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Widespread regeneration failure in forests of Greater Yellowstone under scenarios of future climate and fire

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Abstract

Changing climate and disturbance regimes are increasingly challenging the resilience of forest ecosystems around the globe. A powerful indicator for the loss of resilience is regeneration failure, that is, the inability of the prevailing tree species to regenerate after disturbance. Regeneration failure can result from the interplay among disturbance changes (e.g., larger and more frequent fires), altered climate conditions (e.g., increased drought), and functional traits (e.g., method of seed dispersal). This complexity makes projections of regeneration failure challenging. Here we applied a novel simulation approach assimilating data-driven fire projections with vegetation responses from process modeling by means of deep neural networks. We (i) quantified the future probability of regeneration failure; (ii) identified spatial hotspots of regeneration failure; and (iii) assessed how current forest types differ in their ability to regenerate under future climate and fire. We focused on the Greater Yellowstone Ecosystem (2.9×10^6 ha of forest) in the Rocky Mountains of the USA, which has experienced large wildfires in the past and is expected to undergo drastic changes in climate and fire in the future. We simulated four climate scenarios until 2100 at a fine spatial grain (100 m). Both wildfire activity and unstocked forest area increased substantially throughout the 21st century in all simulated scenarios. By 2100, between 28% and 59% of the forested area failed to regenerate, indicating considerable loss of resilience. Areas disproportionally at risk occurred where fires are not constrained by topography and in valleys aligned with predominant winds. High-elevation forest types not adapted to fire (i.e., *Picea engelmannii–Abies lasiocarpa* as well as non-serotinous *Pinus contorta* var. *latifolia* forests) were especially vulnerable to regeneration failure. We conclude that changing climate and fire could exceed the resilience of forests in a substantial portion of Greater Yellowstone, with profound implications for carbon, biodiversity, and recreation.

KEYWORDS
deep learning, forest resilience, future fire and climate regimes, Greater Yellowstone Ecosytem, regeneration failure, simulation modelling, SVD

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1 | INTRODUCTION

Anthropogenic climate change will likely lead to major changes in vegetation composition globally. The rate of climate change could exceed climatic tolerances of many plant species, pushing them out of their climatic niches (Urban, 2015). Furthermore, the pace of climate change may limit the ability of many species—especially weak dispersers—to cope with these changes via migration (Corlett & Westcott, 2013). As many plant and animal species have coevolved with and are adapted to specific vegetation types, such a reassembly of the biosphere would likely cause significant loss of habitat, further aggravating the ongoing biodiversity crisis (Chase et al., 2020). Furthermore, it could have significant impacts on forest functions, such as the ability of forest ecosystems to take up and store carbon from the atmosphere (Henne et al., 2020; Thom et al., 2017). Given expected changes in vegetation composition and its potential consequences, a key challenge for ecology is to quantify the risk that prevailing vegetation types undergo climate-induced regime shifts, that is, lasting transitions to a fundamentally different state (see Folke, 2006; Ratajczak et al., 2018).

Disturbances are catalysts of change (Sousa, 1984). Natural disturbances such as high-severity wildfire result in mortality of the established tree cohort and free up resources for reorganization (Coop et al., 2020). The window of regeneration after a disturbance is thus a pivotal time in the context of forest resilience (here defined as the ability to absorb disturbance without shifting to a qualitatively different system): Either regenerating trees initiate a new cycle of self-replacement, or the system sets on a trajectory to a new state if the prevailing species fail to regenerate. Regeneration is thus a key process for forest resilience (Albrich, Rammer, Turner, et al., 2020; Johnstone et al., 2016). As young trees can be more sensitive to their environment than adult trees of the same species, regeneration is of particular importance for understanding ecosystem dynamics (Grubb, 1977) and the resilience of forests to climate change (Davis et al., 2019; Stevens-Rumann et al., 2018). If tree species are able to regenerate post-disturbance, they are likely to determine the system's state for many decades. However, if prevailing tree species fail to regenerate in sufficient number, then a transition to a fundamentally different vegetation state is likely (Frelich & Reich, 1999). Failure to regenerate is thus a powerful indicator of resilience in forests, yet it remains difficult to quantify. Whether a disturbed forest has failed to regenerate can only be determined decades after a disturbance (Thrippleton et al., 2018). An important indicator of regeneration failure may be the forest area that is unstocked at a given point in time, which represents the integral over the area affected by disturbance and the ability of the system to recover from disturbance (Turner et al., 1993; Watt, 1947). In many forested parts of the world, phases of sparse tree cover are transient and succeeded quickly by the re-establishing cohort of trees. However, if disturbances increase or regeneration decreases due to climate change, the proportion of the landscape that is effectively unstocked will increase (McDowell et al., 2020).

Natural disturbances are increasing in forests around the globe due to climate change (Seidl et al., 2017; Sommerfeld et al., 2018). However, many tree species are well adapted to the historical natural disturbance regimes, and numerous response strategies for persisting in the face of disturbance have evolved. In the context of wildfire, for instance, response strategies include development of a canopy seed bank that is released after disturbance (serotiny; Tinker et al., 1994), the ability to recolonize disturbed areas via seed dispersal (Harvey et al., 2016), and the capacity to regenerate via resprouting (Clarke et al., 2013). Forest types adapted to disturbance might thus be resilient even to increased levels of disturbance frequency and severity (Turner et al., 2003). In contrast, forest types that did not evolve response traits due to historically low exposure to disturbance might suffer disproportionately from elevated levels of disturbance activity in the future. To assess the probability of future vegetation changes, it is thus important (i) to understand how disturbance regimes are likely to change; and (ii) to quantify whether the increase in disturbances projected for the future will overwhelm the adaptation mechanisms of different vegetation types and lead to regeneration failure.

