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ARTICLE
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Simulated postfire tree regeneration suggests reorganization of Greater Yellowstone forests during the 21st century

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Abstract

Tree regeneration underpins forest resilience, but how pathways of postfire tree regeneration will unfold with future climate and fire regimes is difficult to anticipate. We conducted a simulation study in the Greater Yellowstone Ecosystem (GYE; United States) using a process-based model, iLand, to ask how rates, composition, and spatial patterns of postfire tree regeneration vary with 21st-century climate. Subalpine forest and fire dynamics were simulated through 2100 under four climate scenarios, 2 × 2 factorial of aridity (wet and dry) and temperature (warm and hot), in five GYE landscapes. We tallied postfire tree seedling density by species in simulated fires (>400 ha) at five years postfire. To assess changes in regeneration rates (total and by species) to 2100 in each landscape × climate scenario combination, we fit generalized linear models of regeneration versus time and estimated slope coefficients. To analyze spatial patterns of recovery, we compared regeneration to prefire forest state. Postfire regeneration rates were maintained through 2100 in wet scenarios but declined in the hot-dry scenario. Seedling composition was generally consistent throughout the simulations across wet scenarios, except for declines of Engelmann spruce (*Picea engelmannii*). Regeneration of fire-sensitive species declined in the hot-dry scenario, with Engelmann spruce experiencing the steepest declines (−20% to −71%) and failing by late century. Lodgepole pine (*Pinus contorta* var. *latifolia*) and subalpine fir (*Abies lasiocarpa*) declined in the hot-dry scenario, but regeneration never failed. Regeneration of fire-tolerant Douglas-fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) was sustained or increased in dry scenarios (+4% to +6%). The proportion of burned area where regeneration failed increased in all dry scenarios but never exceeded 20%. Declining tree regeneration and shifts in dominant tree species revealed that changes in forest structure and composition—and not a conversion to non-forest—are the dominant response to future climate across broad swaths of the simulation landscapes. Our results suggest

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that postfire reorganization may be widespread during the 21st century and enable forests to persist in a warming climate with more fire.

KEYWORDS
climate change, disturbance, fire ecology, forest ecology, forest resilience, Northern Rocky Mountains, simulation modeling

INTRODUCTION

Future forest dynamics are increasingly uncertain due to changing climate and disturbance regimes (McDowell et al., 2020; Turner, 2010; Turner & Seidl, 2023). Detecting and predicting forest change is difficult because trees are long-lived, natural disturbances are stochastic, and stand development can take centuries (Aitken et al., 2008; Hughes et al., 2013). Tree regeneration underpins forest resilience (i.e., the ability of a forest to recover its pre-disturbance structure, composition, and function; Coop et al., 2020; Gunderson & Holling, 2003; Hansen & Turner, 2019; Holling, 1973; Seidl & Turner, 2022), thus anticipating how tree regeneration will change following future disturbances is critical to anticipate future forest change. The early years following high-severity disturbances are especially important for conifer regeneration (Kemp et al., 2016; Petrie et al., 2016) because early seedling establishment can shape stand development for decades to centuries (Anderson-Teixeira et al., 2013; Kashian et al., 2005). However, while the rates and composition of tree regeneration following disturbance can be sensitive sentinels of forest change, whether they signal a loss of resilience or a shift toward a state better aligned with a warming climate is not known.

Slowing rates of tree regeneration could indicate declining forest resilience that precedes conversion of forest to non-forest vegetation (Coop et al., 2020; Van Nes & Scheffer, 2007). Theoretical studies suggest that post-disturbance recovery rates will decline as ecosystems approach tipping points leading to collapse (Van De Leemput et al., 2018; Nijp et al., 2019), and numerous studies suggest that tree regeneration declines as the size and frequency of high-severity disturbances increase (Falk et al., 2022; Ramiadantsoa et al., 2023; Turner et al., 1998; Van De Leemput et al., 2018). Tree regeneration is already declining following fire (Davis et al., 2023; Fairman et al., 2022; Kukavskaya et al., 2016), especially in areas of western North America (Baltzer et al., 2021; Harvey et al., 2013; Kiel & Turner, 2022; Turner et al., 2019; Willson & Hurteau, 2024). Reduced postfire regeneration can result from multiple mechanisms, including immaturity risk due to short fire-return intervals (Brown & Johnstone, 2012; Hart et al., 2019; Keeley et al., 1999; Turner et al., 2019), limited seed dispersal into large burned areas (Gill et al., 2021, 2022; Harvey et al., 2016), and climate conditions in the years following fire that are unsuitable for tree seedling establishment (Davis et al., 2019; Stevens-Rumann et al., 2022; Wolf et al., 2021). While a decline in postfire regeneration rates may suggest loss of resilience, declines could also signal restructuring of forests toward sparser stands better suited to future climate (Pausas & Keeley, 2014; Seidl & Turner, 2022).

Compositional changes in postfire tree regeneration could also buffer forests from conversion to non-forest if regeneration of species that are more tolerant of a warming climate is favored (Anderson-Teixeira et al., 2013; Smith et al., 2014; Urza & Sibold, 2017). Interspecific variation in climatic tolerances and fire adaptations (e.g., resprouting, serotiny, bark thickness) can lead to differences between pre- and postfire community assemblages and species dominance (Pausas & Keeley, 2014; Seidl & Turner, 2022). For example, the relative abundance of deciduous species (e.g., *Populus* spp., *Betula* spp.) has increased following high-severity fire in boreal conifer forests (Whitman et al., 2019). Theoretical studies have shown that diverse regeneration strategies enhance forest resilience to declining fire rotations (Ramiadantsoa et al., 2023). Empirical studies have also shown shifts in species assemblages following disturbances toward species that may be better suited for future climates (Germain et al., 2025; Hoecker & Turner, 2022; Seidl et al., 2024; Urza & Sibold, 2017). Thus, the nature of change in the rates and composition of postfire tree regeneration could signal either an erosion of forest resilience or the reorganization of forests responding to a warming climate (Falk et al., 2022; Seidl & Turner, 2022; Swanson et al., 2011).

Field observations alone cannot predict how regeneration rates and composition may change with future climate change. However, process-based simulation models can project such dynamics because they incorporate key mechanisms underpinning forest resilience and allow for interactions among causal processes (Albrich et al., 2020; Bugmann & Seidl, 2022; Gustafson, 2013; Loehman et al., 2020). In the Greater Yellowstone Ecosystem (GYE), recent simulation studies suggest that forests will decline

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(Clark et al., 2017; Hansen et al., 2018; Henne et al., 2021; Rammer et al., 2021; Turner et al., 2022), but studies have not assessed whether changes in the rates, composition, and spatial patterns of postfire tree regeneration suggest a loss of resilience or forest reorganization.

The GYE is an ideal region for assessing postfire tree regeneration rates and composition under alternative future climate scenarios. The historical fire regime is well understood (Higuera et al., 2011; Romme, 1982; Stegner et al., 2019), and forest responses to historical fires have been well studied (e.g., Braziunas et al., 2023; Kiel et al., 2025; Romme et al., 2011; Turner et al., 2007). The forests include tree species with varied adaptations to fire, including "avoiders" (Engelmann spruce [*Picea engelmannii*], subalpine fir [*Abies lasiocarpa*], non-serotinous lodgepole pine [*Pinus contorta* var. *latifolia*]) that are fire sensitive and obligate seeders; "evaders" (serotinous lodgepole pine) that rely on in situ aerial seed banks; "endurers" (aspen [*Populus tremuloides*]) that can resprout; and "resisters" (thick-barked Douglas-fir [*Pseudotsuga menziesii* var. *glauca*]) that can survive surface fire (Agee, 1993; Baker, 2009; Harvey et al., 2016).

Here, analyzing climate and fire simulations first presented by Turner et al. (2022), we focused explicitly on postfire tree regeneration within burned areas to ask: How do simulated rates and composition of postfire tree regeneration and spatial patterns of forest change vary with 21st-century warming and fire activity in the GYE? We expected rates of total postfire tree regeneration density (all species) to decline under dry climate scenarios, with steeper declines under hotter temperatures, but to remain stable under wet climate scenarios. Among species, we expected rapid declines for fire-sensitive obligate seeders (e.g., Engelmann spruce, subalpine fir, and lodgepole pine). We expected regeneration of lodgepole pine to decline only in hot-dry scenarios in which successive short-interval fires could deplete seed supply. We expected increased regeneration of fire resisters (Douglas-fir) and endurers (aspen) with warming, and the most rapid increases in dry scenarios where regeneration of other species would decline. Lastly, we expected forests could reorganize if trees regenerated after fire and postfire cohorts differed from prefire forests in their density (i.e., sparse or dense) and/or dominant tree species.

METHODS

Study region

Centered on Yellowstone (YELL) and Grand Teton (GRTE) National Parks, the GYE spans over 10 million hectares in the northern US Rocky Mountains (Figure 1). From 1991 to 2020, mean annual temperature was 1.3°C, average maximum temperature for summer (June, July, August) was 22.2°C, and average minimum temperature for winter (December, January, February) was −17.0°C; total annual precipitation averaged 65.1 cm and annual snowfall depth averaged 197.0 cm (Old Faithful, Wyoming Station; NOAA NCEI, 2025). Climate in the GYE has warmed considerably since 1950, as annual average temperature has risen by 1.3°C and snowfall decreased by about 25% (Hostetler et al., 2021). Throughout the Holocene, subalpine forests of the GYE experienced large stand-replacing fires at 100- to 300-year intervals and lower montane forests experienced fires at 50- to 100-year intervals (Higuera et al., 2011; Loope & Gruell, 1973; Romme, 1982). However, fire activity is increasing with a warming climate, and this trend is expected to continue throughout the century (Hostetler et al., 2021; Westerling et al., 2011).

Study overview

We assessed postfire tree regeneration across five landscapes, each encompassing about 60,000 ha of forested area and spanning topographic and environmental gradients representative of the GYE (Figure 1). Turner et al. (2022) simulated these landscapes under future climate scenarios and analyzed landscape-level changes in forest type, stand age, density, and basal area of mature trees, and aboveground carbon stocks through 2100. However, they did not assess postfire tree regeneration rates and composition. Here, we conducted a complementary study in which we analyzed postfire tree regeneration within the perimeters of fires simulated by Turner et al. (2022).

Simulation landscapes

We briefly summarize the five study landscapes (Figure 1) here; but see Turner et al. (2022) for further details. Northern Yellowstone is a topographically complex landscape, ranging from lower elevation steppe to upper tree line (1828–3145 m). Lower montane forests dominated by Douglas-fir and aspen transition to lodgepole pine forests and then to mixed forests that include Engelmann spruce and subalpine fir at higher elevations. Western Yellowstone is at mid-elevation (2100–2400 m) and dominated by serotinous lodgepole pine, with limited Douglas-fir and aspen at lower elevations. Much of this landscape burned in 1988, and over 15,000 ha of recovering lodgepole pine forests burned again in 2016 (Turner et al., 2019). Two Ocean Plateau is a high-elevation landscape (2400–2700 m) dominated by non-serotinous

