation | 0.41*** | -0.54*** | -0.41*** |
| Precipitation: Temperature | -0.14* | | |
| Frost events: Precipitation | | 0.22** | 0.07 |
| Frost events: soil water potential | | | 0.04 |
| Precipitation: soil water potential | | | -0.02 |
| Random effects | | | |
| FRI | | 0.26 | 0.45 |
| Distance to seed source | 0.83 | 0.37 | 0.38 |

Notes: Regeneration failure frequency was logit transformed. Density differences for serotinous lodgepole pine was transformed to the $\sqrt{}$. Coefficients of all continuous variables were standardized to z scores and significance levels are presented for fixed effects. Standard deviations are presented for random effects.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

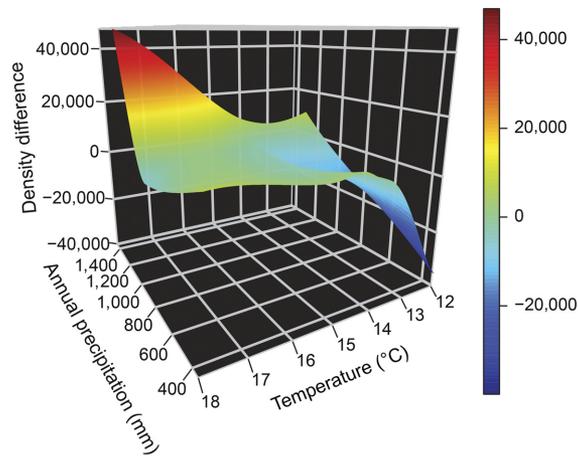


FIG. 4. Differences in early postfire (30 yr) Douglas-fir stand density between historical and 21st-century climate periods vs. 21st-century annual precipitation (mm) and growing season mean temperature ($^{\circ}\text{C}$). Values are predictions from a loess fit.

related to future climate and fire regimes, some that constrain regeneration and others that enhance it. Overall, postfire regeneration of Douglas-fir and lodgepole pine was surprisingly resilient to the substantial changes in climate and fire regimes projected for Yellowstone, particularly when drivers were considered individually. Simulated regeneration failure generally required multiple changing drivers (Fig. 2). Stand-level simulation experiments cannot predict how and where forests will change across the landscape, and results could differ in mixed-species stands. However, this study reveals complex responses to multiple changing drivers and offers insights into the mechanisms underpinning forest resilience (Reyer et al. 2015, Trumbore et al. 2015).

What causes regeneration failure (or success?)

Distance to seed source explained nearly all variation in regeneration failure for Douglas-fir and non-serotinous lodgepole pine, consistent with our hypotheses (Table 1). This finding suggests there are large consequences associated with projections of increased area burned during the 21st century (Westerling et al. 2011), as the size and shape of high-severity burn patches strongly determines regeneration of conifers that lack a canopy seed bank. Indeed, most regeneration following recent fires in the northern Rocky Mountains has occurred within 150 m of the unburned edge (Donato et al. 2016, Harvey et al. 2016a, Kemp et al. 2016). Our findings are consistent with prior studies that emphasize the importance of biotic residuals (i.e., propagules or surviving trees within large disturbed patches) for regeneration following large, infrequent disturbances (Franklin and Forman 1987, Turner et al. 1994, 1998, Franklin et al. 2002, Seidl et al. 2014, Johnstone et al. 2016, Tepley et al. 2017).

Regeneration failure was uncommon in serotinous lodgepole pine stands, which develop canopy seedbanks. Regeneration failure only occurred in stands far from seed source when fires burned again before the development of the canopy seed source (Fig. 2). Serotiny is an effective fire adaptation expressed in a variety of species globally (Lamont et al. 1991, He et al. 2012). Dense seed rain from

cones that open after fire enables serotinous tree species to establish rapidly in postfire environments where a flush of resources is available and competition is low (Tinker et al. 1994, Keeley et al. 2005, Causley et al. 2016). Serotiny may also buffer against other drivers of postfire regeneration failure, including poor substrates for establishment (Johnstone and Chapin 2006, Johnstone et al. 2009), seed predation (Lamont et al. 1991, though see Benkman and Siepielski 2004), and postfire drought (Lamont and He 2017). This prolific production of seed may partly explain the lack of sensitivity to climate conditions in our simulation study. After the 1988 Yellowstone fires, postfire regeneration density in stands where prefire serotiny was high commonly exceeded 100,000 stems/ha. Even if hostile conditions reduce stand density by 90% a robust forest will grow back. Serotiny can be an effective bet-hedging strategy for species facing variable environments (Buma et al. 2013).

