Forest Ecology and Management 572 (2024) 122326

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Multi-decadal aspen dynamics show recruitment bottleneck across complex mountain community

Michael T. Stoddard [a,*], Kyle C. Rodman [a], Connor D. Crouch [b], David W. Huffman [a], Peter Z. Fulé [c], Kristen M. Waring [c], Margaret M. Moore [c]

[a] Ecological Restoration Institute, Northern Arizona University, Flagstaff, AZ 86011, USA
[b] USDA Forest Service, Northern Research Station, Columbia, MO 65211, USA
[c] School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA

ARTICLE INFO

Keywords:
Populus tremuloides
Tree mortality
Tree regeneration
Southwestern United States
Montane forests
Ecological disturbance

ABSTRACT

Changes in forest structure and shifts in tree species composition have occurred globally due to climate change and altered disturbance regimes. With climate trending toward warmer and drier conditions, these altered forest communities may reorganize in diverse and unpredictable ways. This is especially true in mountain environments where a range of vegetation types and abiotic conditions coexist. In this study, we used long-term permanent plot data from a site spanning broad environmental gradients to assess regeneration and mortality patterns in populations of aspen (*Populus tremuloides*). The study site, located on the San Francisco Peaks, Arizona, USA, is near the hot, dry edge of the species' range and has experienced compounding pressure from extreme drought, chronic ungulate browsing, and wildfire in the past two decades. Over a 20-year study period, spanning one of the most prolonged drought periods in at least 1200 years, aspen overstory mortality averaged 42 % and was most common in smaller, younger trees and at lower elevations. Aspen regeneration density increased 13 % and was found in a greater proportion of study sites. However, we observed a noticeable lack of stems in the tallest regeneration size class (>200 cm) and the smaller tree size class (2.5–15 cm in diameter), potentially indicating a demographic bottleneck whereby few trees are recruiting into the overstory. Likewise, prolific aspen suckering occurred after a 2001 wildfire, although regeneration density eventually decreased to pre-fire levels, with <1 % of individuals reaching heights >200 cm. Aspen regeneration densities showed the greatest increases in cool, wet sites and beneath open forest canopies. Disturbances function as catalysts for aspen regeneration, but persistence of aspen stands depends on recruitment of stems into overstory size classes, a process that is limited, particularly on lower and more exposed sites.

1. Introduction

Globally, forests are undergoing abrupt changes in structure and composition due to the synergistic effects of climate change, altered disturbance regimes, and persistent environmental pressures (Seidl et al., 2017; Batllori et al., 2020; Turner et al., 2020). While forest dynamics fluctuate substantially over time due to complex interactions between climate variability and disturbances (Calder et al., 2015; Crausbay et al., 2017), recent changes in disturbance regimes have led to the emergence of novel forest conditions (Johnstone et al., 2016; Hessburg et al., 2019). In the past several decades, the southwestern United States has experienced some of the most extreme drought conditions in over 1000 years (Williams et al., 2020), contributing to widespread disturbances such as wildfires, insect outbreaks, and drought-caused tree die-off events (O'Connor et al., 2015; Hart et al., 2017; Mueller et al., 2020). Changing climate conditions and disturbance regimes are likely to catalyze changes in species distributions by altering the survival of mature trees and limiting tree regeneration (Dobrowski et al., 2015; Coop et al., 2020; Stevens-Rumann et al., 2022). Combined with additional biotic pressures, such as chronic browsing by introduced herbivores (Leopold et al., 1947; Nuñez et al., 2010,), these novel interacting disturbances compromise an ecosystem's adaptive capacity (i.e., the ability to adjust composition, structure, and function in response to external forces) (Millar et al., 2007; Nagel et al., 2017). Understanding and anticipating species' responses to these pressures offers insight into how managers can sustain forest

* Corresponding author.
E-mail address: mike.stoddard@nau.edu (M.T. Stoddard).

https://doi.org/10.1016/j.foreco.2024.122326
Received 28 June 2024; Received in revised form 1 October 2024; Accepted 3 October 2024
Available online 19 October 2024

ecosystems.

In diverse mountain environments, tree species are likely to respond in complex ways to shifting climate and disturbance regimes (Donato et al., 2009; Rodman et al., 2022; Davis et al., 2023). In western North America, suitable environmental niche space for many tree species is predicted to move both upslope and to more northern latitudes (Rehfeldt et al., 2006; Prasad et al., 2020) in response to further temperature increases and altered precipitation patterns (Abatzoglou et al., 2019; Triepke et al., 2019). In reality, species range may not always track changes in suitable climate conditions depending on dispersal ability and available growing space (Jump and Peñuelas, 2005; McDowell et al., 2020; Alsos et al., 2022). Furthermore, broad-scale models of climate suitability may ignore microclimate, which has a direct influence on demographic processes such as tree regeneration (Bell et al., 2014; Dobrowski et al., 2015) and mortality (Marsh et al., 2022). While climate may be the primary factor influencing species distributions, disturbances are likely to be catalysts for in-situ changes in forest structure and composition (Donato et al., 2016; Rodman et al., 2022), as well as migration to newly available habitat (Hill and Field, 2021). Given the complexities of shifting climates and ecological dynamics, tree species exhibit varying capacities for adaptation. Certain early-seral disturbance-adapted species, including aspen (*Populus tremuloides* Michx.), may exhibit heightened adaptive capacity and resilience, enabling them to track favorable climates and thrive in the presence of disturbances, despite the challenges posed by changing environmental conditions.

Aspen is the most broadly distributed tree species in North America and provides critical wildlife habitat, economic value, and recreation opportunities to local communities (Perala, 1990; McCool, 2001; Rogers et al., 2014). Though there are isolated aspen populations in mountain environments throughout Mexico, the southern end of the species' core distribution is found in the southwestern United States (i.e., Arizona and New Mexico) (Martínez González and González-Villarreal, 2005; Crouch et al., 2023). Aspen covers less than 3 % of forested land in the Southwest (Goeking and Menlove, 2017; Shaw et al., 2018) yet supports disproportionately greater biodiversity than neighboring conifer forests (Chong et al., 2001; Kuhn et al., 2011). The conservation of aspen communities has gained increased attention in recent decades due to the species' rapid and extensive mortality across the Southwest (St. Clair et al., 2010; Worrall et al., 2013; Anderegg et al., 2015). Aspen mortality has been particularly acute at lower elevations during the late twentieth and early twenty-first centuries, driven primarily by regional warming trends and prolonged drought (Fairweather et al., 2008; Zegler et al., 2012; Ireland et al., 2014). Over a climate gradient spanning southern New Mexico to northern Wyoming, aspen communities in the south have been shown to be the most sensitive to rising temperatures in the late 20th and early 21st centuries, exhibiting the largest growth declines during drought events (Ayres et al., 2024). Additionally, in the past decade, oystershell scale (*Lepidosaphes ulmi*), an invasive insect originating from Europe, has triggered widespread aspen mortality, especially among small trees at lower elevations (Crouch et al., 2021, 2024). Loss of aspen has also been documented at higher elevations (>2500 m), driven by regional climate change and seral replacement by shade-tolerant conifer species (Bartos, 2001; Cocke et al., 2005; Ireland et al., 2014). While drought, successional displacement, fire, insects, pathogens, and ungulate browse collectively pose significant challenges to aspen communities (Kolb et al., 2016; Crouch et al., 2023) their impacts are particularly pronounced in diverse mountainous environments where different vegetation types coexist and disturbance regimes have been altered (Cocke et al., 2005; Donato et al., 2009; Stoddard et al., 2018).

Aspen is a disturbance-resilient species, capable of persisting at a site through vegetative reproduction (Schier et al., 1985). Many studies have documented prolific aspen regeneration after fire (Bailey and Whitham, 2002; Romme et al., 2001; Margolis et al., 2007, 2011; Waltz et al., 2014; Yocom-Kent et al., 2015; Stoddard et al., 2018), as well as upslope migration and range expansion from seed (Fairweather et al., 2014; Kreider and Yocom, 2021; Nigro et al., 2022), Such dual regeneration strategies may allow aspen to persist in southwestern forests under expected climate change. On the San Francisco Peaks (hereafter, Peaks) in northern Arizona, tree ring evidence and fire history records indicate that the 1879 fire played a crucial role in the establishment and expansion of aspen, highlighting the importance of fire in aspen ecology (Margolis et al., 2011; Fulé et al., 2023). Historical fire regimes were characterized by frequent and patchy fires, especially on drier, south-facing slopes, and were instrumental in shaping aspen stand composition and distribution across the Peaks

(Margolis et al., 2011; Heinlein et al., 2005; Fulé et al., 2023). The exclusion of fire since 1879 has changed the species composition on the Peaks and altered aspen regeneration and stand dynamics (Cocke et al., 2005). Slective mortality of conifers due to prolonged drought, insect outbreaks, and fire may provide new, in-situ opportunities for aspen to establish or expand (Andrus et al., 2021; Nigro et al., 2022; Rodman et al., 2022). However, the positive effect of disturbance depends on aspen's ability to adapt to a changing climate and persist in the face of biotic threats such as chronic ungulate browse and invasive insect outbreaks (Dobrowski et al., 2015; Crouch et al., 2021, 2024). For example, the introduction of non-native Rocky Mountain elk (*Cervus canadensis*) to the Peaks, as well as other areas in the Southwest, has further complicated aspen stand dynamics by preventing post-disturbance suckers from recruiting into the overstory (Rolf, 2001; Binkley et al., 2006; Fairweather et al., 2008; Rogers et al., 2013; Crouch et al., 2023, 2024). Investigation of aspen regeneration, recruitment, and mortality on the San Francisco Peaks provides key insights into changes in forest communities in this local hotspot of biodiversity (Waring, 2018), as well as in other southwestern mountain environments.

In this study, we used a network of long-term plots on the Peaks to monitor changes in aspen populations over a two-decade-long drought and elucidate the role of regional and local pressures such as climate, disturbance, herbivory, and competition on population demographics. Specifically, we asked the following questions: (1) How has the structure of high-elevation aspen populations changed between the periods 2000–2003 and 2021–2022 on the south face of the San Francisco Peaks? (2) What abiotic and biotic factors are affecting patterns of aspen regeneration and mortality on these southerly exposed communities? (3) What are the long-term dynamics and growth of aspen suckers after a severe wildfire? Answering these questions provides insight into processes that influence the persistence of this economically and biologically valuable species.