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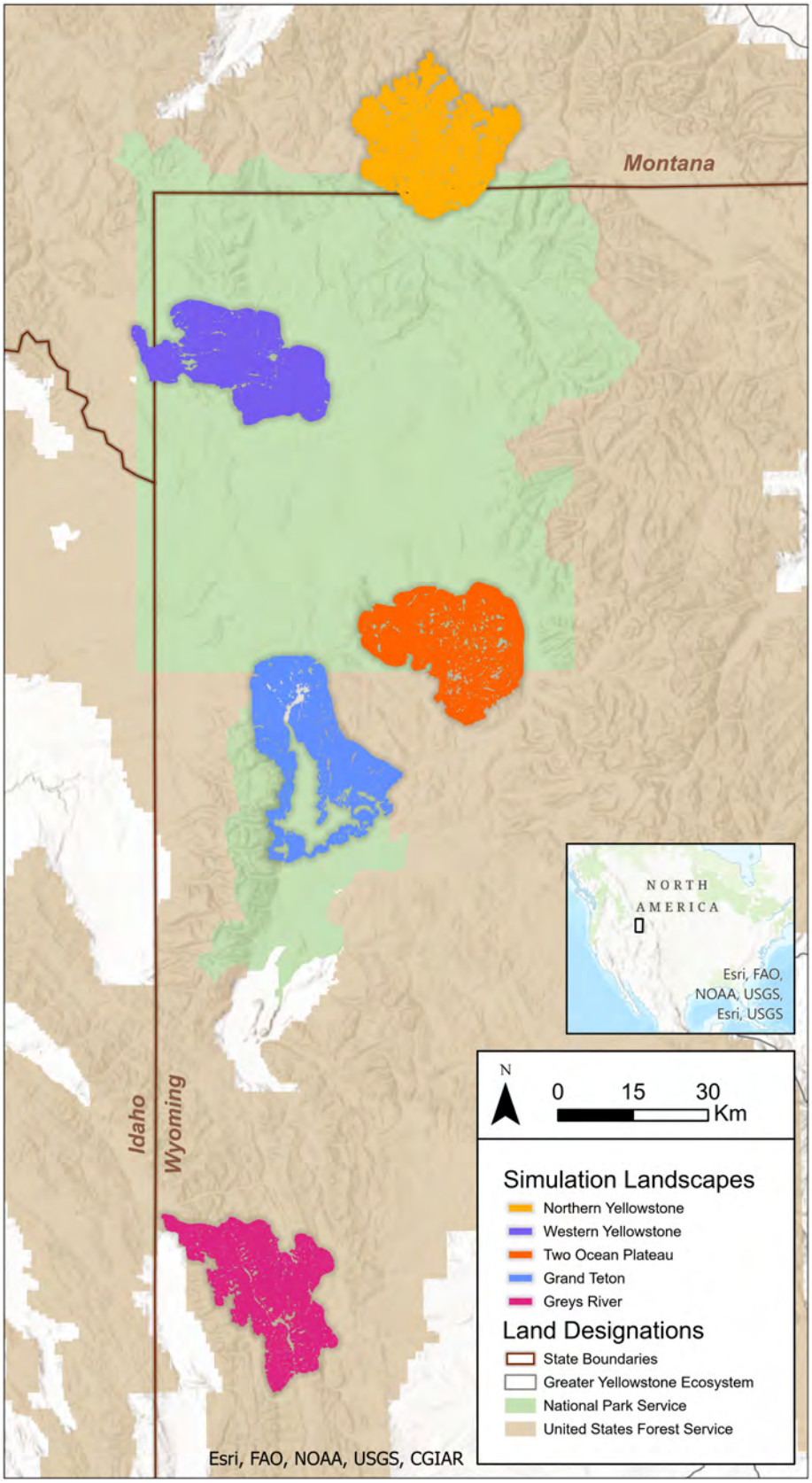

FIGURE 1 Locations of the five simulation landscapes in the Greater Yellowstone Ecosystem. Colors represent each individual landscape. Light brown areas are federally owned lands under the jurisdiction of the US Forest Service, and light green areas are under the jurisdiction of the US National Park Service. Esri World Hillshade basemap was created by Esri (2025).

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lodgepole pine and spruce-fir forests. One-third of this landscape burned in 1988, much of which was forest ≥300 years old (Romme & Despain, 1989). Grand Teton is at mid-elevation (2100–2400 m) and includes most of the forested area in GRTE. Lodgepole pine, Douglas-fir, and spruce-fir forests are all present. Some of this landscape burned in 1988, and additional fires have occurred through 2016. At the southern end of the GYE, Greys River is a lower elevation (1700–2300 m) rugged landscape located on the Bridger-Teton National Forest, representative of lower montane forests. This landscape has a greater prevalence of Douglas-fir and aspen and has burned less than central locations in the GYE.

Model overview

Simulations were conducted with iLand, a process-based simulation model of forest and disturbance dynamics (Rammer et al., 2024; Seidl et al., 2012) that has been parameterized and tested in the GYE (Braziunas et al., 2018; Hansen et al., 2018; Hessburg et al., 2019; Turner et al., 2022). In iLand, growth, competition, and mortality are simulated for individual trees >4 m height (see full model documentation at https://iland-model.org). Trees compete for available resources, including light, water, and nutrients. Soil, water, and nutrient availability are represented at 1-ha resolution and are homogeneous within a grid cell. Tree regeneration is modeled at 2-m × 2-m resolution. Seed dispersal is represented as a probabilistic dispersal kernel around mature trees, and seedling establishment is a function of soil water availability, temperature, and light availability. Tree regeneration is tracked for cohorts (<4 m height) within these 2-m × 2-m grid cells, with cohorts characterized by height and species. When cohorts reach 4 m in height, they transition to trees and are modeled as individuals. In this study, we aggregated regeneration outputs to 1-ha grid cells. All data processing and analyses were conducted in R Statistical Software (version 4.4.1, R Core Team, 2024) using the stats (version 4.4.1), tidyverse (Wickham et al., 2019), raster (Hijmans et al., 2025a), terra (Hijmans, 2025b), RSQLite (Müller et al., 2017), MASS (Ripley et al., 2013), and data.table (Dowle et al., 2019) packages.

We focused on five dominant tree species in the GYE: Engelmann spruce, subalpine fir, lodgepole pine, Douglas-fir, and aspen; species parameters are available in Thom et al. (2024). For lodgepole pine, we simulated serotinous and non-serotinous individuals separately to reflect intraspecific variation in this life history strategy, then pooled them to species prior to analyses. Although whitebark pine (*Pinus albicaulis*) was included in simulations, we did not analyze regeneration of this species. Simulations did not include key mechanisms of recent mortality, including native bark beetles and a non-native pathogen that have caused >75% mortality of mature whitebark pines (Goeking et al., 2019; Macfarlane et al., 2013; Thoma et al., 2019). Thus, we were not confident in the simulated distribution of mature seed sources.

Simulation landscapes were initialized with a 300-year spin-up using historical climate, after which the patterns of the actual fires that burned from 1984 to 2016 were imposed to represent the stand-age mosaic correctly. This initialization procedure approximated forest composition and structure well; further details can be found in Turner et al. (2022).

Simulation experiment

We used a 2 × 2 factorial design with four climate scenarios that project a dry versus wet future (represented by two global climate models from CMIP5; Taylor et al., 2012): HadGEM2-ES (Jones et al., 2011) and CanESM2 (Yang & Saenko, 2012, respectively) and warm versus hot temperatures (using representative concentration pathways RCP 4.5 and 8.5, respectively). Temperature increases similarly in the two global climate models for the same RCP (+4.1 to 4.2°C for RCP 4.5, +6.6 to 6.8°C for RCP 8.5), but there are sharp differences in summer precipitation (June–August), coincident with the fire and growing season. The wet scenario (CanESM2) projects an increase (+1.5 to 3.3 cm) in summer precipitation, whereas the dry scenario projects a decrease (−1.8 to 2.4 cm) by 2100. Climate projections were obtained from the Multivariate Adaptative Constructed Analogs (MACA) and METDATA gridded datasets at 4-km resolution (Abatzoglou & Brown, 2012; Abatzoglou, 2013).

Each combination of climate scenario ($n = 4$) × landscape ($n = 5$) was simulated with 20 replicate simulations in which annual fire occurrence, location, and maximum potential size were generated probabilistically based on statistical models for large (>400 ha) fires (total $n = 400$ simulations). Fire spread was simulated dynamically in iLand, where the probability of fire spread to adjacent cells was determined by fuel load, wind, and topography (Seidl et al., 2014), up to the maximum potential fire size determined by the statistical models (see Turner et al., 2022 for additional detail). Burn severity was recorded as the percentage of crown kill within a 1-ha grid cell. We tracked the year, location, size, and burn severity for every simulated fire and summed the area burned by simulation in 5-year bins because fire did not occur in every year in each landscape.

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Rates of postfire tree regeneration

Postfire tree regeneration was analyzed in large fires (> 400 ha), consistent with the MTBS data and because large fires account for most of the area burned (e.g., Schoennagel et al., 2006). Since we focused specifically on early postfire tree regeneration, we tallied the density of tree seedlings by species within fires (i.e., for each cell within burn perimeters across all burn severities) at 5 years postfire in each replicate simulation. Thus, for a fire simulated in 2050, postfire tree seedling regeneration was quantified in 2055. We chose a 5-year window because most tree seedling establishment in the GYE occurs in the first few years following fire (Turner et al., 1999), although some species (e.g., Douglas-fir) can recruit over a longer window (Donato, Harvey, & Turner, 2016; Harvey et al., 2016). We calculated the average seedling density per hectare (total and by species) within all simulated fires for each simulation year. Again, because large fires did not occur each year in all landscapes, we calculated average postfire regeneration densities across all fire patches that occurred within a replicate simulation during each 5-year bin.

To estimate rates of change in postfire regeneration density, we fit generalized linear models (GLMs) to the average postfire regeneration densities (seedlings ha^{-1}) in each 5-year bin versus time for each landscape × climate scenario using the "glm.nb" function within the "MASS" package R (Version 4.4.1). Each GLM was fit with a negative binomial distribution and log-link function to ensure that postfire densities remained ≥ zero and to account for overdispersion with the initial dispersion parameter (theta; θ) values set to 0.5. Negative-binomial regression is suitable for modeling over-dispersed count data (Ver Hoef & Boveng, 2007) and uses a dispersion parameter within the model to relax the assumption that variance is equal to the mean; theta parameter estimates are provided in Appendix S1: Table S1. Negative-binomial regression requires response variables to be integer values; thus, we rounded average postfire regeneration densities for each bin to the nearest integer. Densities were typically hundreds to thousands per hectare, so rounding should not introduce meaningful error. We estimated slope coefficients and 95% CIs to determine whether postfire regeneration remained stable throughout the century (CIs included zero) or whether rates increased or decreased between 2021 and 2100 (positive or negative slopes, respectively, with CIs not including zero). Where regeneration rates exhibited steep declines (which occurred in the hot-dry scenario), we plotted cumulative frequency distributions of postfire regeneration density across all 1-ha grid cells within all large fires (across 20 replicate simulations) in each time period. We then determined the proportion of area burned in which postfire regeneration failed (defined as <50 seedlings ha^{-1}) in the middle (2030–2055) and late century (2075–2100).

Composition of postfire tree regeneration

To characterize the composition of postfire seedling cohorts over time, we summed the regeneration densities by species within 5-year bins across the 20 replicate simulations for each landscape × climate scenario and generated stacked-area graphs using the mean regeneration densities across the 20 iterations. We also contrasted mean postfire regeneration densities by species in the middle and late century and computed their relative density and the net percent change between these two periods.

Spatial patterns of postfire forest change

We next mapped the spatial patterns of tree regeneration and contrasted the pre- and postfire communities. For each burned 1-ha cell per replicate simulation, we recorded tree density and species composition 1 year before the first simulated fire and compared this to regeneration density and composition 5 years after the last simulated fire. We next calculated the relative pre- and postfire density of each tree species in each cell. A species was considered dominant if it accounted for ≥60% of stems within a cell; otherwise, the cell was classified as mixed forest. Because stem densities in the GYE vary substantially between mature forests and postfire seedlings (e.g., Kashian et al., 2005; Turner et al., 1997), we developed separate density classes for scoring cells as sparse, moderate, or dense (Table 1). Because the

TABLE 1 Stem-density categories used to characterize mature prefire stands and postfire regeneration cohorts by structural categories.

Stem density category	Prefire stem density (trees ha^{-1})	Postfire regeneration density (seedlings ha^{-1})
Non-forest	<50	<50
Sparse	50–200	50–2000
Moderate	201–400	2001–10,000
Dense	>400	>10,000

Note: Further background rationale for density categories and a sensitivity analysis is available in the supplemental information (Appendix S2).

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categories are somewhat arbitrary, we also conducted an analysis to understand the sensitivity of our results to these density classes (Appendix S2).

We next assigned differences in pre- and postfire structure and composition to one of four recovery pathways (Figure 2) based on Seidl and Turner (2022). For each replicate per landscape × climate scenario, we classified cells as resilient if they had the same density class and dominant species pre- and postfire. If cells shifted in density class (e.g., dense to sparse) but retained the same dominant species, we classified the cell as "restructuring." If dominant species changed but density classes did not, we classified the cell as "reassembly." If a cell's density class and dominant species both changed, we classified the cell as "replacement." Lastly, if a cell changed from forest to non-forest (<50 stems ha^{-1}), or non-forest to forest (i.e., forest cover was gained), we considered that a "regime shift." We then determined the most frequent classification across the 20 simulations for each landscape × climate scenario and assigned that as the final pathway for each cell. The final postfire pathways were mapped for each landscape × climate scenario, and the proportion of area burned represented by each pathway was calculated. To further understand the nature of changes in forest structure, we identified and mapped cells that shifted up, down, or remained in the same density class. To understand the nature of compositional change, we created alluvial plots for pre- and postfire species dominance.

RESULTS

From 2021 to 2100, there were 6594 large fires (>400 ha) that accounted for 97% of the total area burned across all simulations. Sixty percent of individual fires and 72% of the total area burned occurred in the dry climate scenarios. Area burned increased throughout the century in the dry scenarios and was greatest in the hot-dry scenario (Appendix S1: Figure S1).