Serotinous stands lose their advantage if fires reoccur before trees are reproductively mature (Johnstone and Chapin 2006, Buma et al. 2013). Thus, postfire densities of serotinous species could be substantially reduced by short-interval fires, consistent with other systems where fire intervals are shortening (Keeley et al. 1999, Enright et al. 2015, Bowman et al. 2016). For example, serotinous black spruce (*Picea mariana*) seed supply was reduced 90% after short-interval fires in the Yukon Territories, Canada (Brown and Johnstone 2012). However, short FRIs alone were insufficient to initiate regeneration failure of simulated serotinous lodgepole pine stands in Yellowstone; burned stands also had to be far from seed source, limiting the seed supply from neighboring unburned stands.

Climate effects on regeneration failure differed by forest type. Warming enhanced Douglas-fir regeneration because frost events became less frequent during the growing season. Although growing season frost became rare in simulations under 21st-century conditions, warming could expose seedlings to winter frost damage if snow cover is reduced because snow insulates seedlings from temperature fluctuations (Batllori et al. 2009, Renard et al. 2016). Reductions in winter snowpack are projected to be greatest at mid elevations in Yellowstone vs. high elevations, where snowpack is projected to remain consistent (Tercek and Rodman 2016), or low elevations, where snow pack is already less. Winter warming could also delay sapling spring growth initiation if chilling requirements are no longer met (Ford et al. 2016). The insulating effect of snow and winter chilling is not currently represented in iLand, and further study is needed to determine how winter climate change may counter effects of declining growing season frost.

Our study suggests substantial resilience of lodgepole pine stands to projected warming; non-forest states rarely occurred in the simulation with the combinations of factors considered here, although tree density could change substantially in the future (e.g., Schoennagel et al. 2006). In part, this may reflect our conservative definition of regeneration failure (< 50 stems/ha at postfire year 30) relative to the prolific regeneration capacity of lodgepole pine and its ability to produce cones at a young age (Turner et al. 2007). Our results are relatively consistent with climate suitability projections of 21st-century lodgepole pine and Douglas-fir distributions in Yellowstone, which suggest range reductions

and distributional shifts to higher elevations. (Bartlein et al. 1997, Crookston et al. 2010, Coops and Waring 2011, Gray and Hamann 2013, Bell et al. 2014, Hansen and Phillips 2015). While our approach takes a step beyond climate suitability studies by considering the processes that are important during a sensitive life-history stage (regeneration), we still only consider the responses of individual tree species to changing climate and fire. However, the abundance and distribution of a species can be strongly shaped by competitive interactions, particularly at local to landscape scales (Copenhaver-Parry et al. 2017), and process-based models are a promising tool for determining where and why interspecific biotic interactions might modulate how tree species respond to climate change.

What explains changing stand densities?

Postfire stand densities for all three forest types were sensitive to both fire and climate drivers, with fire frequency and size influencing potential establishment and climate conditions largely affecting survival and growth. As hypothesized, warming led to increased density of Douglas-fir in our simulations, particularly when precipitation also increased (Fig. 4). Densification of Douglas-fir regeneration under warmer climate is consistent with expectations for a tree species at the leading edge of its distribution (Hansen and Phillips 2015) and with the fossil pollen record in Yellowstone. Conditions were warmer than present during the early to mid Holocene, and Douglas-fir expanded to higher elevations, but only on andesite substrate (Whitlock 1993). The lack of edaphic constraints on Douglas-fir regeneration in our simulations suggests other factors (e.g., competition among tree species) may have shaped Douglas-fir distributions in response to past climate variation.