The Greater Yellowstone Ecosystem (GYE) is an archetype of the complexities of climate- and fire-driven vegetation changes. Situated in the Northern Rocky Mountains of the USA, it received considerable public and scientific attention due to 709,000 ha of wildfires that burned in 1988. While the vast majority of burned stands recovered from the 1988 event (Turner et al., 2016), projections for the region suggest weather conditions conducive to large fires as in 1988 could become 10–20 times more frequent by the end of the century (Westerling et al., 2011). Recent experiments (Gill et al., 2021; Hansen & Turner, 2019; Hoecker et al., 2020) and emerging observational evidence (Stevens-Rumann et al., 2018) highlight the limited resilience of these forests to warmer–drier conditions and larger and more frequent fires. While it appears that changing climate and fire regimes will exceed the resilience of some forests in the GYE, the extent of forest loss is unclear, along with what forest types and sub-regions are most susceptible.

Here, our objective was to assess the probability of regeneration failure in forests of the GYE, given projected future climate and fire scenarios. Specifically, we asked (i) how the unstocked forest area of the GYE (i.e., the area that supported forest in the past but is stocked with <50 stems per hectare) changes throughout the 21st century; and (ii) how much of the currently prevailing forest types experience regeneration failure (i.e., here defined as the inability to regenerate to >50 stems per hectare 30 years after disturbance). Using a novel high-resolution simulation approach, we (iii) identified spatial hotspots of likely regeneration failure within the GYE and (iv) assessed the differential sensitivity of the prevailing forest types to future regeneration failure.

We hypothesized that area burned, unstocked forests, and regeneration failure will all increase with climate change (Stevens-Rumann et al., 2018; Westerling, 2016). We expected area burned to be considerably more sensitive to climate than the other two indicators, as the forests of the GYE have considerable ability to recover

from fire (Romme et al., 2011). Furthermore, we hypothesized that the fire adaptation of a forest type has a stronger influence on its risk of regeneration failure than its exposure to increased wildfire. In other words, forest types with low levels of fire adaptation will be more prone to regeneration failure than fire-adapted forest types, despite the fact that the latter could burn more frequently.

2 | MATERIALS AND METHODS

2.1 | Study system

Centered on Yellowstone and Grand Teton National Parks, the GYE encompasses ~8 million ha in the northern US Rocky Mountains. Pre-Columbian flora and fauna are largely intact, and conifer forests have dominated for the past 10,000 years (Whitlock et al., 2008). Almost 3 Million ha in the GYE are forested, with *Pinus contorta* var. *latifolia* (Dougl. ex Loud.) dominating the subalpine plateaus; *Picea engelmannii* (Parry ex Engelm.), *Abies lasiocarpa* (Hook.), and *Pinus albicaulis* (Engelm.) abundant at higher elevations, and *Pseudotsuga menziesii* (Mirb.) and *Populus tremuloides* (Michx.) in the lower montane. Forests transition to sagebrush (*Artemisia* spp.) steppe and meadows as elevation declines. This conifer-dominated landscape has long been shaped by fire. Large, stand-replacing fires have burned subalpine forests at 100–300 year intervals during warm, dry periods throughout the Holocene (Higuera et al., 2011; Millspaugh et al., 2000, 2004); fire intervals of 75–100 years characterized lower elevation forest-steppe vegetation (Huerta et al., 2009; Whitlock et al., 2008). In general, the biota of the GYE are well adapted to infrequent, severe fire. Forests recovered rapidly after the 1988 Yellowstone Fires (e.g., Romme et al., 2011; Turner et al., 2016), which burned during the driest summer in the modern record (Renkin & Despain, 1992). Although the climate is characterized by cold, snowy winters and dry, mild summers, temperatures have warmed by 2.5°C since 1982 (Notaro et al., 2019). Continued warming and associated increases in aridity are projected to increase fire frequency, fire size, and annual area burned substantially during the 21st century (Hansen et al., 2020; Westerling et al., 2011).

2.2 | Data

We compiled a consistent data set for vegetation, soil, and climate that covers the entire forested area of GYE with a base resolution of 100 m. Soil depth and texture were derived from CONUS-SOIL (Miller & White, 1998). Plant-available nitrogen, as derived by Coops et al. (2012), was used as a metric for soil fertility. Gridded data for current and future climatic conditions were obtained from a data-product based on the Multivariate Adaptive Constructed Analogs method (MACA, Abatzoglou & Brown, 2012) with a 4 km resolution and daily time step. MACA is a method for statistical downscaling and bias correction of Global Circulation Models (GCMs). We used information from three CMIP5 GCMs, namely CanESM2 (Chylek et al., 2011), HadGEM2-CC, and HadGEM2-ES (Collins et al., 2011), forced with two representative concentration pathways (RCP), RCP 4.5 (a lower emission scenario), and RCP 8.5 (a high emission scenario; van Vuuren et al., 2011) for future climate projections. While the models project similar trends of warming throughout the 21st century (+ 2.9 and +5.8°C until 2100 under RCP 4.5 and 8.5, respectively, see Figure A2), future trends in precipitation diverged. Specifically, precipitation increased over time in CanESM2, whereas HadGEM2-CC and HadGEM2-ES have no significant precipitation trend over time, resulting in increased aridity. We selected the two HadGEM2 models because, while both show increased aridity during the 21st century, the timing of extended periods of drought varies. Contrary to our initial expectations, we found that the differences in drought timing and intensity caused only small differences in our analyses, and we therefore only included HadGEM2-CC in the main text, showing results for HadGEM2-ES in the Supporting Information S7.