Rates of postfire tree regeneration

In the wet climate scenarios, rates of total (all species) postfire tree regeneration did not change over time (slopes did not differ from zero) except in Grand Teton, where postfire regeneration increased (3.2% and 6.0% per 5-year bin in the warm and hot scenarios, respectively) and in Northern Yellowstone, where regeneration increased in the hot scenario (5.8% per 5-year bin; Figure 3). In contrast, in the dry climate scenarios, rates

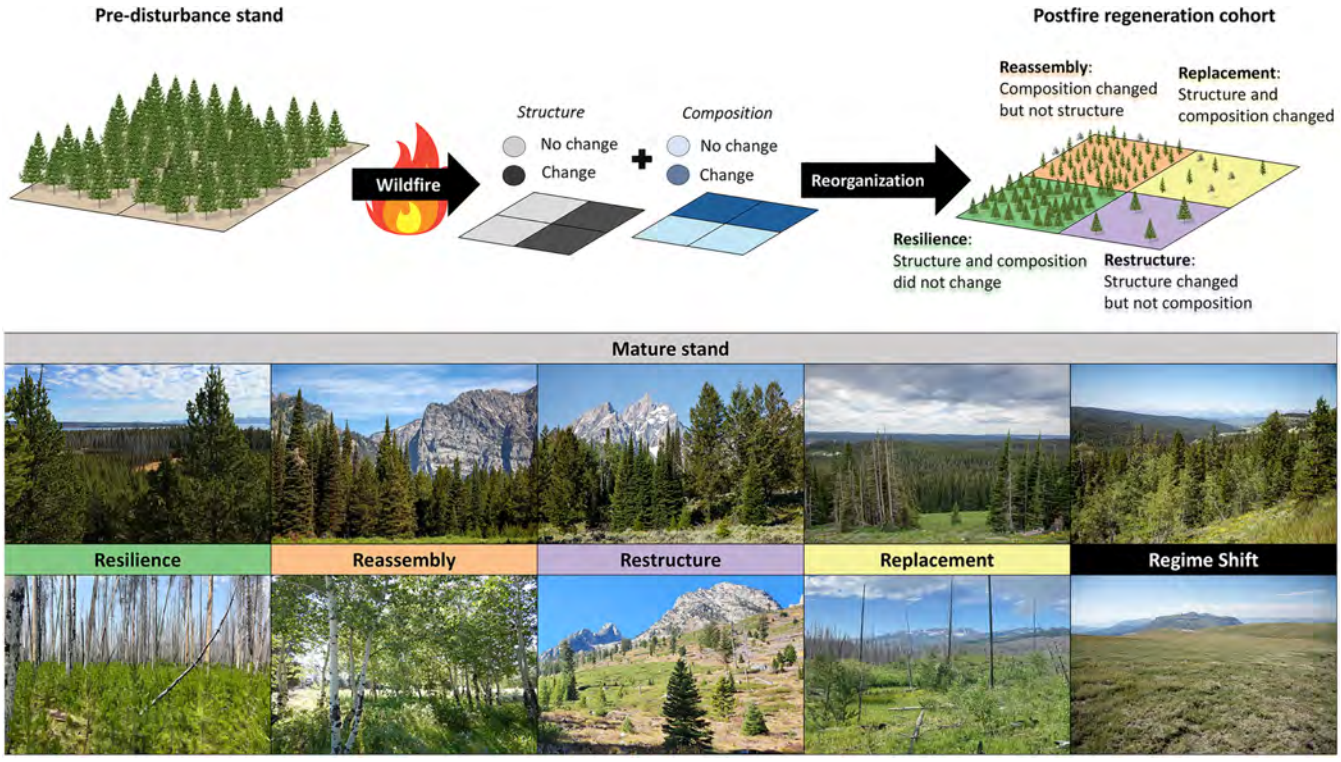

FIGURE 2 Conceptual figure of postfire reorganization pathways and photo representations of pre- versus postfire differences in stand structure and composition. Reorganization pathways follow Seidl and Turner et al. (2022). Photo credits: Garrett J. Knowlton, Timon T. Keller, and Monica G. Turner.

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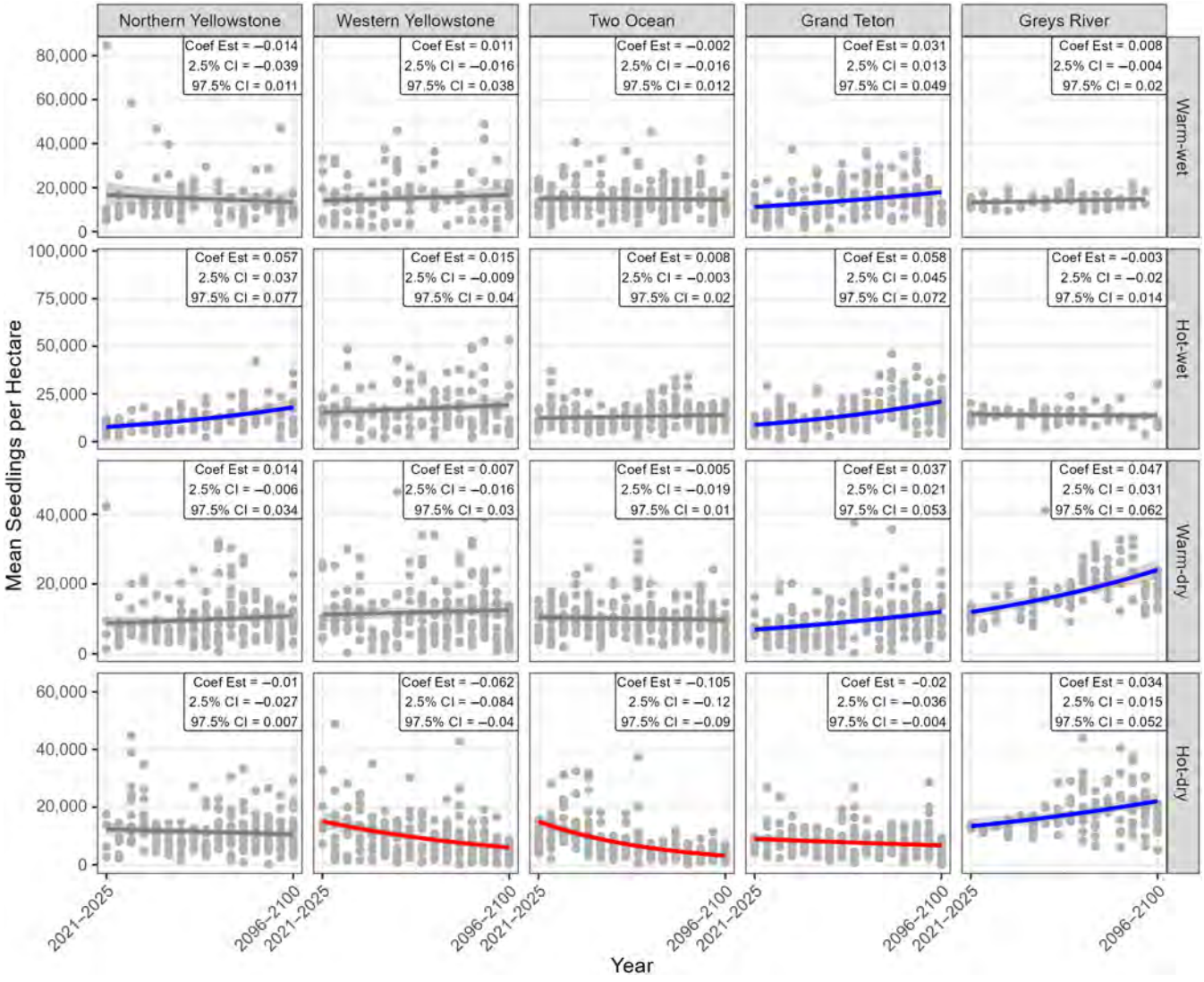

FIGURE 3 Total seedling regeneration rates (for all species) across scenarios and landscapes. Generalized linear models (trend lines) were fit to 5-year averages of the total regeneration density per hectare across all species from 2021 to 2100. Gray lines indicate no change in regeneration (95% CI on slope estimate includes zero), blue lines indicate an increasing rate (positive slope), and red lines indicate a decreasing rate (negative slope). Note differing *y*-axes among rows.

of total postfire tree regeneration varied in magnitude and direction. In the warm-dry scenario, postfire regeneration increased in Grand Teton and Greys River (3.7% and 4.8% per 5-year bin, respectively) but did not change in the other landscapes (Figure 3). In the hot-dry scenario, postfire regeneration declined in Western Yellowstone, Two Ocean Plateau, and Grand Teton (−6.0%, −10.0%, and −2.0% per 5-year bin, respectively), did not change in Northern Yellowstone, and increased in Greys River (3.4% per 5-year bin; Figure 3).

Rates of change in postfire regeneration differed substantially among species, but species responses were generally consistent across landscapes for a given climate scenario (Figure 4). Engelmann spruce regeneration declined through 2100 in nearly all climate scenarios; declines were very steep in the hot scenarios (−19.8% to −71.4% per 5-year bin across landscapes), regardless of aridity, and were the steepest among species (Figure 4). Subalpine fir regeneration changed little or increased in wet scenarios and changed little or declined in dry scenarios, with the steepest declines in the hot-dry scenario (−8.5% to −18.8% per 5-year bin; Figure 4). Lodgepole pine regeneration remained the same or increased under wet scenarios, showing no change in the warm-wet scenario and increasing in the hot-wet scenario in Northern Yellowstone, Two Ocean Plateau, and Grand Teton (8.1%, 4.2%, and 7.2% per 5-year bin, respectively) while decreasing in Greys River (−12.4% per 5-year bin). However, lodgepole pine regeneration rates declined steeply across all landscapes in the hot-dry scenario

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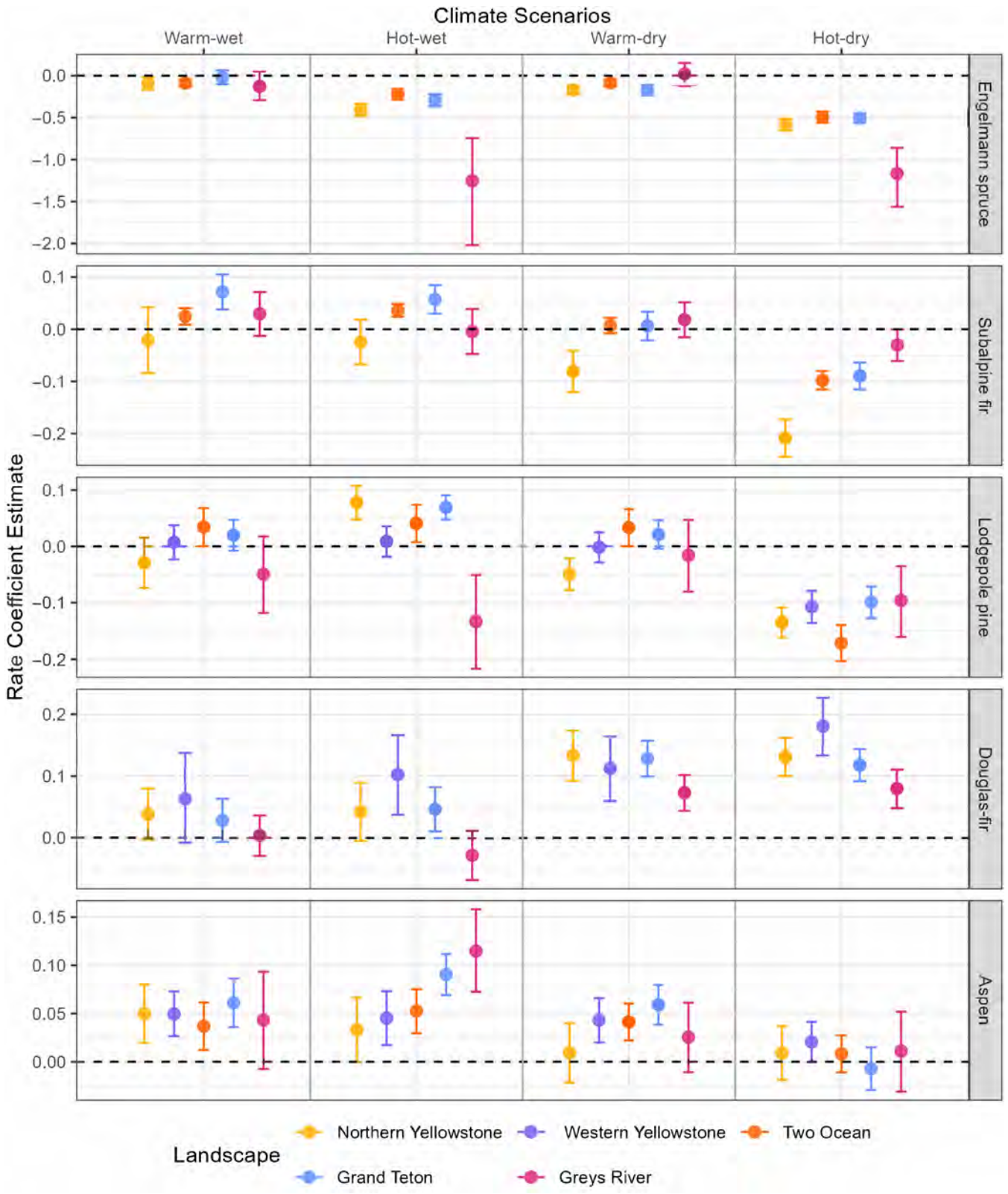

FIGURE 4 Regeneration rate (slope) coefficient estimates and 95% confidence interval by species, based on generalized linear models fit to each seedling density per hectare in every landscape–climate scenario combination from 2021 to 2100. Different colors represent the five study landscapes. Note that the *y*-axis differs among rows.

