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Where are the trees? Extent, configuration, and drivers of poor forest recovery 30 years after the 1988 Yellowstone fires

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A B S T R A C T

Postfire recovery of fire-adapted forests remains uncertain as climate and fire regimes continue to change. Areas of poor postfire tree regeneration following late-20th-century fires may reveal characteristics associated with increased vulnerability to forest decline. However, sufficient time must have elapsed and pre- and postfire forest cover must be compared to distinguish areas that have not recovered. We used remotely sensed data and the Normalized Difference Vegetation Index (NDVI) to detect areas of poor forest recovery across > 250,000 ha of area burned as stand-replacing fire 30 years after the 1988 Yellowstone fires. We asked three questions: (1) What is the extent and configuration of sparse and reduced forest recovery? (2) How do vegetation characteristics compare between areas of sparse and reduced recovery vs. recovered forest? (3) What environmental characteristics explain the distribution and patch size of sparse and reduced recovery? We related postfire (2013–14) NDVI to field-measured stem density to establish an NDVI threshold of sparse tree regeneration, and we contrasted pre- (1986–87) and postfire (2018–19) NDVI as a proxy for pre- and postfire forest cover. Sparse and reduced forest recovery occupied ~ 41,000 ha across the burned area, about half of which was ≥ 150 m from *ex situ* seed sources. Patches of poor recovery were generally large, with ~ 13,400 ha in patches ≥ 50 ha and an area-weighted mean patch size of 97 ha. Vegetation was short (<2 m) in areas of sparse and reduced recovery and non-evergreen biomass was three times greater than in recovered forest. Sparse and reduced recovery was more likely at high elevations, on steep slopes, and far from *ex situ* seed sources, and patches were larger at high elevations and far from seed sources. It took 20 years for sparse and reduced recovery to be distinguishable from recovered forest using NDVI, suggesting a time lag before remotely sensed data can detect alternative pathways of postfire forest recovery. Now, 30 years after the 1988 fires, ~16 % of the forest burned as stand-replacing fire has failed to recover. The extent and configuration of these areas suggest some may persist as sparse or non-forest for the foreseeable future, with implications for biodiversity and ecosystem processes.

1. Introduction

Changing climate and fire regimes are altering postfire tree regeneration and eroding forest resilience (i.e., the ability to recover to predisturbance structure and function; Holling, 1973) throughout western North America (Johnstone et al., 2016, Stevens-Rumann et al., 2018, Coop et al., 2020). Anomalous short-interval fires in forests adapted to infrequent high-severity fire can reduce postfire regeneration due to immaturity risk (Keeley et al., 1999, Brown and Johnstone, 2012, Bowman et al., 2014, Whitman et al., 2019), whereas increased fire severity and tree mortality in forests adapted to frequent low-severity fire can eliminate seed supply (Kemp et al., 2016, Rother and Veblen ,2016, Littlefield, 2019). Even if seeds are available, hot, dry postfire conditions may limit seedling establishment (Tepley et al., 2017, Hansen and Turner, 2019, Rodman et al., 2020), especially in water-limited lower montane forests (Davis et al., 2019). However, postfire regeneration varies widely within fire perimeters, and it remains difficult to explain where and why forests do or do not recover. Many studies emphasize postfire regeneration over relatively short timeframes (<10 yrs; Stevens-Rumann and Morgan, 2019), but analyses that span several decades and contrast areas of variable recovery within large fire events are needed to address this knowledge gap.

Sparse regeneration following recent fires has been observed in lower montane forests, but recovery of high-elevation, mesic coniferous forests is of growing concern. Such forests have often been considered less susceptible to forest loss (Stevens-Rumann et al., 2018) in part

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because upslope tree migration with climate warming could contribute to recovery (Aitken et al., 2008, Harsch et al., 2009, Piekielek et al., 2015, Hill and Field, 2021). However, fires are advancing upslope (Alizadeh et al., 2021) and recent modeling studies suggest high-elevation forests could be vulnerable to postfire regeneration failure (Hansen and Phillips, 2015, Pansing et al., 2020, Rammer et al., 2021). Historical fire return intervals often spanned two to four centuries (Turner and Romme, 1994, Schoennagel et al., 2003, Baker, 2009), and dominant tree species such as Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and non-serotinous populations of lodgepole pine (*Pinus contorta* var. *latifolia)* are fire-sensitive, obligate seeders that lack adaptations to survive fire (e.g., thick bark) or regenerate rapidly (e.g., serotiny, resprouting). Natural postfire tree establishment then relies on seeds from live trees within the burn perimeter or from surrounding forest (Lyon and Stickney, 1974, McCaughey et al., 1986, Alexander, 1987), contributing to sparse early tree regeneration where distances to live seed source are long (Pierce and Taylor, 2011, Harvey et al., 2016a, Hansen et al., 2018). Thus, it may take decades to assess trends in postfire recovery reliably (e.g., Hemstrom and Franklin, 1982, Little et al., 1994, Coop et al., 2010).

Widespread availability of remotely sensed data offers opportunities to quantify broad-scale spatial patterns of postfire recovery over long timeframes, including in areas where lack of access hinders field campaigns. The Normalized Difference Vegetation Index (NDVI; Tucker, 1979) has been widely used to quantify postfire vegetation dynamics (Lentile et al., 2006, Yang et al., 2017) and is well-suited to characterize postfire forest recovery patterns using decades of Landsat imagery. The NDVI is correlated with forest structural characteristics like leaf area index (Spanner et al., 1990), live aboveground biomass (Tucker et al., 1985, Jakubauskas and Price, 1997, Cabrera-Bosquet et al., 2011, Wani et al., 2015) and tree density (Ingram et al., 2005, Wani et al., 2021). Further, it can be used to distinguish evergreen from deciduous vegetation (Buma, 2012, Vanderhoof and Hawbaker, 2018, Vanderhoof et al., 2020), including herbaceous understories that may compete with tree seedlings.

The extent and spatial pattern of sparse forest recovery is likely to drive landscape patterns of forest structure and ecosystem processes. If patches of sparse recovery are small and/or close to seed sources, trees should gradually reestablish, and the age and size structure resulting from continual infilling may generate structurally complex forests (Donato et al., 2012). If patches of sparse recovery are large and/or far from seed sources, sparsely or non-forested areas are likely to persist, with reduced canopy cover altering plant and lichen communities (Miller et al., 2018, Stevens et al., 2019, Paulson et al., 2021) and prolonging or precluding recovery of aboveground carbon stocks (Smithwick et al., 2009, Alexander et al., 2012). For fires that burned in the 1980′s, when the recent uptick in fire activity in western US forests began (Westerling et al., 2006, Dennison et al., 2014, Abatzoglou and Williams, 2016), sufficient time has elapsed for the extent and spatial pattern of sparse forest recovery to be assessed.