A combination of data products was used to inform our modeling regarding the spatial distribution and characteristics of the currently prevailing forest types in the GYE. First, we derived the stockable area, that is, area that is currently or potentially forested given the biophysical conditions, by combining the Environmental Site Potential and the Existing Vegetation Types data sets from LANDFIRE (LANDFIRE, 2013). Second, we assembled maps of current forest vegetation from different national forests and national parks and reclassified the custom vegetation categories to four common forest types: Douglas-fir dominated (Psme), non-serotinous lodgepole pine dominated (Pico), serotinous lodgepole pine dominated (Pico-S), and mixed subalpine fir and Engelmann spruce (Pien-Abla; Figure 1). To differentiate between seed-producing mature forests and early seral immature forests in the initial vegetation condition, we used time since stand-replacing fire provided from the Monitoring Trends in Burn Severity (MTBS, Eidenshink et al., 2007) data set. We excluded riparian areas, human infrastructure, and small isolated forest stands from our analysis (thus removing 2.4% of stockable area). The compiled vegetation layer represented conditions in 2005 and included 2.93 million ha of forested area. See Supporting Information S1 for additional details.

We projected the potential number, maximum size, and location of fires in the GYE under future climate scenarios using an extension of previously developed statistical methods (Westerling et al., 2011). Logistic regression to predict the probability of large fires (>400 ha) was combined with a generalized Pareto distribution model to predict fire size. The models were fitted against MTBS data (Eidenshink et al., 2007) from 1984 to 2014 for forests across the Northern US Rocky Mountains (approx. three times the area of the GYE). As predictors, we used gridded climate (monthly temperature and precipitation) and site variables (topography, geographic location) at 1/16th degree spatial resolution (n = 9506) and monthly temporal resolution. For each climate scenario, these models were used to generate 20 replicates of monthly fire occurrence, potential maximum area burned per fire, and location of fire ignition through 2099. The location of ignitions was selected randomly from the forested area

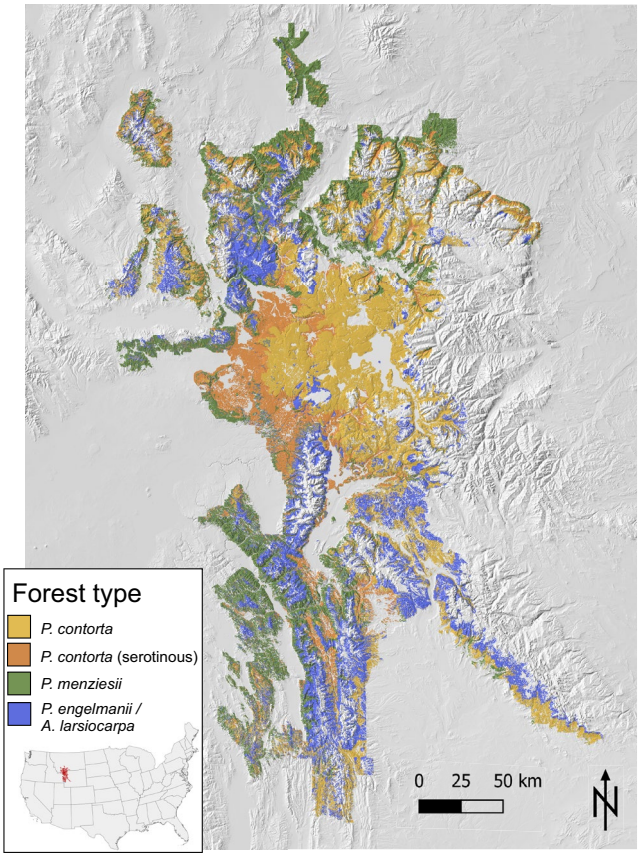

FIGURE 1 Major current forest types of the Greater Yellowstone Ecosystem (GYE). The inset shows the location of GYE in the US. Grey areas indicate unforested areas within the perimeter of the study area as well as areas outside the GYE

within a 1/16th degree cell. Actual area burned was subsequently determined using a dynamic vegetation modeling framework (see below). See Supporting Information S2 for additional details on the statistical fire modeling.

2.3 | Simulating vegetation dynamics

We used the scaling vegetation dynamics (SVD) modeling approach (Rammer & Seidl, 2019a) to simulate future fire regimes and their effects on regeneration success and failure. SVD applies deep learning to simulate vegetation transitions across large spatial scales. Conceptually, SVD follows a state and transition approach (Bestelmeyer et al., 2009), where vegetation is classified into discrete states, and transitions between states are probabilistic. In SVD, transition probabilities are determined by deep learning (LeCun et al., 2015), and are conditional on environmental drivers as well as the local neighborhood of a cell. Deep learning is a new branch of machine learning that has been successfully applied to tasks as diverse as image and speech recognition, automatic language translation, and autonomous driving. Deep learning provides new opportunities for Earth system science (Reichstein et al., 2019) and ecology (Rammer & Seidl, 2019b).

A key element in the application of machine learning are the data used to train the algorithm. Here, we trained the deep neural network (DNN) at the core of SVD on data generated by the process-based model iLand (Seidl et al., 2012). Our modeling approach consisted of two distinct phases: First, training data were generated by simulating regeneration success or failure after fire disturbance over a wide range of environmental conditions in the GYE with iLand. This phase was concluded by training the DNN on these data, yielding a metamodel of the post-fire regeneration response of the process-based model. Second, the trained DNN was used in the dynamic simulation of vegetation transitions in the GYE under different climate and fire scenarios within the SVD model (Figure 2). The spatial grain of SVD simulations was the stand scale (i.e., a 100 × 100 m cell), and the time step was annual.

We selected the most parsimonious path model that allowed us to address our research questions regarding unstocked areas and regeneration failure (Figure 2d). After fire, regeneration success was determined by the DNN, considering climate (temperature, precipitation) and site (soil depth, soil texture, nutrient supply) conditions as well as distance to seed source. Cells transitioned to "Regeneration" in case of success, or to "Regeneration failure" when no trees were able to establish in the first 30 years after fire. Cells that successfully regenerated transitioned to seed-producing "Adult" stands once a forest-type-specific maturation age was reached. Serotinous lodgepole pine (Pico-S) stands started producing a canopy seed bank at the age of 50 years (Schoennagel et al., 2003; Tinker et al., 1994). Distance to seed source was determined as the minimum distance to an "Adult" cell of the corresponding forest type. Since we focused on regeneration failure of the current vegetation as an indicator of potential future regime shifts, transitions from one forest type to another were not simulated. A detailed description of our modeling approach as well as forest type specific parameters is given in Supporting Information S4.