Postfire lodgepole pine stand density was influenced by multiple climate factors, acting in opposing directions. Decreasing annual precipitation, which mainly falls as snow in Yellowstone, increased lodgepole pine densities. Reduced spring snowpack can lead to increased early postfire densities of tree species by lengthening growing seasons (Hansen et al. 2016), when there is sufficient soil moisture and little frost damage. However, soil drying decreased non-serotinous lodgepole pine densities. Effects of soil drying on lodgepole pine seedlings are well documented. Stand densities were substantially reduced in the northern Rockies when recent fires were followed by hot-dry vs. cool-wet conditions (Harvey et al. 2016a). Disentangling effects of opposing climate drivers of postfire regeneration could be explored more fully with experimental approaches.

Considered together, our simulations of postfire regeneration suggest that forest-landscape patterns could become increasingly coarse-grained in the future, as climate changes and fires become larger and more frequent. The number and size of non-forest patches could increase, due to regeneration failure, but the surrounding forests may actually become more dense. This could have important consequences for forest susceptibility to subsequent disturbance agents (Seidl et al. 2016a) and the provision of ecosystem services (Turner et al. 2013, Spies et al. 2017). Changes in spatial patterns of forest cover and structure could also be sensitive indicators of forest resilience (Scheffer et al. 2012,

Ghazoul et al. 2015, Seidl et al. 2016b). Increased regeneration failure over multiple fire cycles or shifting spatial patterns can indicate slowing of ecosystem recovery and impending transitions to alternate states (Kéfi et al. 2007, Dakos et al. 2011, Walker et al. 2016, Ghazoul and Chazdon 2017). Establishing resilience indicators for forest systems is particularly important because forests can respond slowly to drivers, and marginal changes may go unrecognized if postfire recovery dynamics are not monitored through time (Paine et al. 1998, Hughes et al. 2013, Lindenmayer et al. 2016).

CONCLUSIONS

Tree regeneration is a resilience linchpin in forests where large high-severity disturbances occur (Gauthier et al. 2015, Johnstone et al. 2016, Turetsky et al. 2016). Simulated post-fire regeneration of two widespread subalpine conifers was surprisingly resilient to future climate and fire regimes. Multiple drivers were often required for regeneration to fail, distance to seed source, paired with cold temperature for Douglas-fir or with short FRIs for serotinous lodgepole pine (Fig. 2), and such relationships may well apply to other obligate seeders. It appears that the indirect effects of 21st-century warming, causing an increase in the size and frequency of stand-replacing fire (Westerling et al. 2011, Harvey et al. 2016b), could exceed the direct effects of warming on early postfire conifer regeneration in Yellowstone.

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LITERATURE CITED

- Abatzoglou, J. T., and T. J. Brown. 2012. A comparison of statistical downscaling methods suited for wildfire applications. *International Journal of Climatology* 32:772–780.
- Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences USA* 113: 11770–11775.
- Bartlein, P. J., C. Whitlock, and S. L. Shafer. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conservation Biology* 11:782–792.
- Barton, K. 2016. MuMIn: Multi-Model inference. <https://cran.r-project.org/web/packages/MuMIn/index.html>
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Battlori, E., J. J. Camarero, J. M. Ninot, and E. Gutiérrez. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. *Global Ecology and Biogeography* 18:460–472.