The well-studied 1988 Yellowstone fires, which burned across a range of elevations and forest types, are an ideal natural experiment for assessing postfire forest recovery dynamics across a large landscape. The prevalence of serotinous lodgepole pine led to remarkable resilience in much of the burned area (e.g., Turner, 2010, Romme et al., 2011, Turner et al., 2016), contributing to greater positive change in NDVI over time within the 1988 burn perimeter than outside it (Potter, 2019). However, nearly 16,000 ha of areas burned as stand-replacing fire were > 200 m from live forest (Turner et al., 1998). Early postfire studies also reported low tree seedling establishment in some high-elevation locations (Turner et al., 1997, 2003, 2004, 2016), with one-third of the landscape exhibiting relatively sparse postfire densities 10 years postfire (Kashian et al., 2004). Furthermore, regeneration of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) was sparse or absent on south-facing aspects near lower treeline (Donato et al., 2016). Our study is distinct from prior work in that we aimed to identify previously forested areas that appear not to have recovered after the 1988 fires and are exceptions to the rapid recovery that characterizes much of the burned area (Turner et al., 2016).

Here, we focused on forest recovery 30 years after the 1988 fires to address three questions: (1) What is the extent and configuration of sparse and reduced forest recovery? (2) How do vegetation characteristics compare between areas of sparse and reduced recovery vs. recovered forest? (3) What environmental characteristics explain the distribution and patch size of sparse and reduced recovery? We expected sparse and reduced recovery to occur in high-elevation areas dominated pre-fire by fire-sensitive tree species; at lower elevations on drier landscape positions; on steep, southwest facing slopes; and in relatively large patches far from *ex situ* seed sources. We further hypothesized that herbaceous or shrubby vegetation would be more abundant in areas of sparse recovery due to the high light environment and reduced competition with trees. Finally, we expected larger patches of sparse and reduced recovery to be at higher elevations, farther from seed sources, and on steeper, drier landscape positions.

2. Materials and methods

2.1. Study area

The Greater Yellowstone Ecosystem (GYE) is an extensive, intact temperate-zone landscape containing Yellowstone and Grand Teton National Parks (YNP and GTNP, respectively) and surrounding national forests and wilderness areas. Vegetation in the GYE transitions from shrubland steppe and lower montane forests dominated by Douglas-fir and lodgepole pine (~1500–2000 m asl) to subalpine forests dominated by lodgepole pine, Engelmann spruce, and subalpine fir (~2000–2600 m asl), with whitebark pine prevalent at the highest elevations below treeline (Despain, 1990). Annual precipitation is variable and falls primarily during the winter as snow (Hostetler et al., 2021). From 1981 through 2010, the average maximum temperature was 23.6 °C in July, the average minimum temperature was −17.8 °C in January, and the average annual precipitation was ~ 592 mm (data from Old Faithful, Wyoming, station #486845; Western Regional Climate Center). Most soils are derived from infertile volcanic substrates including rhyolite and andesite (Despain, 1990).

Infrequent stand replacing fires have occurred in Yellowstone's subalpine forests at 100–300-yr fire return intervals throughout the Holocene (Romme and Despain, 1989, Schoennagel et al., 2003, Higuera et al., 2011). Tree regeneration following the 1988 Yellowstone fires, which burned > 250,000 ha of forest as stand replacing fire, was dense across much of the landscape (Turner et al., 2004, 2016), indicating widespread forest resilience.

2.2. Question 1: Extent and configuration of sparse and reduced postfire tree recovery

We constrained this study to areas that burned as stand-replacing fire [>92.5 % of basal area killed, corresponding to a Relative differenced Normalized Burn Ratio (RdNBR) ≥ 625; Harvey, 2015] in 1988 and had not burned again through 2019 (~40 % of area within the 1988 burn perimeter; Fig. A.1). We first related satellite-derived NDVI to field-collected postfire stem density data, then used NDVI at 30 years postfire to identify areas that were both sparse (low postfire tree density) and reduced (relative to pre-fire biomass).

2.2.1. Relating NDVI to postfire stem density

Data sources. Thirty-meter-resolution Landsat Top of Atmosphere (TOA) Reflectance imagery was retrieved from Google Earth Engine (Gorelick et al., 2017) for 2013 and 2014 (Landsat 8) to create a postfire greenest pixel composite, with two years of data needed to collect enough cloud-free pixels. These were chosen as the years nearest the year in which postfire stem density data were collected (2012) that avoid scanner line correction failure on the Landsat 7 satellite, the only Landsat sensor available in 2012. Although Landsat Surface Reflectance (SR) imagery is recommended for use in most remote sensing contexts (Young et al., 2017), Landsat TOA imagery was used because it better explained variation in postfire stem density compared to SR imagery (Table A.1). The NDVI was calculated by the normalized difference between bands 5 (near infrared) and 4 (red) for all pixels within and adjacent to YNP. Because of minor differences between sensors, Landsat 8 NDVI values were harmonized to Landsat 5 equivalents prior to analysis (Roy et al., 2016). We removed NDVI values < 0.01 and > 0.9 across all images in each year to avoid erroneous NDVI classification. We developed a postfire greenest pixel composite using NDVI values from both "spring" (January 1 to June 5) and "fall" (September 9 to December 31) to ensure our composite included biomass from evergreen vegetation (i.e., recovering coniferous forest) and excluded biomass from deciduous vegetation during summer. Each pixel in our spring and fall composite thus represents the highest NVDI value for that pixel across 2013–14 spring and fall dates (hereafter, evergreen NDVI). Imagery during snow cover likely contributes little to our spring and fall composite given our date range spans snow-free periods before green-up (late May-early June) and after senescence (September-early October) and maximum NDVI values were used for each pixel.

Postfire tree density (stems ha^{-1}) data were obtained from 71 plots (50 m $\times$ 50 m), all burned as stand-replacing fire and widely distributed, that were sampled in 2012 (i.e., 24 years postfire; see Turner et al., 2016; Fig. A.2). Postfire stem density was recorded within three belt transects (50 m $\times$ 2 m) in each plot and averaged for the plot.

