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RESEARCH ARTICLE

Reducing Fire Severity and Extent Bolsters Subalpine Forest Resilience to Global Change Through Key Demographic Pathways

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ABSTRACT

High-elevation subalpine forests are experiencing rapid changes in climatic conditions, biological disturbances, and wildfire regimes. Despite this, evidence is mixed as to whether they will undergo major ecological transformation or be resilient to a confluence of global change drivers. Here we use subalpine fir (*Abies lasiocarpa*) and Englemann spruce (*Picea engelmannii*), which form co-dominant forests through much of the western United States, to investigate how species' demographic responses to global change influence forest community-wide resilience. We do this by adapting and building on an existing framework for post-disturbance ecological reorganization. With forest inventory data from the United States Forest Service Forest Inventory and Analysis (FIA) program, we quantify population trends for subalpine fir and Engelmann spruce across their joint distribution and organize them in a new conceptual framework for categorizing forest community trajectories. We then build hierarchical Bayesian demographic models of subalpine fir and Engelmann spruce mortality, regeneration, and recruitment as functions of climate, disturbance extent and severity, and forest structural predictors. We bring demographic predictions together in a multinomial classification model to quantify how combinations of demographic rates influence overall forest community trajectories. Finally, we apply future climate and disturbance scenarios to our demographic models to explore how subalpine forest resilience may change in the future. We found strong negative relationships between the demography of both species and disturbance extent and severity, and climatic responses in line with an energy-limited forest system. Future scenario model predictions indicate that reducing wildfire extent and severity can greatly bolster overall subalpine forest resilience; the preferred way to do this will vary according to fire history, forest type, biophysical setting, and land tenure. Opportunities for high-impact management interventions are concentrated in the northern Rocky Mountains, with centers of ongoing resilience in parts of the Oregon and Washington Cascades.

1 | Introduction

The compounding effects of anthropogenic climate change and intensifying physical and biological disturbances are driving the ecological transformation of forest systems around the world (Allen, Breshears, and McDowell 2015; Coop et al. 2020; Hoecker et al. 2023; Seidl and Turner 2022). This is particularly pronounced in high-elevation subalpine forests,

which are experiencing rapid rates of climate warming (Pepin et al. 2022) and unprecedented levels of disturbance from wildfires, insects, and diseases (Davis et al. 2022; Higuera, Shuman, and Wolf 2021; Maclauchlan 2016). In mountainous regions of the western United States, for example, the interactive effects of these stressors are evidenced by widespread population declines among high-elevation species like whitebark pine (*Pinus albicaulis*) (Aguilera et al. 2021; Dudney et al. 2020; Goeking and Windmuller-Campione 2021) and subalpine fir (*Abies lasiocarpa*) (Harvey et al. 2021; Lalande et al. 2020; Perret et al. 2023). Correspondingly, there is evidence that high-elevation subalpine forests are experiencing widespread changes in forest structure and composition, and may continue doing so in the future (Hoecker et al. 2023). However, there is also potential for considerable resilience in these systems under certain conditions (Davis et al. 2023; Jaffe et al. 2023; Wolf et al. 2023). Effectively responding to ongoing changes and managing for anticipated future changes thus requires a nuanced understanding of when and where we should expect ecological reorganization versus resilience.

While a growing body of work is building our understanding of how individual tree species respond to global change drivers (e.g., Bell, Bradford, and Lauenroth 2014; Evans et al. 2024; Iverson et al. 2008; Perret et al. 2023; Perret, Evans, and Sax 2024; Stanke et al. 2021), few studies have been able to make the critical link between individual species and the broader trajectories of the forest systems they comprise (Seidl and Turner 2022). This is an important step because the population trends of individual species may be poor or incomplete indicators of system-wide resilience. For example, a single wildfire disturbance event may have dramatically different demographic consequences for co-occurring species, depending on those species' life history strategies and adaptations to fire disturbance (Keeley et al. 2011; Keeley and Zedler 1998). Fire may cause very high mortality followed by rapid regeneration for one species (e.g., as for lodgepole pine, *Pinus contorta*), but low mortality followed by increased growth and delayed regeneration for another co-occurring species (e.g., as for ponderosa pine, *Pinus ponderosa*). The post-disturbance response of either species in isolation would give a picture of forest-wide trends that is incomplete or even misleading. Host-specific biological disturbance agents can have similar effects, insofar as they disproportionately impact certain tree species over others. There is also abundant evidence that species' responses to climate can vary widely, even among those that currently co-occur or form well-known species associations (Jackson and Overpeck 2000; Overpeck, Webb, and Webb 1992; Roberts and Hamann 2015; Van der Geer et al. 2012). The ephemeral emergence of species assemblages during past glacial–interglacial cycles that have no modern analog serve as an example of why we should not assume that currently-associated species will respond similarly to ongoing and future climate change (Williams and Jackson 2007).

On the other hand, these same dynamics create the potential for a sole focus on ecological communities, assemblages, or forest types to be similarly misleading as to the trajectories of their component species. It has long been appreciated that species are individualistic in their responses to climate, which in turn gives rise to the distribution of ecological communities and species assemblages (Gleason 1926; Whittaker 1967). While fully mechanistic understandings of complex systems like ecological communities are not always necessary for gaining useful insight (Scholes 2017), a purely phenomenological approach may not be sufficient for predicting future outcomes. Indeed, recent work using spatial networks of tree-ring time series has demonstrated that emergent large-scale patterns in tree growth can be severely misleading when used to predict the future growth responses of individuals and populations (Evans et al. 2024; Perret, Evans, and Sax 2024). In light of this, it is important that we build our understanding of how forests respond to global change across levels of biological organization (i.e., from individual trees to ecological communities) and spatial scales (i.e., from stands to landscapes).

In subalpine forests across western North America, both interspecific differences and emergent patterns are likely to influence system-wide responses to ongoing and future global change. Subalpine fir (*A. lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) provide a particularly good example of this. These two species form co-dominant stands across most of their shared distribution in subalpine forests across western North America, comprising an estimated 9.24 ± 0.12 million hectares of forest area (USDA Forest Service 2023). Prior work has found that codominance of Engelmann spruce and subalpine fir is maintained by interspecific differences in key life history traits and associated vital rates. Specifically, the faster growth and more prolific regeneration of subalpine fir is balanced by higher survival and longevity of Engelmann spruce (Andrus et al. 2018). While shade-tolerant subalpine fir seedlings can establish and persist in the understory, sufficient spruce regeneration may rely on canopy gaps provided by large tree mortality or periodic disturbance (Shea 1985). This interspecific trait and life history variation may underlie differential responses to both host-specific and non-discriminant forest disturbances, as reflected in recent findings of significant differences in the importance of major mortality sources among co-occurring subalpine tree species (Perret et al. 2023). These two species may also respond differently to directional climatic shifts through time, as suggested by palaeoecological evidence. Indeed, the subalpine fir—Engelmann spruce association we observe today may not have existed during certain periods of the past. For example, during the last glacial maximum (21,000 years before present), the bulk of Engelmann spruce's distribution was in the southern interior highlands of western North America (i.e., in the current US states of Arizona, New Mexico, and Colorado), whereas subalpine fir was more widely distributed across interior basins in the Northern Rockies and along coastal refugia in the Pacific northwest (Roberts and Hamann 2015). These sorts of interspecific differences create the potential for either subalpine fir or Engelmann spruce to be a misleading indicator of broader trends in the subalpine forests they form.

A conceptual framework recently proposed by Seidl and Turner (2022) provides a useful structure for linking from individuals to landscapes by relating tree species' demographic responses to global change drivers to forest community reorganization trajectories (see Box 1). Seidl and Turner (2022) present four paths that a forest system can follow in response to a discrete disturbance event: *resilience*, *restructuring*, *reassembly*, and *replacement*. In this framework, systems move away from *resilience* and toward one of the other non-resilient pathways

BOX 1 | Conceptual framework for linking single-species population trends to community-level trajectories.

Changes in either abundance or basal area can be caused by a variety of processes, including stand development, disturbance-related turnover, or mortality. To disentangle these processes, we combined abundance and basal area estimates for each species using a binary categorization scheme (Figure 1; Perret et al. 2023) with four population trajectory categories: *Densification* (increases in both basal area and abundance), *development* (declining abundance but increasing basal area), *turnover* (increasing abundance but declining basal area), and *decline* (decreases in both basal area and abundance).

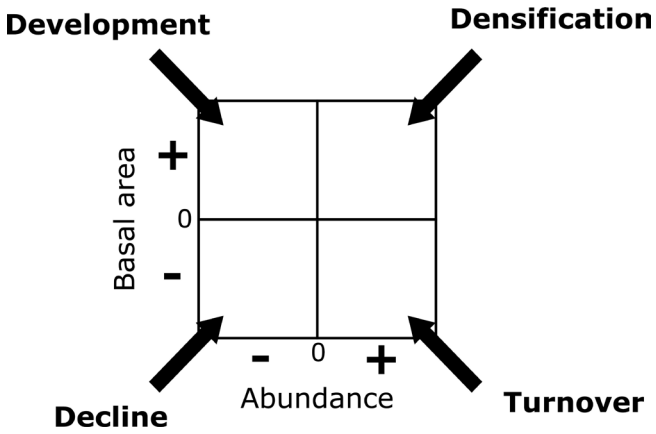

FIGURE 1 | Binary categorization scheme combining trends in abundance and basal area for a single species.