- Bell, D. M., J. B. Bradford, and W. K. Lauenroth. 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography* 23:168–180.
- Benkman, C. W., and A. M. Siepielski. 2004. A keystone selective agent? Pine squirrels and the frequency of serotiny in lodgepole pine. *Ecology* 85:2082–2087.
- Bowman, D. M. J. S., G. L. W. Perry, and J. B. Marston. 2015. Feedbacks and landscape-level vegetation dynamics. *Trends in Ecology and Evolution* 30:255–260.
- Bowman, D. M. J. S., G. J. Williamson, L. D. Prior, and B. P. Murphy. 2016. The relative importance of intrinsic and extrinsic factors in the decline of obligate seeder forests. *Global Ecology and Biogeography* 25:1166–1172.
- Brown, C. D., and J. F. Johnstone. 2012. Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *Forest Ecology and Management* 266:34–41.
- Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* 6:1–15.
- Buma, B., C. D. Brown, D. C. Donato, J. B. Fontaine, and J. F. Johnstone. 2013. The impacts of changing disturbance regimes on serotinous plant populations and communities. *BioScience* 63:866–876.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer-Verlag, New York, New York, USA.
- Burns, R. M., and B. H. Honkala. 1990. Silvics manual volume 1-conifers and volume 2-hardwoods. Second edition. U.S. Department of Agriculture, Forest Service, Washington, D.C.
- Causley, C. L., W. Fowler, B. B. Lamont, and T. He. 2016. Fitness benefits of serotiny in fire- and drought-prone environments. *Plant Ecology* 217:779.
- Chambers, M. E., P. J. Fornwalt, S. L. Malone, and M. A. Battaglia. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine dominated forests of the Colorado Front Range. *Forest Ecology and Management* 378:57–67.
- Chazdon, R. L., P. H. S. Brancalion, L. Laestadius, A. Bennett-Curry, K. Buckingham, C. Kumar, J. Moll-Rocek, I. C. G. Vieira, and S. J. Wilson. 2016. When is a forest a forest? Forest concepts and definitions in the era of forest and landscape restoration. *Ambio* 45:538–550.
- Chmura, D. J., P. D. Anderson, G. T. Howe, C. A. Harrington, J. E. Halofsky, D. L. Peterson, D. C. Shaw, and J. B. St.Clair. 2011. Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. *Forest Ecology and Management* 261:1121–1142.
- Clark, J. S., et al. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity. *Global Change Biology* 22:2329–2352.
- Clark, J. A., R. A. Loehman, and R. E. Keane. 2017. Climate changes and wildfire alter vegetation of Yellowstone National Park, but forest cover persists. *Ecosphere* 8:e01636.
- Coops, N. C., and R. H. Waring. 2011. A process-based approach to estimate lodgepole pine (*Pinus contorta* Dougl.) distribution in the Pacific Northwest under climate change. *Climatic Change* 105:313–328.
- Copenhaver-Parry, P. E., B. N. Shuman, and D. B. Tinker. 2017. Toward an improved conceptual understanding of North American tree species distributions. *Ecosphere* 8:e01853.
- Crookston, N. L., G. E. Rehfeldt, G. E. Dixon, and A. R. Weiskittel. 2010. Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics. *Forest Ecology and Management* 260:1198–1211.
- Dakos, V., S. Kéfi, M. Rietkerk, E. H. van Nes, and M. Scheffer. 2011. Slowing down in spatially patterned ecosystems at the brink of collapse. *American Naturalist* 177:E153–E166.