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(−9.2% to −15.7% per 5-year bin; Figure 4). Aspen regeneration rates increased in both wet scenarios (from 3.4% to 12.2% per 5-year bin for warm and hot temperatures, respectively) and in the warm-dry scenario but changed little in the hot-dry scenario (Figure 4). Douglas-fir regeneration rates increased in nearly all scenarios, with more rapid increases in the dry scenarios (7.6% to 19.8% per 5-year bin; Figure 4).

In association with declining tree regeneration rates in the hot-dry scenario, the proportion of area burned in which postfire regeneration failed (<50 seedlings ha^{-1}) increased in all landscapes between middle century (2030–2055) and late century (2075–2100) (Figure 5). In middle century, four landscapes experienced regeneration failure in only 2% to 4% of the area burned, and by late century, regeneration failed in 7% to 18% of the area burned. Greys River was the exception, with only 1% of burned area failing to regenerate even in the hot-dry scenario (Figure 5).

Composition of postfire regeneration

Composition of seedling cohorts through 2100 varied among climate scenarios (Figure 6, Table 2). In the wet scenarios, the composition of postfire seedling cohorts remained similar, except for declines in Engelmann spruce regeneration in most landscapes (−58% to −100% across landscapes) and increased aspen regeneration in Greys River (61% to 132% across landscapes) (Figure 6, Table 2). In the dry scenarios, the composition of postfire cohorts changed considerably. Douglas-fir dominated regeneration in Northern Yellowstone and Greys River by late century in both dry scenarios (Figure 6) and

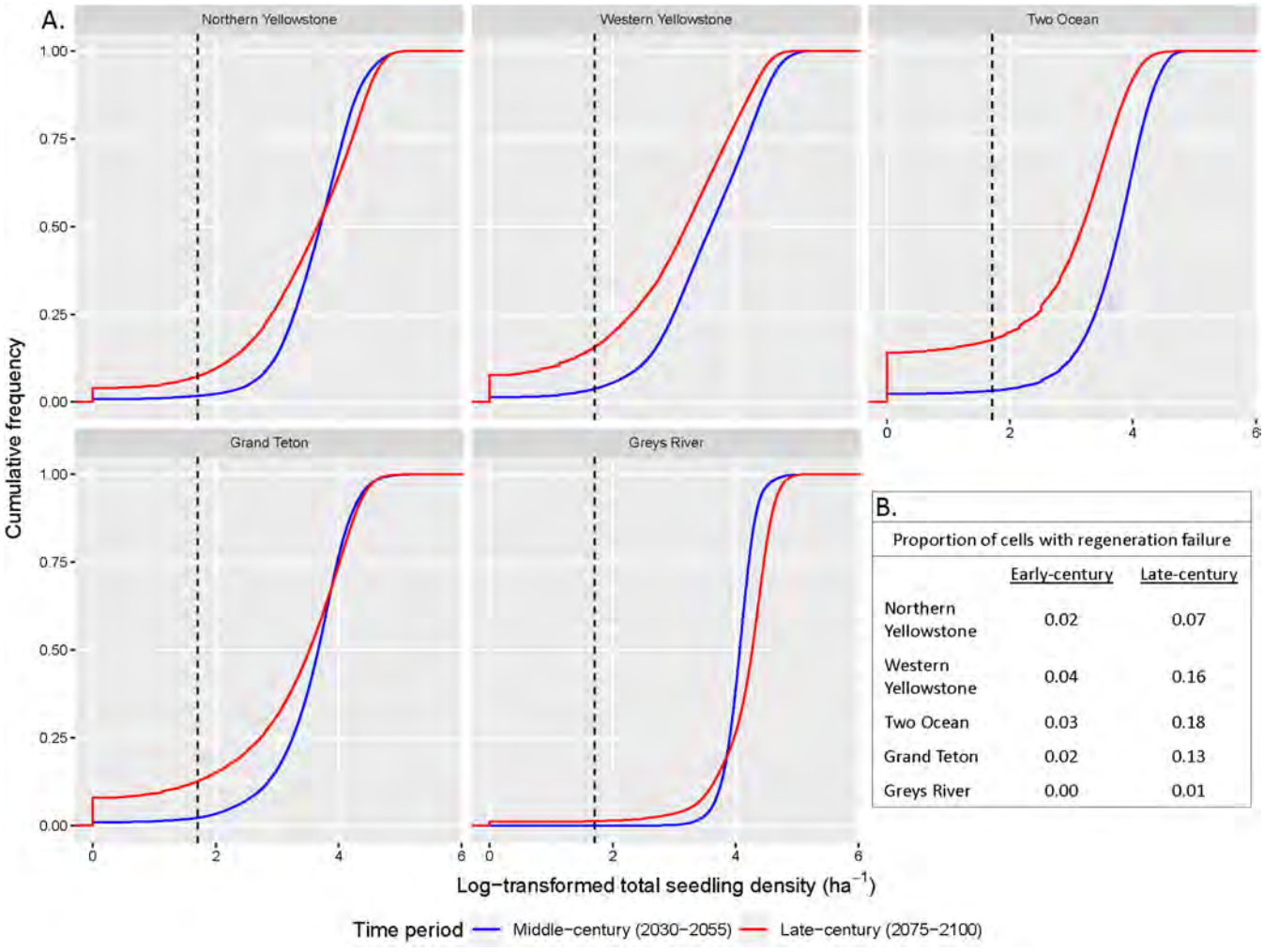

FIGURE 5 (A) Cumulative frequency distribution of seedling density per hectare ($\log_{10}$ transformed) at 5 years postfire for each landscape in the hot-dry scenario (HadGEM2-ES; RCP 8.5) with the blue and red lines showing middle century (2030–2055) and late century (2075–2100). The vertical dashed line is at 50 seedlings per hectare to indicate the threshold used to identify regeneration failure. (B) Proportion of cells in which early postfire tree regeneration failed for each landscape and time period.

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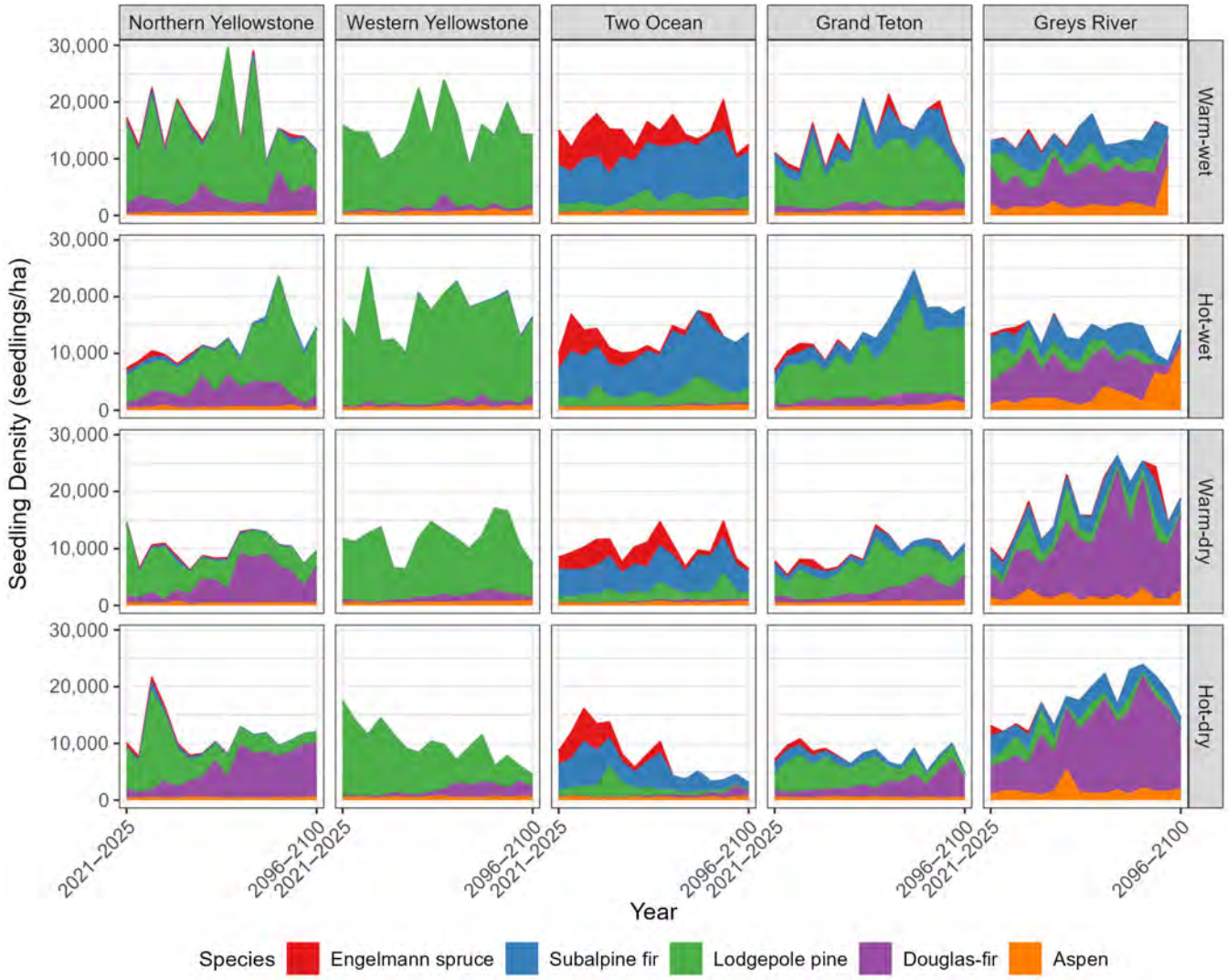

FIGURE 6 Mean simulated seedling densities by species for 5-year bins from 2021 to 2100. For each graph, the *y*-axis sums to mean total regeneration density for each 5-year bin, and the contribution of each species is indicated by color.

accounted for 76% of late-century regeneration in the hot-dry scenario (8734 and 16,660 Douglas-fir seedlings ha^{-1}; Table 2). Lodgepole pine dominated postfire regeneration in West Yellowstone and Grand Teton in mid-century across scenarios, but low regeneration densities reduced lodgepole pine dominance in both landscapes (e.g., 4365 and 1808 lodgepole pine seedlings ha^{-1}, respectively, accounting for 63% and 26% of total regeneration density in the hot-dry scenario; Table 2). In the hot-dry scenario, Engelmann spruce was eliminated from the postfire seedling community across all landscapes (Figure 6), and even on the high-elevation Two Ocean Plateau, it accounted for only 15% of late-century regeneration in the warm-dry scenario (Table 2). Subalpine fir and aspen never dominated postfire seedling recruitment, but presence was maintained in all landscapes and climate scenarios (Table 2).

Spatial patterns of forest change

Forest recovery pathways varied substantially with climate scenarios and among landscapes (Figure 7). In the wet scenarios, large areas of three landscapes were unaffected by fire, whereas fire affected almost the entirety of four landscapes in the dry scenarios (Figure 7). Postfire resilience was lower across all landscapes in the dry versus wet climate scenarios, but other postfire pathways were variable among landscapes. Restructuring was common in both Northern Yellowstone and Western Yellowstone (Figure 7), which largely shifted to less-dense forests (Appendix S1: Figure S2). In both landscapes, Douglas-fir increased as a dominant forest type (Appendix S1: Figure S3). Western Yellowstone also sustained areas of resilience where lodgepole pine

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TABLE 2 Mean seedling regeneration (seedlings per hectare) across all simulations for large (>400 ha) fires in middle century (2030–2055) to late century (2075–2100) and net change between the two periods.