In a simple community comprised of two species, continued coexistence requires positive population trajectories for both species (i.e., *development* or *densification*, described above). In contrast, if one species is experiencing decline, the system may shift to single-species dominance or undergo other compositional changes. We used the single-species population trajectories described above to categorize these possibilities (Figure 2) after the post-disturbance reorganization schema presented by Seidl and Turner (2022). These possibilities include: (1) *resilience*—both species are either undergoing changes corresponding with normal stand development or are actively increasing in density; (2) *restructuring*—one or both species have experienced significant turnover of individuals, indicating that future trajectories may depend on post-disturbance recovery and survival of new recruits; (3) *reassembly*—one species is in decline while the other is either undergoing normal stand development or increasing in density, suggesting that one species will become dominant over the other; and (4) *replacement*—indicating that both species are in decline, and the system may be replaced entirely. We note that the resilience concept has been applied to forest systems in various ways; here, *resilience* is interpreted as relative to any drivers impacting the forest system, including both climate and disturbance.

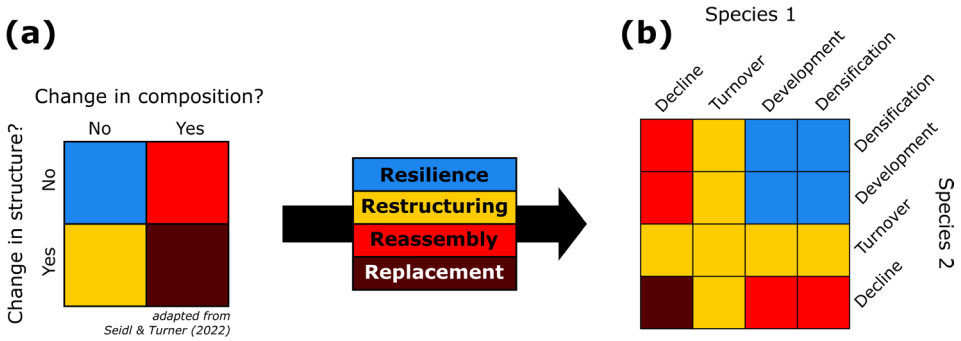

FIGURE 2 | The post-disturbance reorganization categories (a) described by Seidl and Turner (2022) can be mapped onto a bivariate classification scheme comprised of the population trajectories of two co-occurring species (b).

when critical processes related to community assembly and forest development are disrupted. While Seidl and Turner (2022) focus on post-disturbance ecological reorganization (i.e., following wildfire, insect or disease outbreaks, physical disturbance), their framework could be applied in any context where some change driver is altering tree species' demography. While discrete disturbance events like wildfire may have obvious and immediate impacts on tree survival, the long-term demographic impact of disturbance depends heavily on the climatic context in which it occurs (Enright et al. 2015). Further, increases in both climate variability and the frequency of extreme climate events are impacting tree species' demography in ways that are comparable to physical or biological disturbances. Between 2012 and 2015, for example, sustained drought and anomalously warm temperatures across large swaths of the Sierra Nevada mountains in California induced large-scale mortality and

regeneration failure of certain tree species, potentially leading to long-term changes in forest structure and composition (Fettig et al. 2019; Goulden and Bales 2019).

Here we leverage USDA Forest Inventory and Analysis (FIA) data to investigate how changing climate and disturbance influence the resilience of subalpine fir—Engelmann spruce forests across the western United States. We do this by first estimating trends in both species' abundance and basal area within ecoregion subsections where they co-occur between 2000–2009 and 2010–2019 inventory periods. We combine these trends using a new conceptual framework building on Seidl and Turner (2022) to identify areas where spruce-fir forests display demographic signatures of *resilience*, *reassembly, restructuring*, and *replacement* (Box 1). We then build a series of hierarchical Bayesian demographic models that estimate the effect of mean climatic conditions, climate anomalies, and disturbance on individual mortality, regeneration, and recruitment. We use these models to assess how projected future climate and disturbance scenarios influence the distribution of forest community trajectories and demonstrate how this information can support conservation and management decision-making.

2 | Methods

2.1 | Forest Inventory Data

The FIA database provides a nationally-consistent, randomized sample of forest measurements across all forest lands in the United States. In most of the western United States, plots are remeasured on an average rotation of 10 years, facilitating estimates of decadal-scale changes in forest attributes and tree vital rates. In brief, each FIA plot consists of nested subplots on which adult trees (> 12.7 cm DBH) are inventoried, microplots on which seedlings (< 2.54 cm DBH and > 15.24 cm height) and saplings (2.54–12.7 cm DBH) are inventoried, and macroplots on which large trees are inventoried (in certain Western states; size threshold varies by state). FIA field crews collect a vast array of information, including physical tree measurements, tree damages, putative causes of mortality, and disturbance type and extent. For a complete description of FIA sampling and measurement protocols, refer to the FIA user guide and FIA field manual (Burrill et al. 2015; USDA Forest Service 2024).

We queried the FIA database for plots that had been remeasured during the 2010–2019 inventory period, and contained both subalpine fir and Engelmann spruce. Following Perret et al. (2023), we included all plots that contained at least one live or dead individual of both species with a DBH > 2.54 cm during at least one plot measurement. We intentionally retained plots that only contained dead individuals of either or both species, in order to avoid excluding plots that had experienced high mortality rates since the previous measurement. Every plot we included in our analyses could be linked back to a previous plot measurement; because Wyoming transitioned to the annualized sampling design later than other western States, initial plot measurements in the state came from the previous periodic survey design. In total, this yielded 2972 plots with two measurements between the 2000–2009 and 2010–2019 inventory periods (Figure S1), containing 34,989 subalpine fir individuals and 27,944 Engelmann spruce individuals.

2.2 | Population Trajectories

We used standard FIA estimation procedures (Bechtold and Patterson 2005), modified from implementation in the rFIA package (Perret et al. 2023; Stanke et al. 2020), to estimate decadal changes in the abundance and basal area of both subalpine fir and Engelmann spruce at the ecoregion subsection scale (Cleland et al. 2007). These estimation procedures leverage the FIA program's randomized sampling design to make post-stratified, area-based estimates of multiple forest attributes. Because we were specifically interested in processes influencing the coexistence of subalpine fir and Engelmann spruce, we restricted these estimates to FIA plots containing live individuals of both species as described above ($N = 2972$ plots). Basal area and abundance trends were calculated between 2000–2009 and 2010–2019 annualized inventory periods, except in Wyoming, where the most recent annualized plot measurements were linked back to the most recent previous periodic survey (Perret et al. 2023). Trees smaller than 12.7 cm DBH could not be linked back to periodic inventories in Wyoming; for this reason, we calculated range-wide population trajectories for trees larger than 12.7 cm DBH.

We combined ecoregion subsection-level trend estimates of abundance and basal area for each species using the single-species population trajectory scheme described in Box 1 (Figure 1). In cases where trend estimates were statistically indistinguishable from zero (i.e., sampling error was equal or greater to the magnitude of the change), we treated the estimate as though it were positive. We used the joint trajectory framework described in Box 1 (Figure 2) to combine single-species trajectories and categorize community-level trends in subalpine fir—Engelmann spruce forests. These resulting joint trajectories observed between 2000–2009 and 2010–2019 inventories were then related to species' demographic rates and responses, as described below, and assessed under several future climate and disturbance scenarios.

2.3 | Demographic Models

We built a series of statistical models for each species predicting individual mortality, seedling presence, and recruitment presence as the linear combination of several predictor variables and their interactions related to tree condition (mortality only), forest stand structure, climate, and disturbance. Because our response variables were binary states (i.e., the presence or absence of mortality, seedlings, or recruitment), we modeled each as the outcome of a single Bernoulli trial using a generalized linear mixed model with a logit link function, implemented in a Bayesian framework with non-informative priors. All response and predictor variables are described below for each model, and summarized in Table S1. We used the "brms" package (Bürkner 2018) in the R4.2.1 statistical programming environment (R Core Team 2023) to build all of our models. All models were trained with uninformative flat priors over 10,000 "burn-in" iterations and 10,000 sampling iterations across four sampling chains. Model convergence was assessed using Ruben-Gelman statistics for

each estimated model parameter and visual inspection of sampling chains.