To interface statistical projections of potential fire activity (described above) with dynamic simulations of vegetation, we developed a fire module for SVD. This module simulates wildfire spatially explicitly at a resolution of 100 m, and conceptually follows the wildfire module described by Seidl et al. (2014). After an ignition (determined from the statistical models), fires spread dynamically through the landscape using a cellular automaton approach, considering wind conditions, terrain, and the burn probabilities specified for each vegetation state. A fire keeps spreading until it stops intrinsically (e.g., when the combustible biomass is exhausted and no further burnable adjacent cells are available), or when the statistically determined maximum fire size is reached. Currently, the module simulates high-severity fires only, and multiple fires can start in any given year. Fire effects are homogeneous at the level of a 100 m grid cell, but a mosaic of burned and unburned patches emerges dynamically within a fire perimeter during the simulations, depending on fuels, topography, and wind. More details on our approach to model wildfire are given in Supporting Information S3. We evaluated the new fire module for SVD against independent data to ensure that the fires emerging from the simulations realistically captured observed

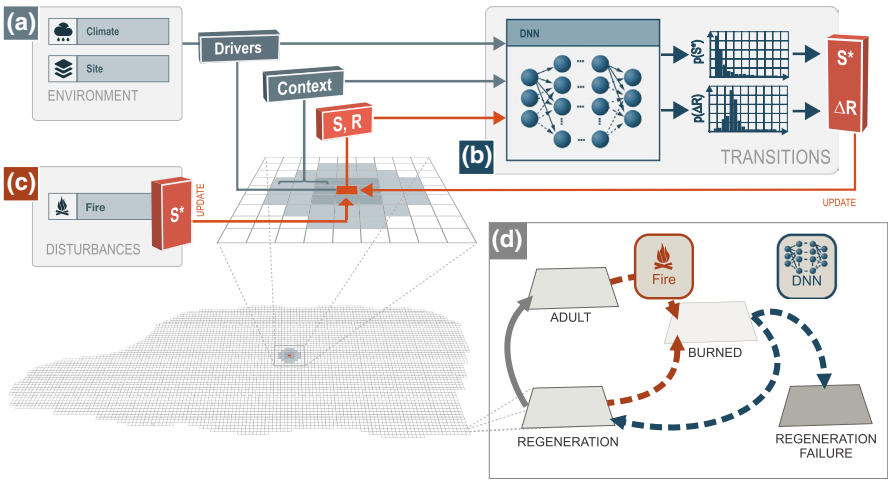

FIGURE 2 Conceptual overview of the scaling vegetation dynamics (SVD) framework (a–c), and the specific vegetation states and transition pathways (d) used in this study. In SVD, transitions between vegetation states are predicted by a Deep Neural Network at the level of individual 100 m cells (b) and depend on environmental drivers (a), the current state (S) and residence time of a cell (R), as well as the spatial context (here: distance to seed source). Dynamically simulated fire (c) adds an additional pathway of state change. (d) Adult and regenerated cells transition to a burned state when affected by fire, with regeneration success or failure determined by the DNN. The transition from regeneration to adult states is deterministic based on species-specific maturation age

fire dynamics in the GYE. Specifically, we compared spatial properties of simulated fires (e.g., proportion of unburned area within the fire perimeter) with a remote-sensing-based analysis of fire patches in western North America (Kolden et al., 2012; see Supporting Information S3 for details).

2.4 | Forest regeneration under future climate and fire regimes

We used the individual-based forest landscape and disturbance model iLand (Seidl et al., 2012) to determine regeneration success or failure under future climate and disturbance regimes. iLand was successfully parameterized, evaluated, and applied in the GYE previously (Braziunas et al., 2018; Hansen et al., 2018; Hansen et al., 2020; Turner et al., 2019). Specifically, we conducted a factorial simulation experiment with iLand, in which we experimentally varied seed supply and seed delivery (represented by different fire frequencies and sizes) as well as the climate conditions influencing seed establishment (e.g., post-fire drought) to determine regeneration success or failure for each forest type. Our factorial simulation experiment followed the approach described by Hansen et al. (2018) and was extended to the four major forest types and the full environmental gradient of forests in the GYE. We selected 1296 unique combinations of site factors, representing the climate and soil conditions of the GYE. For each factor combination, we simulated different fire return intervals (FRI), distances to seed source, and climate scenarios. Specifically, we considered four forest types, four levels of FRI (11, 20, 50 and 100 years), 25 levels of distance to the nearest seed source (from 50 to 1250 m in 50 m increments), 18 soil types, and 72 different climate conditions (resulting in 1,296 combinations of different site conditions), and we covered the climate expected for the 21st century by simulating five climate forcings from different RCPs. Only stand-replacing fire was considered. All factorial combinations were simulated, resulting in a total of 2.59×10^6 simulated regeneration trajectories. More information on the generation of regeneration data under future climate and fire conditions and the evaluation of iLand in the GYE is found in Supporting Information S5.