2. Methods

2.1. Study area

The study area was on the south face of the Peaks within or directly adjacent to the Kachina Peaks Wilderness on the Coconino National Forest, north of Flagstaff, Arizona (35°18' N, 111°41' W). The Kachina Peaks Wilderness was designated in 1984 and covers 7536 ha. The Peaks include the highest point in Arizona (Humphreys Peak; 3852 m), are sacred to many Native American peoples, and are revered by outdoor enthusiasts. They were also home to early influential research on climate-vegetation interactions, including providing inspiration for C. Hart Merriam's life zone concept (Waring, 2018). The south face of the Peaks comprises a mixture of forest types arranged in close proximity, along a steep elevation gradient (2440 m to 3569 m) that burned historically with a mix of frequencies and severities (Fulé et al., 2023). Mean fire intervals (MFI) ranged from 4 to 19.7 years, typically increasing with elevation (Fulé et al., 2023). Tree-ring evidence indicates that most canopy dominant aspen on the Peaks established following a large fire in 1879, which also coincides with the onset of modern fire exclusion (Margolis et al., 2011). Cocke et al. (2005) established a systematic grid of 135 plots describing the broad range of

contemporary and historical tree species covering the south face of the Peaks, though this study focuses specifically on aspen communities within the larger plot network. Age distribution of aspen trees cored indicated that 80 % established between 1862 and 1901 and less than 1 % established after 1930 (Cocke et al., 2005; Fulé et al., 2023). Aspen occupies ~30 % of the study area and ranges in elevation from 2497 m to 3208 m (Cocke et al., 2005). Aspen (POTR) stands on the Peaks can also include ponderosa pine (*Pinus ponderosa var. scopulorum,* PIPO) at lower elevations, white pine (*Pinus flexilis,* PIFL, *Pinus strobiformis,* PIST, or their hybrid (Steinhoff and Andresen, 1971; Menon et al., 2018) and Douglas-fir (*Pseudotsuga menziesii*, PSME) at intermediate elevations, and corkbark fir (*Abies lasiocarpa* var. *arizonica,* ABLA), Engelmann spruce (*Picea engelmannii,* PIEN) and bristlecone pine *(Pinus aristata,* PIAR*)* at higher elevations. Rocky Mountain elk, introduced after the extirpation of Merriam's elk in the early 1900s, are the wildlife species that have the greatest effects on forest communities in the Kachina Peaks Wilderness (Bechta and Ripple 2010). Concerns regarding elk populations and their effect on aspen regeneration following fires in the area have led to cooperative agreements between the US Forest Service and AZ Game and Fish to increase the availability of public elk hunting permits (U.S. Forest Service#: 17-MU-11030408–009). Between 1991 and 2020, mean annual temperatures ranged from 3.1°C to 6.9°C across plots with aspen with average January minimums ranging −10.4°C to −7.4°C, and average July maximums ranging 20.3°C to 25.6°C (PRISM Climate Group, 2024). Annual precipitation ranged from 69.2 cm to 107.0 cm, with an average of 30 % received during the summer months (June-September) (PRISM Climate Group, 2024). An extensive and severe drought began during the initial monitoring of this study area and continues to this day (Stoddard et al., 2018; Fulé et al. 2022). Like many western forests, over a century of fire exclusion and favorable climatic conditions resulted in compositional shifts toward shade-tolerant conifers (Cocke et al., 2005). Formal wilderness designation and associated management policies implemented in the early 1980's, and the proximity of the study area to the city of Flagstaff have further solidified these forest trajectories by maintaining fire exclusion and restricting active management. Coinciding with drought since the early 2000s, aspen forests on the Peaks have become increasingly susceptible to insects and pathogens (Fairweather et al., 2008; Ganey and Vojta, 2011). The study area also includes the footprint of the Leroux Fire (Fig. 1), a human-ignited wildfire that started on June 11th, 2001, burning ~500 ha (details described in Cocke et al., 2005; Stoddard et al., 2018). In recent decades, large areas of the Peaks were burned by the Schultz (2010), Museum (2019), Pipeline (2022), and Tunnel (2022) fires, driven by extreme wind, drought conditions, dense forest conditions and over a century of forest fuel accumulation. The Pipeline Fire burned through the eastern portion of the study area with moderate to high severity, leading to 100 % tree mortality rates and substantial soil erosion in severely burned areas. These fires caused significant damage as well as millions of dollars in flood destruction in the nearby city of Flagstaff, Arizona (Colavito et al., 2021; Edgeley and Colavito, 2022)

2.2. Field methods and data collection

Between 2000 and 2003, 135 permanent plots (0.1 ha; 20 ×50 m)

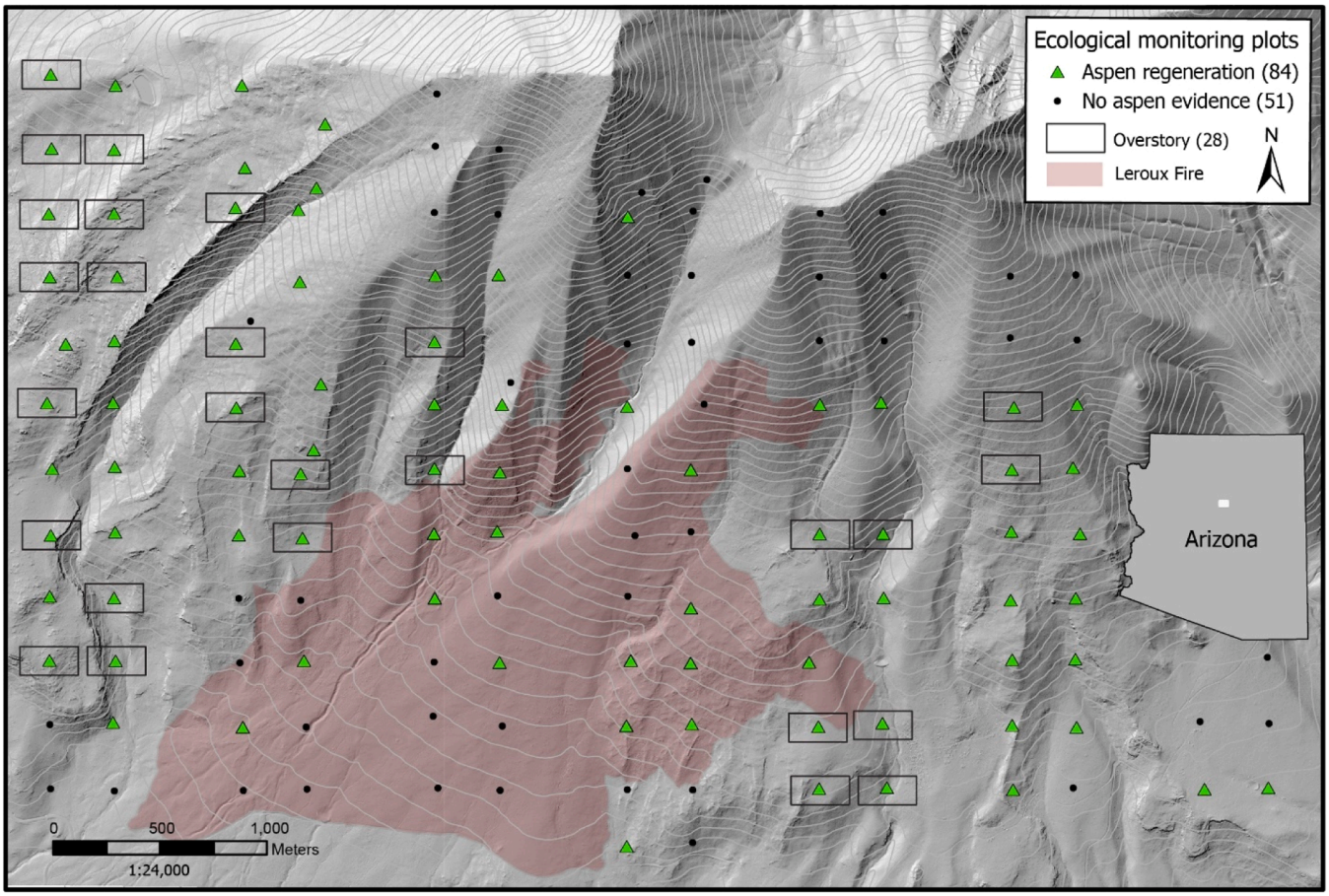

Fig. 1. Map of our study area in the Kachina Peaks Wilderness on the south face of the San Fransico Peaks, AZ, USA showing locations of permanent ecological monitoring plots established by Cocke et al., (2005). Green triangles located outside of the Leroux Fire are plots identified as having evidence of aspen and used for regeneration linear model and describing aspen regeneration (70 plots). Boxes are randomly selected plots use for aspen mortality generalized linear mixed model and describing aspen overstory (28 plots).

were established to examine historical and contemporary forest structure and composition over a high elevational gradient on the south face of the Peaks (Cocke et al., 2005). Plots were installed on a systematic grid with 300- x 600-m spacing. Stems of all tree species located in study plots were classified into two categories and surveyed using separate methods: 1) 'overstory' includes trees ≥ 15 cm diameter at breast height (dbh); and saplings 2.5–15.0 cm dbh and 2) 'regeneration' stems < 2.5 cm dbh. All overstory trees and saplings were permanently tagged and mapped during initial surveys, and measurements included species, tree condition class, dbh, total height and crown base height. Overstory trees were measured across the entire 0.1-ha plot, and saplings were measured on a 0.025-ha subplot. Increment cores were also collected in the original survey period (2000–2003) at 40 cm above ground level for all trees likely to pre-date fire exclusion (1879) and for 10 % of trees (< 37.5 dbh for conifers; < 20 cm dbh for aspen) that had likely established after this period. Regeneration was tallied by species, condition, and height classes (≤ 30 cm, 30.1–200 cm, >200 cm) in a 0.005-ha subplot. Aspen regeneration stems >200 cm in height are considered to have reached a regeneration-recruitment threshold, above which they are less likely to be negatively impacted by browsing (Campbell and Bartos, 2001; Kitchen et al., 2019)

In 2021, we relocated 132 of the original 135 plots and remeasured regeneration in each 0.005-ha subplot. Because the sites are remote and overstory sampling is labor-intensive, overstory trees were remeasured on a subset of plots (N =28) in 2022 (Fig. 1). To be included in the selection for remeasurement, overstory plots had to exhibit evidence of a least a single aspen stem (based on original surveys from Cocke et al., 2005), be located outside the 2001 Leroux Fire footprint, and cover a range of elevations. New live overstory trees and saplings (ingrowth) identified in 2022 were measured and mapped. Aspen regeneration on the 28 overstory plots was assessed for browsing evidence. We also noted insect, pathogen, and animal damage at the tree- and plot-level in the 2022 remeasurements to provide context for observed changes.

2.3. Analyses

To assess long-term changes in aspen populations, we compared overstory structure and regeneration densities on plots outside the Leroux Fire perimeter (Fig. 1) between the two surveys with two-sided Wilcoxon signed-ranked tests. Aspen overstory structure and composition were described, compared, and modeled between two spans of time: one from approximately 2000 to 2003 and the other from 2022, using the 28 remeasured overstory plots. Analysis for aspen regeneration was restricted to plots that had any evidence of live or dead aspen stems in either the original surveys or in the 2021 observations (N = 70). Transitions in overstory species dominance for each plot were assessed using an importance value calculated by summing relative tree density and relative basal area (ba) for each tree species (Curtis and McIntosh, 1951). Transitions in regeneration composition for each plot were evaluated using species' densities (stems ha^{-1}). In addition, the percentage of plots stocked with aspen regeneration (plots containing any live aspen stem < 2.5 cm dbh) was calculated for each measurement year and compared using two-way contingency tables and z-tests of proportions (N=70). We used an *alpha* level of 0.05 to determine statistical significance in these tests.