	Wet climate (CanESM2)						Dry climate (HadGEM2-ES)					
	Warm (RCP 4.5)			Hot (RCP 8.5)			Warm (RCP 4.5)			Hot (RCP 8.5)		
Landscape	Middle	Late	Δ (%)	Middle	Late	Δ (%)	Middle	Late	Δ (%)	Middle	Late	Δ (%)
Engelmann spruce												
Northern Yellowstone	589	246	−58	413	10	−98	274	47	−83	433	1	−100
Western Yellowstone	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Two Ocean	5605	1937	−65	3157	378	−88	3218	1274	−60	2708	8	−100
Grand Teton	849	354	−58	641	14	−98	638	89	−86	569	2	−100
Greys River	290	42	−86	227	0	−100	326	359	10	296	0	−100
Subalpine fir												
Northern Yellowstone	663	577	−13	537	613	14	364	166	−54	603	106	−82
Western Yellowstone	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Two Ocean	7342	9387	28	6407	10,046	57	4566	5286	16	4681	1940	−59
Grand Teton	2029	3473	71	2288	3498	53	1180	1161	−2	1425	705	−51
Greys River	3450	4303	25	3453	3480	1	2421	2774	15	2382	2435	2
Lodgepole pine												
Northern Yellowstone	10,592	7609	−28	5061	11,801	133	4687	3422	−27	7952	2229	−72
Western Yellowstone	13,209	15,599	18	13,903	15,474	11	9502	9798	3	10,829	4365	−60
Two Ocean	1643	2165	32	1876	3226	72	1700	1674	−2	2075	471	−77
Grand Teton	7071	8890	27	6275	12,638	101	4314	4895	13	4627	1808	−61
Greys River	2484	1626	−35	1682	1013	−50	2369	1646	−31	2252	978	−57
Aspen												
Northern Yellowstone	383	556	45	454	580	28	294	381	30	365	378	4
Western Yellowstone	469	706	51	411	632	54	392	630	61	405	529	31
Two Ocean	464	615	33	429	664	55	310	551	78	396	423	7
Grand Teton	399	684	71	486	1173	141	360	699	94	444	361	−19
Greys River	1568	2518	61	1859	4314	132	1546	1703	10	1761	1524	−13
Douglas-fir												
Northern Yellowstone	2685	3776	41	2787	3063	10	2614	6278	140	2437	8734	258
Western Yellowstone	518	579	12	567	1209	113	442	1577	257	444	1992	349
Two Ocean	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Grand Teton	884	1265	43	1151	1433	25	978	3618	270	1225	4123	237
Greys River	5367	5514	3	6377	4880	−23	8455	13,582	61	6907	16,660	141

Note: Means were computed across for the 25-year window across all 20 simulations of each climate × landscape combination. NA indicates not applicable, as each species was not present in each landscape.

remained dominant and dense (Appendix S1: Figures S2 and S3). Replacement and reassembly were the most frequent postfire pathways on Two Ocean Plateau (Figure 7), reflecting a shift to sparser forests dominated by subalpine fir (Appendix S1: Figures S2 and S3). Replacement and restructuring were most prominent in Grand Teton (Figure 7), with increased dominance of Douglas-fir and areas of both sparser and denser forests (Appendix S1: Figures S2 and S3). In Greys River, reassembly was the most frequent recovery pathway within areas that burned (Figure 7). Most burned forests remained in the same density class, but mixed forests shifted to Douglas-fir dominance (Appendix S1: Figures S2 and S3).

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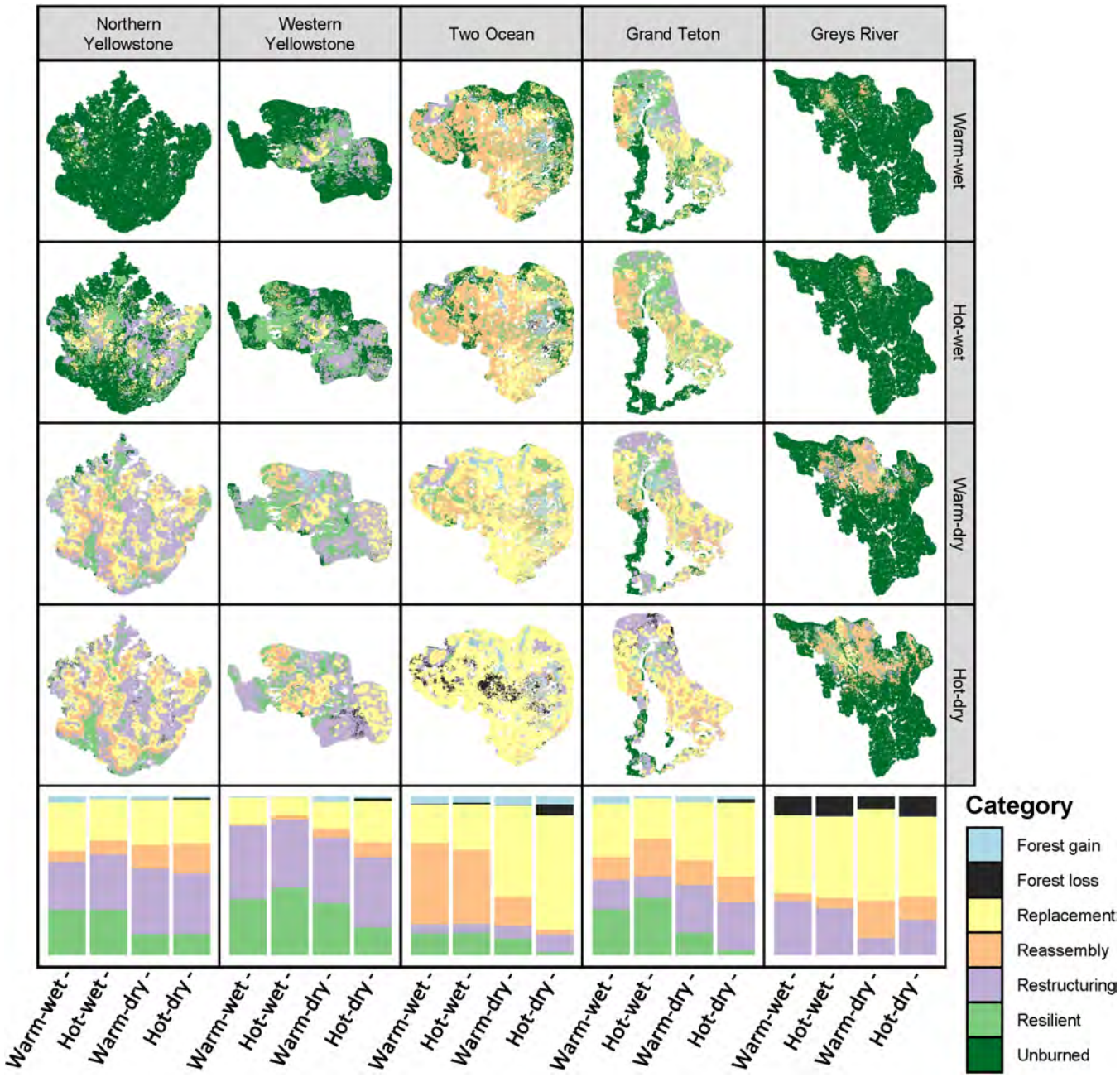

FIGURE 7 Maps of unburned areas or postfire reorganization trajectories across each landscape–climate scenario as indicated by the difference between prefire stand structure before the first time the cell burned and postfire regeneration following the last simulated fire. Categories were assigned based on the most frequent categorization across the 20 simulations. Stacked bar charts indicate the proportion of burned areas across the landscapes in each reorganization category. Colors across the maps and bar charts indicate the reorganization category.

DISCUSSION

Our simulation results found that declining rates of early postfire tree regeneration and shifts in species composition were prevalent in the 21st century, but regeneration failure never exceeded 20% of the area burned. With a wet future climate or modest warming, fire activity did not rise substantially, and early postfire tree regeneration density and composition were sustained except in the high-elevation landscape. With a drier future climate and greater warming, fire activity increased, and postfire tree regeneration rates declined sharply, especially for fire avoiders. However, declines in regeneration of some species (e.g., Engelmann spruce or lodgepole pine) were often countered by increases in regeneration of others (e.g., Douglas-fir, subalpine fir, aspen). Shifts in both the

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structure and composition of postfire tree regeneration initiated a wide range of recovery pathways across the GYE. Resilience per se (i.e., recovery to prefire structure and composition) was uncommon following simulated fires, but fire-catalyzed forest reorganization was prevalent. Reduced early regeneration densities combined with the increase in fire-tolerant resisters or endurers suggest the potential for forests to shift toward lower densities and species assemblages better aligned with a warming climate.

Rates and composition of early postfire tree regeneration

Total early regeneration was maintained under the wet climate scenarios, as expected, but we were surprised that total early regeneration did not decline in all dry climate scenarios. Dry conditions are a strong environmental filter on tree seedling establishment (Kueppers et al., 2017; Lazarus et al., 2018), especially in the lower montane zone (Davis et al., 2019; Donato, Fontaine, & Campbell, 2016; Stevens-Rumann et al., 2018) when drought years follow high-severity fires (Harvey et al., 2016), or when loss of canopy cover and snags leads to hotter, drier soils (Hoecker et al., 2020; Wolf et al., 2021). However, some subalpine forests in the Northern Rocky Mountains may retain a climate suitable for tree regeneration through mid-century, even with warming (Davis et al., 2023). Regeneration is often sustained in mesic locations even after high-severity fire and recent reburns (Clark-Wolf et al., 2022; Jaffe et al., 2023; Povak et al., 2020). Relaxation of cold limitations for some species (e.g., Douglas-fir) might also enhance tree establishment and growth with moderate temperature increases (Carroll et al., 2021; Körner & Paulsen, 2024), but see Klesse et al. (2020) who predicted declining growth rates for Douglas-fir in the Rocky Mountains with future warming. Thus, local variation in topographic and biophysical context may help sustain postfire tree regeneration even with some drying if species' physiological thresholds for temperature or moisture are not surpassed.

Regeneration of fire-sensitive, higher-elevation conifers declined as expected, consistent with reduced recruitment of subalpine fir and Engelmann spruce in association with warmer temperatures, low snowpack, and altered precipitation (Andrus et al., 2018). The failure of Engelmann spruce regeneration under hot scenarios reflects its lack of heat tolerance and underscores that this species may be increasingly restricted to cool, mesic microsites (e.g., north aspects at high elevations) as climate warms (Seidel, 1986). In contrast, although regeneration of subalpine fir declined under hot and dry scenarios, its persistent regeneration suggests viability under moderate warming, sustained precipitation, and moderate changes in wildfire regimes (Perret et al., 2025). Subalpine fir and Engelmann spruce co-occur in high-elevation forests, but subalpine fir is also co-dominant with Douglas-fir in lower elevation portions of the GYE (M.G. Turner, personal observations), suggesting a wide range of climate tolerance. The persistence of lodgepole pine in all scenarios likely reflects its dual life history strategy (serotinous and non-serotinous trees; Schoennagel et al., 2003; Tinker et al., 1994; Turner et al., 2007), rapid growth, and capacity to produce cones at a young age (Turner et al., 2007). Overall, our results suggest that the presence of tree species with complementary regeneration strategies could promote postfire recovery pathways that allow forests to adapt to a warmer world with more fire (Keeley & Pausas, 2022; Seidl & Turner, 2022).

Our findings that regeneration failure did not dominate burned areas, even during the late century, might initially appear contradictory to recent studies documenting forest transitions to non-forest (e.g., Petrie et al., 2023; Stevens-Rumann et al., 2018). Indeed, postfire regeneration failure has been documented in portions of fires in the US Northern Rockies, including areas of compound disturbance (e.g., Hoecker et al., 2020; Turner et al., 2019); in topographic positions where environmental conditions hinder seedling establishment, such as south-facing slopes at lower treeline (e.g., Donato, Fontaine, & Campbell, 2016; Hansen & Turner, 2019); and at distances far from live-tree seed sources (e.g., Harvey et al., 2013; Kiel et al., 2025). While postfire regeneration failure attributed to climate and high-severity fire has occurred in southwestern forests of the United States (Coop et al., 2020; Hurteau et al., 2025; Petrie et al., 2023), to our knowledge, regeneration has not yet failed throughout an entire fire in the Northern Rocky Mountains. Our analyses also differ from an earlier simulation study that predicted widespread loss of resilience in a hot-dry future climate (Rammer et al., 2021). The Rammer et al. study defined regeneration failure as the inability of the species currently dominating an area to regenerate after fire, assumed all fires were high-severity (stand-replacing), and did not allow tree species to move across the landscape. The plethora of regeneration pathways (Figure 7) and lack of resilience sensu stricto is thus consistent with conclusions drawn by Rammer et al. (2021).

Other studies in the GYE have projected changes in forest composition under future climate that are generally consistent with our results. Landscapes and scenarios with the greatest declines in postfire regeneration were also consistent with landscapes for which Turner et al. (2022) reported the greatest declines in the extent of mature forest. Simulations using LANDIS-II emphasized

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carbon dynamics but reported reduced conifer regeneration after mid-century (Henne et al., 2021). However, their results projected regeneration failure of both Engelmann spruce and Douglas-fir after 2070 with the same hot-dry scenario. Simulations using FIRE-BGCv2 reported a shift in basal area dominance from lodgepole pine to Douglas-fir with moderate warming in the central plateau of YELL (Clark et al., 2017), although dispersal of Douglas-fir seeds to areas far from mature individuals seems unlikely.