2.4 | Climate Data

To capture both spatial and temporal climatic variation relevant to tree demography, we calculated mean reference period climatic conditions and local climate anomalies for FIA plots using the ClimateNA software package (Wang et al. 2016). ClimateNA uses a dynamic local downscaling approach to generate scale-free climate data for specific locations based on underlying gridded monthly PRISM data (Daly et al. 2008). More details on ClimateNA are provided on the project website (https://www.climatena.ca) and by Wang et al. (2016). Past work has demonstrated that tree demography in temperate forests is both strongly limited by local temporal variation in moisture availability (Davis et al. 2019, 2023; Littlefield et al. 2020) and structured by spatial variation in mean climatic conditions (Klesse et al. 2020; Perret, Evans, and Sax 2024). We thus focused on climate variables that reflect these two sources of variability—mean annual temperature, mean climatic moisture deficit, maximum annual temperature anomalies, and maximum climatic moisture deficit anomalies. We used historical climate data from ClimateNA to calculate mean annual temperature and mean climatic moisture deficit for each FIA plot in our dataset during a reference period comprising the 30 years preceding each site's initial measurement (typically between 2000 and 2009). We then calculated the maximum mean annual temperature and climatic moisture deficit anomalies each plot experienced between its initial measurement and remeasurement relative to the reference period means. These maximum anomalies were converted to z-scores using variation observed during the reference period, following the procedures of Littlefield et al. (2020) and Davis et al. (2023). These anomalies capture the maximum degree to which climatic conditions at each FIA plot departed from historical baselines during the period reflecting our population trajectory estimates. In all our demographic models, we incorporated interactions between climate anomalies and reference mean conditions, allowing for regional variation in demographic responses to local temporal climatic variation.

2.5 | Mortality Models

We modeled individual-level survival as an interval probability over the length of time between plot remeasurements (Kubo et al. 2000; Sheil, Burslem, and Alder 1995). In most western US states, FIA plots began being remeasured in approximately 10-year rotations in the year 2000. For the vast majority of plots, there thus exists an initial measurement between 2000 and 2009, and a single remeasurement approximately 10 years later between 2010 and 2019. However, regional delays in implementing this annualized sampling design, variation in field crew efficiency, and seasonal field hazards (e.g., wildfires) all create variability around this intended 10-year remeasurement period. We accounted for this interval variability in our model by representing survival as an annual probability that is converted to an interval probability using the observed remeasurement period:

$$y_{\mathrm{ipr}} \sim \mathrm{Bernoulli}\left(S_{\mathrm{ipr}}^{(t_2-t_1)}\right) \tag{1}$$

$$\mathrm{logit}\left(S_{\mathrm{ipr}}\right)^{-1} = X_{\mathrm{ipr}}\beta + \gamma_{\mathrm{r}} + \varepsilon_{\mathrm{ipr}} \tag{2}$$

where y_{ipr} is the observed status (live or dead) of individual tree "i" on plot "p" in ecoregion "r", S_{ipr} is that tree's annual predicted survival probability, $t_2 - t_1$ is the number of years between plot measurements, β is the vector of regression parameters, X_{ipr} is the design matrix containing all observations and corresponding independent variables, γ_{r} is an ecoregion-level random effect distributed as $N(0, \tau^2)$, and $\varepsilon_{\mathrm{ipr}}$ is a tree-level error distributed as $N(0, \sigma^2)$.

We implemented this model for remeasured adult (DBH > 12.7 cm) subalpine fir and Engelmann spruce from the 2972 plots on which they co-occurred ($N = 34{,}989$ subalpine fir and 27,944 Engelmann spruce). Each species' model had an identical design matrix X_{ipr} that included individual-, plot-, and ecoregion-level predictors. Individual-level predictors included the diameter at breast height (cm), crown ratio (unitless), and damage status of tree i at time t_1. Damage status was coded as 0 if the tree was undamaged, and 1 if any fire, insect, or disease damage was recorded. Plot-level predictors included the total stand basal area ($m^2\,ha^{-1}$) within each plot at t_1, as well as climate normals during the 30-year reference period preceding the initial plot measurement, recent climate anomalies observed between time t_1 and time t_2, and their interactions. Because we incorporated both annual temperature and climatic moisture deficit variables, described above, these climate predictors comprised two climate normals, two climate anomalies, and their four associated interactions. Landscape-level predictors included the proportion of spruce-fir forest in each ecoregion impacted by fire mortality or biological disturbance agent mortality between time t_1 and time t_2. Because most field-derived measurements of disturbance severity involve quantifying the proportional or total mortality induced by the disturbance in question, using a plot-level disturbance metric to predict individual mortality would be unavoidably circular. This is especially the case in a system where the vast majority of mortality is disturbance-related (Perret et al. 2023). We thus chose to quantify disturbance at the ecoregional scale, reflecting landscape-level patterns in disturbance prevalence and extent, after Perret et al. (2023). Briefly, we used tree-level mortality attribution to identify disturbed plots, and plot expansion factors derived from the FIA sampling design to calculate the corresponding proportion of spruce-fir forest in each ecoregion. We chose this approach to retain information about low-severity disturbances, in contrast to other approaches that use a mortality or damage threshold (Fitts, Domke, and Russell 2022). The model also included selected cross-scale interactions, namely between tree size, climate anomalies, and disturbed area. Modeled probabilities were subtracted from one to reflect the probability of mortality over the remeasurement period for all subsequent analyses.

2.6 | Regeneration Models

FIA field procedures define seedlings as individual trees with a diameter of less than 2.54 cm and a height of at least 15 cm.

Seedlings are inventoried on smaller microplots (13.5 m^2) nested within subplots (168.1 m^2); because of this, seedling density estimates have more uncertainty than those for adults and may be unreliable when there is high spatial heterogeneity. We thus chose to model subalpine fir and Engelmann spruce regeneration using seedling presence rather than seedling densities. For each species, we used a generalized linear mixed model to predict the probability of seedling presence at an FIA plot at its remeasurement:

$$y_{pr} \sim \text{Bernoulli}\left(R_{pr}\right) \tag{3}$$

$$\text{logit}\left(R_{pr}\right)^{-1} = X_{pr}\beta + \gamma_r + \varepsilon_{pr} \tag{4}$$

where seedling presence or absence y in plot "p" nested in ecoregion r is the outcome of a Bernoulli trial with estimated probability of success R_{pr}, which is modeled as the linear combination of a vector of regression parameters β, a design matrix X_{pr}, an ecoregion-level random effect γ_r distributed as $N(0, \tau^2)$, and a plot-level error ε_{pr} distributed as $N(0, \sigma^2)$. The design matrix X_{pr} incorporated plot-level predictors including the severity of fire disturbance on a plot between t_2 and t_1, calculated as the proportion of adult trees of all species living on the plot at t_1 that had died due to fire by t_2. We took this approach, instead of an ecoregional approach as in the mortality models described above, because past work has shown a clear link between fire severity and the biophysical environment necessary for seedling establishment and survival (Davis et al. 2023; Littlefield et al. 2020; Wolf et al. 2021). Other predictors included total stand basal area at t_1, reference period climate normals (CN), and remeasurement period climate anomalies (CA), as described for the mortality models above. Because the presence or absence of seedlings reflects processes that occurred in the several years prior to observation regardless of the remeasurement period, we did not account for variable intervals as in the survival models described above.

2.7 | Recruitment Models

Previous work on subalpine fir population trends has demonstrated that sapling recruitment (i.e., the number or proportion of trees that transition from seedling to sapling) presents a critical demographic bottleneck for the species across its distribution (Perret et al. 2023). However, saplings are defined by FIA field protocol as trees with a diameter between 2.54 and 12.7 cm, and are inventoried on microplots similarly to seedlings. We thus chose to model sapling recruitment similarly to seedling regeneration; as the presence or absence of new sapling recruits recorded on the microplot at remeasurement. While we acknowledge that these tree size thresholds are to some degree arbitrary and create artificial groups along a continuous size distribution (Monleon and Lintz 2015), it is likely that different demographic processes are being captured within each category (e.g., seedling establishment versus recruitment) given the generally slow growth rates expected in cold subalpine forests. Sapling recruitment models were structured identically to seedling regeneration models (Equations 3 and 4) for both species.

2.8 | Joint Trajectory Classification

We modeled observed joint trajectories (classified as *resilience*, *restructuring*, *reassembly*, or *replacement*; Box 1) as the outcome of a single multinoulli trial with probabilities predicted by the mean posterior predictions of mortality, regeneration, and recruitment for Engelmann spruce and subalpine fir within ecoregion subsections occupied by both species. Because the population trends incorporated in our joint trajectory framework (Box 1) reflect multiple demographic processes acting in concert, this model incorporated two- and three-way interactions between all demographic rates for each species:

$$\text{JT}_r \sim \text{Multinoulli}\left(p_{\text{JT},r}\right) \tag{5}$$

$$p_{\text{JT},r} = X_r\beta + \varepsilon_{\text{JT},r} \tag{6}$$

where JT is the joint trajectory (i.e., *resilience*, *restructuring*, *reassembly*, or *replacement*; Box 1) observed in each ecoregion subsection r, and $p_{\text{JT},r}$ is the estimated probability of each outcome JT in each ecoregion subsection r. These probabilities are modeled as the linear combination of a design matrix X_r, a vector of estimated regression parameters β, and an ecoregion-level error term ε for each outcome JT. The design matrix included interactions between mean posterior estimates of survival, regeneration, and recruitment, averaged across ecoregion subsections, for subalpine fir and Engelmann spruce respectively. Model coefficients were estimated in a Bayesian framework using the "brms" R package (Bürkner 2018) over 5000 sampling iterations with non-informative priors. Model convergence was assessed using Ruben-Gelman statistics and visual inspection of sampling chains.