To identify biophysical drivers of overstory tree mortality and changes in aspen regeneration, we used Generalized Linear Mixed Models (GLMMs) and linear regressions. Tree-level mortality was modeled using a logistic GLMM with a Bernoulli error structure and a logit link function. We incorporated 'plot' as a random intercept term in the model to address the spatial structure of data collection, where multiple trees were sampled within each plot. Biophysical covariates of tree mortality included plot-level variables related to terrain, competition, and damaging agents (Table 1) and a tree-level covariate for tree dbh. We modeled plot-level changes in aspen regeneration densities between the two surveys using ordinary least squares regression with potential biophysical covariates selected based on prior knowledge from local studies (Zegler et al., 2012; Crouch et al., 2023, 2024) (see Table 1). After fitting full models with all potential covariates, as described above, we performed an all-possible-subsets model selection procedure to identify the best combination of predictors of each response variable, selecting the top-performing model as the one that minimized Akaike's information criterion (AICc) and showed no evidence of overfitting. Following model selection and fitting, we ensured that all model assumptions (i.e., homogeneity of residuals, lack of collinearity, spatial independence of residuals) were met. All statistical analyses were performed in R v. 4.3.1 (R Core Team, 2023). We used the base "stats" package for Wilcoxon signed-rank tests, the "glmmTMB" package for linear regressions and GLMMs (Brooks et al., 2017), and the "MuMIn" package for model selection (Bartón, 2018). We used the "DHARMa" (Hartig, 2018) and "ncf" packages (Bjornstad, 2019) to

Table 1
A list of predictor variables tested for inclusion for the linear regression model and generalized linear mixed model, respectively.

Model predictors	Descriptions	Changes in regeneration	Probability of aspen mortality
Plot level			
Elevation	Height above sea level (m)	+	-
Heat load index (HLI)	Heat load index. Estimate of solar heating that combines slope angle, latitude, and aspect (McCune and Keon, 2002)	-	x
Topographic position index (TPI)	Topographic position index. Elevation of area in relationship to it surrounding	x	x
Change in canopy cover	Based on vertical projections (% change)	-	
Basal area (BA) (2000–2003)	Cross sectional area (m^2 ha^{-1}) of trees at 1.37 m in height	-	
Aspen importance Value (IV) (2000–2003)	Index value summing relative tree density and relative BA (Curtis and McIntosh, 1951)	x	x
Conifer seedling density (2000–2003)	Abundance of seedlings (trees ha^{-1}) <1.37 m in height	x	
Forest floor depth (2000–2003)	Depth (cm) of organic horizon	x	
Coarse wood debris (CWD) (2000–2003)	Dead and down logs > 7.6 cm (mg ha^{-1})	x	
Root disease evidence (2022)	Evidence of *Armillaria spp.* (presence/absence)		x
Tree level			
DBH (2000–2003)	Diameter (cm) of a tree at 1.37 m in height		-
Pathogen evidence (2022)	Evidence of canker causing diseases on aspen (presence/absence)		x
Insect damage evidence (2022)	Evidence of wood boring insect damage on aspen boles (presence/absence)		+
Animal damage evidence (2022)	Evidence of animal induce wounds on aspen (presence/absence)		x

Lower case letter "x" indicates that a variable was tested for inclusion in the full model and bold +/- indicate inclusion and direction of effects in the full model (i.e., after model selection). Values in parentheses indicate the sampling year data used for models.

evaluate model residuals and the "performance" package (Lüdecke et al., 2021) to evaluate multicollinearity. For the logistic GLMM model, we calculated goodness of fit using the marginal pseudo-R^2 (variance explained by fixed effects) and conditional pseudo-R^2 (variance explained by both fixed and random effects) values (Bartón, 2018). For the linear model, we summarized the model's R^2. Additionally, we included the AUC (Area Under the Curve) result for the logistic GLMM to further evaluate model performance, utilizing the 'pROC' package in R (Robin et al., 2011).

Finally, to describe the long-term dynamics of aspen suckers after the Leroux Fire, we utilized data from 14 plots within the fire's extent. This analysis builds on previous research and extends the field monitoring efforts to 20 years post-fire. Cocke et al. (2005) developed a burn severity map for the initial response to the Leroux Fire. Stoddard et al. (2018) examined overstory and regeneration dynamics of several species at 10- and 15-years post-fire (corresponding to 2011 and 2016, respectively). Our study extends this work by tracking the post-fire dynamics specific to aspen regeneration, using data collected across five sampling periods: pre-fire (2000) and post-fire (2002, 2011, 2016, and 2021). Plots in the Leroux Fire were selected based on the presence of aspen regeneration recorded either in the original surveys or in the 2021 observations (see Fig. 1).

3. Results

3.1. Mortality and changes in aspen overstory structure and composition

In 2022, two decades after initial observations, mean aspen overstory (≥2.5 cm dbh) tree densities had declined significantly (V= 378, $p < 0.01$) by 42 % to 196.7 tree ha^{-1} (± 145.5 standard deviation (sd)). Aspen mortality occurred primarily in the smaller diameter sizes (Fig. 2). Between 2000 and 2022, 81 % of overstory aspen stems < 20 cm dbh died. In 2022, 65 % of live aspen trees were >30 cm dbh (Fig. 2). Aspen basal area decreased significantly (V=355, $p < 0.01$) by 21 % throughout the study period to 19.7 m^2 ha^{-1} (± 15.3 sd). Overstory plots where aspen had the highest ecological importance value in the initial survey tended to remain dominated by aspen in 2022 (Fig. 2). All 28 overstory plots we remeasured still had aspen trees, though one plot had only a single live aspen sapling (2.5–15.0 cm dbh). Overall mortality across all species was evident over the study duration, especially within smaller-diameter trees and mesic species (Fig. S1).

Aspen mortality was best predicted in our logistic GLMM using a combination of dbh, aspen importance value, elevation, and the proportion of live aspen trees with evidence of insect damage (ΔAICc = −0.65 from the next best model). During model selection, top-performing models (i.e., ΔAICc <2) indicated that elevation and DBH had consistent, negative relationships with aspen mortality, whereas aspen importance value and insect damage had less consistent effects. Aspen overstory mortality was greatest in smaller diameter trees, at lower elevations, and in areas with high concentrations of damaging insects (Fig. 3). Additionally, aspen importance value is negatively associated with mortality, indicating that aspen are dying more frequently in stands that were predominantly conifer-dominated at the start of the study. Fixed effects explained just 7 % of the variance in mortality (marginal pseudo-$r^2 = 0.07$), and random effects explained an additional 7 % (conditional pseudo-$r^2 = 0.14$), and the model had modest discriminatory power (AUC = 0.73).

3.2. Changes in densities and distribution of aspen regeneration

Live aspen regeneration density increased by 13 % or 208.6 stems ha^{-1} (±2858.7 sd) over the study period. Though increases were not statistically significant (V = 559.5, p = 0.08), there was a clear a shift in height class distribution (Fig. 4a). Aspen stems in the 30–200 cm height class (V = 276, $p < 0.01$) increased by 2021, with no significant differences in the ≤ 30 cm (V = 853, p = 0.34) or > 200 cm height classes (V = 0, p = 0.37) when compared to 2000–2003. Stems in the > 200 cm and < 2.5 cm dbh regeneration height class were rare in 2021, representing < 1 % of all aspen stems. Ninety-one percent of aspen regeneration surveyed in 2022 showed signs of browse by large mammals. Significantly more plots had aspen regeneration present ($\chi^2 = 4.06$; $p < 0.05$) in 2021 (77 %) compared to 2000–2003 (61 %) in the 70 regeneration plots. Between surveys, stem densities increased in 50 % of regeneration plots, decreased in 29 % of plots, and remained the same in 21 % of plots. Aspen regeneration replaced conifers as the dominant regeneration species in 47 % of the plots that were initially dominated

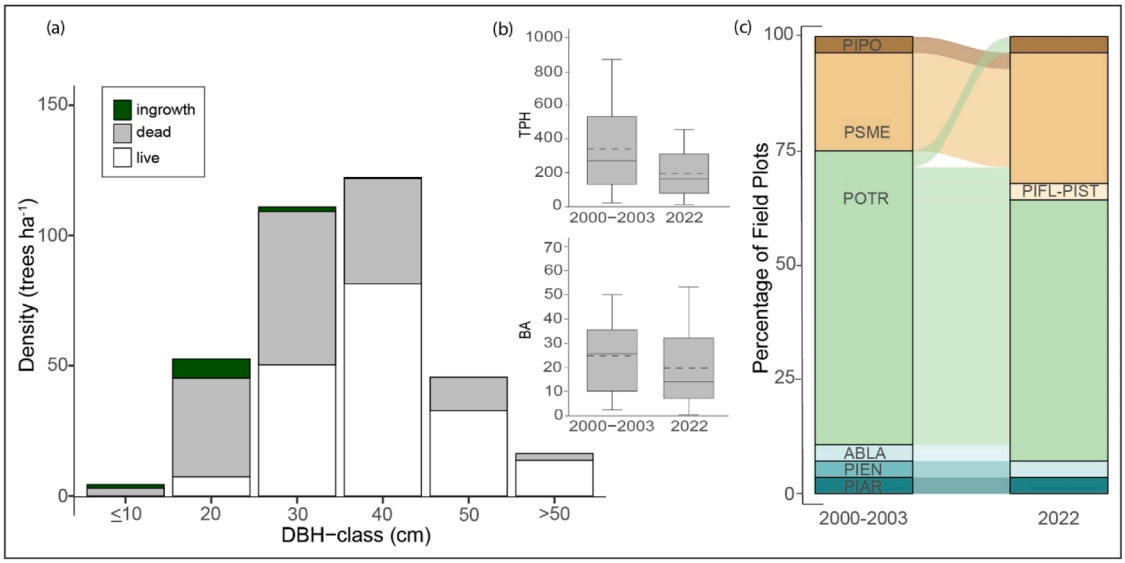

Fig. 2. (a) Diameter (dbh ≥2.5 cm) distribution of aspen overstory, based on 2000–2003 diameter classes, includes density (trees ha^{-1}; TPH) of both dead and live trees observed in 2022. Ingrowth refers to new trees first observed in 2022. (b) Box plots represent live aspen overstory tree density and basal area (BA; m^2 ha^{-1}) 25th, 50th and 75th percentiles, whiskers represent 10th and 90th percentiles and dotted lines represent means, (c) Bars represent species dominance, expressed as importance value (the sum of relative tree density and relative basal area) across field plots (n = 28) for two time periods. Chord colors indicate the directional transition in species importance, with the size of each chord proportional to its contribution, so that the total of all chords equals 100 % of the original sample period. Note the different scales for density on a) and b) panel. See methods to reference species code definitions.