Analysis. The postfire spring and fall greenest pixel composite was sampled using plot centers of the 71 postfire plots, where evergreen NDVI was extracted from the 30 m $\times$ 30 m pixel that intersected plot center. Regression analysis was used to relate 2013–14 evergreen NDVI to postfire lodgepole pine density. Stem density was log-transformed prior to analyses to satisfy the assumption of equal variance. Spatial structure in model residuals was assessed with semivariograms. We also tested for relationships between pre-fire stem density and pre-fire evergreen NDVI using a greenest pixel composite for 1986–87, but no relationship was found (Appendix A).

2.2.2. *Identifying sparse and reduced postfire tree recovery*

Distinguishing areas of poor forest recovery from recovered forest requires determining whether postfire regeneration is both sparse and reduced relative to pre-fire density (sensu Coop et al., 2020). Thus, postfire stem density must be quantified throughout a burned area, and pre- and postfire densities must be compared. We used a threshold of 1000 stems ha^{-1} to differentiate sparse from intermediate and dense postfire tree density. This value is sparse relative to the mean (21,738 stems ha^{-1}) and median (4050 stems ha^{-1}) stem density 24 years after the 1988 fires (Turner et al., 2016) and is below the density to which stands converge after $\sim$ 175 years of development (1170 stems ha^{-1}; Kashian et al., 2005a). We used the regression between postfire evergreen NDVI and postfire stem density to identify the NDVI threshold that would distinguish present-day stands (2018–19) with sparse postfire tree densities ($\leq$1000 stems ha^{-1}) from stands where recovery was robust.

To identify areas of reduced postfire tree recovery, pre-fire (1986–87) and present-day (2018–19) spring and fall greenest pixel composites were created using methods described above (section 2.2.1). We then subtracted pre- from postfire evergreen NDVI and identified pixels in which postfire evergreen NDVI exhibited a net decline > 0.1 relative to pre-fire. This conservative definition of reduced recovery targets areas with a marked decline in biomass and avoids areas with marginal changes in evergreen NDVI that may not be ecologically meaningful (Appendix B). We next identified all pixels in the present-day spring and fall composite that were (i) below the sparse recovery threshold and (ii) had a decline in evergreen NDVI > 0.1 (defined as sparse and reduced forest recovery). We also identified all pixels that were (i) above the sparse recovery threshold and (ii) had no decline or an increase in evergreen NDVI (defined as recovered forest).

To quantify the configuration of sparse and reduced recovery, we identified all patches > 1 ha in size (using an 8-neighbor rule), computed the cumulative frequency distribution of patches and area by patch size, and calculated the area-weighted mean patch size (AREA_AM; ha) using the landscapemetrics package in R (Hesselbarth et al., 2019). To determine the extent to which seed limitations may be limiting recovery, we calculated the amount of this area that was ≥ 150 m from areas that were unburned or burned at low severity (<50 % of basal area killed by fire, corresponding to a RdNBR ≤ 288; Harvey, 2015) in 1988, a distance that exceeds typical seed dispersal distances for non-serotinous conifers in the study area (Greene and Johnson, 1996).

2.2.3. *Accuracy assessment and sensitivity analysis*

We assessed the accuracy of our classification of sparse and reduced recovery by counting all dead snags and logs, and live trees in a subset of points of sparse and reduced recovery in the Google Earth Engine 'satellite' view (Appendix B). To assess the sensitivity of our results to our methods, we varied the thresholds of both sparse forest and reduced recovery and tested the effects of choosing different pre- and postfire years (Appendix B).

2.3. *Question 2: Distinctions between sparse and reduced vs. Recovered forest*

We randomly sampled 1000 pixels within areas of both sparse and reduced recovery and recovered forest, with all sample pixels ($n = 2000$) separated by $\geq$ 500 m. As indicators of differences in vegetation conditions, we extracted the following at each sample location: (i) net change in evergreen NDVI from pre- to postfire; (ii) vegetation height (m), retrieved from the Global Forest Canopy Height database (Potapov et al., 2020); and (iii) the proportion of total NDVI represented by non-evergreen vegetation [the difference between the postfire spring and fall (2018–19) greenest pixel composite and a greenest pixel composite at peak biomass considering all dates between January 1, 2018, and December 31, 2019]. One hundred and forty-nine sample locations were removed from consideration for vegetation height because data were not available. Inherent spatial and temporal structure in remotely sensed imagery (Fig. A.3; Ives et al., 2021) and large sample sizes pose several problems for common statistical methods, particularly in the interpretation of statistical significance. As such, we focused our interpretation on whether differences are ecologically meaningful rather than statistically significant.

To determine the length of time since fire needed to distinguish sparse and reduced recovery from recovered forest, we created spring and fall greenest pixel composites for each pair of years from 1985 to 86 to 2019–20 (excluding 2012–13 due to inadequate cloud-free imagery) using the above methods (section 2.2.1). Pairs of years were used to reduce variability owing to the availability of cloud-free imagery. Each spring and fall greenest pixel composite was sampled using the same 1000 points from each sparse and reduced recovery and recovered forest classified using 1986–87 and 2018–19 imagery and mean ($\pm$SD) values were plotted by year pairs. We considered the year at which standard deviations from each recovery type no longer overlapped to indicate the time required to distinguish sparse and reduced from recovered forest.

2.4. *Question 3: Environmental predictors of distribution and patch size*

We next extracted four potential predictors at each sample location to identify pixel- and patch-level drivers of the distribution of sparse and reduced recovery vs. recovered forest. Three predictors were associated with abiotic conditions that could potentially influence tree establishment and growth [elevation (m), slope (degrees), and Topographic Moisture Index (TMI; cosine-transformed aspect: 0 = dry, southwest facing; 2 = moist, northeast facing; Beers et al., 1966), all derived from a