Spatial patterns of forest change

Our results suggest that wildfires could promote widespread shifts in species dominance and stand structure that reorganize rather than eliminate forests in the GYE (cf. Figure 2). Recovery pathways with altered densities and/or dominant species (e.g., restructuring, replacement, and reassembly) were common across most landscapes, even with hotter temperatures and drier climates. We found two landscapes (Northern Yellowstone, Western Yellowstone) where restructuring, with a decrease in regeneration, was the most prevalent pathway. Western Yellowstone lies on gentle terrain where fires can readily spread due to continuous forests, and short-interval fires can reduce regeneration densities of serotinous lodgepole pine because of immaturity risk (e.g., Turner et al., 2019). The prevalence of replacement on Two Ocean Plateau is likely due to seed limitations that reduce stem density (Kiel et al., 2025) and the loss of Engelmann spruce, which increased the dominance of subalpine fir. The prevalence of replacement in Grand Teton reflected both increased and decreased regeneration density and increased dominance of Douglas-fir. Greys River had the least area burned and may experience less forest change in the future. If fire occurred, reassembly was most common as the dominance of Douglas-fir and aspen both increased. Although future climate remains uncertain, trends in the GYE since 1950 have already led to hotter, drier summers and more area burned (Hostetler et al., 2021). These trends show no signs of stopping, and thus we suggest that forest reorganization is increasingly likely (Davis et al., 2019; Dollinger et al., 2024; Hessburg et al., 2019; Hoecker et al., 2023). Collectively, our results suggest that there will be substantial fire-catalyzed changes in GYE forests by 2100.

Our findings of variation in postfire recovery pathways across landscapes are consistent with studies following recent fires in western North America. Postfire replacement and reassembly have been observed in the Northern Rocky Mountains, where there is greater diversity in tree species (Hoecker & Turner, 2022; Urza & Sibold, 2017) and in the boreal forest, where fire-adapted deciduous species have replaced conifer-dominated forests (Whitman et al., 2019). In contrast, restructuring and regime shifts have been observed in drier climates and where forest communities are more homogeneous (Rodman et al., 2020; Rother & Veblen, 2016; Turner et al., 2019). These observations further suggest that varied postfire recovery trajectories will continue to emerge following 21st-century wildfires.

CAVEATS

We simulated 20 replicate fire sequences for each climate scenario × landscape to explore plausible futures, but in reality, only one climate-fire trajectory will unfold. Current trends are consistent with longer, drier summers and extended fire seasons relative to historical conditions (Reidmiller et al., 2017), suggesting that drier futures are more likely in the GYE. We also recognize that the effects of microclimate on tree regeneration could be stronger than our model suggests. Our simulations used climate downscaled to 4-km × 4-km resolution, which cannot account for local variation in microclimate (Tercek et al., 2021). Downscaling to finer resolution (e.g., 1 ha as in Dollinger et al., 2024) and the consideration of microclimatic buffering below the canopy (Braziunas et al., 2025) could yield different results. In addition to fire, tree regeneration can be affected by factors not considered in our study, such as seed predation or seedling herbivory (e.g., Painter et al., 2015; Romme et al., 1995), and other natural disturbances, such as outbreaks of native bark beetles (*Dendroctonus* spp.) that structure forests during fire-free intervals (Donato et al., 2013; Simard et al., 2012).

CONCLUSIONS

Our simulations suggest that changes in postfire tree regeneration in GYE forests may lead to a reorganization rather than loss of forests during the 21st century, and that forests may adapt to tolerate a warmer climate. Results also indicate that limiting temperature increases (as in RCP 4.5) could sustain postfire tree regeneration across much of the GYE and enable persistence of cold-adapted species such as Engelmann spruce. Tree regeneration failure is likely to increase across western North America (Stevens-Rumann et al., 2022), but it is not the only pathway of change. Monitoring postfire tree regeneration during the reorganization window is especially important as an indicator of how forests are likely to develop and for evaluating simulated projections of

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forest change (Halofsky et al., 2018). Fire could allow forests to reorganize toward less dense stands composed of tree species better able to persist in a warming climate.

AUTHOR CONTRIBUTIONS

Garrett J. Knowlton, Rupert Seidl, and Monica G. Turner designed the study. Garrett J. Knowlton and Timon T. Keller analyzed the data. Garrett J. Knowlton and Monica G. Turner wrote the manuscript with input from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Knowlton et al., 2025) are available from the Environmental Data Initiative (EDI) Data Portal: https://doi.org/10.6073/pasta/43f2f62f84495380fc7e2aa42ff90828.

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REFERENCES

Abatzoglou, J. T. 2013. "Development of Gridded Surface Meteorological Data for Ecological Applications and Modelling." *International Journal of Climatology* 33(1): 121–131. https://doi.org/10.1002/joc.3413.

Abatzoglou, J. T., and T. J. Brown. 2012. "A Comparison of Statistical Downscaling Methods Suited for Wildfire Applications." *International Journal of Climatology* 32(5): 772–780. https://doi.org/10.1002/joc.2312.

Agee, J. K. 1993. *Fire Ecology of Pacific Northwest Forests*, Vol. 499. Washington, DC: Island Press.

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. "Adaptation, Migration or Extirpation: Climate Change Outcomes for Tree Populations." *Evolutionary Applications* 1(1): 95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x.

Albrich, K., W. Rammer, and R. Seidl. 2020. "Climate Change Causes Critical Transitions and Irreversible Alterations of Mountain Forests." *Global Change Biology* 26(7): 4013–27. https://doi.org/10.1111/gcb.15118.

Anderson-Teixeira, K. J., A. D. Miller, J. E. Mohan, T. W. Hudiburg, B. D. Duval, and E. H. DeLucia. 2013. "Altered Dynamics of Forest Recovery under a Changing Climate." *Global Change Biology* 19(7): 2001–21. https://doi.org/10.1111/gcb.12194.

Andrus, R. A., B. J. Harvey, K. C. Rodman, S. J. Hart, and T. T. Veblen. 2018. "Moisture Availability Limits Subalpine Tree Establishment." *Ecology* 99(3): 567–575. https://doi.org/10.1002/ecy.2134.

Baker, W. L. 2009. *Fire Ecology in Rocky Mountain Landscapes*. Washington, DC: Island Press.

Baltzer, J. L., N. J. Day, X. J. Walker, D. Greene, M. C. Mack, H. D. Alexander, D. Arseneault, et al. 2021. "Increasing Fire and the Decline of Fire Adapted Black Spruce in the Boreal Forest." *Proceedings of the National Academy of Sciences* 118(45): e2024872118. https://doi.org/10.1073/pnas.2024872118.

Braziunas, K. H., W. D. Hansen, R. Seidl, W. Rammer, and M. G. Turner. 2018. "Looking Beyond the Mean: Drivers of Variability in Postfire Stand Development of Conifers in Greater Yellowstone." *Forest Ecology and Management* 430(December): 460–471. https://doi.org/10.1016/j.foreco.2018.08.034.

Braziunas, K. H., N. G. Kiel, and M. G. Turner. 2023. "Less Fuel for the Next Fire? Short-Interval Fire Delays Forest Recovery and Interacting Drivers Amplify Effects." *Ecology* 104(6): e4042. https://doi.org/10.1002/ecy.4042.

Braziunas, K. H., W. Rammer, P. De Frenne, J. Díaz-Calafat, P.-O. Hedwall, C. Senf, D. Thom, F. Zellweger, and R. Seidl. 2025. "Microclimate Temperature Effects Propagate across Scales in Forest Ecosystems." *Landscape Ecology* 40(2): 37. https://doi.org/10.1007/s10980-025-02054-8.

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(2): 34–41. https://doi.org/10.1016/j.foreco.2011.11.006.

Bugmann, H., and R. Seidl. 2022. "The Evolution, Complexity and Diversity of Models of Long-Term Forest Dynamics." *Journal of Ecology* 110(10): 2288–2307. https://doi.org/10.1111/1365-2745.13989.

Carroll, C. J. W., A. K. Knapp, and P. H. Martin. 2021. "Higher Temperatures Increase Growth Rates of Rocky Mountain Montane Tree Seedlings." *Ecosphere* 12(3): e03414. https://doi.org/10.1002/ecs2.3414.

Clark, J. A., R. A. Loehman, and R. E. Keane. 2017. "Climate Changes and Wildfire Alter Vegetation of Yellowstone

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National Park, but Forest Cover Persists." *Ecosphere* 8(1): e01636. https://doi.org/10.1002/ecs2.1636.

Clark-Wolf, K., P. E. Higuera, and K. T. Davis. 2022. "Conifer Seedling Demography Reveals Mechanisms of Initial Forest Resilience to Wildfires in the Northern Rocky Mountains." *Forest Ecology and Management* 523(November): 120487. https://doi.org/10.1016/j.foreco.2022.120487.

Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, S. D. Crausbay, P. E. Higuera, M. D. Hurteau, A. Tepley, et al. 2020. "Wildfire-Driven Forest Conversion in Western North American Landscapes." *Bioscience* 70(8): 659–673. https://doi.org/10.1093/biosci/biaa061.

Davis, K. T., S. Z. Dobrowski, P. E. Higuera, Z. A. Holden, T. T. Veblen, M. T. Rother, S. A. Parks, A. Sala, and M. P. Maneta. 2019. "Wildfires and Climate Change Push Low-Elevation Forests across a Critical Climate Threshold for Tree Regeneration." *Proceedings of the National Academy of Sciences* 116(13): 6193–98. https://doi.org/10.1073/pnas.1815107116.

Davis, K. T., M. D. Robles, K. B. Kemp, P. E. Higuera, T. Chapman, K. L. Metlen, J. L. Peeler, et al. 2023. "Reduced Fire Severity Offers near-Term Buffer to Climate-Driven Declines in Conifer Resilience across the Western United States." *Proceedings of the National Academy of Sciences* 120(11): e2208120120. https://doi.org/10.1073/pnas.2208120120.

Dollinger, C., W. Rammer, K. F. Suzuki, K. H. Braziunas, T. T. Keller, Y. Kobayashi, J. Mohr, A. S. Mori, M. G. Turner, and R. Seidl. 2024. "Beyond Resilience: Responses to Changing Climate and Disturbance Regimes in Temperate Forest Landscapes across the Northern Hemisphere." *Global Change Biology* 30(8): e17468. https://doi.org/10.1111/gcb.17468.

Donato, D. C., J. B. Fontaine, and J. L. Campbell. 2016. "Burning the Legacy? Influence of Wildfire Reburn on Dead Wood Dynamics in a Temperate Conifer Forest." *Ecosphere* 7(5): e01341. https://doi.org/10.1002/ecs2.1341.

Donato, D. C., B. J. Harvey, W. H. Romme, M. Simard, and M. G. Turner. 2013. "Bark Beetle Effects on Fuel Profiles across a Range of Stand Structures in Douglas-Fir Forests of Greater Yellowstone." *Ecological Applications* 23(1): 3–20. https://doi.org/10.1890/12-0772.1.

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(8): e01410. https://doi.org/10.1002/ecs2.1410.

Dowle, M., A. Srinivasan, J. Gorecki, M. Chirico, P. Stetsenko, T. Short, S. Lianoglou, et al. 2019. "Package 'Data. Table'. Extension of 'Data. Frame'." 596. 952.

Esri. World Hillshade (Basemap). 2025. "Esri, Maxar, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap, and the GIS User Community." https://www.arcgis.com/home/item.html?id=1b243539f4514b6ba35e7d995890db1d

Fairman, T. A., C. R. Nitschke, and L. T. Bennett. 2022. "Carbon Stocks and Stability Are Diminished by Short-Interval Wildfires in Fire-Tolerant Eucalypt Forests." *Forest Ecology and Management* 505(2): 119919. https://doi.org/10.1016/j.foreco.2021.119919.

Falk, D. A., P. J. van Mantgem, J. E. Keeley, R. M. Gregg, C. H. Guiterman, A. J. Tepley, D. J. N. Young, and L. A. Marshall. 2022. "Mechanisms of Forest Resilience." *Forest Ecology and Management* 512(5): 120129. https://doi.org/10.1016/j.foreco.2022.120129.

Germain, S. J., W. D. Hansen, and C. D. Canham. 2025. "Reassembly of Disturbed Forests Portends Climate Resilience but Diversity Loss." *Ecosystems* 28(1): 1–16. https://doi.org/10.1007/s10021-024-00959-0.

Gill, N. S., T. J. Hoecker, and M. G. Turner. 2021. "The Propagule Doesn't Fall Far from the Tree, Especially after Short-Interval, High-Severity Fire." *Ecology* 102(1): e03194. https://doi.org/10.1002/ecy.3194.