2.9 | Future Scenarios

We used demographic vital rate models to predict survival, regeneration, and recruitment of subalpine fir and Engelmann spruce under a range of future climate and fire scenarios. We evaluated three fire scenarios—high disturbance, observed disturbance, and low disturbance. High- and low-disturbance scenarios corresponded to the high end (50% area burned at 90% mortality) and low end (5% area burned at 50% mortality), respectively, of what was observed in spruce-fir forests between 2000–2009 and 2010–2019 inventory periods. The observed fire disturbance scenario reflected fire extent and severity as estimated between 2000–2009 and 2010–2019 inventory periods. We evaluated each of these scenarios under projected climatic conditions for 2040–2050 and 2070–2080, using an ensemble of 13 global circulation model projections for the CMIP6 SSP3-7.0 pathway (Eyring et al. 2016; Mahony et al. 2022), obtained and downscaled using ClimateNA v7.42 (Wang et al. 2016). Evidence suggests that this mid-severity pathway is most in line with recent emission trends (IPCC 2021). All future predictions reflect mean posterior predictions from 1000 model draws.

Recent work has suggested that ecological responses to spatial and temporal climatic variation may not be equivalent or substitutable (Evans et al. 2024; Perret, Evans, and Sax 2024). We

thus chose to use a partial space-for-time approach in making our future predictions. Specifically, we followed the approach of Klesse et al. (2020) by forcing our demographic vital rate models using only projected future climate anomalies, while leaving reference period mean variables at the values used for model fitting. Because our model structures incorporate interaction terms between reference period mean variables and climate anomalies, this allows for flexible responses to climate anomalies that vary across each species' distribution but are invariant through time.

We used our multinomial classification model to predict joint trajectories (i.e., *resilience*, *restructuring*, *reassembly*, or *replacement*) for each future climate and disturbance scenario, given mean posterior vital rate predictions. For each ecoregion subsection, we calculated the proportion of 1000 posterior predictive draws in each trajectory category (i.e., the posterior probability of *resilience*, *restructuring*, *reassembly*, *replacement*). We then calculated the sum of these proportions across all ecoregion subsections weighted by the estimated spruce-fir area in each subsection. This weighted sum represents the model-predicted area of spruce-fir forest in each trajectory category, calculated in such a way as to incorporate the prediction uncertainty.

3 | Results

3.1 | Observed Population Trajectories

We found that 35.7% of all forest area in which Engelmann spruce and subalpine fir co-occur fell in the *resilience* category, with neutral or positive population trajectories for both species during the inventory remeasurement period. *Restructuring*, characterized by significant turnover among one or both species, comprised 15.0% of the shared distribution. In 26.5% of the shared distribution, population trajectories were mismatched between the two species such that one was in decline while the other was not, forming the *reassembly* category. Both species were in decline across 22.8% of the shared distribution, indicating possible *replacement*. We found notable differences in estimated joint trajectories between regions and mountain ranges (Figure 3). The northern Rocky Mountains in northern Idaho and northwestern Montana formed the largest

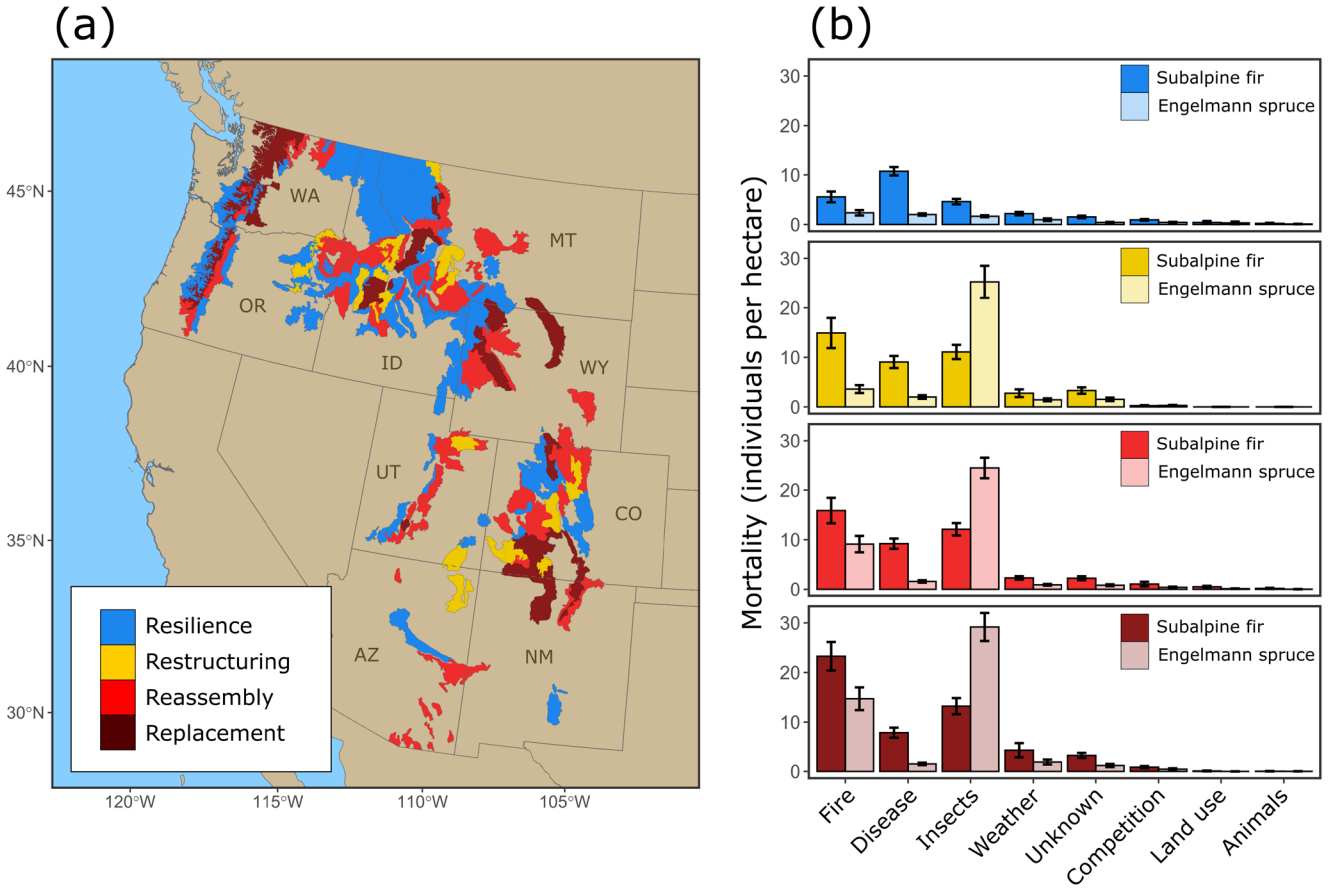

FIGURE 3 | Distribution of joint species trajectory categories (colors), as estimated at the ecoregion subsection level across the shared range of subalpine fir and Engelmann spruce (a), and the estimated mortality of both species in each category caused by broad classes of mortality agents (b). Mortality is quantified as the estimated density of subalpine fir or Engelmann spruce individuals that died between inventory remeasurements per hectare of spruce-fir forest area; error bars represent the standard error of this estimate. Colors correspond with the categories in Box 1. Selected U.S. state abbreviations include Arizona (AZ), Colorado (CO), Idaho (ID), Montana (MT), New Mexico (NM), Oregon (OR), Utah (UT), Washington (WA), and Wyoming (WY). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

area of estimated *resilience* across the species' joint range. In contrast, the central Idaho mountains, which have experienced significant large-scale wildfire events and insect/disease outbreaks between inventory periods, were characterized by a mixture of *restructuring*, *reassembly*, and *replacement*. The largest estimated areas of *replacement* were found in southern Colorado and northern New Mexico. Where spruce-fir forests were undergoing *replacement*, we found that Douglas fir (*Pseudotsuga menziesii*) was the most common species undergoing densification, followed by species typically associated with more arid forest types, including Gambel oak (*Quercus gambelii*), ponderosa pine (*P. ponderosa*), Rocky Mountain juniper (*Juniperus scopulorum*), Utah juniper (*J. osteosperma*), and common pinyon (*Pinus edulis*; Figure S2).

The major sources of mortality for each species differed between joint trajectory categories (Figure 3). For Engelmann spruce, insects were the largest mortality source across all categories except *resilience*, probably reflecting severe spruce beetle outbreaks in parts of the species' range. In contrast, fire was the largest mortality source for subalpine fir except in the *resilience* category, where diseases caused the most mortality. Overall mortality levels were comparable across all non-resilient joint trajectories (Figure 3).

3.2 | Demographic Models

All demographic models converged adequately, indicated by Gelman-Rubin statistics equal to 1.0 for all covariate estimates and visual inspection of sampling chains.

3.3 | Mortality

Individual probability of mortality on average was substantially higher for subalpine fir than for Engelmann spruce (Figure 4). For both species, probability of mortality increased with tree size, though the effect was marginally stronger for subalpine fir than for Engelmann spruce (Figure S3). Tree condition was also an important influence on mortality, with higher crown ratios associated with lower probability of mortality and insect/disease damage associated with higher probability of mortality. For both species, higher temperature anomalies were associated with lower mortality (Figure 4a). Reference climatic moisture deficit did not have a substantial effect on mortality for either species, though there was some weak evidence that subalpine fir mortality was higher in drier regions. CMD anomalies, however, had more substantial impacts, with higher deficits associated with higher mortality risk for Engelmann spruce, especially in drier regions (Figure 4b; Figure S8). Fire disturbance increased the probability of mortality similarly for both species (Figure 4c; Figure S3). Increasing stand density was associated with lower mortality risk for subalpine fir, and slightly higher mortality risk for Engelmann spruce.