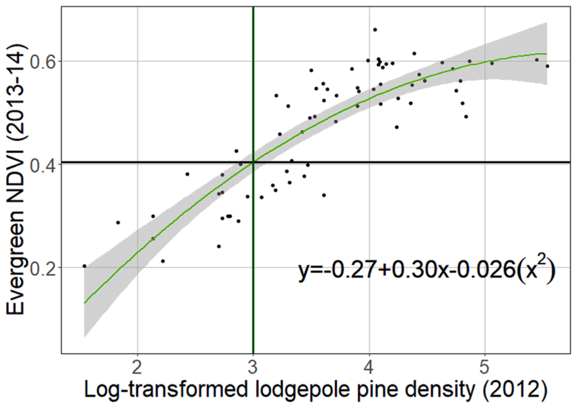

Fig. 1. Polynomial regression line (light green) with 95 % confidence interval for 2013–14 evergreen NDVI fitted to lodgepole pine density in 71 plots sampled in 2012 ($R^2 = 0.74$). The dark vertical line indicates sparse tree recovery (log-transformed lodgepole pine density = 3, or 1000 stems ha^{-1}), and the dark horizontal line indicates the predicted NDVI at this sparse tree recovery threshold. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

30-m resolution digital elevation model], and the fourth predictor chosen as a proxy for seed supply (distance to *ex situ* seed sources, defined as unburned areas or areas burned at low severity). Elevation is also a proxy for pre-fire forest composition, particularly the presence of serotinous lodgepole pines, which are common at elevations < 2300 m and rare at elevations ≥ 2300 m (Schoennagel et al., 2003). We did not include burn severity, because all sampled locations burned as stand-replacing fire; pre-fire forest composition, which varies strongly with elevation; or soil type, which does not relate to variability in postfire sapling density (Turner et al., 2004). We used a classification tree to identify relevant predictors of sparse and reduced recovery vs. recovered forest at the pixel level using the 'ctree' function in the partykit package in R (Hothorn et al., 2006, Hothorn and Zeileis, 2015).

Finally, we used a generalized linear model to relate patch sizes of sparse and reduced recovery to the above four predictors. Patch-level values for each predictor were calculated as the average of pixel-level values within a patch, except for distance to *ex situ* seed source, which was averaged only for edge pixels to avoid conflating distance to seed source with patch size. Predictors were standardized prior to modeling so model coefficients estimate the effect size for each predictor, and patch size as the response variable was treated as count data (i.e., number of pixels per patch). A zero-truncated negative binomial distribution with a log-link function was used to account for overdispersion (tested for using the DHARMa package; Hartig, 2021). This model was fit using the glmmTMB package (Brooks et al., 2017), and top models were identified using the 'dredge' function in the MuMIn package (Barton, 2020), where AICc was compared among possible models. If multiple models were identified as top models within an AICc < 2, the model with the fewest number of parameters was chosen as the most parsimonious. Because of spatial structure in the model residuals (Fig. A.4) contributing to inflated Type I error, confidence intervals were not included with standardized coefficient estimates. All analyses were conducted in R (R Core Team, 2020).

3. Results

3.1. Relationship between NDVI and stem density

Postfire lodgepole pine stem density averaged 22,044 ± 6480 stems

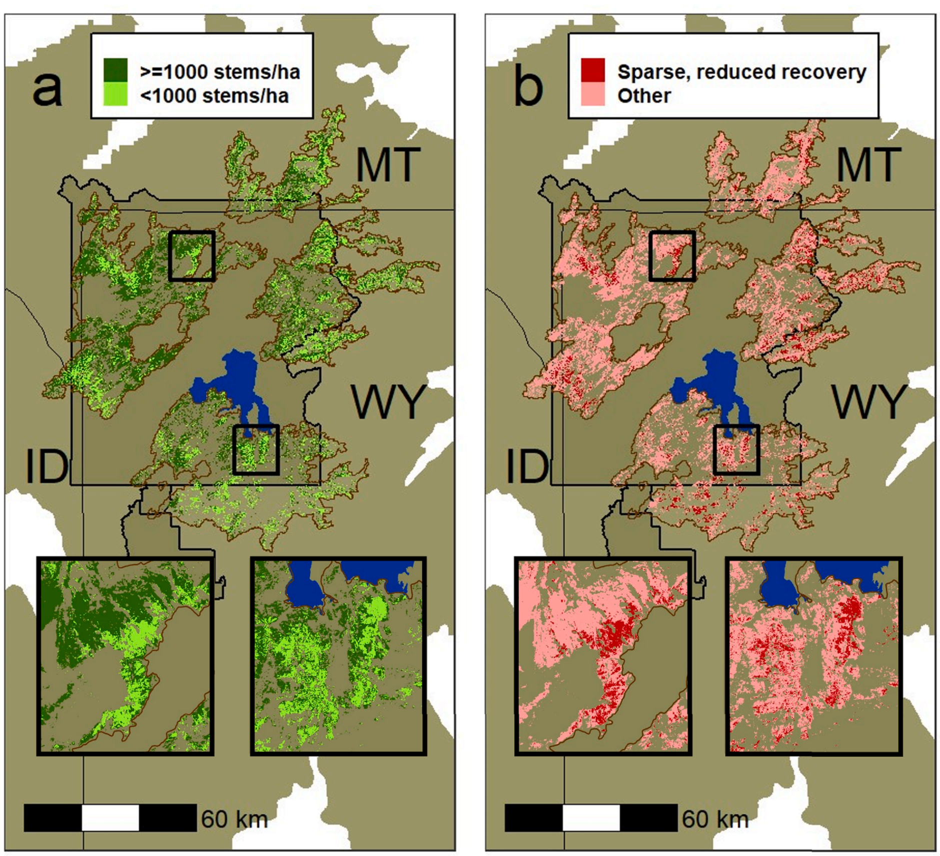

Fig. 2. (a) Areas of sparse postfire tree recovery (<1000 stems ha^{-1}) and intermediate and dense recovery (≥1000 stems ha^{-1}) 30 years after the 1988 Yellowstone fires. (b) Areas of sparse and reduced postfire tree recovery (<1000 stems ha^{-1}, >0.1 NDVI decline pre- to postfire) 30 years after the 1988 Yellowstone fires.