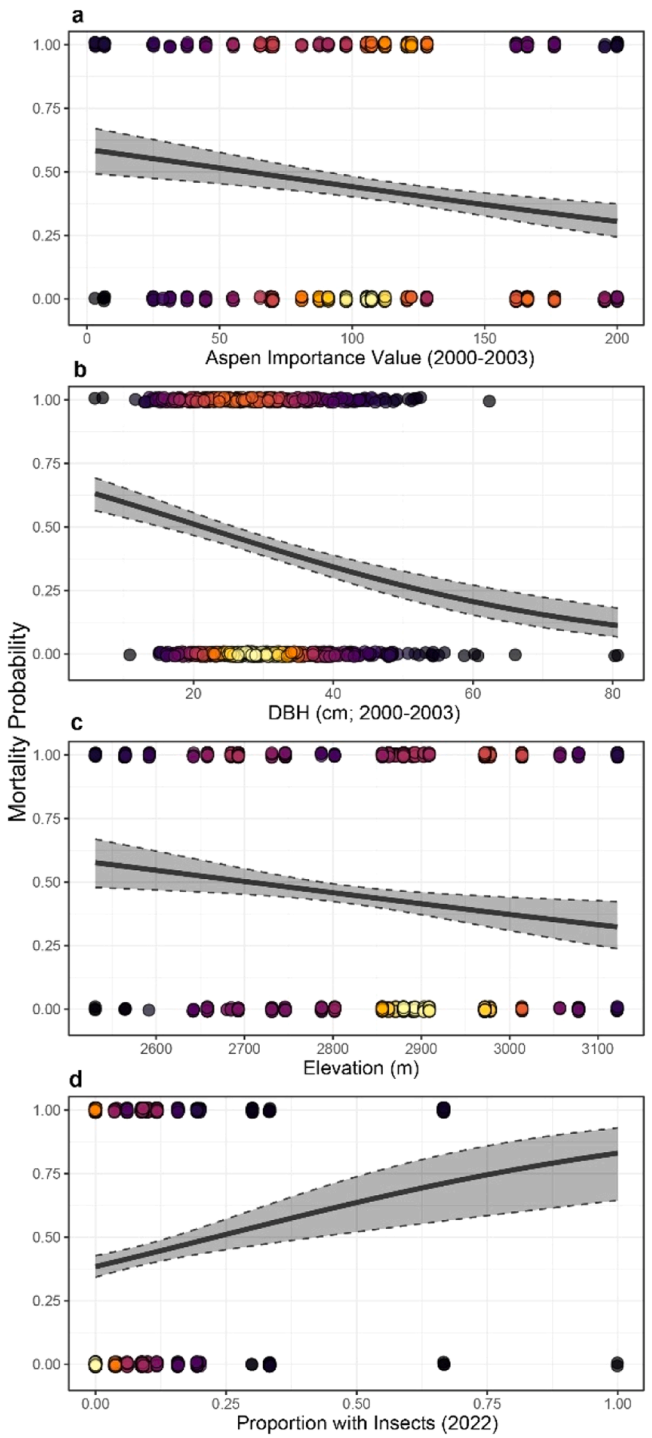

Fig. 3. Marginal effects plots of terms included in the final logistic model of tree-level aspen mortality. Solid lines show model-predicted values of changes in aspen mortality (y-axis) at a specific value of a predictor (x-axis), conditional on mean values of the other predictors and of random effects. Ribbons are the 95 % prediction interval (±1.96x standard error). Points show the observed data for individual aspen trees that survived (0) or died (1) during the study period. Point colors are scaled by local point density, from yellow (highest density) to black (lowest density), to reduce the effects of overplotting. Total tree observations = 872 and plots = 28.

by conifer seedlings (Fig. 4c).

Using a linear model, change in aspen regeneration (stems ha^{-1}) was best predicted using a combination of elevation, heat load index (HLI), change in tree canopy cover (across all species), and initial basal area for all tree species (ΔAICc = 4.61 from the next best model). Aspen regeneration tended to increase at higher elevations, in areas with low HLI (i.e., cool and wet slopes; less southwesterly aspects), in plots with a decrease in overstory canopy cover throughout the study period, and in stands that had low BA in the initial survey (Fig. 5). These terms explained 26 % of the variance (adjusted pseudo-R^2) in aspen regeneration density changes.

3.3. Growth and changes in aspen regeneration following the 2001 Leroux Fire

Though aspen regeneration density increased immediately following the Leroux Fire, suggesting fire-driven increases in aspen suckering, this increase diminished over time (Fig. 6). For example, in 2002, one year after the Leroux fire, we observed a > 500 % increase in aspen regeneration relative to pre-fire levels sampled in 2000–2003 (see Stoddard et al., 2018). However, by 2021 aspen regeneration densities were similar to pre-fire densities (15 % more in 2021 compared to pre-fire), though there were clear changes in the height class distribution. By 2021, the majority of aspen stems were in the 30–200 cm height class, and stems in this height class had significantly (V = 0, p = 0.04) increased by nearly 2000 % when compared to pre-fire densities. Across the study period, stems > 200 cm were exceedingly rare in the Leroux Fire area (Fig. 6).

4. Discussion

4.1. Changes in aspen communities over two decades (2000–2022) on the south face of the San Francisco Peaks

Aspen communities on the San Francisco Peaks, a biodiverse montane ecosystem near the warm, dry edge of the species' range in North America, have undergone notable changes in forest structure and distribution. Using a network of permanent research plots established in the early 2000s, we tracked shifts in forest structure and composition over a 20-year period on the Peaks during a prolonged drought period (Williams et al., 2020). Our findings indicate that aspen tree densities have declined by 42 %, while basal area has decreased by 21 %. Patterns of overstory mortality and changes in tree regeneration suggest that while aspen populations at lower elevations may face increased stress, those at higher elevations could be poised for potential expansion under certain conditions. Nonetheless, aspen faces several key barriers to both in-situ persistence and expansion. Our study highlights three key findings: (1) on mesic sites, aspen mortality was low and regeneration has increased since the early 2000s, (2) recruitment of aspen regeneration into the overstory was limited, and (3) disturbances such as fire have the potential to influence aspen dynamics, though their role in enhancing aspen dominance may depend on the presence of suitable environmental conditions that can support regeneration and growth.

4.2. Key abiotic and biotic factors affecting aspen populations

Taken together, our predictive models of aspen tree mortality and changes in regeneration densities suggest that sites at high elevations and with low heat load index values (i.e., non-southwesterly plots) are better suited for aspen populations. Specifically, overstory mortality on our plots was 34 % higher below 2700 m compared to wetter, higher-elevation sites. Since the early 2000s, aspen mortality has been widespread across western North America, primarily due to extreme drought and associated biotic factors such as insects and pathogens (Worrall et al., 2013; Rogers et al., 2014). Moreover, mortality patterns vary at local scales; rates are often highest on warm, dry sites that were already marginal for the species (Hanna and Kulakowski, 2012; Kane and Kolb, 2014; Ireland et al., 2014), aligning with our findings on the Peaks. While our model revealed significant trends, the small percentage of explained variance suggests that other key variables were not captured,

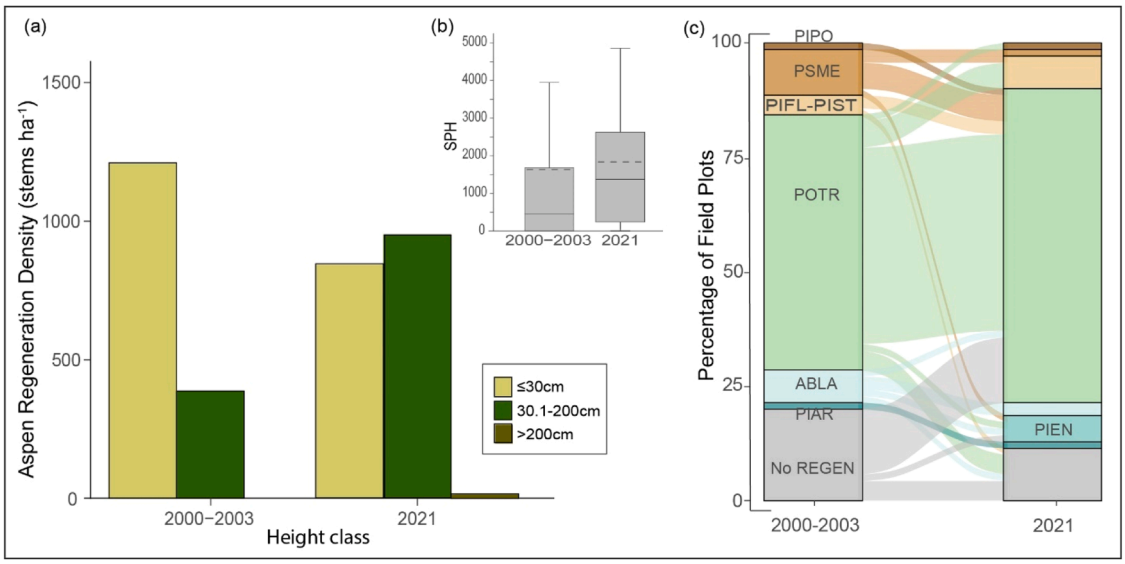

Fig. 4. (a) Mean aspen regeneration (<2.5 cm dbh) by height class and by time (2000–2003, 2021), (b) Box plots represent aspen regeneration as stems per hectare (SPH) 25th, 50th and 75th percentiles, whiskers represent 10th and 90th percentiles and dotted lines represent means, (c) Bars represent species dominance, expressed as importance value (the sum of relative tree density and relative basal area) across field plots (n = 70) for two time periods. Chord colors indicate the directional transition in species importance, with the size of each chord proportional to its contribution, so that the total of all chords equals 100 % of the original sample period. Note the different scales for density on a) and b) panel. See methods to reference species code definitions. No REGEN = plots without observed regeneration.

and the limited number of plots may have affected the robustness of our findings. Despite these limitations, we observed 340 % higher aspen regeneration densities above 2900 m, highlighting the potential for climate refugia and expansion opportunities in these areas. Patterns of regeneration following drought-induced mortality are crucial indicators of forest community shifts and respond to complex interactions between climate and competition (Batllori et al., 2020; Qiu et al., 2021; Shriver et al., 2022). Several studies in northern Arizona emphasize the challenges that warmer, lower-elevation sites pose to aspen regeneration (Fairweather et al., 2008; Zegler et al., 2012; O'Donnell et al., 2018; Crouch et al., 2024). However, in a systematic review of aspen populations in the Southwest, Crouch et al. (2023) found that the influence of climate on aspen regeneration was less influential than the effects of fire and elk browsing. In addition to these immediate factors, long-term successional processes may also contribute to aspen decline in our study area. Historical fires in the late 1800s facilitated aspen regeneration; however, as these stands matured and conifers became established, competition may have further reduced aspen persistence. This gradual shift toward conifer dominance, observed elsewhere in western North America (Kulakowski et al., 2013; Rogers et al., 2014), suggests that aspen decline may also reflect broader successional changes. Overall, these long-term dynamics are essential to consider alongside more immediate climate and disturbance-related pressures.