We considered regeneration to be successful when a density of 50 stems per hectare (counting post-fire seedlings, saplings, and trees of all sizes) was reached in the first 30 years post-fire (Hansen et al., 2018). The threshold value of 50 stems per hectare was chosen to discriminate against other, open land cover types. It is likely lower (i.e., more conservative) than commonly used forest definitions (e.g., a threshold of >10% canopy cover for areas to be identified as open forest; Chazdon et al., 2016). For reference, the average stem density of forests in the GYE is currently at 1008 trees ha^{-1} (SD ± 529 trees ha^{-1}), and forests regenerating from fire in 1988 had an average tree density of 22,030 ± 6389 stems ha^{-1} 24 years after fire (Turner et al., 2016). Thirty years was selected as the length of the regeneration period because it accounts for the short post-fire establishment window for most tree species (Turner et al., 1999) but also accommodates the more protracted establishment window of conifers that lack a canopy seedbank (Donato et al., 2016) and captures the effects of climate on young trees. The length of the regeneration period of 30 years was further corroborated with empirical evidence, indicating that two to three decades after fire approximately 99% of the stands had >50 stems per hectare in our study system (Turner et al., 2016). The information on regeneration success or failure from the iLand simulation experiment was subsequently used to train the DNN of SVD. The network learned to predict the success or failure of regeneration contingent on FRI, distance to seed source, site, and climate conditions. We tested different DNN architectures and settings, and monitored

the predictive performance of the network using 11% of the training data set aside for evaluation. The best-performing network was consequently used in SVD for the dynamic simulations across the entire GYE. It replicated the responses of iLand very well and achieved an accuracy for predicting regeneration success or failure of 0.941 and an F1 score (harmonic mean of precision and recall) of 0.954 on the independent evaluation data set. See Supporting Information S6 for additional information on the DNN as well as its training and testing.

2.5 | Analyses

To assess the effects of changing climate and fire regimes on regeneration success, we ran SVD simulations at a grain of 1 ha for 2,926,494 ha of the GYE. Each simulation started with the same initial conditions derived from the GYE vegetation layer for the year 2005. For each of the six climate scenarios, we ran 20 replicate simulations, with each replicate corresponding to a unique series of predicted fires derived from statistical fire modeling (but the same climate). The focus of our analysis was the years 2005–2100, but in order to assess whether fires burning at the end of the 21st century result in regeneration failure 30 years after the disturbance, we continued simulating vegetation dynamics until 2130 (with climate resampled from the period 2080–2100 for the period 2100–2130). No additional fires were simulated over this period.

To address our research questions, we focused on two indicators, the unstocked forest area and the area where the current forest type fails to regenerate. Unstocked forests are areas that currently support forests (i.e., excluding the current steppe and parkland systems of the GYE) but have stem densities of <50 stems ha^{-1} in the simulation. Unstocked forest area thus combines areas that are temporarily open because of a recent disturbance and areas that are permanently open because of regeneration failure. Unstocked forest area was assessed for every single year of the 95-year study period.

The total area of regeneration failure was assessed at the end of the simulation in 2130 for each scenario, accounting for the effects of all fires simulated until 2100. For the analysis of spatial hotspots, we calculated for each scenario the probability of regeneration failure as the proportion of the 20 replicated simulations that indicated failure at the level of 100 m cells. Analysis of regeneration failure at the level of forest types was based on their current spatial distribution and tallied as absolute area and percentage of current area lost. All analyses of simulation results were conducted with the R Project for Statistical Computing (R Core Development Team, 2019), specifically using the *tidyverse* (Wickham et al., 2019) and *raster* packages (Hijmans, 2019).

3 | RESULTS

3.1 | Area burned and unstocked forest area

Annual area burned and unstocked forest area increased substantially throughout the 21st century under all climate scenarios (Table 1). Annual area burned was around 1% per year in the first decades of the simulation for all scenarios, with slightly higher values for scenarios that are drier in that period (e.g., CanESM2 4.5). The area burned reached on average 5.3% per year during the late century for the dry and warm HadGEM2 scenario under RCP 8.5 forcing. The increasing fire activity led to a sharp increase in unstocked area in the GYE (Figure 3). Trajectories among climate scenarios were similar during the first three decades of the simulation (i.e., the 95th percentile confidence intervals of the scenarios overlapped), but diverged among climate scenarios in the second half of the 21st century. The highest unstocked forest area proportion of the landscape was found under the HadGEM2 scenarios, regardless of RCP. Variability among individual replicated simulations was considerable due to differences in the number, size, and sequence of fires, but variability in unstocked area generally decreased over time (Table 1). Observed annual area burned in the period with empirical data (2005–2018) was well within the range of our simulations (Figure A3).

TABLE 1 Unstocked forest area (<50 stems per hectare) and area burned in the Greater Yellowstone Ecosystem under different climate scenarios. Values are averaged per replicate and period and reported as mean annual values ± SD among replicates

Period	Climate scenario (GCM-RCP)	Unstocked area		Area burned	
		km²	%	km²	%
Early century (2005–2030)	CanESM2 4.5	3251 ± 1216	11.1 ± 4.2	393 ± 179	1.3 ± 0.6
	CanESM2 8.5	2378 ± 1025	8.1 ± 3.5	316 ± 118	1.1 ± 0.4
	HadGEM2-CC 4.5	1924 ± 589	6.6 ± 2	246 ± 73	0.8 ± 0.2
	HadGEM2-CC 8.5	3115 ± 1238	10.6 ± 4.2	356 ± 143	1.2 ± 0.5
Mid century (2035–2065)	CanESM2 4.5	6886 ± 1597	23.5 ± 5.5	275 ± 102	0.9 ± 0.3
	CanESM2 8.5	7090 ± 1562	24.2 ± 5.3	391 ± 131	1.3 ± 0.4
	HadGEM2-CC 4.5	7567 ± 1622	25.9 ± 5.5	455 ± 195	1.6 ± 0.7
	HadGEM2-CC 8.5	10,267 ± 1082	35.1 ± 3.7	771 ± 222	2.6 ± 0.8
Late century (2070–2100)	CanESM2 4.5	8709 ± 1407	29.8 ± 4.8	325 ± 129	1.1 ± 0.4
	CanESM2 8.5	10,013 ± 1419	34.2 ± 4.8	444 ± 124	1.5 ± 0.4
	HadGEM2-CC 4.5	13,142 ± 1039	44.9 ± 3.6	713 ± 195	2.4 ± 0.7
	HadGEM2-CC 8.5	17,210 ± 418	58.8 ± 1.4	1564 ± 330	5.3 ± 1.1

3.2 | Regeneration failure

By the end of the 21st century, current forest types were unable to regenerate on a substantial proportion of the GYE, ranging from 21.7% in the most optimistic scenario (CanESM2 RCP4.5) to 61.3% in the most pessimistic scenario (HadGEM2-CC RCP8.5; Figure 4). We found clear differences among climate scenarios, with differences between climate models having a stronger effect on the results than differences between RCPs. Specifically, simulations under CanESM2 climate (projecting increased precipitation for the future) had much less area of regeneration failure (22%–39%) compared to simulations with HadGEM2-CC (36%–62%).