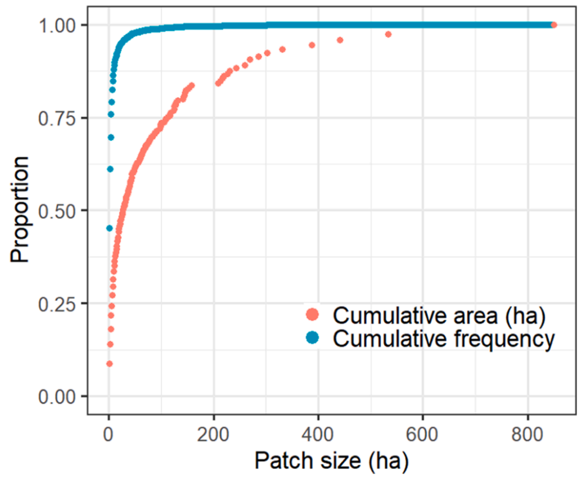

Fig. 3. Cumulative area (ha; red) and frequency (blue) distributions by size of patches of sparse and reduced recovery 30 years after stand-replacing fire during the 1988 Yellowstone fires. Patches range from 1 to 850 ha. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ha^{-1} and ranged from 33 to 344,067 stems (Turner et al., 2016). Postfire evergreen NDVI values in these plots (n = 71) averaged 0.47 ± 0.014 and ranged from 0.20 to 0.66. Postfire evergreen NDVI increased non-linearly with increasing lodgepole pine density in these 24-yr old forests ($F_{2,68}$ = 97.41, p < 0.001, R^2 = 0.74; Fig. 1). No spatial structure was present in model residuals (Fig. A.5).

3.2. Extent and configuration of sparse and reduced recovery

The evergreen NDVI threshold for sparse postfire recovery (<1000 stems ha^{-1}) was determined to be 0.40 (Fig. 1), which correctly identified 62 of 71 (87 %) field plots. Within the 253,966 ha of forest that burned as stand-replacing fire in 1988, 34 % (86,644 ha) fell below this threshold in 2018–19 (Fig. 2a). When intersected with areas that also showed reduced biomass recovery, 16 % (40,861 ha total; 33,477 ha in patches > 1 ha) of the area exhibited both sparse and reduced recovery in 2018–19 (Fig. 2b), of which half (20,164 ha) was ≥ 150 m from *ex situ* seed source and in patches > 1 ha. Our classification methods performed well, with 92 % of 249 sampled plots accurately classified as reduced recovery and all plots correctly identified as sparse. Our results were sensitive to varying the pre- and postfire NDVI years, with an order of magnitude difference in the area identified as sparse and reduced recovery depending on the combination of dates chosen (~5 % to ~ 40 %; Table B.3). However, evergreen NDVI in our chosen postfire years (2018–19) tracked postfire evergreen NDVI trajectories well and was notably more accurate than either 2016–17 or 2017–18 (Fig. 4). Our results proved less sensitive to differences in the stem density threshold used to detect sparse forest (500, 1000, or 1500 stems ha^{-1}) or the reduced NDVI threshold used to identify reduced recovery (0.05, 0.1, or 0.15; Table B.3).

We tallied 4,553 patches of sparse and reduced recovery, ranging in size from 1 ha to 850 ha. Nearly 50 % of the patches were very small (1–2 ha), but these accounted for < 10 % of the area. Conversely, 2.2 % of the patches were large (≥50 ha, n = 100), and these accounted for ~ 40 % of area (Fig. 3). The area-weighted mean patch size was 97 ha.

3.3. Characteristics of sparse and reduced vs. Recovered forest

Pre-fire evergreen NDVI was ~ 0.45 and was similar in areas subsequently classified as either sparse and reduced recovery or recovered forest (Fig. 4). The evergreen NDVI trajectories of recovery began to separate (i.e., no overlap in SD) in 2009–10, ~20 years postfire (Fig. 4). Further, the standard deviations about evergreen NDVI in sparse and reduced recovery never included our threshold of sparse forest (Fig. 4), lending confidence in it as an appropriate and ecologically meaningful threshold to distinguish these areas across years.

Although pre-fire evergreen NDVI was similar in areas classified as sparse and reduced recovery vs. recovered forest, present-day evergreen NDVI was ~ 40 % lower in sparse and reduced recovery than in recovered forest (Fig. 5a-b). Further, present-day evergreen NDVI increased by ~ 25 % relative to pre-fire in recovered forests but declined by ~ 30 % in areas of sparse and reduced recovery (Fig. 5c). Present-day non-evergreen NDVI was nearly three times greater in areas of sparse and reduced recovery compared to recovered forest (Fig. 5d). Estimated mean vegetation height was < 2 m in areas of sparse and reduced recovery but > 9 m in areas where forest had recovered (Fig. 5e).

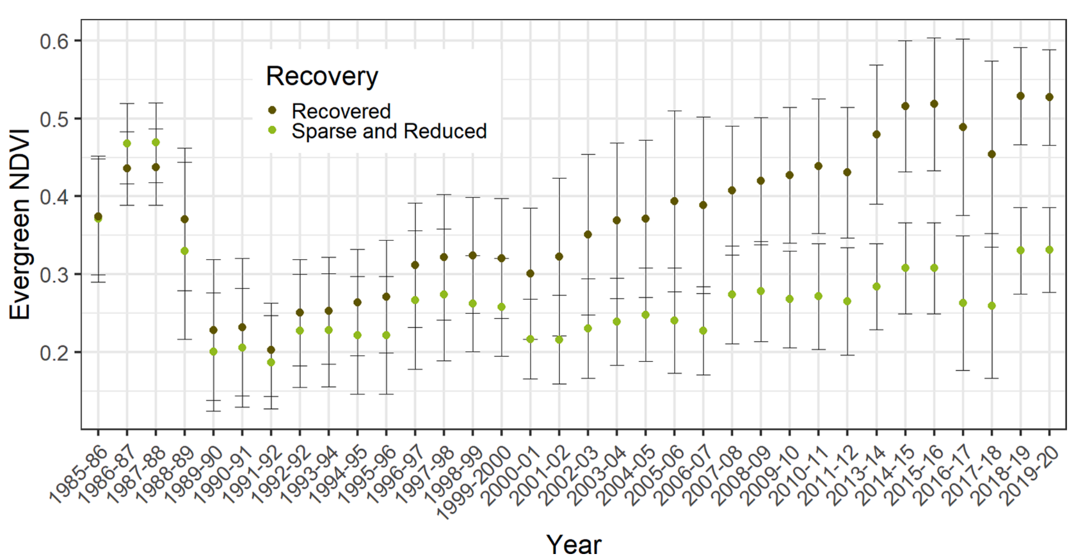

Fig. 4. Recovery of evergreen NDVI through time (mean ± SD) for areas identified as recovered (dark green) and sparse and reduced recovery (light green) following the 1988 Yellowstone fires using 1986–87 and 2018–19 imagery. The evergreen NDVI for each pair of years was calculated using methods outlined in section 2.2.1 and sampled using the same 1000 points in each sparse and reduced recovery and recovered forest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