Gill, N. S., M. G. Turner, C. D. Brown, S. I. Glassman, S. L. Haire, W. D. Hansen, E. R. Pansing, S. B. St Clair, and D. F. Tomback. 2022. "Limitations to Propagule Dispersal Will Constrain Postfire Recovery of Plants and Fungi in Western Coniferous Forests." *Bioscience* 72(4): 347–364. https://doi.org/10.1093/biosci/biab139.

Goeking, S. A., D. K. Izlar, and T. C. Edwards. 2019. "A Landscape-Level Assessment of Whitebark Pine Regeneration in the Rocky Mountains, USA." *Forest Science* 65(1): 87–99. https://doi.org/10.1093/forsci/fxy029.

Gunderson, L. H., and C. S. Holling. 2003. *Panarchy: Understanding Transformations in Human and Natural Systems*. Washington, DC: Island Press.

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(8): 1429–37. https://doi.org/10.1007/s10980-013-9927-4.

Halofsky, J. S., D. C. Donato, J. F. Franklin, J. E. Halofsky, D. L. Peterson, and B. J. Harvey. 2018. "The Nature of the Beast: Examining Climate Adaptation Options in Forests with Stand-Replacing Fire Regimes." *Ecosphere* 9(3): e02140. https://doi.org/10.1002/ecs2.2140.

Hansen, W. D., K. H. Braziunas, W. Rammer, R. Seidl, and M. G. Turner. 2018. "It Takes a Few to Tango: Changing Climate and Fire Regimes Can Cause Regeneration Failure of Two Subalpine Conifers." *Ecology* 99(4): 966–977. https://doi.org/10.1002/ecy.2181.

Hansen, W. D., and M. G. Turner. 2019. "Origins of Abrupt Change? Postfire Subalpine Conifer Regeneration Declines Nonlinearly with Warming and Drying." *Ecological Monographs* 89(1): e01340. https://doi.org/10.1002/ecm.1340.

Hart, S. J., J. Henkelman, P. D. McLoughlin, S. E. Nielsen, A. Truchon-Savard, and J. F. Johnstone. 2019. "Examining Forest Resilience to Changing Fire Frequency in a Fire-Prone Region of Boreal Forest." *Global Change Biology* 25(3): 869–884. https://doi.org/10.1111/gcb.14550.

Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2013. "Influence of Recent Bark Beetle Outbreak on Fire Severity and Postfire Tree Regeneration in Montane Douglas-Fir Forests." *Ecology* 94(11): 2475–86. https://doi.org/10.1890/13-0188.1.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. "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*

21508925, 2025, 10, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.70415 by University Of Wisconsin - Madison, Wiley Online Library on [28/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Biogeography 25(6): 655–669. https://doi.org/10.1111/geb.12443.

Henne, P. D., T. J. Hawbaker, R. M. Scheller, F. Zhao, H. S. He, W. Xu, and Z. Zhu. 2021. "Increased Burning in a Warming Climate Reduces Carbon Uptake in the Greater Yellowstone Ecosystem despite Productivity Gains." *Journal of Ecology* 109(3): 1148–69. https://doi.org/10.1111/1365-2745.13559.

Hessburg, P. F., C. L. Miller, S. A. Parks, N. A. Povak, A. H. Taylor, P. E. Higuera, S. J. Prichard, et al. 2019. "Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests." *Frontiers in Ecology and Evolution* 7: 239. https://doi.org/10.3389/fevo.2019.00239.

Higuera, P. E., C. Whitlock, and J. A. Gage. 2011. "Linking Tree-Ring and Sediment-Charcoal Records to Reconstruct Fire Occurrence and Area Burned in Subalpine Forests of Yellowstone National Park, USA." *The Holocene* 21(2): 327–341. https://doi.org/10.1177/0959683610374882.

Hijmans, R. 2025a. "raster: Geographic Data Analysis and Modeling." R Package Version 3.6–31. https://CRAN.R-project.org/package=raster.

Hijmans, R. 2025b. "terra: Spatial Data Analysis." R Package Version 1.8–15. https://CRAN.R-project.org/package=terra.

Hoecker, T. J., W. D. Hansen, and M. G. Turner. 2020. "Topographic Position Amplifies Consequences of Short-Interval Stand-Replacing Fires on Postfire Tree Establishment in Subalpine Conifer Forests." *Forest Ecology and Management* 478: 118523. https://doi.org/10.1016/j.foreco.2020.118523.

Hoecker, T. J., S. A. Parks, M. Krosby, and S. Z. Dobrowski. 2023. "Widespread Exposure to Altered Fire Regimes under 2°C Warming Is Projected to Transform Conifer Forests of the Western United States." *Communications Earth & Environment* 4(1): 1–12. https://doi.org/10.1038/s43247-023-00954-8.

Hoecker, T. J., and M. G. Turner. 2022. "A Short-Interval Reburn Catalyzes Departures from Historical Structure and Composition in a Mesic Mixed-Conifer Forest." *Forest Ecology and Management* 504: 119814. https://doi.org/10.1016/j.foreco.2021.119814.

Holling, C. S. 1973. "Resilience and Stability of Ecological Systems." *Annual Review of Ecology and Systematics* 4: 1–23. http://www.jstor.org/stable/2096802.

Hostetler, S., C. Whitlock, B. Shuman, D. Liefert, C. Drimal, and S. Bischke. 2021. *Greater Yellowstone Climate Assessment: Past, Present, and Future Climate Change in Greater Yellowstone Watersheds* 260. Bozeman MT: Montana State University, Institute on Ecosystems. https://doi.org/10.15788/GYCA2021.

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 & Evolution* 28(3): 149–155. https://doi.org/10.1016/j.tree.2012.08.022.

Hurteau, M. D., R. Baker, K. Gonterman, A. Granath, J. Lopez-Binder, M. D. Taylor, L. S. Rojas, et al. 2025. "Changing Climate and Disturbance Effects on Southwestern US Forests." *Forest Ecology and Management* 575: 122388. https://doi.org/10.1016/j.foreco.2024.122388.

Jaffe, M. R., M. R. Kreider, D. L. R. Affleck, P. E. Higuera, C. A. Seielstad, S. A. Parks, and A. J. Larson. 2023. "Mesic Mixed-Conifer Forests Are Resilient to Both Historical High-Severity Fire and Contemporary Reburns in the US Northern Rocky Mountains." *Forest Ecology and Management* 545(10): 121283. https://doi.org/10.1016/j.foreco.2023.121283.

Jones, C. D., J. K. Hughes, N. Bellouin, S. C. Hardiman, G. S. Jones, J. Knight, S. Liddicoat, et al. 2011. "The HadGEM2-ES Implementation of CMIP5 Centennial Simulations." *Geoscientific Model Development* 4(3): 543–570. https://doi.org/10.5194/gmd-4-543-2011.

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(3): 643–654. https://doi.org/10.1890/03-0828.

Keeley, J. E., G. Ne'eman, and C. J. Fotheringham. 1999. "Immaturity Risk in a Fire-Dependent Pine." *Journal of Mediterranean Ecology* 1(8): 41–48.

Keeley, J. E., and J. G. Pausas. 2022. "Evolutionary Ecology of Fire." *Annual Review of Ecology, Evolution, and Systematics* 53(1): 203–225. https://doi.org/10.1146/annurev-ecolsys-102320-095612.

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(3): 619–636. https://doi.org/10.1007/s10980-015-0268-3.

Kiel, N. G., E. F. Mavencamp, and M. G. Turner. 2025. "Sparse Subalpine Forest Recovery Pathways, Plant Communities, and Carbon Stocks 34 Years after Stand-Replacing Fire." *Ecological Monographs* 95(1): e1644. https://doi.org/10.1002/ecm.1644.

Kiel, N. G., and M. G. Turner. 2022. "Where Are the Trees? Extent, Configuration, and Drivers of Poor Forest Recovery 30 Years after the 1988 Yellowstone Fires." *Forest Ecology and Management* 524(11): 120536. https://doi.org/10.1016/j.foreco.2022.120536.

Klesse, S., R. J. DeRose, F. Babst, B. A. Black, L. D. L. Anderegg, J. Axelson, A. Ettinger, et al. 2020. "Continental-Scale Tree-Ring-Based Projection of Douglas-Fir Growth: Testing the Limits of Space-for-Time Substitution." *Global Change Biology* 26: 5146–63. https://doi.org/10.1111/gcb.15170.

Knowlton, G. J., T. T. Keller, R. Seidl, and M. G. Turner. 2025. "Data for: Simulated Postfire Tree Regeneration Suggests Reorganization of Greater Yellowstone Forests during the 21st Century ver 2." Environmental Data Initiative. https://doi.org/10.6073/pasta/43f2f62f84495380fc7e2aa42ff90828

Körner, C., and J. Paulsen. 2024. "A World-Wide Study of High Altitude Treeline Temperatures." *Journal of Biogeography* 31(5): 713–732. https://doi.org/10.1111/j.1365-2699.2003.01043.x.

Kueppers, L. M., E. Conlisk, C. Castanha, A. B. Moyes, M. J. Germino, P. de Valpine, M. S. Torn, and J. B. Mitton. 2017. "Warming and Provenance Limit Tree Recruitment across and Beyond the Elevation Range of Subalpine Forest." *Global Change Biology* 23(6): 2383–95. https://doi.org/10.1111/gcb.13561.

Kukavskaya, E. A., L. V. Buryak, E. G. Shvetsov, S. G. Conard, and O. P. Kalenskaya. 2016. "The Impact of Increasing Fire Frequency on Forest Transformations in Southern Siberia." *Forest Ecology and Management* 382(12): 225–235. https://doi.org/10.1016/j.foreco.2016.10.015.

21508925, 2025, 10, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.70415 by University Of Wisconsin - Madison, Wiley Online Library on [28/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Lazarus, B. E., C. Castanha, M. J. Germino, L. M. Kueppers, and A. B. Moyes. 2018. "Growth Strategies and Threshold Responses to Water Deficit Modulate Effects of Warming on Tree Seedlings from Forest to Alpine." *Journal of Ecology* 106(2): 571–585. https://doi.org/10.1111/1365-2745.12837.

Loehman, R. A., R. E. Keane, and L. M. Holsinger. 2020. "Simulation Modeling of Complex Climate, Wildfire, and Vegetation Dynamics to Address Wicked Problems in Land Management." *Frontiers in Forests and Global Change* 3: 3. https://doi.org/10.3389/ffgc.2020.00003.

Loope, L. L., and G. E. Gruell. 1973. "The Ecological Role of Fire in the Jackson Hole Area, Northwestern Wyoming." *Quaternary Research* 3: 425–443. https://doi.org/10.1016/0033-5894(73)90007-0.

Macfarlane, W. W., J. A. Logan, and W. R. Kern. 2013. "An Innovative Aerial Assessment of Greater Yellowstone Ecosystem Mountain Pine Beetle-Caused Whitebark Pine Mortality." *Ecological Applications* 23(2): 421–437. https://doi.org/10.1890/11-1982.1.

McDowell, N. G., C. D. Allen, K. Anderson-Teixeira, B. H. Aukema, B. Bond-Lamberty, L. Chini, J. S. Clark, et al. 2020. "Pervasive Shifts in Forest Dynamics in a Changing World." *Science* 368(6494): eaaz9463. https://doi.org/10.1126/science.aaz9463.

Müller, K., H. Wickham, D. A. James, S. Falcon, and L. Healy. 2017. "Package 'RSQLite'."

Nijp, J. J., A. J. A. M. Temme, G. A. K. van Voorn, L. Kooistra, G. M. Hengeveld, M. B. Soons, A. J. Teuling, and J. Wallinga. 2019. "Spatial Early Warning Signals for Impending Regime Shifts: A Practical Framework for Application in Real-World Landscapes." *Global Change Biology* 25(6): 1905–21. https://doi.org/10.1111/gcb.14591.

NOAA NCEI. 2025. "U.S. Climate Normals; National Oceanic and Atmospheric Association, National Centers for Environmental Information." National Centers for Environmental Information (NCEI). https://www.ncei.noaa.gov/products/land-based-station/us-climate-normals#:~:text=The%20product%20suite%20includes%20monthly%20climate

Painter, L. E., R. L. Beschta, E. J. Larsen, and W. J. Ripple. 2015. "Recovering Aspen Follow Changing Elk Dynamics in Yellowstone: Evidence of a Trophic Cascade?" *Ecology* 96(1): 252–263. https://doi.org/10.1890/14-0712.1.

Pausas, J. G., and J. E. Keeley. 2014. "Evolutionary Ecology of Resprouting and Seeding in Fire-Prone Ecosystems." *New Phytologist* 204(1): 55–65. https://doi.org/10.1111/nph.12921.

Perret, D. L., D. M. Bell, and H. S. J. Zald. 2025. "Reducing Fire Severity and Extent Bolsters Subalpine Forest Resilience to Global Change Through Key Demographic Pathways." *Global Change Biology* 31(2): e70052. https://doi.org/10.1111/gcb.70052.