- Despain, D. G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart Publishers, Boulder, Colorado, USA.
- Dietze, M. C. 2017. Ecological forecasting. Princeton University Press, Princeton, New Jersey, USA.
- Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. Regeneration of montane forests 24 years after the 1988 Yellowstone fires: A fire-catalyzed shift in lower treelines? *Ecosphere* 7:e01410.
- Enright, N. J., J. B. Fontaine, B. B. Lamont, B. P. Miller, and V. C. Westcott. 2014. Resistance and resilience to changing climate and fire regime depend on plant functional traits. *Journal of Ecology* 102:1572–1581.
- Enright, N. J., J. B. Fontaine, D. M. Bowman, R. A. Bradstock, and R. J. Williams. 2015. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment* 13:265–272.
- Ford, K. R., C. A. Harrington, S. Bansal, P. J. Gould, and J. B. St. Clair. 2016. Will changes in phenology track climate change? A study of growth initiation timing in coast Douglas-fir. *Global Change Biology* 22:3712–3723.
- Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology* 1:5–18.
- Franklin, J. F., et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155:399–423.
- Gauthier, S., P. Bernier, T. Kuuluvainen, A. Z. Shvidenko, and D. G. Schepaschenko. 2015. Boreal forest health and global change. *Science* 349:819–822.
- Ghazoul, J., and R. Chazdon. 2017. Degradation and recovery in changing forest landscapes: a multiscale conceptual framework. *Annual Reviews of Environment and Resources* 42:1–28.
- Ghazoul, J., Z. Burivalova, J. Garcia-Ulloa, and L. A. King. 2015. Conceptualizing forest degradation. *Trends in Ecology and Evolution* 30:622–632.
- Gray, L. K., and A. Hamann. 2013. Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change* 117:289–303.
- Grimm, V., and U. Berger. 2016. Structural realism, emergence, and predictions in next-generation ecological modelling: synthesis from a special issue. *Ecological Modelling* 326:177–187.
- 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. *Landscape Ecology* 28:1429–1437.
- Hansen, A. J., and L. B. Phillips. 2015. Which tree species and biome types are most vulnerable to climate change in the US Northern Rocky Mountains? *Forest Ecology and Management* 338:68–83.
- Hansen, W. D., W. H. Romme, A. Ba, and M. G. Turner. 2016. Shifting ecological filters mediate postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone. *Forest Ecology and Management* 362:218–230.
- Harvey, B. J., D. C. Donato, and M. G. Turner. 2016a. High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Global Ecology and Biogeography* 25:655–669.
- Harvey, B. J., D. C. Donato, and M. G. Turner. 2016b. Drivers and trends in spatial patterns of burn severity in forests of the US Northern Rocky Mountains (1984–2010). *Landscape Ecology* 31:2367–2383.
- He, T., J. G. Pausas, C. M. Belcher, D. W. Schwilk, and B. B. Lamont. 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytologist* 194:751–759.
- Hirota, M., M. Holmgren, E. H. van Nes, and M. Scheffer. 2011. Global resilience of tropical forest and savanna to critical transitions. *Science* 334:232–235.
- Hoffmann, W. A., E. L. Geiger, S. G. Gotsch, D. R. Rossatto, L. C. R. Silva, O. L. Lau, M. Haridasan, and A. C. Franco. 2012. Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters* 15:759–768.