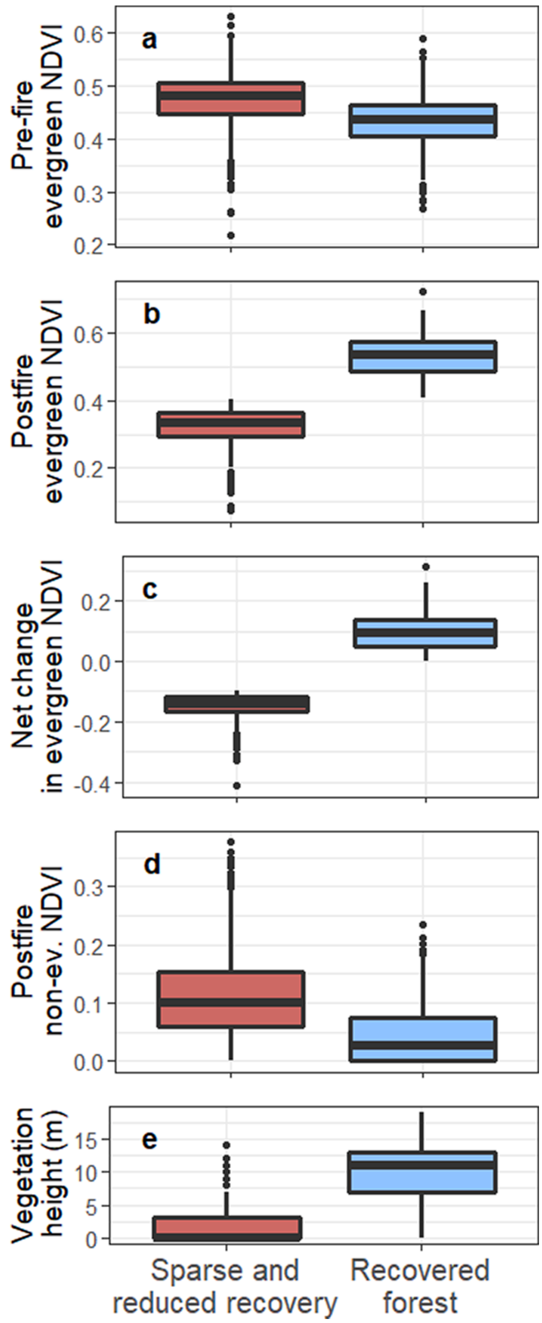

Fig. 5. Vegetation characteristics of areas classified as sparse and reduced recovery (red, left) and recovered forest (blue, right) 30 years after the 1988 Yellowstone fires. (a) pre-fire evergreen NDVI; (b) postfire evergreen NDVI; (c) Net change in evergreen NDVI, where negative values indicate greater pre- than postfire NDVI, and positive values indicate greater post- than pre-fire NDVI; (d) Postfire non-evergreen NDVI, or the difference in NDVI between the growing and non-growing (i.e., spring and fall) seasons; (e) vegetation height (m), retrieved from the Global Forest Canopy Height database (Potapov et al. 2020). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.4. *Predictors of distribution and patch size of sparse and reduced recovery*

Pixels of sparse and reduced recovery occurred at higher elevations and on steeper slopes than recovered forest (Fig. 6, Table 1), with ~ 85 % of the area found above 2500 m (Fig. A.6). Distance to *ex situ* seed source was greater in areas of recovered forest across the landscape (Table 1) but emerged as a predictor of sparse and reduced recovery at high elevations, where greater distance to *ex situ* seed source indicated a greater likelihood of sparse and reduced recovery (Fig. 6). Topographic moisture index did not differ between the two categories of forest recovery.

Larger patches were more likely to occur farther from *ex situ* seed source and at higher elevations than smaller ones (Table 2), with distance to seed source having roughly twice as strong an effect on patch size than elevation. Of the models within two AICc of one another, the most parsimonious model for explaining patch sizes of sparse and reduced recovery included only distance to *ex situ* seed source (m) and elevation (m; Table 2). Patch size was minimally influenced by slope or TMI.

4. Discussion

Although the 1988 Yellowstone fires serve as a well-documented example of forest resilience (Romme et al., 2011), our study revealed that 16 % of the forested area burned as stand-replacing fire had not recovered after 30 years. Additionally, we found that these patterns related to environmental and disturbance characteristics, with a lack of forest recovery at high elevations, far from seed sources, and on steep slopes potentially related to the pre-fire species distributions and postfire establishment limitations. Our results also suggest that a substantial proportion of the landscape burned as stand-replacing fire in 1988 may persist as sparse or non-forest for the foreseeable future, as ~ 20,000 ha of poor forest recovery exist beyond seed dispersal distances of the dominant tree species in the region.

4.1. *Extent and configuration of sparse and reduced forest recovery*

We found spring and fall NDVI to effectively characterize postfire tree density and thus evergreen biomass, with a stronger positive correlation between spring and fall NDVI and stem density at 24 years postfire than at eight to 18 years postfire (Buma, 2012, Franks et al., 2013). The lack of relationship between spring and fall NDVI and pre-fire stem density was unsurprising because many forests were well over 100 years old when they burned in 1988 (Romme and Despain, 1989), and among-stand variation in biomass and productivity converges 100 to 200 years postfire (Kashian et al., 2005a, 2005b, Bradford et al., 2008). Postfire trends in evergreen NDVI also indicate it took ~ 20 years for divergent trajectories of forest recovery to become evident. In boreal forests of Alaska, immediate NDVI increases following fire were largely driven by deciduous cover, where compositional shifts to conifer-dominated lower and upper canopies only occurred by 50 years postfire (Fiore et al., 2020). While climate-driven greening and browning does influence NDVI in our study region, disturbance remains the dominant driver (Emmett et al., 2019).

Forested areas that have not yet recovered from stand-replacing fires in 1988 were widely distributed throughout the burned area. Our estimate of sparse and reduced recovery was comparable to that found in black spruce-dominated boreal forests of North America, where regeneration failure occurred in 18 % of 1140 sites following recent (1989–2014) fires (Baltzer et al., 2021). Further, the amount of sparse forest 30 years after the 1988 fires was similar to estimates based on field data and false-color infrared aerial photos from 10 years postfire (Kashian et al., 2004), suggesting forest recovery trajectories that established early have persisted. However, our methods using spring and fall NDVI cannot detect small tree seedlings that could be infilling beneath herbaceous vegetation. Indeed, under historical climate and fire regimes, postfire tree regeneration in high-elevation *Picea-Abies* forests of the Rocky Mountains can occur over a 40–70-yr range (Peet, 1988). Field measurements would be required to detect evidence of ongoing tree seedling recruitment.