Petrie, M. D., A. M. Wildeman, J. B. Bradford, R. M. Hubbard, and W. K. Lauenroth. 2016. "A Review of Precipitation and Temperature Control on Seedling Emergence and Establishment for Ponderosa and Lodgepole Pine Forest Regeneration." *Forest Ecology and Management* 361(February): 328–338. https://doi.org/10.1016/j.foreco.2015.11.028.

Petrie, M. D., R. M. Hubbard, J. B. Bradford, T. E. Kolb, A. Noel, D. R. Schlaepfer, M. A. Bowen, L. R. Fuller, and W. K. Moser. 2023. "Widespread Regeneration Failure in Ponderosa Pine Forests of the Southwestern United States." *Forest Ecology and Management* 545: 121208. https://doi.org/10.1016/j.foreco.2023.121208.

Povak, N. A., D. J. Churchill, C. A. Cansler, P. F. Hessburg, V. R. Kane, J. T. Kane, J. A. Lutz, and A. J. Larson. 2020. "Wildfire Severity and Postfire Salvage Harvest Effects on Long-Term Forest Regeneration." *Ecophere* 11(8): e03199. https://doi.org/10.1002/ecs2.3199.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*_. Vienna: R Foundation for Statistical Computing. https://www.R-project.org.

Ramiadantsoa, T., Z. Ratajczak, and M. G. Turner. 2023. "Regeneration Strategies and Forest Resilience to Changing Fire Regimes: Insights from a Goldilocks Model." *Ecology* 104(6): e4041. https://doi.org/10.1002/ecy.4041.

Rammer, W., K. H. Braziunas, W. D. Hansen, Z. Ratajczak, A. L. Westerling, M. G. Turner, and R. Seidl. 2021. "Widespread Regeneration Failure in Forests of Greater Yellowstone under Scenarios of Future Climate and Fire." *Global Change Biology* 27(18): 4339–51. https://doi.org/10.1111/gcb.15726.

Rammer, W., D. Thom, M. Baumann, K. Braziunas, C. Dollinger, J. Kerber, J. Mohr, and R. Seidl. 2024. "The Individual-Based Forest Landscape and Disturbance Model iLand: Overview, Progress, and Outlook." *Ecological Modelling* 495: 110785. https://doi.org/10.1016/j.ecolmodel.2024.110785.

Reidmiller, D. R., C. W. Avery, D. R. Easterling, K. E. Kunkel, K. L. M. Lewis, T. K. Maycock, and B. C. Stewart. 2017. "Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II."

Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, D. Firth, and M. B. Ripley. 2013. "Package 'Mass'." *Cran r* 538(113–120): 822.

Rodman, K. C., T. T. Veblen, T. B. Chapman, M. T. Rother, A. P. Wion, and M. D. Redmond. 2020. "Limitations to Recovery Following Wildfire in Dry Forests of Southern Colorado and Northern New Mexico, USA." *Ecological Applications* 30(1): e02001. https://doi.org/10.1002/eap.2001.

Romme, W. H. 1982. "Fire and Landscape Diversity in Subalpine Forests of Yellowstone National Park." *Ecological Monographs* 52(2): 199–221. https://doi.org/10.2307/1942611.

Romme, W. H., M. S. Boyce, R. Gresswell, E. H. Merrill, G. W. Minshall, C. Whitlock, and M. G. Turner. 2011. "Twenty Years after the 1988 Yellowstone Fires: Lessons about Disturbance and Ecosystems." *Ecosystems* 14(7): 1196–1215. https://doi.org/10.1007/s10021-011-9470-6.

Romme, W. H., and D. G. Despain. 1989. "Historical Perspective on the Yellowstone Fires of 1988." *Bioscience* 39(10): 695–99. https://doi.org/10.2307/1311000.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. "Aspen, Elk, and Fire in Northern Yellowstone Park." *Ecology* 76(7): 2097–2106. https://doi.org/10.2307/1941684.

Rother, M. T., and T. T. Veblen. 2016. "Limited Conifer Regeneration Following Wildfires in Dry Ponderosa Pine Forests of the Colorado Front Range." *Ecosphere* 7(12): e01594. https://doi.org/10.1002/ecs2.1594.

Schoennagel, T., M. G. Turner, D. M. Kashian, and A. Fall. 2006. "Influence of Lodgepole Pine Stand Age and Density across the Yellowstone National Park (USA)." *Landscape Ecology* 21: 1281–96. https://doi.org/10.1007/s10980-006-0028-5.

21508925, 2025, 10, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.70415 by University Of Wisconsin - Madison, Wiley Online Library on [28/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Schoennagel, T., M. G. Turner, and W. H. Romme. 2003. "The Influence of Fire Interval and Serotiny on Postfire Lodgepole Pine Density in Yellowstone National Park." *Ecology* 84(11): 2967–78. https://doi.org/10.1890/02-0277.

Seidel, K. W. 1986. "Tolerance of Seedlings of Ponderosa Pine, Douglas-Fir, Grand Fir, and Engelmann Spruce for High Temperatures." *Northwest Science* 60(1): 1–7.

Seidl, R., M. Potterf, J. Müller, M. G. Turner, and W. Rammer. 2024. "Patterns of Early Post-Disturbance Reorganization in Central European Forests." *Proceedings of the Royal Society B* 291(2031): 20240625. https://doi.org/10.1098/rspb.2024.0625.

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(4): 87–100. https://doi.org/10.1016/j.ecolmodel.2012.02.015.

Seidl, R., W. Rammer, and T. A. Spies. 2014. "Disturbance Legacies Increase the Resilience of Forest Ecosystem Structure, Composition, and Functioning." *Ecological Applications* 24(8): 2063–77. https://doi.org/10.1890/14-0255.1.

Seidl, R., and M. G. Turner. 2022. "Post-Disturbance Reorganization of Forest Ecosystems in a Changing World." *Proceedings of the National Academy of Sciences of the United States of America* 119(28): e2202190119. https://doi.org/10.1073/pnas.2202190119.

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(5): 556–567. https://doi.org/10.1111/j.1466-8238.2011.00710.x.

Smith, A. L., D. Blair, L. McBurney, S. C. Banks, P. S. Barton, W. Blanchard, D. A. Driscoll, A. M. Gill, and D. B. Lindenmayer. 2014. "Dominant Drivers of Seedling Establishment in a Fire-Dependent Obligate Seeder: Climate or Fire Regimes?" *Ecosystems* 17(2): 258–270. https://doi.org/10.1007/s10021-013-9721-9.

Stegner, M. A., M. G. Turner, V. Iglesias, and C. Whitlock. 2019. "Post-Fire Vegetation and Climate Dynamics in Low-Elevation Forests over the Last Three Millennia in Yellowstone National Park." *Ecography* 42(6): 1226–36. https://doi.org/10.1111/ecog.04445.

Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. "Evidence for Declining Forest Resilience to Wildfires under Climate Change." *Ecology Letters* 21(2): 243–252. https://doi.org/10.1111/ele.12889.

Stevens-Rumann, C. S., S. J. Prichard, E. Whitman, M.-A. Parisien, and A. J. H. Meddens. 2022. "Considering Regeneration Failure in the Context of Changing Climate and Disturbance Regimes in Western North America." *Canadian Journal of Forest Research* 52(10): 1281–1302. https://doi.org/10.1139/cjfr-2022-0054.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. "The Forgotten Stage of Forest Succession: Early-Successional Ecosystems on Forest Sites." *Frontiers in Ecology and the Environment* 9(2): 117–125. https://doi.org/10.1890/090157.

Taylor, K. E., R. J. Stouffer, and G. A. Meehl. 2012. "An Overview of CMIP5 and the Experiment Design." *Bulletin of the American Meteorological Society* 93(4): 485–498. https://doi.org/10.1175/bams-d-11-00094.1.

Tercek, M. T., A. Rodman, S. Woolfolk, Z. Wilson, D. Thoma, and J. Gross. 2021. "Correctly Applying Lapse Rates in Ecological Studies: Comparing Temperature Observations and Gridded Data in Yellowstone." *Ecosphere* 12(3): e03451. https://doi.org/10.1002/ecs2.3451.

Thom, D., W. Rammer, K. Albrich, K. H. Braziunas, L. Dobor, C. Dollinger, W. D. Hansen, et al. 2024. "Parameters of 150 Temperate and Boreal Tree Species and Provenances for an Individual-Based Forest Landscape and Disturbance Model." *Data in Brief* 55: 110662. https://doi.org/10.1016/j.dib.2024.110662.

Thoma, D. P., E. K. Shanahan, and K. M. Irvine. 2019. "Climatic Correlates of White Pine Blister Rust Infection in Whitebark Pine in the Greater Yellowstone Ecosystem." *Forests* 10(8): 666. https://doi.org/10.3390/f10080666.

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(5): 897–903. https://doi.org/10.1139/x94-118.

Turner, M. G. 2010. "Disturbance and Landscape Dynamics in a Changing World." *Ecology* 91(10): 2833–49. https://doi.org/10.1890/10-0097.1.

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(6): 511–523. https://doi.org/10.1007/s100219900047.

Turner, M. G., K. H. Braziunas, W. D. Hansen, and B. J. Harvey. 2019. "Short-Interval Severe Fire Erodes the Resilience of Subalpine Lodgepole Pine Forests." *Proceedings of the National Academy of Sciences* 116(23): 11319–28. https://doi.org/10.1073/pnas.1902841116.

Turner, M. G., K. H. Braziunas, W. D. Hansen, T. J. Hoecker, W. Rammer, Z. Ratajczak, A. L. Westerling, and R. Seidl. 2022. "The Magnitude, Direction, and Tempo of Forest Change in Greater Yellowstone in a Warmer World with More Fire." *Ecological Monographs* 92(1): e01485. https://doi.org/10.1002/ecm.1485.

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, Wyoming." *International Journal of Wildland Fire* 9(1): 21–36. https://doi.org/10.1071/wf99003.

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(4): 411–433. https://doi.org/10.2307/2963464.

Turner, M. G., and R. Seidl. 2023. "Novel Disturbance Regimes and Ecological Responses." *Annual Review of Ecology, Evolution, and Systematics* 54(1): 63–83. https://doi.org/10.1146/annurev-ecolsys-110421-101120.

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(2–3): 119–126. https://doi.org/10.1016/j.foreco.2006.12.032.

Urza, A. K., and J. S. Sibold. 2017. "Climate and Seed Availability Initiate Alternate Post-Fire Trajectories in a Lower Subalpine

21508925, 2025, 10, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.70415 by University Of Wisconsin - Madison, Wiley Online Library on [28/10/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Forest." *Journal of Vegetation Science* 28(1): 43–56. https://doi.org/10.1111/jvs.12465.

Van De Leemput, I. A., V. Dakos, M. Scheffer, and E. H. Van Nes. 2018. "Slow Recovery from Local Disturbances as an Indicator for Loss of Ecosystem Resilience." *Ecosystems* 21(1): 141–152. https://doi.org/10.1007/s10021-017-0154-8.

Van Nes, E. H., and M. Scheffer. 2007. "Slow Recovery from Perturbations as a Generic Indicator of a Nearby Catastrophic Shift." *The American Naturalist* 169(6): 738–747. https://doi.org/10.2307/4136993.

Ver Hoef, J. M., and P. L. Boveng. 2007. "Quasi-Poisson vs. Negative Binomial Regression: How Should We Model Overdispersed Count Data?" *Ecology* 88(11): 2766–72. https://doi.org/10.1890/07-0043.1.

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* 108(32): 13165–70. https://doi.org/10.1073/pnas.1110199108.

Whitman, E., M.-A. Parisien, D. K. Thompson, and M. D. Flannigan. 2019. "Short-Interval Wildfire and Drought Overwhelm Boreal Forest Resilience." *Scientific Reports* 9(1): 18796. https://doi.org/10.1038/s41598-019-55036-7.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. D'Agostino McGowan, R. François, G. Grolemund, et al. 2019. "Welcome to the Tidyverse." *Journal of Open Source Software* 4(43): 1686.

Willson, K. G., and M. D. Hurteau. 2024. "Abiotic Factors Modify Ponderosa Pine Regeneration Outcomes after High-Severity Fire." *Ecosystems* 27(4): 606–620. https://doi.org/10.1007/s10021-024-00911-2.

Wolf, K. D., P. E. Higuera, K. T. Davis, and S. Z. Dobrowski. 2021. "Wildfire Impacts on Forest Microclimate Vary with Biophysical Context." *Ecosphere* 12(5): e03467. https://doi.org/10.1002/ecs2.3467.

Yang, D., and O. A. Saenko. 2012. "Ocean Heat Transport and its Projected Change in CanESM2." *Journal of Climate* 25(23): 8148–63. https://doi.org/10.1175/jcli-d-11-00715.1.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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