- Hughes, T. P., C. Linares, V. Dakos, I. A. van de Leemput, and E. H. van Nes. 2013. Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in Ecology and Evolution* 28:149–155.
- Inouye, D. W. 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters* 3:457–463.
- Johnstone, J. F., and F. S. Chapin. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems* 9:14–31.
- Johnstone, J. F., L. Boby, E. Tissier, M. Mack, D. Verbyla, and X. Walker. 2009. Postfire seed rain of black spruce, a semiserotinous conifer, in forests of interior Alaska. *Canadian Journal of Forest Research* 39:1575–1588.
- Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16:1281–1295.
- Johnstone, J. F., et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14:369–378.
- Kashian, D. M., M. G. Turner, W. H. Romme, and C. G. Lorimer. 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. *Ecology* 86:643–654.
- Keane, R. E., D. McKenzie, D. A. Falk, E. A. H. Smithwick, C. Miller, and L. K. B. Kellogg. 2015. Representing climate, disturbance, and vegetation interactions in landscape models. *Ecological Modelling* 309–310:33–47.
- Keeley, J. E., G. Ne'eman, and C. J. Fotheringham. 1999. Immaturity risk in a fire-dependent pine. *Journal of Mediterranean Ecology* 1:41–48.
- Keeley, J. E., C. J. Fotheringham, and M. Baer-Keeley. 2005. Determinants of postfire recovery and succession in mediterranean climate shrublands of California. *Ecological Applications* 15:1515–1534.
- Kéfi, S., M. Rietkerk, C. L. Alados, Y. Pueyo, V. P. Papanastasis, A. Elaich, and P. C. de Ruiter. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449:213–217.
- Kemp, K. B., P. E. Higuera, and P. Morgan. 2016. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. *Landscape Ecology* 31:619–636.
- Lamont, B. B., and N. J. Enright. 2000. Adaptive advantages of aerial seed banks. *Plant Species Biology* 15:157–166.
- Lamont, B. B., and T. He. 2017. Fire-proneness as a prerequisite for the evolution of fire-adapted traits. *Trends in Plant Science* 22:278–288.
- Lamont, B. B., D. C. Maitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. *Botanical Review* 57:277–317.
- Lenton, T. M., H. Held, E. Kriegler, J. W. Hall, W. Lucht, S. Rahmstorf, and H. J. Schellnhuber. 2008. Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Sciences USA* 105:1786–1793.
- Lindenmayer, D., C. Messier, and C. Sato. 2016. Avoiding ecosystem collapse in managed forest ecosystems. *Frontiers in Ecology and the Environment* 14:561–568.
- Littell, J. S., D. L. Peterson, K. L. Riley, Y. Liu, and C. H. Luce. 2016. A review of the relationships between drought and forest fire in the United States. *Global Change Biology* 22:1–17.
- Martínez-Vilalta, J., and F. Lloret. 2016. Drought-induced vegetation shifts in terrestrial ecosystems: the key role of regeneration dynamics. *Global and Planetary Change* 144:94–108.
- Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349:823–826.
- Millsbaugh, S. H., C. Whitlock, and P. J. Bartlein. 2000. Variations in fire frequency and climate over the past 17,000 yr in central Yellowstone National Park. *Geology* 28:211–214.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1:535–545.
- Pechony, O., and D. T. Shindell. 2010. Driving forces of global wildfires over the past millennium and the forthcoming century. *Proceedings of the National Academy of Sciences USA* 107:19167–19170.
- Pedro, M. S., W. Rammer, and R. Seidl. 2015. Tree species diversity mitigates disturbance impacts on the forest carbon cycle. *Oecologia* 177:619–630.
- Peters, D. P., R. A. Pielke, B. T. Bestelmeyer, C. D. Allen, S. Munson-mcgee, and K. M. Havstad. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences USA* 101:15130–15135.
- Peters, D. P., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross-scale interactions and changing pattern-process relationships: consequences for system dynamics. *Ecosystems* 10:790–796.
- Power, M. J., C. Whitlock, and P. J. Bartlein. 2011. Postglacial fire, vegetation, and climate history across an elevational gradient in the Northern Rocky Mountains, USA and Canada. *Quaternary Science Reviews* 30:2520–2533.
- R Core Team 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Renard, S. M., E. J. B. McIntire, and A. Fajardo. 2016. Winter conditions, not summer temperature, influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec. *Journal of Vegetation Science* 27:29–39.
- Reyer, C. P., et al. 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. *Journal of Ecology* 103:5–15.
- Savage, M., and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research* 35:967–977.
- Savage, M., J. N. Mast, and J. J. Feddema. 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. *Canadian Journal of Forest Research* 583:570–583.
- Scheffer, M. 2009. *Critical transitions in nature and society*. Princeton University Press, Princeton, New Jersey, USA.
- Scheffer, M., M. Hirota, M. Holmgren, E. H. van Nes, and F. S. Chapin. 2012. Thresholds for boreal biome transitions. *Proceedings of the National Academy of Sciences USA* 109:21384–21389.
- Schoennagel, T., M. Turner, D. Kashian, and A. Fall. 2006. Influence of fire regimes on lodgepole pine stand age and density across the Yellowstone National Park (USA) landscape. *Landscape Ecology* 21:1281–1296.
- Seidl, R. 2017. To model or not to model, that is no longer the question for ecologists. *Ecosystems* 20:222–228.
- Seidl, R., et al. 2011. Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling* 222:903–924.
- Seidl, R., W. Rammer, R. M. Scheller, and T. A. Spies. 2012. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecological Modelling* 231:87–100.
- Seidl, R., W. Rammer, and T. A. Spies. 2014. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecological Applications* 24:2063–2077.
- Seidl, R. D. C., K. F. Raffa, Donato, and M. G. Turner. 2016a. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. *Proceedings of the National Academy of Sciences USA* 113:13075–13080.
- Seidl, R., T. A. Spies, D. L. Peterson, S. L. Stephens, and J. A. Hicke. 2016b. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology* 53:120–129.
- Seidl, R., et al. 2017. Forest disturbances under climate change. *Nature Climate Change* 7:395–402.
- Simard, M., E. N. Powell, K. F. Raffa, and M. G. Turner. 2012. What explains landscape patterns of tree mortality caused by bark beetle outbreaks in Greater Yellowstone? *Global Ecology and Biogeography* 21:556–567.
- Smith, P., et al. 2016. Biophysical and economic limits to negative CO₂ emissions. *Nature Climate Change* 6:42–50.