3.4 | Regeneration

On average, seedling presence was far more likely for subalpine fir than for Engelmann spruce (Figure 4; Figure S4). While regeneration probability was higher in colder regions (i.e., low MAT) for both species, responses to temperature anomalies varied (Figure S7). Subalpine fir regeneration had a slight negative response to mean annual temperature anomalies during the remeasurement period (Figure 4e) in all but the warmest locations. In contrast, the response of Engelmann spruce regeneration to temperature anomalies was slightly negative in warm regions, and positive in colder regions (Figure S7). CMD anomalies had no substantive effect on either subalpine fir or Engelmann spruce regeneration under mean conditions (Figure 4f), though higher deficit anomalies were associated with higher Engelmann spruce regeneration in dry regions (Figure S8). Fire severity, as estimated by the proportion of adult trees on a plot killed by fire between remeasurements, had a strongly negative effect on regeneration probability for both species, but especially for subalpine fir (Figure 4g). Stand density, on the other hand, had a strong negative effect on Engelmann spruce regeneration but no effect on subalpine fir regeneration, potentially reflecting differences in the shade-tolerance of the two species.

3.5 | Recruitment

The probability of sapling recruitment was higher on average for subalpine fir than for Engelmann spruce, similarly to our seedling regeneration results. We found that Engelmann spruce sapling recruitment was less likely in regions with warmer reference temperatures; we found a similar but weaker effect for subalpine fir. For both species, higher remeasurement period temperature anomalies were associated with a lower probability of sapling recruitment (Figure S5). This relationship was stronger for Engelmann spruce than for subalpine fir, especially in colder regions (Figure S7). Moisture availability, as represented in the model by reference period mean CMD and remeasurement period CMD anomalies, had no effect on subalpine fir sapling recruitment. For Engelmann spruce, however, higher moisture deficit anomalies were associated with higher sapling recruitment probabilities in drier regions, and lower recruitment in wetter regions (Figure S8). Fire severity was negatively related to sapling recruitment for both species, with an especially strong effect for Engelmann spruce. Stand density had a similarly negative effect on sapling recruitment for both species (Figure 4k–m).

3.6 | Trajectory Classification

The classification model converged adequately, and posterior predictive checks indicated that the model was able to reproduce the observed data distribution well. Classification accuracy was highest for the *resilience* category (74.5%), lowest for *restructuring* (21.31%), and 56.79% across all categories (Table S3). The null accuracy of the model (i.e., the classification accuracy of an uninformative model that only predicts the most common class) was 43%. When holding other demographic rates constant, the model predicted high probability of *resilience* in demographic situations corresponding with low mortality (i.e., <0.25) of both species or high probability of Engelmann spruce recruitment (Figure 5a,c). Conversely, *replacement* was predicted with high probability in situations with high subalpine fir mortality (i.e.,

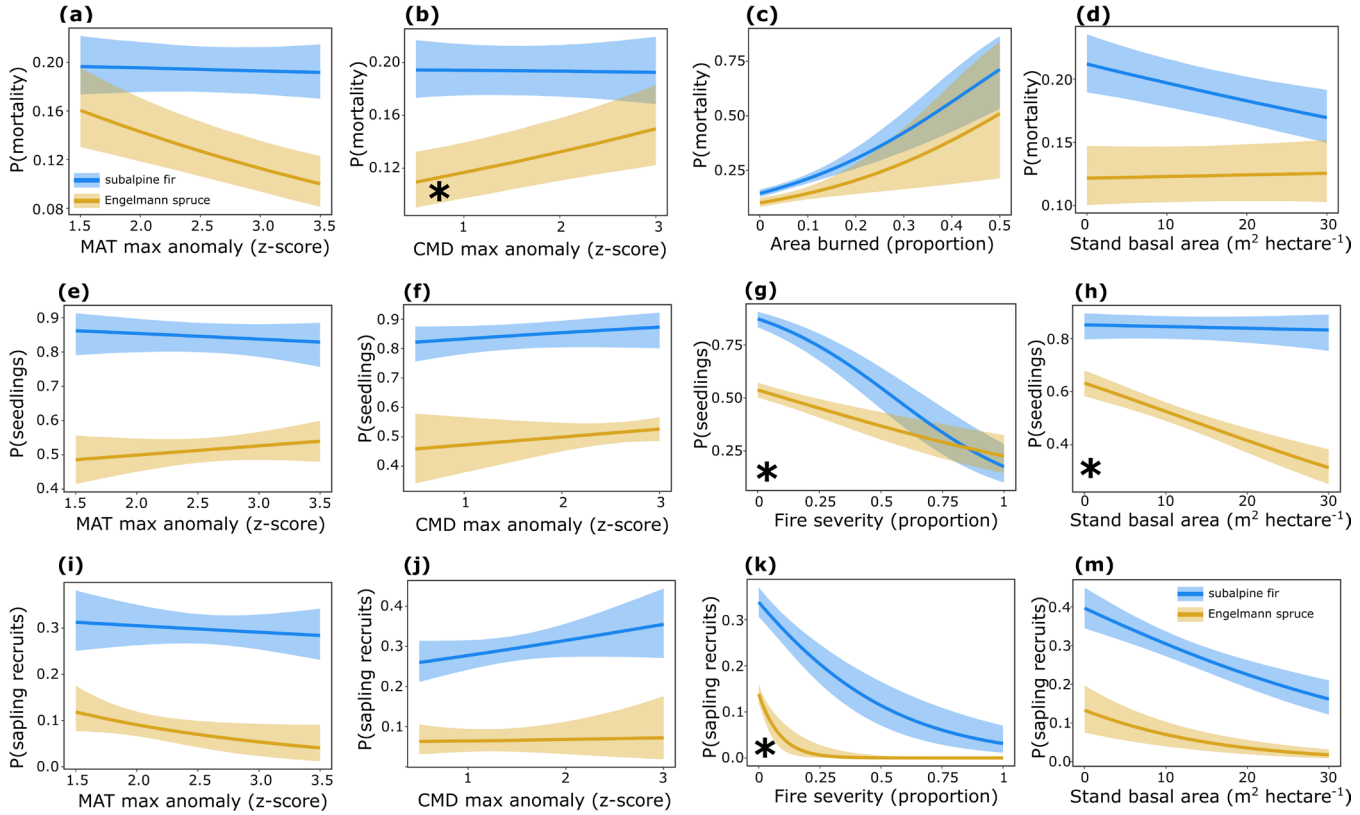

FIGURE 4 | Modeled partial effects for selected demographic model covariates, for both subalpine fir (blue lines and shading) and Engelmann spruce (gold lines and shading). Panels (a–d) correspond to mortality models (y-axis shows the predicted individual probability of mortality over a 10 year remeasurement period), panels (e–h) correspond to seedling regeneration models (*y*-axis shows the probability of seedling presence at plot remeasurement), and panels (i–m) correspond to sapling recruitment models (*y*-axis shows the probability of new sapling recruitment at plot remeasurement). Covariates on *x*-axes are the maximum mean annual temperature anomaly during remeasurement periods (panels a, e, i), maximum climatic moisture deficit anomaly during remeasurement periods (panels b, f, j), fire disturbance expressed as the proportion of subalpine forests impacted by fire mortality during the remeasurement period (panel c) or fire severity expressed as the proportion of adult trees in a plot killed by fire during the remeasurement period (panels g, k), and total plot basal area (m^2 $hectare^{-1}$) at initial measurement. Lines and shading indicate marginal mean posterior predictions and 94% credible intervals, respectively, for subalpine fir (blue) and Engelmann spruce (gold). Partial effects are generated by holding all other predictor variables at their mean value and varying the covariate of interest within the range of observed values. Asterisks (*) indicate cases where the 95% credible intervals for the indicated effects do not overlap.

> 0.5), regardless of Engelmann spruce mortality (Figure 5a). *Restructuring* was most likely in situations where Engelmann spruce had a higher probability of regeneration than subalpine fir (Figure 5b), likely reflecting higher post-disturbance regeneration of a shade-intolerant species. *Reassembly* was indicated in a wide variety of demographic situations, potentially reflecting a greater range of pathways towards either subalpine fir or Engelmann spruce dominance. In particular, *reassembly* was most likely when Engelmann spruce mortality was high but subalpine fir mortality was low (Figure 5a) or when subalpine fir recruitment was high and Engelmann spruce recruitment was low (Figure 5c), likely leading toward dominance by subalpine fir.