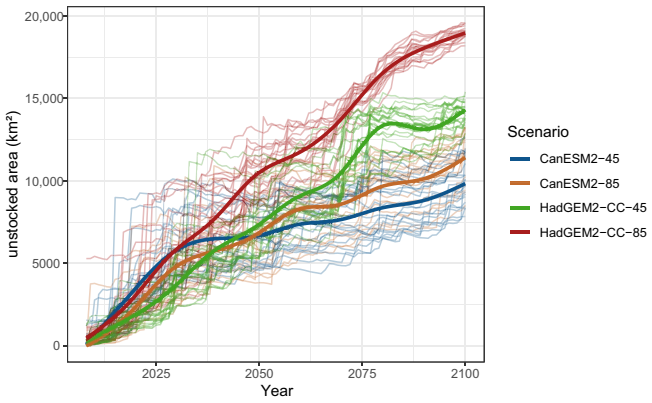

FIGURE 3 Trajectories of unstocked forest area (<50 stems per hectare) in the Greater Yellowstone Ecosystem under different climate scenarios. Thin lines denote replicated simulations; bold lines are smoothed averages (using generalized additive model smoothing)

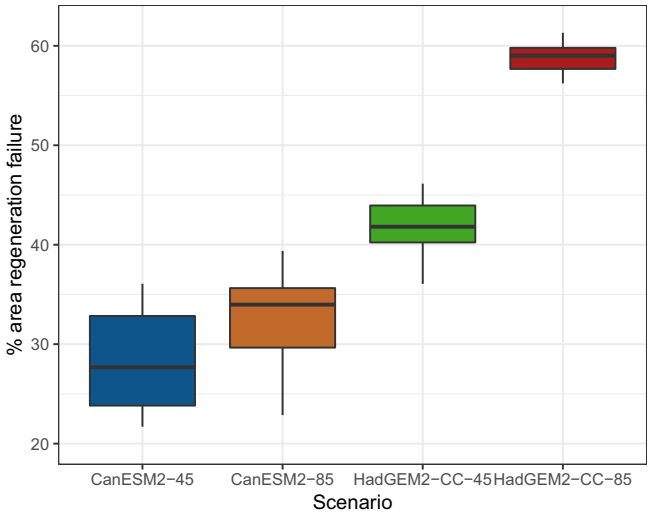

FIGURE 4 Percent of forest area where the currently prevailing forest type failed to regenerate by 2100 due to simulated climate and fire regimes. Boxplots indicate the variation among 20 replicates for each scenario, with boxes denoting the interquartile range (IQR), bold horizontal lines showing the median, and whiskers extending to 1.5 × IQR

3.3 | Spatial hotspots of regeneration failure

The central Yellowstone plateau was particularly vulnerable, with >50% probability of regeneration failure by 2100 under the more optimistic climate scenarios (Figure 5). This area within the GYE supports particularly large and increasingly frequent fires (Figure A9) and may be at high risk for losing current forest types. The probability of regeneration failure also increased for other parts of the GYE, such as lower elevation portions of the landscape, under more severe climate change scenarios.

3.4 | Sensitivity of forest types to regeneration failure

Forest types differed in area burned and regeneration failure (Figure 6; Table A9). Lodgepole pine forests currently make up 49% of the forested area, but 67%–70% of fires throughout the 21st century were burning in areas currently occupied by this forest type. However, only between 5.5% (serotinous lodgepole pine) and 17.6% (non-serotinous lodgepole pine) of the area burned failed to regenerate under scenario HadGEM2-CC 8.5. In contrast, the proportion of regeneration failure was considerably higher in Douglas-fir forests (32.8%) and subalpine fir/spruce forests (31.3%). Generally, differences among forest types were conserved across all climate scenarios (Figure 6). In absolute terms (i.e., accounting for the different prevalence of each forest type on the landscape), serotinous lodgepole pine was least vulnerable to regeneration failure. Less than 10% of the forest type failed to regenerate by the end of the simulation period in three out of four climate scenarios, and even in the most extreme climate scenario (HadGEM2-CC 8.5) the area of regeneration failure remained <25% (Table A9). Non-serotinous lodgepole pine was considerably more vulnerable, failing to regenerate on between 40% and 77% of its current area. The ranking of proportion of forest area lost per forest type was consistent over all climate scenarios, with non-serotinous lodgepole pine>Engelman spruce/subalpine fir>Douglas-fir>serotinous lodgepole pine.