Quantifying differences between pre- and postfire evergreen NDVI (e.g., Yang et al., 2017) likely improved assessments of the extent and

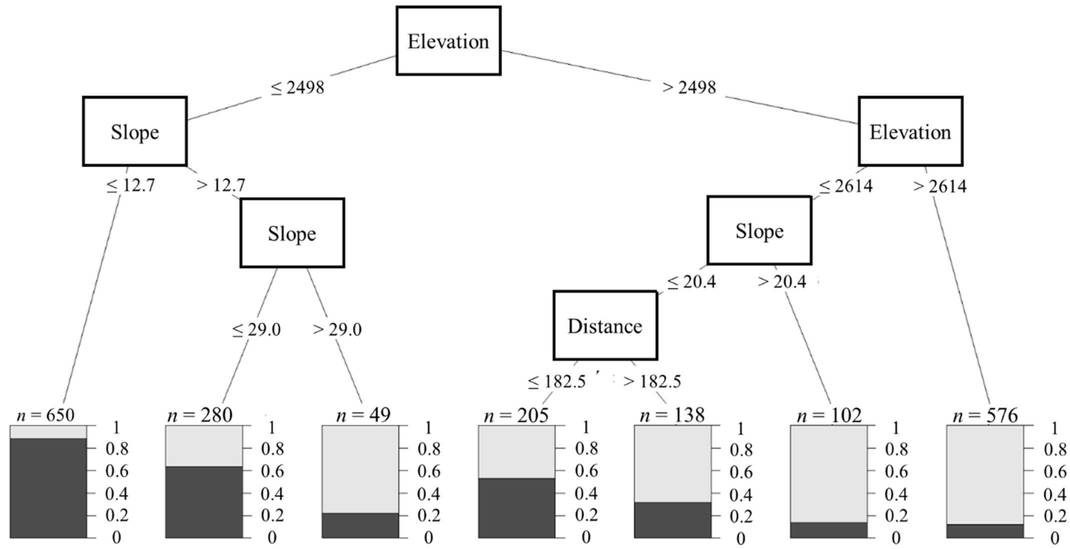

Fig. 6. Classification tree of pixels of sparse and reduced recovery (light grey) and recovered forest (dark grey) for areas burned as stand-replacing fire in the 1988 Yellowstone fires differentiated into groups by elevation (m), slope (degrees), and distance to *ex situ* seed source ('Distance'; m).

Table 1
Environmental characteristics (mean ± SE) of areas classified as sparse and reduced post-fire tree recovery and recovered forest (n = 1000 for each) in Greater Yellowstone 30 years after the 1988 Yellowstone Fires.

Factor	Sparse and Reduced Recovery	Recovered Forest
Elevation (m)		
Mean ± SE	2606 ± 5	2403 ± 5
Median	2616	2405
Range (min – max)	1923–3106	1910–2943
Slope (degrees)		
Mean ± SE	16 ± 0.3	9 ± 0.2
Median	15.2	6.8
Range (min – max)	0–59.2	0–40.5
Topographic Moisture Index		
Mean ± SE	1.01 ± 0.02	1.04 ± 0.02
Median	1.01	1.14
Range (min – max)	0–2	0–2
Distance to nearest ex situ seed source (m)		
Mean ± SE	180 ± 5	201 ± 6
Median	127	150
Range (min – max)	30–1231	30–1355

configuration of forest recovery compared to only tracking trends in postfire NDVI (e.g., with a postfire Landsat timeseries; Goetz et al., 2006, Pickell et al., 2016, White et al., 2017). By accounting for locations that were sparsely treed before 1988 and separating evergreen from non-evergreen biomass, our estimates of poor forest recovery are likely more robust. For example, the area-weighted mean patch size of sparsely forested areas (without accounting for pre-fire tree density) at 10 years postfire was 179 ha (Turner et al., 2004), nearly twice our estimate of 97 ha for sparse and reduced recovery. Thus, short-term postfire stem density alone may be insufficient to predict poor forest recovery. Resilience of subalpine forests to large, stand-replacing fires can be better assessed by also incorporating return to pre-fire conditions.

4.2. Vegetation characteristics in sparse and reduced vs. recovered forest

The short stature of vegetation and increased abundance of non-evergreen biomass in areas of sparse and reduced recovery suggest the potential for understory vegetation (e.g., *Calamagrostis canadensis*; Lieffers et al., 1993) to constrain future tree seedling establishment. However, the long-term effect of the herbaceous layer on tree seedling establishment remains unclear, as competitive, facilitative, and neutral effects have all been documented depending on the tree and shrub species studied (Anderson and Romme, 1991, Cain, 1996, Gärtner et al., 2014, Klutsch et al., 2015, Castro and Leverkus, 2019, Urretavizcaya and Defossé, 2019). Additional studies are needed to quantify effects of non-tree vegetation on stand development and determine whether a non-forested state is likely to persist.

4.3. Explaining distribution and patch size of sparse and reduced recovery

Distance to *ex situ* seed source was important for distinguishing sparse and reduced recovery from recovered forest and was the strongest predictor of patch size of sparse and reduced recovery. Distance to seed source has been long-recognized as a driver of variable tree regeneration (Greene et al., 1999) and postfire regeneration in western US forests (Harvey et al., 2016a, Stevens-Rumann and Morgan, 2019, Hoecker and Turner, 2022a). Our results suggest that forest recovery may be precluded for the foreseeable future in ~ 20,000 ha of sparse and reduced recovery that are ≥ 150 m from live tree seed sources. However, trees that established soon after fire will in time produce cones (Alexander, 1987, Arno and Hoff, 1989, Lotan and Critchfield, 1990, McCaughey

Table 2
Top models (≤2 AICc) explaining variation in patch size (number of 30-m by 30-m square pixels) of sparse and reduced recovery 30 years after the 1988 Yellowstone fires. The first model was considered the most parsimonious because it contained the fewest predictors. Standardized coefficient estimates for each distance to *ex situ* seed source (m), elevation (m), topographic moisture index (TMI), and slope (degrees) are provided for each model.