3.7 | Future Scenarios

Future scenarios indicated that the distribution of predicted joint trajectories is more sensitive to the amount and severity of fire on the landscape than to predicted climate change under the SSP3-7.0 emissions scenario (Figure 6). In all three disturbance scenarios (low, observed, and high), the proportion of spruce-fir forest area range-wide predicted to fall within each joint trajectory category was largely constant across time periods (2010–2019, 2040–2050, 2070–2080; Figure 6a–c). However, we found major differences between disturbance scenarios for any single time period—for example, moving from a low-disturbance to high-disturbance scenario in the near-future period (2040–2050) led to the predicted area of *replacement* approximately tripling while *resilience* decreased by ~80%.

To explore how these results may inform near-term conservation and management decision-making, we highlighted the predicted geographic distribution of certain trajectories in three specific cases (Figure 6). These are: (1) *replacement* under a low-disturbance scenario, highlighting regions where spruce-fir forests are unlikely to persist even under benign conditions; (2) *resilience* under a high-disturbance scenario, highlighting regions unlikely to undergo decline even under the most challenging conditions; and (3) the change in the probability of *resilience* when moving from high to low-disturbance scenarios, highlighting regions that are sensitive to changes in severity and extent of fire on the landscape. We assessed these three cases under

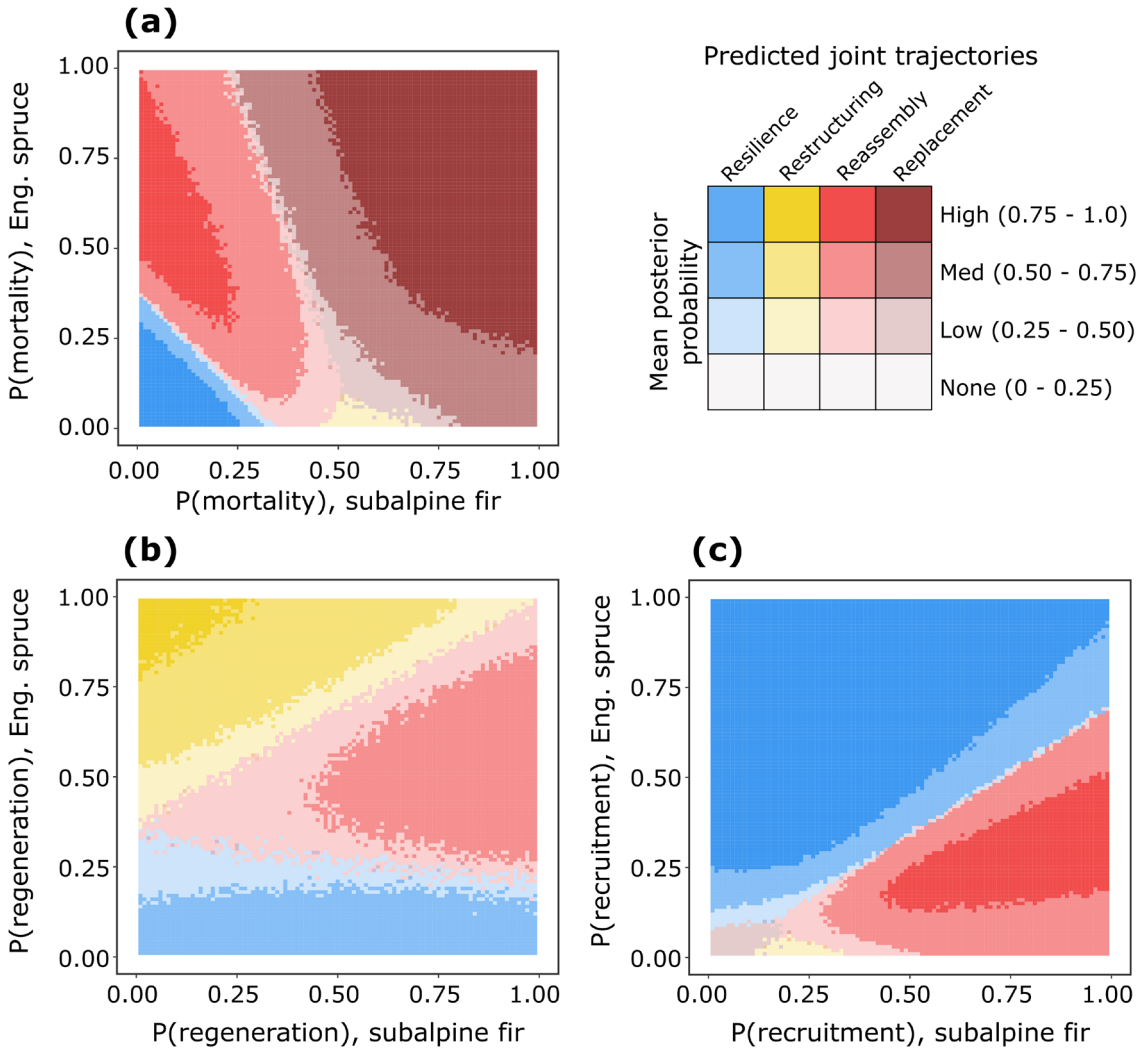

FIGURE 5 | Multinomial classification model predictions of joint trajectories in response to combinations of mortality (a), regeneration (b), and recruitment (c) probabilities for subalpine fir (*x*-axes) and Engelmann spruce (*y*-axes). Colors correspond to joint trajectories: Resilience (blue), restructuring (gold), reassembly (red), and replacement (maroon). Color shade reflects the mean posterior probability of the most likely predicted trajectory. Predictions reflect partial model effects generated by holding the other two demographic rates constant at their observed mean while varying mortality (a), regeneration (b) or recruitment (c) independently for each species.

projected 2040–2050 climatic conditions, to reflect the decadal timescales that forest management planning typically reflects. We found regions with an elevated probability of *replacement* even under low levels of disturbance in high-elevation parts of the Oregon and Washington Cascades, parts of northern Idaho, and scattered pockets in the central and southern Rocky Mountains (e.g., central Wyoming, southern Colorado; Figure 6d). *Resilience* was still highly likely in high-disturbance scenarios in lower-elevation regions of the Oregon and Washington Cascades, in northeastern Oregon and western Idaho, and in parts of the Rocky Mountain Front in central Colorado (Figure 6e). When moving from a high-disturbance scenario to a low-disturbance scenario, the probability of *resilience* increased by more than 0.75 across large swaths of the northern Rocky Mountains in northwestern Washington, Idaho, and western Montana, as well as parts of central Idaho. Probability of *resilience* decreased in the same scenario along the western slope of the Oregon and Washington Cascades, and in isolated pockets in Colorado (Figure 6f). Posterior predictions for all future climate and disturbance scenarios are presented in Figure S9.

4 | Discussion

Our analyses indicate that wildfire extent and severity will have larger impacts on the future trajectories of subalpine forests than projected climate change alone by the end of the century. Under constant levels of forest disturbance, we found that future projected climate change under a realistic emissions scenario (IPCC SSP3-7.0; Eyring et al. 2016) did not substantially change the distribution of predicted trajectories in subalpine fir—Engelmann spruce forests (Figure 6). However, these trajectories were highly sensitive to the amount of disturbance on the landscape at all future timesteps, such that increasing fire extent and severity induced a loss of resilient forest area and an increase in forest area projected to undergo replacement of some kind.

In light of recent projections of intensifying wildfire disturbance in subalpine and other forest types across western North America (Parks et al. 2023), our findings suggest that there may be opportunities for targeted management to increase the