- Spies, T. A., et al. 2017. Using an agent-based model to examine forest management outcomes in a fire-prone landscape in Oregon, USA. *Ecology and Society* 22:art25.
- Staal, A., S. C. Dekker, M. Hirota, and E. H. van Nes. 2014. Synergistic effects of drought and deforestation on the resilience of the south-eastern Amazon rainforest. *Ecological Complexity* 22:65–75.
- Stevens-Rumann, C., and P. Morgan. 2016. Repeated wildfires alter forest recovery of mixed-conifer ecosystems. *Ecological Applications* 26:1842–1853.
- Tepley, A. J., J. R. Thompson, H. E. Epstein, and K. J. Anderson-Teixeira. 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. *Global Change Biology* 23:4117–4132.
- Tercek, M., and A. Rodman. 2016. Forecasts of 21st century snowpack and implications for snowmobile and snowcoach use in Yellowstone National Park. *PLoS ONE* 11:e0159218.
- Thom, D., W. Rammer, T. Dirnböck, J. Müller, J. Kobler, K. Katzensteiner, N. Helm, and R. Seidl. 2017a. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. *Journal of Applied Ecology* 54:28–38.
- Thom, D., W. Rammer, and R. Seidl. 2017b. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. *Global Change Biology* 23:269–282.
- Tinker, D. B., W. H. Romme, W. W. Hargrove, R. H. Gardner, and M. G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. *Canadian Journal of Forest Research* 24:897–903.
- Trumbore, S., P. Brando, and H. Hartmann. 2015. Forest health and global change. *Science* 349:814–818.
- Turetsky, M. R., J. L. Baltzer, J. F. Johnstone, M. C. Mack, K. Mccann, and E. A. G. Schuur. 2016. Losing legacies, ecological release, and transient responses: key challenges for the future of northern ecosystem science. *Ecosystems* 20:23–30.
- Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849.
- Turner, M. G., W. W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science* 5: 731–742.
- Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67:411–433.
- Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1:511–523.
- Turner, M. G., W. H. Romme, and R. H. Gardner. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, WY. *International Journal of Wildland Management* 9:21–36.
- Turner, M. G., D. Tinker, W. Romme, D. Kashian, and C. Litton. 2004. Landscape patterns of sapling density, leaf area, and above-ground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* 7:751–775.
- Turner, M. G., D. M. Turner, W. H. Romme, and D. B. Tinker. 2007. Cone production in young post-fire *Pinus contorta* stands in Greater Yellowstone (USA). *Forest Ecology and Management* 242:119–126.
- Turner, M. G., D. C. Donato, and W. H. Romme. 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. *Landscape Ecology* 28:1081–1097.
- Turner, M. G., T. G. Whitby, D. B. Tinker, and W. H. Romme. 2016. Twenty-four years after the Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and function? *Ecology* 97:1260–1273.
- Voltaire, A., et al. 2013. The CNRM-CM5.1 global climate model: description and basic evaluation. *Climate Dynamics* 40: 2091–2121.
- Walck, J. L., S. N. Hidayati, K. W. Dixon, K. Thompson, and P. Poschod. 2011. Climate change and plant regeneration from seed. *Global Change Biology* 17:2145–2161.
- Walker, B., L. Gunderson, A. Zinzig, C. Folke, S. Carpenter, and L. Schultz. 2006. A handful of heuristics and some propositions for understanding resilience in social-ecological systems. *Ecology and Society* 11:13.
- Walker, X. J., M. C. Mack, and J. F. Johnstone. 2016. Predicting ecosystem resilience to fire from tree ring analysis in black spruce forests. *Ecosystems* 20:1137–1150.
- Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. *Philosophical Transactions of the Royal Society B* 371:1–10.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313:940–943.
- Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences USA* 108:13165–13170.
- Western Regional Climate Center 2017a. NCDC 1981–2016 monthly normals, Old Faithful, WY. <https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?wy6845>.
- Western Regional Climate Center 2017b. NCDC 1981–2016 monthly normals, Mammoth, WY. <https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?wy9905>.
- Whitlock, C. 1993. Postglacial vegetation and climate of Grand Teton and southern Yellowstone National Parks. *Ecological Monographs* 63:173–198.

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