				Coefficient estimates			
Model	df	Log-likelihood	AICc	Distance	Elevation	TMI	Slope
distance + elevation	4	−23873.3	47754.6	0.56	0.26	*NA*	*NA*
distance + elevation + TMI	5	−23872.6	47755.3	0.55	0.26	0.04	*NA*
distance + elevation + slope	5	−23873.0	47756.0	0.55	0.25	*NA*	−0.02

and Tomback, 2001) and may contribute to a gradual increase in stem density (Kashian et al., 2005a). Thus, a protracted recovery to forest may still be possible given a suitable climate and sufficiently long fire-free interval. However, continued increases in fire size (Riley and Loehman, 2016, Wang et al., 2020) and area of high-severity fire (Harvey et al., 2016c, Singleton et al., 2019, Parks and Abatzoglou, 2020) suggest recovery may become increasingly unlikely with climate change.

Counter to expectations, we did not find sparse and reduced recovery associated with drier topographic positions at lower elevations. The lack of an effect of topographic position on tree regeneration following the 1988 fires is consistent with early field studies (Turner et al., 1999), and it may reflect weather conditions suitable for tree seedling establishment during the initial postfire years. Reduced postfire tree regeneration in lower montane forests has been observed in several studies (e.g., Donato et al., 2016, Davis et al., 2019, Stevens-Rumann and Morgan, 2019). Poor recovery in higher elevation forests has not been widely reported (but see Andrus et al., 2021), but climate has warmed in the GYE since 1988 (Notaro et al., 2019, Hostetler et al., 2021) and topographic position has affected tree seedling establishment following recent short-interval fires (Hoecker et al., 2020).

Sparse and reduced recovery was more prevalent at higher elevations, consistent with previous findings despite different definitions of forest recovery (reaching 10 % canopy cover; Zhao et al., 2016). This likely reflects the distribution of dominant tree species (but see Potter et al., 2012), as serotinous lodgepole pine is prevalent at mid-elevations and fire-sensitive non-serotinous lodgepole pine, Engelmann spruce, and subalpine fir are common at higher elevations (Tinker et al., 1994, Schoennagel et al., 2003, Hansen et al., 2016). Climate may too limit recovery of high-elevation forests, with seedling establishment sensitive to both warm and dry (Harvey et al., 2016a) and cold conditions (Ferrar et al., 1988, Ball et al., 1991, Germino et al., 2002). Indeed, Lubenow and Reinhardt (2020) found a negative relationship between NDVI and elevation across Intermountain West forests, and Coop et al. (2010) predicted no postfire trees near alpine treeline, suggesting abiotic limitations to establishment and growth at high elevations. Alternatively, climate may become increasingly suitable for postfire seedling establishment at upper treeline, but short dispersal distances may preclude seed arrival (Morgan et al., 2018). Our results are also consistent with recent modeling studies that highlight the vulnerability of high-elevation forests to regeneration failure (Rammer et al., 2021, Turner et al., 2022).

Slope was important for distinguishing sparse and reduced from recovered forest, with poor forest recovery more prevalent on steeper slopes. Tree establishment on steep slopes is low elsewhere in the western US (Stueve et al., 2009) and in boreal forests (Albani et al., 2005). Reduced seed interception and moisture retention on steep slopes plus greater soil erosion and snow disturbance (Billings, 1969, Nagamatsu et al., 2002) likely contribute to lower tree seedling establishment, though these influences may be relatively low and localized compared to the effect of either distance to seed source or elevation in our study area.

4.4. Implications and conclusions

The ecological consequences and management implications of sparse postfire forests within the 1988 burned area are myriad. Variable stand-development pathways increase heterogeneity of forest structure, which could influence numerous consumers (Bradstock et al., 2005, Noss et al., 2006, Tingley et al., 2016). For example, forest-dependent wildlife species may find areas of poor forest recovery less habitable (Lindenmayer et al., 2014, Hoecker and Turner, 2022b). However, such areas may be hotspots of plant diversity as the presence of many understory species increases with lower tree densities (Romme et al., 2016). The extent and distribution of sparse postfire forests may also delay or dampen future outbreaks of native bark beetles (Seidl et al., 2016). At the ecosystem level, areas of poor forest recovery may remain C sources for a long time and exhibit very slow rates of C recovery (Kashian et al., 2006, Smithwick et al., 2009), especially in areas far from seed sources (Henne et al., 2021). Remote sensing of postfire forest recovery pathways may thus be useful in assessing landscape-level C dynamics (Goetz et al., 2012, Pastick et al., 2017) and recovery of gross or net primary productivity (Hicke et al., 2003, Bolton et al., 2017).

The potential for forest disturbance-recovery dynamics to change fundamentally in the future is now widely recognized (e.g., Trumbore et al., 2015, Johnstone et al., 2016, Serra-Diaz et al., 2018, Coop et al., 2020, McDowell et al., 2020). Our results underscore the importance of considering postfire stem densities as well as pre- to postfire forest decline when assessing forest recovery and resilience. Though poor recovery at lower treeline may be driven by aridity, we suggest that loss of seed source may be driving sparse and reduced recovery in the upper subalpine zone, a condition unlikely to change even as such areas become potentially more suitable for establishment with climate warming. Under historical climate and fire regimes, areas of sparse and reduced forest recovery would likely recover to their pre-fire state over multiple centuries. However, as continued climate change makes more systems fire prone (Pechony and Shindell, 2010) and increasingly extensive wildfires burn fire-sensitive ecosystems (Godfree et al., 2021), such recovery may be precluded by poor establishment conditions or anomalously frequent fire. In response, wildland fire management efforts could prioritize protection of fire sensitive forests to maintain seed source for burned areas and habitat for forest-dependent species, and/or areas of sparse and reduced forest recovery to provide needed recovery time before fire occurs again. Regardless, the effects of such management decisions long-term will increasingly be mediated by projected changes to climate and fire (Hansen et al., 2019).

Land Acknowledgement

Since before colonization, the Greater Yellowstone Ecosystem was used by numerous Indigenous nations and tribes, notably the Crow, Bannock, and Shoshone. Despite their forced removal following the creation of YNP (Spence, 1999), many nations and tribes remain culturally and spiritually connected to the landscape (https://www.nps.gov/yell/learn/historyculture/associatedtribes.htm; https://native-land.ca/).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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