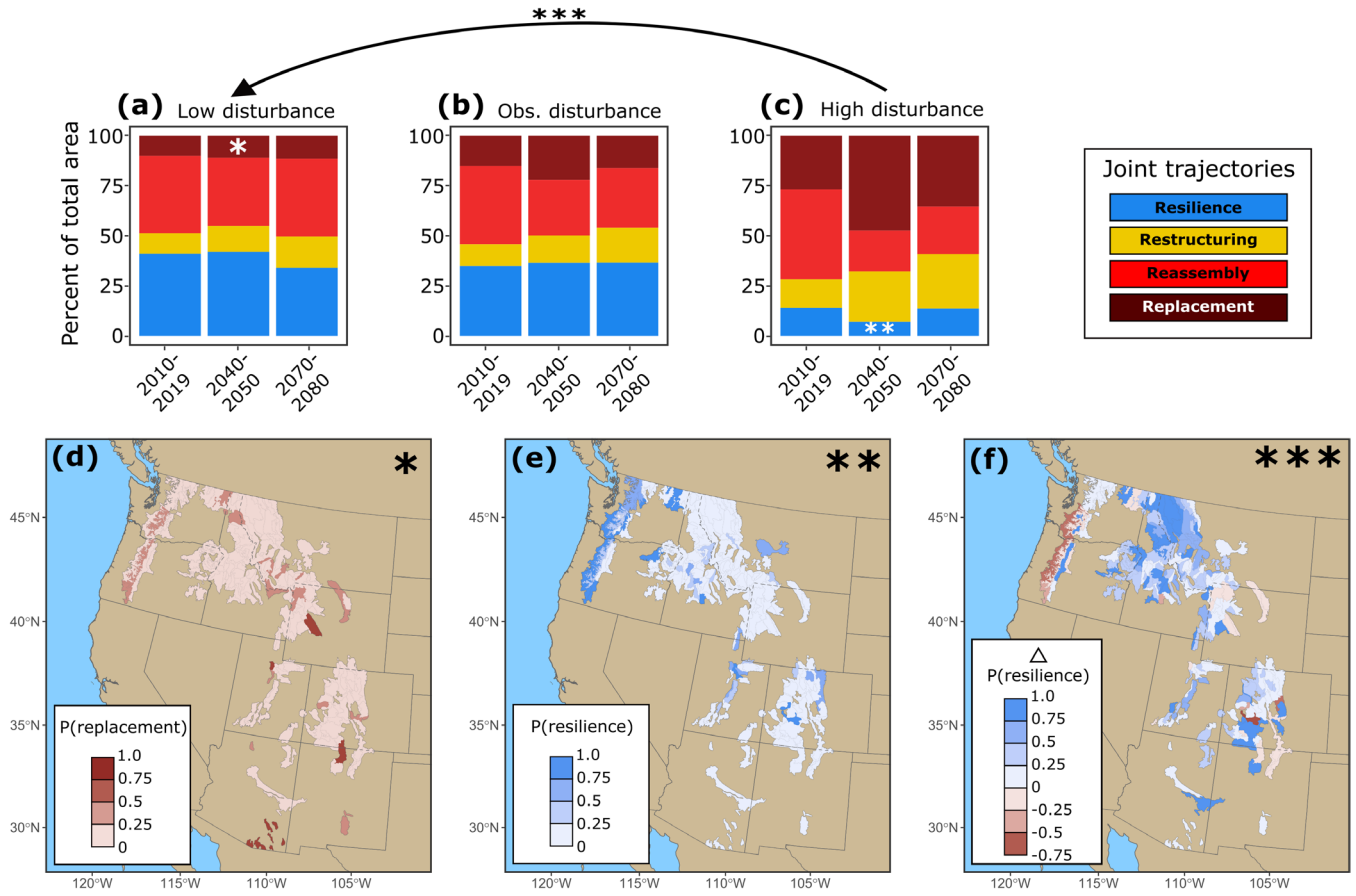

FIGURE 6 | Posterior predictions of subalpine fir-Engelmann spruce joint trajectory probabilities at different timesteps under the SSP3-7.0 emissions scenario, with varying levels of disturbance. Panel (a) shows the range-wide proportion of spruce-fir forest area predicted for each joint trajectory category (*resilience*—blue; *restructuring*—gold; *reassembly*—red; *replacement*—maroon) in a low-disturbance scenario (5% spruce-fir area burned at 50% mortality) at three different time steps (*x*-axis): 2010–2019 (corresponding to past estimated trends), 2040–2050, and 2070–2080. Panels (b, c) show the same for an observed disturbance scenario (area burned and mortality reflect observed rates during 2000–2009 to 2010–2019 inventory period) and a high-disturbance scenario (20% spruce-fir area burned at 90% mortality), respectively. Panel (d) shows the predicted probability of replacement within ecoregion subsections during 2040–2050 in the low-disturbance scenario, corresponding with the (*) in panel (a). Panel (e) shows the predicted probability of resilience for the same time period in a high-disturbance scenario, corresponding with the (**) in panel (c). Panel (f) shows how the predicted probability of resilience changes when moving from a high-disturbance scenario to a low-disturbance scenario, corresponding with the arrow (***) between panels (c) and (a). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

resilience of the subalpine forests we assessed. We found that reducing fire severity and extent in certain regions is likely to have a large impact on forest resilience—in some cases, increasing the probability of a resilient trajectory by more than 75% (Figure 6). These opportunities are concentrated in the northern Rocky Mountains in western Montana and northern Idaho, with smaller areas scattered throughout central Idaho and further south (Figure 6f). Following the Resist–Accept–Direct framework for conservation decision-making and prioritization (Lynch et al. 2021; Schuurman et al. 2020), management aimed at directing future changes toward lower-intensity disturbance regimes may be a highly effective strategy for increasing spruce-fir resilience in these regions. How this strategy relates to historical subalpine forest regimes varies considerably. For example, tree-ring and pollen-based fire regime reconstructions for subalpine forest types prior to Euro-American settlement indicate a wide range of fire return intervals from less than 20 years (Murray, Bunting, and Morgan 1998; Sherriff, Veblen, and Sibold 2001; Sibold and Veblen 2006) to more than 150 years (Anderson et al. 2008; Arno 1980). While fires in subalpine forests tend to be high-severity, there is also evidence for relatively frequent low-severity ground fires in some systems (i.e., moist and cold subalpine forests in the northern Rockies; Arno 1980). This variability may have been instrumental in creating past resilience in subalpine forest systems by promoting landscape-scale disturbance mosaics (Cansler and McKenzie 2014). With this in mind, we note that the spatial scale of our analyses (ecoregion subsections) is fairly large relative to both the spatial scale of biophysical variation in mountainous regions (Dobrowski 2011; Dobrowski and Parks 2016) and the size of typical forest management treatments (10s—100 s ha). As a result, it is likely that considerable heterogeneity in observed forest trajectories, their responses to global change, and the effects of past disturbances exists at smaller scales than those for which our data were suited.

While evidence from subalpine forests is sparse compared to lower-elevation forest types, recent work has highlighted the effectiveness of mechanical thinning and prescribed fire at reducing subsequent wildfire severity (Davis et al. 2024). Besides reducing live fuels available for wildfire, our results

indicate that reducing stand density through thinning may also benefit subalpine forests by increasing the probability of regeneration and recruitment (Figure 4). However, implementation of these treatments in any given landscape depends on more than potential ecological benefit. Given the lack of fire-resistant traits among subalpine tree species, low-severity prescribed burns may be far more difficult to carry out in these forest types than in lower montane forests dominated by thick barked, fire-resistant species like ponderosa pine (*P. ponderosa*) or Douglas fir (*P. menziesii*). Excessive mortality of subalpine tree species could potentially be mitigated through fuel reduction techniques like post-thinning pile burning; however, it is unclear whether these approaches can be scaled up to landscape-level treatments, and whether they induce the same ecological response as broadcast burning or other larger-scale treatments. Further, a recent study focusing on priority landscapes under the US Forest Service Wildfire Crisis Strategy found that operational (e.g., terrain and road access) and administrative constraints reduced the forested area available for mechanical fuel reduction by more than 70% (Woolsey et al. 2024). These constraints may be particularly relevant for management of the subalpine forests we focused on in this study. Across the western United States, 32% of all subalpine fir—Engelmann spruce forest occurs on "reserved" federal land where many management actions are statutorily prohibited (Table S2; USDA Forest Service 2023). This designation includes national parks, monuments, and areas managed under the Wilderness Act of 1964. In the northern Rocky Mountains, where our results indicate reducing disturbance is most likely to increase subalpine forest resilience, 27% of spruce-fir forests are in reserved areas; in the Pacific Northwest, this increases to 57% (Table S2; Figure 6). Further, even in areas without administrative or statutory constraints (e.g., general forest), treatments in many subalpine landscapes may be precluded by remoteness, difficult access, or topography (Woolsey et al. 2024).

An alternative or complementary approach to bolstering subalpine forest resilience in high-impact regions (i.e., those highlighted in Figure 6f) could involve landscape-scale mosaics of fire age, size, and severity (Cansler and McKenzie 2014). Wildfire in cold wet systems like Engelmann spruce—subalpine fir forests can be strongly self-regulating under certain conditions and at certain spatial and temporal scales (Parks et al. 2015). While we were unable to capture these dynamics in our analyses here, there is abundant evidence that previous wildfires are one of the strongest controls on subsequent fire extent and severity (Cansler et al. 2022; Davis et al. 2024; Holsinger, Parks, and Miller 2016; Parks et al. 2015, 2016; Rollins, Morgan, and Swetnam 2002). Though similar stabilizing feedbacks could also be created by prescribed burning or other fuel reduction treatments (Cansler et al. 2022; Davis et al. 2024), natural ignitions have the potential to do so in areas that are operationally or administratively precluded from treatment. A compelling example of this has been observed in certain high-elevation wilderness areas subjected to only limited fire suppression (e.g., the Selway-Bitterroot Wilderness Complex; Morgan et al. 2017; Parks et al. 2015), where subalpine forests have been resilient to both frequent and severe wildfires over the past several decades (Jaffe et al. 2023). Similarly limiting suppression of low-risk natural wildfire ignitions in high-elevation forests (i.e., a "progressive" wildfire suppression strategy, *sensu* Kreider et al. 2024) could be a productive strategy for decreasing future fire activity and supporting the formation of resilient landscape-scale disturbance mosaics. However, given recent increases in wildfire size and severity (Higuera, Shuman, and Wolf 2021; Higuera and Abatzoglou 2021; Parks et al. 2023), this approach needs to be balanced against potential loss of property, natural resource value, and human health and safety.

Our analyses also identified regions where system-wide replacement is likely even in low-disturbance future scenarios (Figure 6d). In these landscapes, it is unlikely that reducing disturbance extent or severity will result in a resilient spruce-fir forest system, either due to underlying demographic constraints or to the effects of projected climatic changes. In some of these regions, subalpine forests may transition to lower-elevation montane forest types as species associated with warmer and drier conditions shift their distributions upslope, as suggested by the trends we estimated in similar regions between 2000–2009 and 2010–2019 (Figure S2). Finally, we identified areas that are highly likely to be resilient even in high-disturbance scenarios. These regions may constitute future refugia from the worst demographic impacts of disturbance for subalpine fir and Engelmann spruce—for example, regions where climatic conditions are such that regeneration and recruitment can more easily offset high levels of disturbance-related mortality. These areas are uncommon, making up only ~7% of current spruce-fir forest area, and may thus constitute priority areas for management or conservation designed to preserve their refugial nature.