We found that insect damage, particularly from wood-boring insects, at the stand level was a meaningful predictor of tree mortality. This finding suggests that insects and other biotic disturbances significantly influence aspen stand dynamics, partially in the context of the prolong drought occurring in the Southwest. Although our data do not specify the exact timing of aspen mortality between 2000 and 2022, local research indicates that elevated mortality coincided with the severe 2002 drought (Fairweather et al., 2008; Ireland et al., 2020; Ganey et al., 2021), followed by further losses due to secondary insect and disease outbreaks (Zegler et al., 2012). While our observed mortality rate of 42 % over 20 years aligns with studies from wetter regions of aspen's range (e.g., Kweon and Comeau, 2019), the punctuated role of drought in our study area may indicate the heightened vulnerability of aspen populations at the southern edge of their range. Our findings are consistent with regional studies that document aspen mortality driven by intermittent droughts, insect attacks, pathogens, and herbivory (Ganey and Vojta, 2011; Zegler et al., 2012; Hoffman et al., 2014; Ireland et al., 2014, 2020), particularly on marginal sites and ecotones (Donato et al., 2009; Worral et al., 2013).

While increases in aspen regeneration density have been robust in portions of our study area, recruitment into larger size classes remains limited, posing challenges to the sustainability of aspen forests on the Peaks. Our tree mortality model indicated that smaller-diameter aspen (e.g., < 20 cm dbh) were particularly susceptible to mortality over the past two decades. This aligns with local research indicating that smaller-sized, aspen trees are dying before transitioning into larger size classes, especially at lower elevations (Zegler et al., 2012; Ireland et al., 2020; Crouch et al., 2024). These trends likely stem from a combination of factors, including reduced juvenile niche space, limited resource storage (Shepperd et al., 2001; Kulakowski et al., 2013), and climate stress, which may particularly impact smaller trees (Bell et al., 2014; Ireland et al., 2014). Moreover, recruitment limitations may be further exacerbated by ungulate browsing, which disproportionately affects regeneration that has not grown beyond the browse line (Rhodes et al., 2018). Alongside higher mortality rates among smaller trees, we observed very few aspen stems in the >200 cm regeneration height class (regeneration-recruitment threshold), suggesting a potential demographic bottleneck in aspen recruitment. In 2021, 91 % of aspen regeneration exhibited signs of browsing, reflecting cumulative impacts over the study's duration (>20 years). However, this browsing data is complicated by its cumulative nature and the limited number of plots sampled, leading to its exclusion from the linear regeneration model. In this context, Crouch et al. (2023), (2024) identified stems >1.37 m in height and <12.7 cm dbh as crucial indicators of aspen stand replacement, revealing this size class to be underrepresented in Southwest aspen forests. Their assessment of aspen stands across Arizona established sustainable thresholds for regeneration (42.5 stems per overstory tree) and recruitment (21.8 stems per overstory tree), with findings indicating that less than 40 % of stands meet these recruitment levels. In our study, only 14 % of plots, both inside and outside the Leroux Fire, met sustainable regeneration criteria and none met recruitment thresholds. This suggesting that while disturbances such as drought and fire initially promoted aspen regeneration, ongoing challenges have hindered

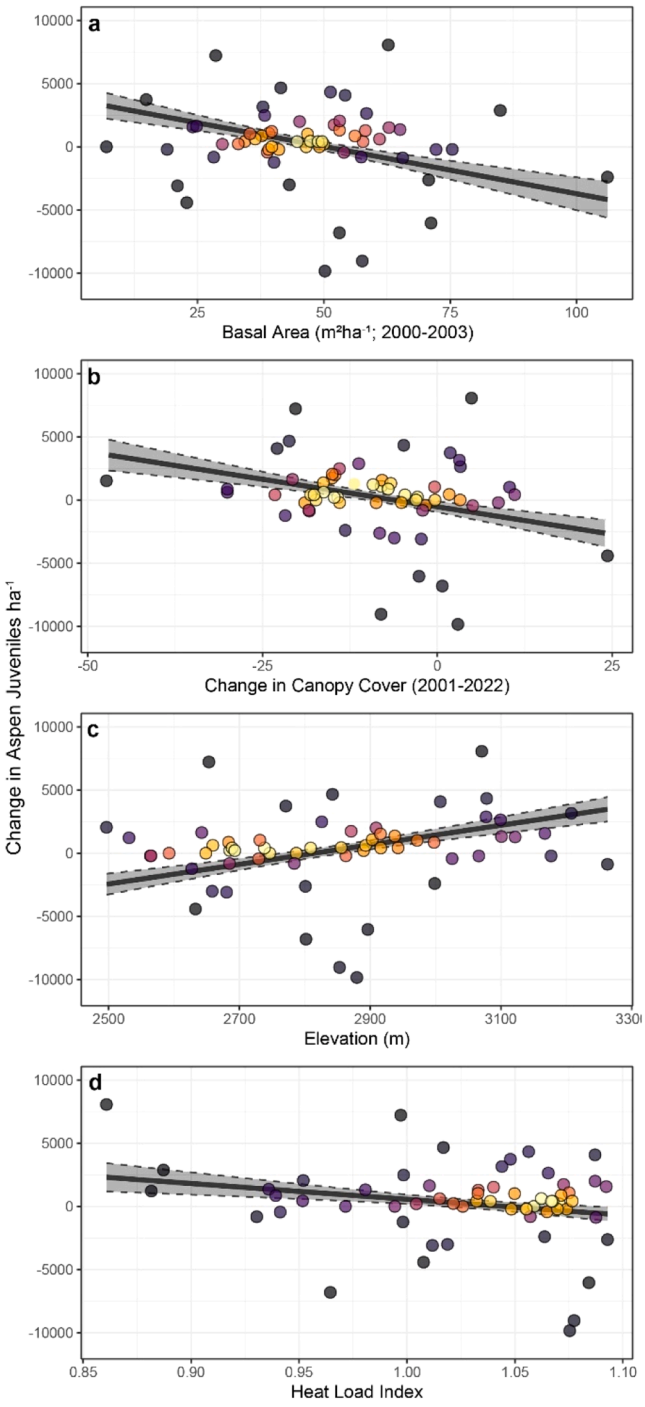

Fig. 5. Marginal effects plots of terms included in the final linear model of plot-level changes (2021 densities minus 2000 densities) in aspen regeneration density. Solid lines show predicted values of changes in aspen juveniles (y-axis) at a specific value of a predictor (x-axis), conditional on mean values of the other predictors. Ribbons are the 95 % prediction interval (± 1.96x standard error). Points show the observed data for each plot. N = 70.

recruitment success. Given that <8 % of live overstory aspen we observed in 2022 were <20 cm dbh (Fig. 2), the lack of sufficient aspen recruitment is not surprising. Additionally, increased hunting pressure on elk has been intermittently implemented on the Peaks over the past two decades (Rolf, 2001; AZ Game and Fish), but it remains unclear whether this has benefited aspen communities. Continued monitoring of aspen populations, including plots impacted by the 2022 Pipeline Fire, could offer valuable insights into the challenges surrounding recruitment.

4.3. *Disturbances vary in promoting aspen populations*

Disturbances such as insect outbreaks and wildfires offer opportunities for early seral species like aspen to thrive, provided that environmental conditions can support recruitment. While literature supports the existence of self-sustaining (non-seral) aspen stands, where adequate rates of regeneration are likely driven by increased light exposure from canopy openings, our findings indicate that increases in regeneration across the southern extent of the Peaks were most pronounced in areas with lower initial total basal area and where canopy cover declined throughout the study period. Although aspen is often considered a disturbance-dependent species, not all disturbances equally promote aspen regeneration (Wolf et al., 2021; Nigro et al., 2022). For instance, in our study, aspen regeneration increased following mortality due to factors other than wildfires, but this response was an order of magnitude lower than the initial surge following the Leroux Fire. Aspen stands experiencing dieback while retaining apical dominance have been found to stimulate limited suckering, likely due to factors such as limited light availability, conifer competition, and inadequate allocation of stored resources to resprouts (Frey et al., 2003; Bailey and Whitman, 2002; Anderegg et al., 2013; Anderegg et al., 2015). Aspen is well adapted to high-severity fire (Yocom-Kent et al., 2015; Crouch et al., 2023, 2024), as exemplified by initial increases in regeneration following the 2001 Leroux Fire. However, the fire-induced pulse in regeneration was insufficient after 20+ years to establish an aspen overstory in the Leroux Fire, unlike in areas on the north aspects of the San Francisco Peaks (Gonzales, 2017) and mesic areas in Arizona (Yocom-Kent et al., 2015; Clement et al., 2019), where aspen successfully established following their respective fires. The Leroux Fire was, however, at lower elevations within our study area, and occurred during a time with significant browse pressure. Disturbances in the presence of chronic ungulate browse could hasten aspen decline (Smith et al., 2016, Crouch et al., 2024). For example, if a disturbance occurs that removes apically dominant stems, but recruitment does not occur, then aspen may be extirpated. More recent fires on the Peaks may present opportunities for aspen to expand or increase, especially given increased hunting pressure on elk. Despite our best efforts to document current aspen stand conditions on the Peaks, our understanding of how aspen will respond to future changes, especially interactions between wildfire and ungulate browse, remains incomplete. Further research following high-severity fires will enhance our understanding of aspen responses to future climate changes, particularly regarding interactions with wildfire and ungulate browsing (Lewis et al., 2024).

5. Management implications and conclusions

While our research provides valuable insights into the patterns of aspen mortality and regeneration, it also underscores the complexities of aspen population dynamics, particularly the influences of fire suppression, long-term successional changes, climate change and browsing pressures. These complexities are exemplified by nearly 140 years of fire regime disruption on the south face of the Peaks, with the exception of the Leroux Fire and the recent Shultz and Pipeline Fire, which have led to structural and compositional shifts (Cocke et al., 2005; Fulé et al., 2023). Based on results from dendroecological reconstructions, Cocke et al. (2005) reported that the basal area of all tree species combined increased by 70–460 % between 1879 and 2000 on these slopes. Contributing influences likely include the natural regrowth of aspen following the late nineteenth-century fires (Margolis et al., 2011). Major changes to forest composition and structure are underway as a result of a couple of key process, such as fire exclusion and recent climate change. While mortality has been significant, aspen density and basal area remain well above historical conditions (Cocke et al., 2005). Increasing temperatures and drought severity will continue to stress existing

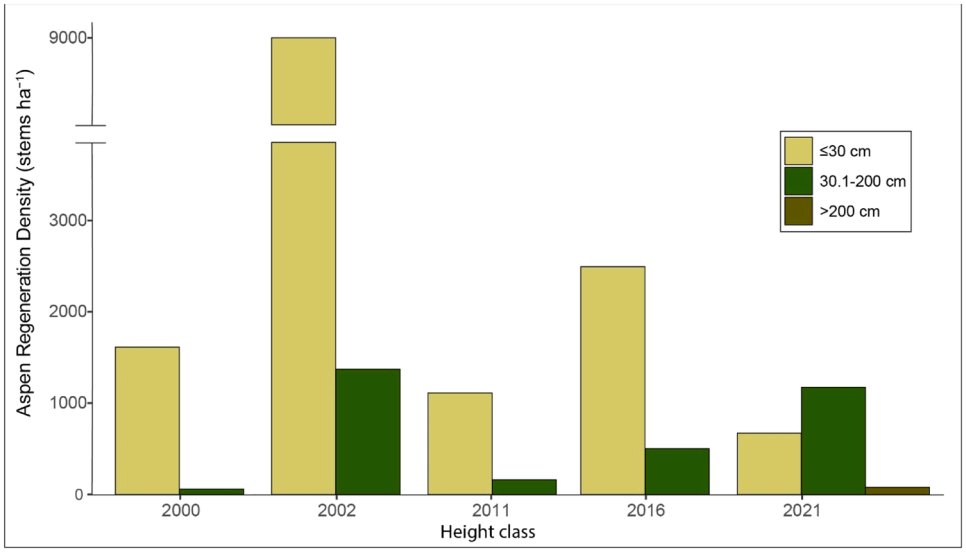

Fig. 6. Mean aspen regeneration (< 2.5 cm dbh) by height classes within the Leroux Fire 2001 by time (pre-fire 2000; post-fire 2002, 2011, 2016 and 2021). Note the scale break on the y-axis. N = 14.

populations, as currently observed throughout the Intermountain West (Rehfeldt et al., 2009; Worrall et al., 2013). Aspen tree size and age distributions are skewed toward larger, older trees with few recruiting juveniles, suggesting a limited capacity for self-replacement. Increased fire frequency and severity projected for forests of the Southwest may provide aspen with more opportunities for regeneration and migration to suitable sites (Krasnow and Stephens, 2015); however, promoting aspen's adaptive capacity and resilience following these disturbances will be crucial for sustaining aspen on these landscapes (Crouch et al., 2021, 2024).

