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RESEARCH ARTICLE

Decadal drivers of quaking aspen decline across the Western United States

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Abstract

1. Although forests serve critical roles maintaining biodiversity and provisioning ecosystem services, many tree species world-wide have experienced population declines due to climate change and other related factors. One such species is quaking aspen (*Populus tremuloides*), the most widely distributed tree species in North America, which has undergone reductions in survival, growth, and/or recruitment in many parts of its range.
2. To understand the patterns in and drivers of aspen performance across its range in six western US states, we evaluated the importance of 44 climatic, topographic, and forest structure variables in explaining mortality, growth and adult recruitment rates in 263 plots over a 9-to-13-year period.
3. Aspen experienced substantial mortality during this study, with 4% of trees on average dying each year. In addition, aspen performed differently from co-occurring conifers, with their dominance declining during the study while conifers increased. Mortality rates for aspen increased with higher aspen canopy dieback and dead aspen in the initial sampling and decreased with increased initial dominance of aspen and conifers as well as increased precipitation and reduced aridity. Growth rates of aspen increased with higher temperatures and winter precipitation, in more upland and south-facing locations, and decreased with warmer and drier conditions relative to the historic baseline, greater initial aspen canopy dieback, higher initial dead aspen and greater initial dominance of aspen and conifers. Increased adult recruitment was associated with higher temperatures and winter precipitation as well as more upland and south-facing locations, whereas reduced recruitment occurred with higher initial aspen and conifer dominance, greater amounts of initial dead aspen, and hotter and drier conditions relative to the historic baseline.
4. *Synthesis*. Across the western United States, the health and dominance of aspen declined during a decade-long study, with annual mortality being three times greater than the recruitment of new adults. We frequently detected long-lasting effects, where areas that were challenging or optimal for aspen at the outset of our study continued to be so over the next decade. Intra- and interspecific

competition as well as hotter and drier conditions associated with climate change adversely influenced aspen populations.

KEYWORDS
aspen, climate change, demographic rates, growth rates, interspecific competition, intraspecific competition, large plot network, mortality rates, *Populus tremuloides*, recruitment rates, western United States

1 | INTRODUCTION

Forests cover 30% of the globe's terrestrial surface area (Keenan et al., 2015) and provide a diverse range of ecosystem services, including the maintenance of biodiversity, hydrological and nutrient cycling, and carbon sequestration (Bonan, 2008; Pan et al., 2011; Trumbore et al., 2015). However, there is growing concern that many tree species are in decline due to extensive tree mortality, contracting stand cover and/or reduced recruitment (Allen et al., 2015; Anderegg et al., 2015; Breshears et al., 2005; Cohen et al., 2016; Hartmann et al., 2018; Hartmann et al., 2022; Luo & Chen, 2015; Millar & Stephenson, 2015; Peng et al., 2011; Trumbore et al., 2015; Van Mantgem et al., 2009). These episodic events can arise gradually or rapidly and involve the widespread loss of tree and stand health and overall vigour, leading to canopy die-off and eventual death. For example, Allen et al. (2010) conducted a global assessment of forest health and reported widespread evidence of increased tree mortality since 1970 in each of the wooded continents on Earth, spanning diverse forest types and climatic zones. McDowell et al. (2018) found that the mortality rates for trees in old-growth forests in the Amazon Basin have been increasing since 1980. In addition, Stanke et al. (2021) reported that five of the eight most abundant tree species in the western United States exhibited rapid population decline from 2001 to 2018.

Increased temperatures and drought associated with anthropogenic climate change are frequently recognized as important drivers of tree decline around the world (Allen et al., 2010, 2015; Hammond et al., 2022; Yi et al., 2022). These factors can themselves lead to tree mortality and can also cause trees to become more susceptible to attack by insect herbivores and plant pathogens (Simler-Williamson et al., 2019; Teshome et al., 2020; Velásquez et al., 2018). However, it is often unclear the degree to which decline is occurring across the full geographic ranges of tree species and the extent to which climatic and topographic factors—along with stand structure, forest composition and biotic agents—mediate tree performance. Thus, understanding the dynamics and spatial extent of tree decline, as well as the many individual and interacting factors that drive such decline, is of great importance, given the essential role that trees play in ecological systems.

A growing number of studies have reported that quaking aspen (*Populus tremuloides*), the most widely distributed tree species in North America (Michaelian et al., 2011; Worrall et al., 2013), is experiencing large-scale mortality as well as reduced recruitment in multiple areas of its geographic range (Crouch et al., 2023; Rogers et al., 2020; Singer et al., 2019; Worrall et al., 2013). For example, in a continent-wide review of data from close to 4000 plots across North America, Refsland and Cushman (2021) reported that mortality rates of aspen increased and growth rates decreased over the past two to three decades in numerous biomes. Such reports are particularly concerning given that aspen is one of the few deciduous trees in otherwise conifer-dominated montane landscapes (Rogers et al., 2007) and is recognized as a foundation and/or keystone species (Rogers et al., 2020) that plays critical roles in carbon cycling (Huang & Anderegg, 2012; Michaelian et al., 2011), mediating fire dynamics (Harris et al., 2025) and supporting high levels of biodiversity (Kuhn et al., 2011).