The overall sensitivity of joint population trajectories to disturbance that we found reflects how subalpine fir and Engelmann spruce mortality, regeneration, and recruitment respond to fire extent and severity. Specifically, fire negatively impacted the demography of both species by raising the probability of mortality while lowering the probability of regeneration and subsequent recruitment (Figure 5). This effect was more pronounced for subalpine fir than for Engelmann spruce, perhaps reflecting subalpine fir's life history strategy of faster growth, lower survival, and more regeneration. Both species' negative demographic responses to fire were stronger than their responses to temperature anomalies, moisture deficit anomalies, or competition (Figure 5; Figures S3–S5). However, we did find evidence of energy limitation in these forests, insofar as warming was associated with lower mortality for both species, and for Engelmann spruce in particular (Figure 5; Figures S3–S5). The effect of temperature and moisture deficit anomalies on the demography of both species did vary with climatic context, such that warming positively impacted their demography by lowering mortality and increasing regeneration and recruitment in colder regions, but not in warmer regions (Figures S7 and S8). While other subalpine and boreal conifers have displayed similar patterns (Dudney et al. 2023; Wilmking et al. 2004), interpreted as evidence of an energy-limitation to moisture-limitation gradient, our findings here were less clear. Such a gradient could result in directionally opposing demographic responses to future climatic changes across a species' distribution; however, in our future projections the impact of fire disturbance far outweighed these climatic effects.

Recent work by Davis et al. (2023) focusing on post-fire regeneration found similar negative relationships between wildfire severity and subalpine fir and Engelmann spruce recruitment probabilities as those revealed by our analyses, such that fire severity and seed availability were dominant constraints on post-disturbance regeneration. However, in contrast to our findings, they also found that mid-century climate impacts may outweigh those of fire severity in some regions (Davis et al. 2023). We attribute this difference to two aspects of our respective analyses. First, our analyses included forest stands that were both disturbed and undisturbed during plot remeasurement intervals. Prior wildfire disturbance can have dramatic impacts on the biophysical environment that establishing seedlings experience (Wolf et al. 2021), suggesting that regeneration and recruitment responses to recent climate anomalies may be stronger in disturbed versus undisturbed stands. Further, an unavoidable consequence of the FIA remeasurement cycle and diameter size thresholds for delineating age classes is that our regeneration analyses are unlikely to actually capture the year of germination and any effects that climate anomalies may have had on germination success. Our results may thus underestimate the sensitivity of regeneration to climate anomalies relative to studies that focus on post-disturbance effects and those with finer temporal resolution. Second, our findings suggest that subalpine fir—Engelmann spruce forests are energy-limited through much of their distribution, except perhaps in the very warmest regions (Figure S7). This is reflected in a negative mortality response to warming temperatures (Figure 4a), such that lower future mortality may demographically offset the impact of warming on regeneration and recruitment (Figure 4e,i).

Our multinomial classification model found that the demography of Engelmann spruce and subalpine fir combine to predict community trajectories in ways that once again reflect differences in the life history strategies of the two species (Figure 5). Specifically, positive community trajectories are possible under a wider range of demographic conditions for subalpine fir, a result of the species' faster, more dynamic demographic strategy. For instance, we found that replacement required high levels of subalpine fir mortality, but was possible even at low levels of Engelmann spruce mortality (Figure 5a). This asymmetry is likely due to different levels of regeneration potential between the two species—subalpine fir tends to have a higher probability of regeneration under most conditions (Figure 4; Andrus et al. 2018), and can thus more easily balance elevated mortality than Engelmann spruce. On the other hand, high levels of Engelmann spruce regeneration mostly corresponded with restructuring trajectories (Figure 5b), indicating high turnover in one or both species (Box 1). It seems that this situation would be most likely in post-disturbance landscapes, where ample canopy gaps allow for easier establishment of shade-intolerant Engelmann spruce seedlings. Resilience was similarly predicted under a wide range of recruitment probabilities for subalpine fir, but only at the upper end of recruitment for Engelmann spruce (Figure 5c). Taken together, this suggests that Engelmann spruce population dynamics may be a better indicator of overall forest resilience in this system than subalpine fir.

Our goal in this set of analyses was to characterize large-scale patterns in how climate and disturbance influence the resilience of subalpine fir—Engelmann spruce forests across the western United States. As a consequence of this large scope, our findings may not represent the best possible predictions of specific future states for individual landscapes or locations, and should not be interpreted as such. This is particularly relevant in light of the patchwork of past management legacies impacting subalpine and other forest types in the western United States. For example, the baseline period against which population change is calculated in our analyses is the 2000–2009 FIA inventory period. Baseline conditions during this period are strongly influenced by geographically-variable contemporary forest management, following more than 100 years of fire suppression and missing cultural burning (Prichard et al. 2021). As a result, the trajectories we estimated between 2000–2009 and 2010–2019 FIA inventory period (Figure 3a) should be interpreted as relative to these modified conditions. For example, *resilience* in some areas may reflect forest densification as a byproduct of recent fire suppression; on the other hand, *restructuring* or *replacement* may represent a return to historical conditions. As such, we caution against assigning normative values to these categories—while our estimates do accurately represent current trends, whether that trend is desirable or not depends heavily on local and historical context.

Finally, in order to make inference at large ecoregional scales, our analyses necessarily sacrifice resolution of smaller-scale local variation in forest conditions and responses to global change in favor of larger landscape-scale patterns. This limits the applicability of our findings to broader scales while also highlighting opportunities for further study. For example, recent work has demonstrated the importance of forest microclimate effects on understory plant community responses to global change (De Frenne et al. 2021; Zellweger et al. 2020). Tree seedling establishment is likely to be highly sensitive to these effects, especially in a post-disturbance context (Wolf et al. 2021). Subsequent work investigating feedbacks between macroclimate-driven and/or disturbance-driven changes to forest microclimates and forest community trajectories would be productive in gaining a better understanding of ecological scaling in these systems. Additional opportunities for further study involve the temporal scales relevant to different forest responses to global change. In the analyses presented here, we combine information from forest stands that are at different stages of development and/or post-disturbance recovery. However, as a forest responds to discrete or continuous change drivers, it likely moves through a succession of trajectories as we define them here. For example, a stand may be on a *replacement* trajectory shortly after a major disturbance, but trend toward *resilience* on longer timescales. Further, these dynamics may take longer than the 20 years reflected in available FIA remeasurement data to develop. Gaining more temporal resolution and depth is thus critical to building a better understanding of transient forest community dynamics in an age of rapid global change. Recent work integrating tree-ring and other timeseries with forest inventory data is especially promising, and has already been productive in this respect (DeRose, Shaw, and Long 2017; Evans et al. 2017; Heilman et al. 2022).

In this study, we linked species' demographic rates and global change responses to forest community trajectories (i.e., resilience, restructuring, reassembly, replacement). In doing so, we applied reorganization concepts from Seidl and Turner (2022) to observed forest changes at large scales and extended them to consider both post-disturbance and climatically-driven cases.

We did this by organizing known or knowable information (i.e., trends in tree basal area and abundance) within and across species to reflect stand development, reorganization, and related forest dynamics (Box 1). While we developed and applied this framework in the context of a simple two-species system, we believe that our approach could be generalized and applied broadly to different forest types and species assemblages. In order to do so, there are several conceptual issues that need to be addressed. For example, in the case of a more diverse species assemblage, it is unclear what proportion of species exhibiting a negative population trend should trigger a corresponding change in the overall community trajectory. A species that is rare or existing in a marginal or sink population might have a more minor impact on a community's trajectory than a species that constitutes a major portion of total stand basal area. Similarly, a species that contributes some unique functional diversity to the forest may have an outsize impact compared to a species that is functionally redundant. Taking a functional traits-based approach could help in this regard, as suggested by Seidl and Turner (2022), and complement the demographic approach we take in this study. Resolving these and similar questions could help in the development of a generalized, practical, and actionable framework for describing forest trajectories and subsequent management priorities in light of pervasive global change drivers.

Author Contributions

Daniel L. Perret: conceptualization, formal analysis, investigation, methodology, writing – original draft, writing – review and editing. **David M. Bell:** conceptualization, funding acquisition, methodology, supervision, writing – review and editing. **Harold S. J. Zald:** conceptualization, funding acquisition, methodology, project administration, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Analytical code supporting the findings of this study is openly available in Zenodo at https://doi.org/10.5281/zenodo.14642265, and GitHub at https://github.com/daniel-perret/SpruceFirResilience/tree/v1.0. The data that support the findings of this study are publicly available from the USDA Forest Service Forest Inventory and Analysis Database at https://research.fs.usda.gov/products/dataandtools/tools/fia-datamart (version 2.0.1) and from ClimateNA at https://climatena.ca/ (version 7.42).

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Supporting Information

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