Our study of aspen populations on the south face of the Peaks highlights three objectives for managing aspen resilience and adaptation: (1) promoting diversity in age structure by enhancing regeneration and recruitment, (2) mitigating the impacts of ungulate browse on recruitment, and (3) enhancing the complexity of forest structure, composition, and function (Crouch et al., 2023). We have shown that the Leroux Fire resulted in a pulse of aspen regeneration that has not successfully recruited into the overstory, likely due to environmental stresses and ungulate browsing. Future fires are likely to provide opportunities for aspen regeneration (suckering or seedling establishment), but subsequent recruitment of stems into the overstory is necessary to sustain aspen populations on the Peaks. The most effective strategy for promoting recruitment may be to reduce ungulate population sizes and increase their movement via further adjustment of hunting permits and regulations (Rolf, 2001; Fairweather et al., 2014; Crouch et al., 2023). Due to the separation of responsibilities between governmental agencies, actions that directly affect wildlife populations are outside the control of federal forest managers (i.e., they are determined by state wildlife managers). Thus, a feasible tactic for forest managers could be to inhibit ungulates from areas targeted for recruitment by manipulating woody material to form natural barriers to ungulate herbivory (e.g., "jackstrawing") (Gonzales, 2017; Crouch et al., 2023). By creating these types of safe sites at higher elevations, managers could address the impacts of ungulates and potentially enhance the adaptive capacity of aspen recruitment. However, the study area's location in a federally designated wilderness area presents unique challenges because active management techniques, such as silvicultural operations and ungulate exclusion, are either restricted or impractical in wilderness (Wilderness Act 16 US Code § 1131, 1964). Although managers are limited in their ability to directly promote aspen populations on the Peaks and other wilderness areas, actions outside of designated wilderness could positively impact aspen inside wilderness. For example, closer coordination between state wildlife managers and federal foresters could be beneficial. Such actions were exemplified following the 2010 Schultz Fire on the Peaks, which led to cooperative agreements between the U.S. Forest Service and Arizona Game and Fish to increase the availability of public elk hunting permits (U.S. Forest Service#: 17-MU-11030408–009) to help promote aspen regeneration. Furthermore, given recent concerns about the efficacy of local ungulate exclusion tactics, particularly fenced enclosures that facilitate outbreaks of the invasive oystershell scale (Crouch et al., 2023, 2024), the limitations imposed by wilderness restrictions may provide opportunities for innovative aspen management.

Compared to reducing the impacts of chronic ungulate browsing, future challenges to aspen management posed by climate change, particularly increased warming and drought, will be much more difficult for managers to address. Strategies for increasing resilience to climate impacts include promoting diverse stand structures and age classes and increasing recruitment (Crouch et al., 2023). In part, these goals may be achieved through pyrosilvicultural approaches (e.g., North et al., 2021). Such approaches include the management of natural wildfire ignitions as well as prescribed fire. With climate change, increasing area burned in the western U.S. (Westerling et al., 2006) is likely to provide opportunities for aspen regeneration through suckering and seedling establishment, given its strong association with fire (Krasnow and Stephens, 2015). Aspen's dual regeneration strategy confers an advantage for its persistence in southwestern forests; however, pre-fire conditions such as conifer basal area, aspen clone vigor, and herbivore pressure influence sprout production, and managers may have limited time to take needed conservation actions. Encouraging managers to allow wildfires to burn within acceptable parameters or to intentionally burn could be ecologically beneficial, though these actions do not come without considerable risk, given contemporary fuel accumulation, overly dense forests, and exacerbated ecological conditions associated with warming and drought (Flatley and Fulé, 2006). Although it is understood that aspen regeneration is typically stimulated by high-severity fire (Crouch et al., 2023), allowing such fires to burn is likely to be acceptable to managers only on the most remote landscapes. Smaller wildfires, such as the Leroux Fire, could increase complexity and structural diversity at stand and landscape scales. In addition, the judicious use of prescribed fire within designated wilderness areas to accomplish restoration and conservation goals is worth consideration (Fire, 2023). Indeed, recent large, uncharacteristic fires near our study area have caused substantial ecological change, cost billions of dollars in flood damage (Colavito et al., 2021),

and underscore the urgent need to address problems associated with historical fire exclusion and interruption of natural fire regimes.

Questions also remain about the social impacts of aspen population dynamics on the Peaks and about the role management might play in sustaining the biological, cultural, and recreational values associated with aspen. For example, if aspen stands continue to age without sustainable self-replacement, the loss of aspen trees is likely to influence tourism and recreation on the Peaks. As large high-severity fires continue to impact the Peaks, how might post-fire dominance by dense monocultures of young aspen influence social perception of the Peaks? Although it may take decades or longer to answer these questions, our unique longitudinal study of aspen on the south face of the Peaks provides insight into how these important communities are responding to environmental change.

CRediT authorship contribution statement

Kristen M. Waring: Review & editing, Validation. **Margaret M. Moore**: Review & editing, Validation. **Mike Stoddard**: Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Kyle C. Rodman**: Writing – review & editing, Writing – original draft, Validation, Methodology, Formal analysis. **Connor D. Crouch**: Writing – review & editing, Writing – original draft, Validation. **David W. Huffman**: Writing – review & editing, Validation, Project administration, Funding acquisition, Conceptualization. **Peter Z. Fulé**: Writing – review & editing, Validation, Data curation.

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.

Data Availability

Data will be made available on request.

Acknowledgments

This study was funded by a grant from the USDA Forest Service. We thank the staff and students at the Ecological Restoration Institute at Northern Arizona University, Coconino National Forest and Forest Health Protection for field and logistical support. Our study area includes the homelands of at least 35 Indigenous nations – we honor their past, present, and future generations, who have lived here for millennia and will forever call this place home.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122326.

References

Abatzoglou, J.T., Williams, A.P., Barbero, R., 2019. Global emergence of anthropogenic climate change in fire weather indices. Geophys. Res. Lett. 46 (1), 326–336.

Alsos, I.G., Rijal, D.P., Ehrich, D., Karger, D.N., Yoccoz, N.G., Heintzman, P.D., PhyloNorway Consortium, 2022. Postglacial species arrival and diversity buildup of northern ecosystems took millennia. Sci. Adv. 8 (39), eabo7434.

Anderegg, L.D., Anderegg, W.R., Abatzoglou, J., Hausladen, A.M., Berry, J.A., 2013. Drought characteristics' role in widespread aspen forest mortality across Colorado, USA. Glob. Change Biol. 19 (5), 1526–1537.

Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A.K., Shaw, J. D., Stephenson, N.L., Tague, C., Zeppel, M., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. N. Phytol. 208. https://doi.org/10.1111/nph.

Andrus, R.A., Hart, S.J., Tutland, N., Veblen, T.T., 2021. Future dominance by quaking aspen expected following short-interval, compounded disturbance interaction. Ecosphere 12 (1), e03345.

Ayres, G.A., Fulé, P.Z., Flatley, W.T., 2024. Response of aspen to a warming climate along a latitudinal gradient in the Rocky Mountains, USA. Can. J. For. Res. https://doi.org/10.1139/cjfr-2024-0001.

Bailey, J.K., Whitham, T.G., 2002. Interactions among fire, aspen, and elk affect insect diversity: reversal of a community response. Ecology 83, 1701–1712.

Bartón, K., 2018. MuMIn: multi-model inference. R. Package.

Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G., (Compilers) (Eds.), Sustaining aspen in western landscapes: Symposium proceedings; 13–15 June 2000; Grand Junction, CO. Proceedings RMRS-P-18. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, pp. 5–14.

Batllori, E., Lloret, F., Aakala, T., Anderegg, W.R., Aynekulu, E., Bendixsen, D.P., Zeeman, B., 2020. Forest and woodland replacement patterns following drought-related mortality. Proc. Natl. Acad. Sci. 117 (47), 29720–29729.

Bell, D.M., Bradford, J., Lauenroth, W.K., 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. Glob. Ecol. Biogeogr. 23, 168–180. https://doi.org/10.1111/geb.12109.

Binkley, D., Moore, M.M., Romme, W.H., Brown, P.M., 2006. Was Aldo Leopold right about the Kaibab Deer herd? Ecosystems 9 (2), 227–241.

Bjornstad, O.N., 2019. ncf: spatial covariance functions. R. Package.

Brooks, M.E., Kristensen, K., van, Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9, 378–400.

Calder, W.J., Parker, D., Stopka, C.J., Jiménez-Moreno, G., Shuman, B.N., 2015. Medieval warming initiated exceptionally large wildfire outbreaks in the Rocky Mountains. Proc. Natl. Acad. Sci. U. S. A. 112, 13261–13266. https://doi.org/10.1073/pnas.1500796112.

Campbell, R.B., Jr., Bartos, D.L., 2001. Aspen ecosystems: Objectives for sustaining biodiversity. In: Shepperd, Wayne D.; Binkley, Dan; Bartos, Dale L.; [et al.], comps. Sustaining aspen in western landscapes: Symposium proceedings; 2000 June 3–15; Grand Junction, CO. Proceedings RMRS-P-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 299–307.

Chong, G.W., Simonson, S.E., Stohlgren, T.J., Kalkhan, M.A., 2001. Biodiversity: Aspen Stands Have the Lead, but Will Nonnative Species Take Over? In Sustaining Aspen in Western Landscapes: Symposium Proceedings, edited by W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, 261–72. USDA Forest Service Gen. Tech. Rep. RMRS–P–18. Fort Collins, CO: Rocky Mountain Research Station.

Clement, M.J., Harding, L.E., Lucas, R.W., Rubin, E.S., 2019. The relative importance of biotic and abiotic factors influencing aspen recruitment in Arizona. For. Ecol. Manag. 441, 32–41.

Cocke, A.E., Fulé, P.Z., Crouse, J.E., 2005. Forest Change on a steep mountain gradient after extended fire exclusion: San Francisco Peaks, Arizona, USA. J. Appl. Ecol. 42 (5), 814–823.