4 | DISCUSSION

Here we show that changes in climate and fire regimes can exceed the resilience of forest ecosystems. Our analyses suggest that up to ~60% of the current forest area in the GYE could be at risk of regeneration failure during the 21st century. While these forests have regenerated vigorously after large fires in the past (Donato et al., 2016; Turner et al., 2016), they could undergo shifts in forest type or transition to non-forested ecosystems in the future. Tree regeneration is crucial to sustaining temperate forest resilience, as the ability or failure to regenerate determines forest development for decades to centuries. In these forests, a transition to a different vegetation state (e.g., a different forest type or a grassland state) is imminent if prevailing tree species fail to recover, rendering regeneration failure

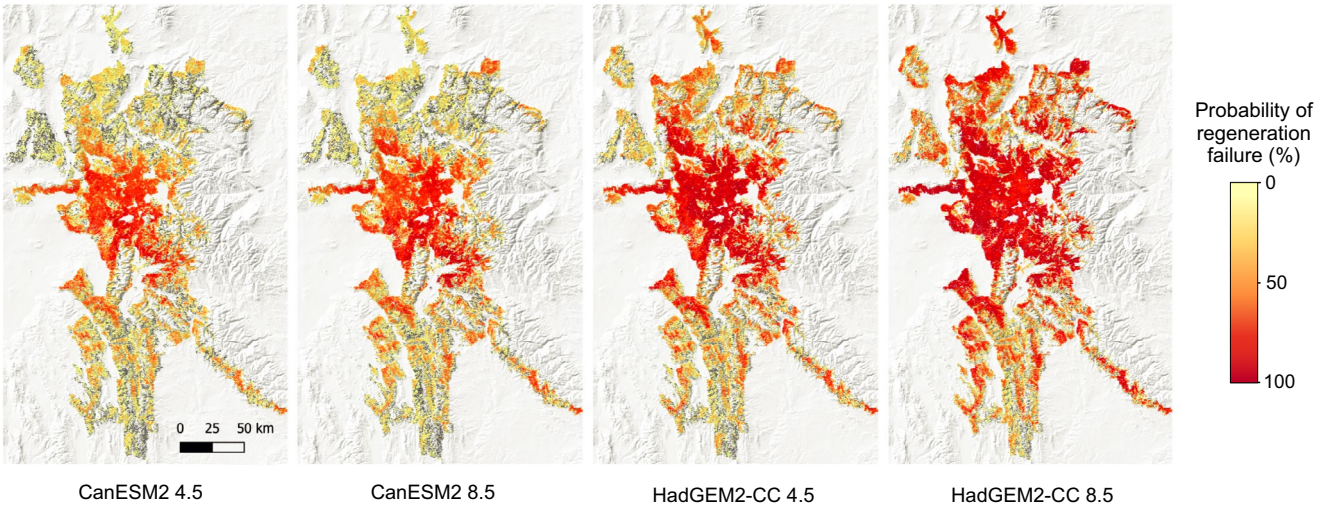

FIGURE 5 Spatial distribution of the probability of regeneration failure under the four climate change scenarios for the year 2100. The probability is calculated as the average over 20 replicated simulations per scenario

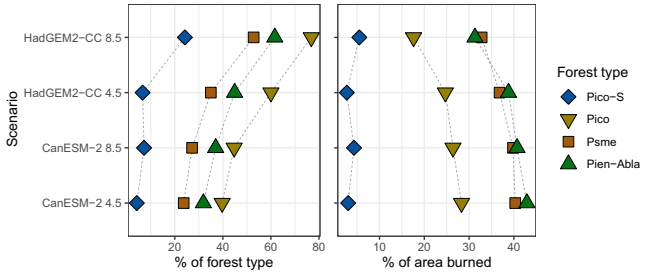

FIGURE 6 The proportion of regeneration failure per forest type and climate scenario relative to the total area per forest type (left), and relative to the cumulative area burned per forest type (right). Pico-S, serotinous lodgepole pine; Pico, non-serotinous lodgepole pine; Psme, Douglas-fir; Pien-Abla, Engelmann spruce/subalpine fir

a powerful indicator of exceeded forest resilience. Our finding of widespread regeneration failure of current forest types in the GYE under climate change suggests regime shifts are likely in coming decades. These findings are congruent with previous analyses suggesting that tree regeneration in the Rocky Mountains is climate and fire sensitive (Davis et al., 2019; Kemp et al., 2019; Stevens-Rumann et al., 2018). While drivers of ecosystem sensitivity differ by region (Mcwethy et al., 2013), our results correspond well with other reports of forest change in North America (e.g., Petrie et al., 2017), South America (e.g., Uriarte et al., 2018), Europe (e.g., Maringer et al., 2020), Asia (e.g., Xu et al., 2017), and Australia (e.g., Fairman et al., 2016), all of which point to losses of forest resilience due to climate change. This body of work, along with this study, suggests that changing climate and disturbance regimes could challenge the resilience of forests at the global scale, and that forested regions, such as the GYE, may be dominated either by different forest types or by non-forest by the end of the 21st century.

The hotspots of future regeneration failure in the GYE result from the complex interplay between future fire dynamics and the distribution of current forest types. Our analyses highlight that the sensitivity of a forest type to changing disturbance regimes cannot be assessed based on disturbance activity or vegetation traits alone, but rather emerges from the interactions between these two factors. In a detailed simulation study analyzing the causes of regeneration failure, Hansen et al. (2018) found that distance to seed source was overall the most important single factor for regeneration failure. However, other factors were also important, such as reduced reburn intervals for serotinous lodgepole pine. Furthermore, topography considerably modulates the interplay between disturbances and vegetation. Areas disproportionally at risk of losing resilience occurred where fires are not constrained by topography and can grow exceedingly large, such as the Yellowstone central plateau, and valleys aligned with predominant winds from the southwest, fueling fire spread. Areas that are already warm and dry, for which warming and increased aridity may limit tree regeneration (e.g., the low elevation northern reaches of the GYE; Hansen & Turner, 2019) or locations subject to sequential high-severity fires (Hoecker et al., 2020) are also at risk. In contrast, cooler (e.g., north-exposed) sites surrounded by complex mountain topography could serve as climate refugia for current forest types (Albrich et al., 2020; Serra-Diaz et al., 2015; Turner et al., 2013).