Colavito, M.M., Combrink, T., Hjerpe, E., Edgeley, C., Burnett, J., Sánchez Meador, A.J., 2021. ERI White Paper—Issues in Forest Restoration. Ecological Restoration Institute. Full-Cost Accounting Remeasurement of the 2010 Schultz Fire: Understanding the Long-term Socio-Economic Implications of High-Severity Wildfire and Post-Wildfire Flooding. Northern Arizona University, p. 45.

Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S., Higuera, P.E., Hurteau, M.D., et al., 2020. Wildfire-driven forest conversion in western North American landscapes. Bioscience 70 (8), 659–673 doi:10. 1093/biosci/biaa061. PMID: 32821066.

R Core Team., 2023. R: A language and environment for statistical computing (4.2.0). R Foundation for Statistical Computing. https://www.r-project.org/.

Crausbay, S.D., Higuera, P.E., Sprugel, D.G., Brubaker, L.B., 2017. Fire catalyzed rapid ecological change in lowland coniferous forests of the Pacific Northwest over the past 14,000 years. Ecology 98 (9), 23562369. https://doi.org/10.1002/ecy.1897. PMID: 28500791.

Crouch, C.D., Grady, A.M., Wilhelmi, N.P., Hofstetter, R.W., DePinte, D.E., Waring, K.M., 2021. Oystershell scale: an emerging invasive threat to aspen in the Southwestern US. Biol. Invasions 23 (9), 2893–2912.

Crouch, C.D., Rogers, P.C., Moore, M.M., Waring, K.M., 2023. Building ecosystem resilience and adaptive cpacity: a systematic review of aspen ecology and management in the Southwest. For. Sci. 69 (3), 334–354. https://doi.org/10.1093/forsci/fxad004.

Crouch, C.D., Wilhelmi, N.P., Rogers, P.C., Moore, M.M., Waring, K.M., 2024. Sustainability and drivers of *Populus tremuloides* regeneration and recruitment near the southwestern edge of its range. For. Int. J. For. Res., cpae018 https://doi.org/10.1093/forestry/cpae018.

Curtis, J.T., McIntosh, R.P., 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32, 476–496.

Davis, K.T., Robles, M.D., Kemp, K.B., Higuera, P.E., Chapman, T., Metlen, K.L., Campbell, J.L., 2023. Reduced fire severity offers near-term buffer to climate-driven declines in conifer resilience across the western United States. Proc. Natl. Acad. Sci. 120 (11), e2208120120.

Dobrowski, S.Z., Swanson, A.K., Abatzoglou, J.T., Holden, Z.A., Safford, H.D., Schwartz, M.K., Gavin, D.G., 2015. Forest structure and species traits mediate projected recruitment declines in Western US tree species. Glob. Ecol. Biogeogr. 24 (8), 917–927. https://doi.org/10.1111/geb.12302.

Donato, D.C., Fontaine, J.B., Robinson, W.D., Kauffman, J.B., Law, B.E., 2009. Vegetation response to a short interval between high severity wildfires in a mixed-evergreen forest. J. Ecol. 97, 142–154.

Donato, D.C., Harvey, B.J., Turner, M.G., 2016. Regeneration of montane forests 24 years after the 1988 Yellowstone fires: a fire catalyzed shift in lower treelines? Ecosphere 7 (8), 1–16.
Edgeley, C.M., Colavito, M.M., 2022. Characterizing divergent experiences with the same wildfire: insights from a survey of households in evacuation, postfire flood risk, and unaffected areas after the 2019 Museum Fire. J. For. 120, 660–675 https:// doi. org/ 10. 1093/ jofore/ fvac0 18.
Fairweather, M.L., Geils, B.W., Manthei, M., 2008. Aspen decline on the Coconino National Forest. In: McWilliams, M.G. (Ed.), Proceedings of the55th Western International Forest Disease Work Conference. Salem, OR: Oregon Department of Forestry, pp. 53–62.
Fairweather, M.L., Rokala, E.A., Mock, K.E., 2014. Aspen seedling establishment and growth after wildfire in central Arizona: an instructive case history. For. Sci. 60 (4), 703–712.
Fire, S.F., 2023. Prescr. Fire US Wilderness Areas.
Flatley, W.T., Fulé, P.Z., 2016. Are historical fire regimes compatible with future climate? Implications for forest restoration. Ecosphere 7 https:// doi. org/ 10. 1002/ ecs2. 1471.
Frey, B.R., Lieffers, V.J., Landhausser, S.M., Comeau, P.G., Greenway, K.J., 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. 33, 1169–1179.
Fulé, P.Z., Barrett, M.B., Cocke, A.E., Crouse, J.E., Roccaforte, J.P., Normandin, D.N., Covington, W.W., Moore, M.M., Heinlein, T.A., Stoddard, M.T., Rodman, K.C., 2023. Fire regimes over a 1070-m elevational gradient, San Fransico Peaks/ Dook'o'ooslííd, Arizona, USA. Fire Ecol. 19, 41. https://doi.org/10.1186/s42408-023-00204-4.
Fulé, P.Z., Sánchez Meador, A.J., Moore, M.M., Covington, W.W., Kolb, T.E., Huffman, D. W., Roccaforte, J.P., 2022. Forest restoration treatments increased growth and did not change survival of ponderosa pines in severe drought, Arizona. Ecol. Appl. 32 (8), e2717.
Ganey, J.L., Iniguez, J.M., Vojta, S.C., Iniguez, A.R., 2021. Twenty years of drought-mediated change in snag populations in mixed conifer and ponderosa pine forest in Northern Arizona. For. Ecosyst. 8 (30). https://doi.org/10.1186/s40663-021-00298-9.
Ganey, J.L., Vojta, S.C., 2011. Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, USA. For. Ecol. Manag. 261, 162–186.
Goeking, S.A., Menlove, J., 2017. New Mexico's forest resources, 2008–2014. Resour. Bull. RMRS-RB-24. Fort Collins, CO: U.S. Department of Agriculture, Forest Service. Rocky Mountain Research Station, p. 68.
Gonzales, L., 2017. Coconino National Forest, AZ. Undergraduate Research Paper, Flagstaff, AZ: ecological Restoration Institute, Northern Arizona University. Five-year Post-treat. Eff. Jackstraw Treat. Aspen Regen. Large Ungulat-.-. Presence Schultz Fire.
Hanna, P., Kulakowski, D., 2012. The influences of climate on aspen dieback. For. Ecol. Manag. 274, 91–98.
Hart, S.J., Veblen, T.T., Schneider, D., Molotch, N.P., 2017. Summer and winter drought drive the initiation and spread of spruce beetle outbreak. Ecology 98 (10), 2698–2707.
Hartig, F., 2018. Package ' Dharma ': Residual Diagn. Hierarchical (Mulit-lev. /Mixed) Regres. Models.
Heinlein, T., A, Moore, M.M., Fulé, P.Z., Covington, W.W., 2005. Fire history and stand structure of two ponderosa pine-mixed conifer sites: San Francisco Peaks, Arizona, USA. Int. J. Wildland Fire 14, 307–320.
Hessburg, P.F., Miller, C.L., Parks, S.A., Povak, N.A., Taylor, A.H., Higuera, P.E., Prichard, S.J., North, M.P., Collins, B.M., Hurteau, M.D., Larson, A.J., Allen, C.D., Stephens, S.L., Rivera-Huerta, H., Stevens-Rumann, C.S., Daniels, L.D., Gedalof, Z., Gray, R.W., Kane, V.R., Churchill, D.J., Hagmann, R.K., Spies, T.A., Cansler, C.A., Belote, R.T., Veblen, T.T., Battaglia, M.A., Hoffman, C., Skinner, C.N., Safford, H.D., Salter, R.B., 2019. Climate, environment, and disturbance history govern resilience of western North American forests. Front. Ecol. Evol. 7, 239. https://doi.org/10.3389/fevo.2019.00239.
Hill, A.P., Field, C.B., 2021. Forest fires and climate-induced tree range shifts in the western US. Nat. Commun. 12 (1), 6583.
Hoffman, C.W., Mathiasen, R.L., Hofstetter, R.W., Fairweather, M.L., Shaw, J.D., Hanna, J.W., Klopfenstein, N.B., 2014. Survey for Armillaria by plant association in Northern Arizona. J. Ariz. Nev. Acad. Sci. 45, 276–286.
Ireland, K.B., Moore, M.M., Fulé, P.Z., Zegler, T.J., Keane, R.E., 2014. Slow lifelong growth predisposes *Populus tremuloides* trees to mortality. Oecologia 175 (3), 847–859.
Ireland, K.B., Moore, M.M., Fulé, P.Z., Yocom, L.L., Zegler, T.J., 2020. Warm, dry conditions inhibit aspen growth, but tree growth and size predict mortality risk in the southwestern United States. Can. J. For. Res. https://doi.org/10.1139/cjfr-2019-0222.
Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L., Schoennagel, T.L., Turner, M.G., 2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ. 14 (7), 369–378. https://doi.org/10.1002/fee.1311.
Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecol. Lett. 8 (9), 1010–1020.
Kane, J.M., Kolb, T.E., 2014. Short- and long-term growth characteristics associated with tree mortality in southwestern mixed conifer forests. Can. J. For. Res. 44 (10), 1227–1235.
Kitchen, S.G., Behrens, P.N., Goodrich, S.K., Green, A., Guyon, J., O'Brien, M., Tart, 2019. Guidelines for aspen restoration in Utah with applicability to the Intermountain West. Gen. Tech. Rep. RMRS-GTR-390. Fort Collins CO: U.S. Department of Agriculture, Forest Service. Rocky Mountain Research Station, p. 55.
Kolb, T.E., Ayres, M.P., Stewart, J.E., 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. For. Ecol. Manag. 380, 321–334. https://doi.org/10.1016/j.foreco.2016.04.051.
Krasnow, K.D., Stephens, S.L., 2015. Evolving paradigms of aspen ecology and management: impacts of stand condition and fire severity on vegetation dynamics. Ecosphere 6, 1–16.
Kreider, M.R., Yocom, L.L., 2021. Low-density aspen seedling establishment is widespread following recent wildfires in the western United States. Ecology 102 (10), e03436. https://doi.org/10.1002/ecy.3436.
Kuhn, T.J., Safford, H.D., Jones, B.E., Tate, K.W., 2011. Aspen (*Populus tremuloides*) stands and their contribution to plant diversity in a semiarid coniferous landscape. Plant Ecol. 212, 1451–1463.
Kulakowski, D., Kaye, M.W., Kashian, D.M., 2013. Long-term aspen cover change in the western US. For. Ecol. Manag. 299, 52–59.
Kweon, D., Comean, P.G., 2019. Relationships between tree survival, stand structure and age in trembling aspen dominated stands. For. Ecol. Manag. 438, 114–122.
Leopold, A., Sowls, L.K., Spencer, D.L., 1947. A survey of over-populated deer ranges in the United States. J. Wildl. Manag. 11 (2), 162–177. https://doi.org/10.2307/3795561.
Lewis, J.S., Clair, S.B.S., Fairweather, M.L.Rubin, E.S., 2024. Fire severity and ungulate herbivory shape forest regeneration and recruitment after a large mixed-severity wildfire. For. Ecol. Manag. *555*, 121692.
Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. performance: an R package for assessment, comparison and testing of statistical models. J. Open Source Softw. 6 (60).
Margolis, E.Q., Swetnam, T.W., Allen, C.D., 2011. Historical stand-replacing fire in Upper Montane forests of the madrean Sky Islands and Mogollon Plateau, Southwestern USA. Fire Ecol. *7*, *88–107* https:// doi. org/ 10. 4996/fireecology. 07030 88.
Margolis, E.Q., Swetnam, T.W., Allen, T.W., C.D, 2007. A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. Can. J. For. Res. 37, 2227–2241. https://doi.org/10.1139/X07-079.
Marsh, C., Krofcheck, D., Hurteau, M.D., 2022. Identifying microclimate tree seedling refugia in post-wildfire landscapes. Agric. For. Meteorol. 313, 108741.
Martínez González, R.E., González-Villarreal, L.M., 2005. Taxonomía y Biogeografía del Género Populus (Salicaceae) en México. Universidad de Guadalajara, Guadalajara, Mexico.
McCool, S.F., 2001. Quaking Aspen and the human experience: dimensions, issues, and challenges. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Eds.), Sustaining Aspen in Western Landscapes: Symposium Proceedings. Fort Collins, CO: Rocky Mountain Research Station.
McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13 (4), 603–606.
McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science 368 (6494), eaaz9463. https://doi.org/10.1126/science.aaz9463.
Menon, M., Bagley, J.C., Friedline, C., Whipple, A., Schoettle, A.W., Leal-Saenz, A., Wehenkel, C., Molina-Freaner, F., Flores-Renteria, L., González-Elizondo, M.S., Sniezko, R., Cushman, S.A., Waring, K.M., Eckert, A.J., 2018. The role of hybridization during ecological divergence of southwestern white pine (*Pinus strobiformis*) and limber pine (*P. flexilis*). Mol. Ecol. 27 (5), 1245–1260. https://doi.org/10.1111/mec.14505.
Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecol. Appl. 17 (8), 2145–2151.
Mueller, S.E., Thode, A.E., Margolis, E.Q., et al., 2020. Climate relationships with increasing wildfire in the southwestern US from 1984 to 2015. For. Ecol. Manag. 460, 117861.
Nagel, L.M., Palik, B.J., Battaglia, M.A., et al., 2017. Adaptive silviculture for climate change: a national experiment in manager-scientist partnerships to apply an adaptation framework. J. For. 115 (3), 167–178.
Nigro, K.M., Rocca, M.E., Battaglia, M.A., Coop, J.D., Redmond, M.D., 2022. Wildfire catalyzes upward range expansion of trembling aspen in beetle-killed forests of the southern Rocky Mountains. J. Biogeogr. 49 (1), 201–214. https://doi.org/10.1111/jbi.14302.
North, M.P., York, R.A., Collins, B.M., Hurteau, M.D., Jones, G.M., Knapp, E.E., Kobziar, L., McCann, H., Meyer, M.D., Stephens, S.L., Tompkins, R.E., Tubbesing, C. L., 2021. Pyrosilviculture needed for landscape resilience of dry western United States forests. J. For. 119, 520–544.
Nuñez, M.A., Bailey, J.K., Schweitzer, J.A., 2010. Population, community and ecosystem effects of exotic herbivores: a growing global concern. Biol. Invasions *12*, 297–301.
O'Connor, C.D., Lynch, A.M., Falk, D.A., Swetnam, T.W., 2015. Post-fire forest dynamics and climate variability affect spatial and temporal properties of spruce beetle outbreaks on a sky island mountain range. For. Ecol. Manag. 336, 148–162 doi: 10.1016/j. foreco.2014.10.021.
O'Donnell, F.C., Flatley, W.T., Springer, A.E., Fulé, P.Z., 2018. Forest restoration as a strategy to mitigate climate impacts on wildfire, vegetation, and water in semiarid forests. Ecol. Appl. 28 (6), 1459–1472.
Perala, D.A., 1990. Populus tremuloides Michx. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, Volume 2. USDA Forest Service, Washington, DC, pp. 555–569.
Prasad, A., Pedlar, J., Peters, M., McKenney, D., Iverson, L., Matthews, S., Adams, B., 2020. Combining US and Canadian forest inventories to assess habitat suitability and migration potential of 25 tree species under climate change. Divers. Distrib. 26 (9), 1142–1159.

PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, data accessed 17 January 2024.
Qiu, T., Sharma, S., Woodall, C.W., Clark, J.S., 2021. Niche shifts from trees to fecundity to recruitment that determine species response to climate change. Front. Ecol. Evol. 9, 719141.
Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S., 2006. Empirical analyses of plant-climate relationships for the western United States. Int. J. Plant. Sci. 167, 1123–1150.
Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. For. Ecol. Manag. 258, 2353–2364.
Rhodes, A.C., Larsen, R.T., Clair, S.B.S., 2018. Differential effects of cattle, mule deer, and elk herbivory on aspen forest regeneration and recruitment. For. Ecol. Manag. 422, 273–280.
Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J., Müller, M., 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinf. 12, 77.
Rodman, K.C., Andrus, R.A., Carlson, A.R., Carter, T.A., Chapman, T.B., Coop, J.D., Hart, S.J., 2022. Rocky Mountain forests are poised to recover following bark beetle outbreaks but with altered composition. J. Ecol. 110 (12), 2929–2949.
Rogers, P.C., Landhäusser, S.M., Pinno, B.D., Ryel, R.J., 2014. A functional framework for improved management of western north American aspen (*Populus tremuloides* Michx.). For. Sci. 60 (2), 345–359.
Rolf, J.A., 2001. Aspen fencing in northern Arizona: a 15-year perspective. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Compilers) (Eds.), Sustaining aspen in western landscapes: Symposium proceedings. Forest Service, Rocky Mountain Research Station, pp. 193–196.
Romme, W.H., Floyd-Hanna, L., Hanna, D.D., Bartlett, E., 2001. Aspen's ecological role in the West. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Compilers) (Eds.), Sustaining aspen in western landscapes: Symposium proceedings. CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 243–260.
Schier, G.A., Jones, J.R., Winokur, R.P., 1985. Vegetative regeneration. P. 29–33 in Aspen: ecology and management in the western United States. In: DeByle, N.V., Winokur, R.P. (Eds.), USDA Forest Service Gen Tech. Rep.
Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Chang 7, 395–402 doi: 10.1038/nclimate3303. Epub 2017 May 31. PMID: 28861124; PMCID: PMC5572641.
Shaw, J.D., Menlove, J., Witt, C., Morgan, T.A., Amacher, M.C., Goeking, S.A., Werstak, C.E., 2018. Arizona's forest resources, 2001–2014. Resour. Bull. RMRS-RB-25. Fort Collins, CO: U.S. Dep. Agric. For. Serv. Rocky Mt. Res. Station.
Shepperd, W.D., Bartos, D.L., Mata, S.A., 2001. Above- and below-ground effects of aspen clonal regeneration and succession to conifers. Can. J. For. Res. 31, 739–745.
Shriver, R.K., Yackulic, C.B., Bell, D.M., Bradford, J.B., 2022. Dry forest decline is driven by both declining recruitment and increasing mortality in response to warm, dry conditions. Glob. Ecol. Biogeogr. 31 (11), 2259–2269.
Smith, D.S., Fettig, S.M., Bowker, M.A., 2016. Elevated Rocky Mountain elk numbers prevent positive effects of fire on quaking aspen (*Populus tremuloides*) recruitment. For. Ecol. Manag. 362, 46–54.
St. Clair, S.B., Guyon, J., Donaldson, J., 2010. Quaking aspen's current and future status in western North America: the role of succession, climate, biotic agents and its clonal nature. Progr. Bot. 71, 371–400.
Steinhoff, R.J., Andresen, J.W., 1971. Geographic variation in *Pinus flexilis* and *Pinus strobiformis* and its bearing on their taxonomic status. Silvae Genet. 20, 159–167.
Stevens-Rumann, C.A., Prichard, S.J., Whitman, E., Parisien, M., Meddens, A.J.H., 2022. Considering regeneration failure in the context of changing climate and disturbance regimes in western North America. Can. J. For. Res. 52 (10), 1281–1302. https://doi.org/10.1139/cjfr-2022-0054.
Stoddard, M.T., Huffman, D.W., Fule, P.Z., Crouse, J.C., Sánchez Meador, A.J., 2018. Forest structure and regeneration response 15 years after wildfire in a ponderosa pine and mixed-conifer ecotone, Arizona, USA. Fire Ecol. 14, 12. https://doi.org/10.1186/S42408-018-0011-Y.
Triepke, F.J., Muldavin, E.H., Wahlberg, M.M., 2019. Using climate projections to assess ecosystem vulnerability at scales relevant to managers. Ecosphere 10 (9), e02854.
Turner, M.G., et al., 2020. Climate change, ecosystems and abrupt change: science priorities. Philos. Trans. R. Soc. B 375, 20190105. https://doi.org/10.1098/rstb.2019.0105.
Waltz, A.E., Stoddard, M.T., Kalies, E.L., Springer, J.D., Huffman, D.W., Sánchez Meador, A.J., 2014. Effectiveness of fuel reduction treatments: assessing metrics of forest resiliency and wildfire severity after the Wallow Fire, AZ. For. Ecol. Manag. 334, 43–52. https://doi.org/10.1016/J.FORECO.2014.08.026.
Waring, G.L., 2018. The Natural History of the San Francisco Peaks. A Sky Island of the American Southwest. Flagstaff: Gwendolyn L. Waring.
Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase Western U.S. Forest wildfire activity. Science 313 (5789), 940–943. https://doi.org/10.1126/science.1128834.
Wilderness Act 16 US Code § 1131, 1964. URL: https://uscode.house.gov/view.xhtml?path=/prelim@title16/chapter23&edition=prelim.
Williams, A.P., Cook, E.R., Smerdon, J.E., Cook, B.I., Abatzoglou, J.T., Bolles, K., Baek, S. H., Badger, A.M., Livneh, B., 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. Science 368 (1979), 314–318. https://doi.org/10.1126/science.aaz9600.
Wolf, K.D., Higuera, P.E., Davis, K.T., Dobrowski, S.Z., 2021. Wildfire impacts on forest microclimate vary with biophysical context. Ecosphere 12, e03467.
Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Marchetti, S.B., Michaelian, M., Gray, L.K., 2013. Recent declines of *Populus tremuloides* in North America linked to climate. For. Ecol. Manag. 299, 35–51.
Yocom-Kent, L.L., Fulé, P.Z., Bunn, P.Z., Gdula, W.A., E.G, 2015. Historical high severity fire patches in mixed-conifer forests. Can. J. For. Res. 45, 1587–1596 https:// doi.org/ 10. 1139/ cjfr- 2015- 0128.
Zegler, T.J., Moore, M.M., Fairweather, M.L., Ireland, K.B., Fulé, P.Z., 2012. *Populus tremuloides* mortality near the southwestern edge of its range. For. Ecol. Manag. 282, 196207.