Indicators of resilience need to jointly consider disturbance impact and recovery (Ingrisch & Bahn, 2018). Assessing forest resilience across large spatial domains remains challenging, because regeneration periods can be protracted and regeneration success or failure can only be determined decades after a disturbance (Thrippleton et al., 2018). Thus, important measures of resilience such as regeneration failure remain difficult to quantify from forest inventory data and remote sensing. Based on simulation modeling, we have shown that focusing solely on area disturbed—that is, an indicator that can be readily derived across large spatial domains from remote sensing (Cohen et al., 2016; Senf & Seidl, 2021)—is insufficient for characterizing forest resilience. Area burned increased

threefold between the most moderate and the most extreme climate scenarios while the area failing to regenerate increased only by a factor of two. This underlines that unstocked forest area, representing an integral measure of disturbance and regeneration processes, is considerably more indicative of forest resilience than area burned. Future work on broad-scale forest resilience, for example, using remote sensing, should thus jointly consider changes in forest disturbances *and* regeneration (e.g., White et al., 2017) in order to capture ongoing shifts in forest ecosystems (McDowell et al., 2020).

Fine-grained, spatially explicit, and mechanistic analyses at broad scales are needed to capture the complexities and feedbacks between future vegetation and fire. Mechanisms potentially leading to regeneration failure are forests re-burning before they can produce seeds (immaturity risk; Enright et al., 2015; Keeley et al., 1999; Stevens-Rumann & Morgan, 2016), burned areas growing so large that seeding in from unburned areas becomes difficult (Harvey et al., 2016), and drought inhibiting successful establishment of trees after fire (Harvey et al., 2016; Walck et al., 2011). Capturing these mechanisms in simulation models at meaningful scales remains challenging (Albrich, Rammer, Turner, et al., 2020), which limits our ability to project future forest resilience. Here we have used SVD, a novel approach to upscaling detailed process-model responses to the regional level using deep learning. This type of meta-modeling has long been recognized as a powerful approach for scaling in ecology (Halofsky et al., 2013; Urban, 2005), and is also a promising field for the application of deep learning methods in Earth system sciences (Reichstein et al., 2019) and ecology (Rammer & Seidl, 2019b). Our modeling framework is unique in that it dynamically integrates fire modeling based on empirical data with vegetation responses simulated in a process-based manner. It allows us to determine the success and failure of forests to regenerate with high resolution (100 m grid cells) across a large spatial domain (close to three million hectares of forests), accounting for spatial interactions between grid cells (e.g., fire spread, seed dispersal). It thus fills a crucial gap between landscape-level simulations (accounting for detailed spatio-temporal vegetation dynamics at fine grain, e.g., Honkaniemi et al., 2020; Thrippleton et al., 2018) and dynamic global vegetation models (simulating continental to global vegetation dynamics but often neglecting detailed regeneration processes and spatial dynamics such as fire spread, e.g., Lasslop et al., 2020; Pugh et al., 2019).

Methodological limitations should be considered when interpreting our findings. A limitation of our work is that while considering the complex interplay among factors leading to regeneration failure, we here did not model the migration of tree species. Owing to this limitation, our projections of regeneration failure must not be interpreted as forest loss, but rather give an indication where and when the resilience of *current* forest types is exceeded. As the ability of species to migrate is an important mechanism of resilience (Albrich, Rammer, Turner, et al., 2020; Johnstone et al., 2016), future work should extend our current approach to allow the quantification of potential forest loss (Hansen et al., 2020). As climate and fire increase monotonically throughout the 21st century in our study region, we did not allow cells to regenerate at a later point in time after an initial regeneration failure was computed. A further limitation is that species of local relevance in the GYE, such as whitebark pine (*P. albicaulis*) and aspen (*P. tremuloides* Michx.), were excluded from the analysis. In addition, other agents beyond fire can cause large-scale disturbances and challenge forest resilience. Notably, global change could also increase the activity of biotic agents such as bark beetles and pathogens (Seidl et al., 2017; Weed et al., 2013) and should be considered explicitly in future efforts. We further assumed that all fires on the level of 100 m cells were stand-replacing, which would eliminate local seed sources from mature trees that could potentially have survived a fire. However, within fire perimeters, a realistic mosaic of unburned patches remained in our simulations, acting as seed source for the surrounding burned areas. Thus, key results of our analysis regarding the share of unstocked forests on the landscape and the failure of current forest types to regenerate are not affected by this methodological limitation.

Differences in fire adaptation and the distribution of species determined which forest types were more resilient than others. For example, in areas where serotinous lodgepole pines dominate, the risk of post-fire regeneration failure was three to eight times lower in our simulations compared to areas dominated by non-serotinous lodgepole pines. This highlights the potential of species adapted to re-establish after fire to better cope with increasing fire activity (Buma et al., 2013). In contrast, fire-sensitive forest types such as high-elevation subalpine fir—Engelman spruce forests are not evolutionarily adapted to frequent fires and are at greater risk of losing resilience. Douglas-fir—currently located at the warm and dry end of our study system and equipped with thick bark to survive fire—was less susceptible to regeneration failure than other forest types because of reduced exposure to fire. Douglas-fir might be able to expand to higher elevations in the future (Hansen et al., 2020) while the species currently forming the timber line (such as subalpine fir–Engelman spruce forests or whitebark pine forests) have limited possibilities for migration (Kueppers et al., 2017). Forests in the upper subalpine zone are thus particularly vulnerable to climate and disturbance changes and should be a priority of future research (Hansen & Phillips, 2015; Ireland et al., 2018). We conclude that climate change could exceed the resilience of forests in a substantial portion of the GYE. The future GYE will likely differ significantly from the GYE of the recent past, with profound implications for carbon, biodiversity, and recreation.

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DATA AVAILABILITY STATEMENT

The code and data that support the findings of this study are openly available at https://github.com/SVDmodel/SVD (https://doi.org/10.5281/zenodo.4810960), and https://github.com/SVDmodel/models (https://doi.org/10.5281/zenodo.4811079).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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