Numerous biotic and abiotic factors have been implicated in the decline of aspen. Many authors have found that anthropogenic climate change and associated water stress are important predictors of aspen dieback and mortality (Anderegg et al., 2013, 2015; Chen et al., 2018; Worrall et al., 2013). Fire suppression and associated conifer encroachment have also been reported to drive aspen mortality (Brewen et al., 2021; Shinneman et al., 2013; St. Clair et al., 2013). Other investigators have shown that fungal pathogens (Marchetti et al., 2011; Zegler et al., 2012) and herbivory by insects (Chen et al., 2018; Crouch et al., 2024) and both wild and domestic ungulates (Beschta & Ripple, 2009; Reikowski et al., 2022; Rhodes et al., 2018) reduce growth, recruitment and overall health of aspen populations. Lastly, forest structure and the presence of competing conifers may influence aspen mortality, growth and recruitment in many parts of its range (Bell et al., 2014; Hember et al., 2017; Kweon & Comeau, 2019; Trugman et al., 2018; Zhang et al., 2015). For example, Strand et al. (2009) identified three unique types of biophysical sites that make aspen more or less vulnerable to competing conifers. In their study, south-facing sites exposed to higher levels of solar radiation and often dominated by rock talus were less susceptible to conifer encroachment compared to more mesic forest sites with deeper soils. Likewise, they found that aspen located near springs or other highly mesic sites showed lower rates of conifer growth compared to the better drained mixed aspen-conifer forests. Similarly, studies of aspen in the Great Basin (Kulakowski et al., 2004; Shinneman & McIlroy, 2019; Yang et al., 2015) have suggested that aspen in arid regions may be less susceptible to conifer encroachment compared to their counterparts in the Rocky Mountains and the Sierra Nevada, yet face greater threats due to climate change because they are already located at the dry end of their range. Hence, it is

critical to understand how topography and geography influence aspen performance by influencing both climate and competition with co-occurring conifers.

Although there is strong evidence for declining health and performance of aspen populations and the importance of various biotic and abiotic drivers, considerable spatial variation in these patterns and mechanisms has been repeatedly observed. For example, Refsland and Cushman (2021) found that mortality rates for aspen in North America varied across the five biomes it inhabits, increasing in boreal forests, montane coniferous forests and prairie parklands, decreasing in mixed deciduous-coniferous forests, and not changing in deciduous forests. Even within each of these biomes, investigators have detected substantial spatial variation in mortality, growth and recruitment (Kulakowski et al., 2013). Similarly, studies have found considerable spatial variation in how well climate, drought, wildfire and various other factors predict aspen performance (Dudley et al., 2015; Huang & Anderegg, 2012; Kane et al., 2014; Michaelian et al., 2011; Shinneman & McIlroy, 2019; Worrall et al., 2013; Zegler et al., 2012). Such variation should not be surprising given the extensive geographic range and immense topographic, climatic and stand structure heterogeneity that aspen experiences. The key is to develop a comprehensive understanding of this variation and the relative contribution of multiple, potentially interacting drivers of demographic rates in different parts of aspen's range. To date, few studies of aspen have quantified their mortality, growth and recruitment rates across broad regions and at decadal time scales and related them to climatic, topographic and vegetation characteristics. Here, we seek to fill this research gap to understand the long-term trends in and drivers of aspen health. Understanding how these multiple—and potentially competing—drivers of demographic rates vary across geographic space is critical for understanding the long-term persistence of this widespread and influential tree species.

We used an extensive network of plots distributed across six states in the western United States to address the following questions: (1) To what extent do the mortality, growth and recruitment rates of mature aspen vary across different geographic regions over a 10- to 13-year period? (2) Do aspen and co-occurring conifers differ in their performance across this plot network during the same time period? and (3) What climatic, topographic and stand structure variables best predict the recruitment, growth and mortality rates of mature aspen over a 10–13 period? By studying aspen populations across a large heterogeneous landscape, we aim to better understand the complex, and potentially opposing, drivers of mortality, growth and recruitment rates of aspen.

2 | METHODS

2.1 | Study system

Our study was conducted in six topographically heterogeneous landscapes in the western United States—California, Nevada, Idaho, Montana, Wyoming and Utah (Figure 1). Mean annual precipitation varied greatly across this study region, being wettest in the Sierra Nevada and Cascade Mountains (368–1449 mm per year) and driest in the Great Basin (264–470 mm per year). The Sierra Nevada and Cascade portion of the study region experienced a Mediterranean-type climate, receiving 5%–10% of their annual precipitation during the summer. The Great Basin received 15%–20% of its precipitation during the summer, while the Rocky Mountains, Wasatch Mountains

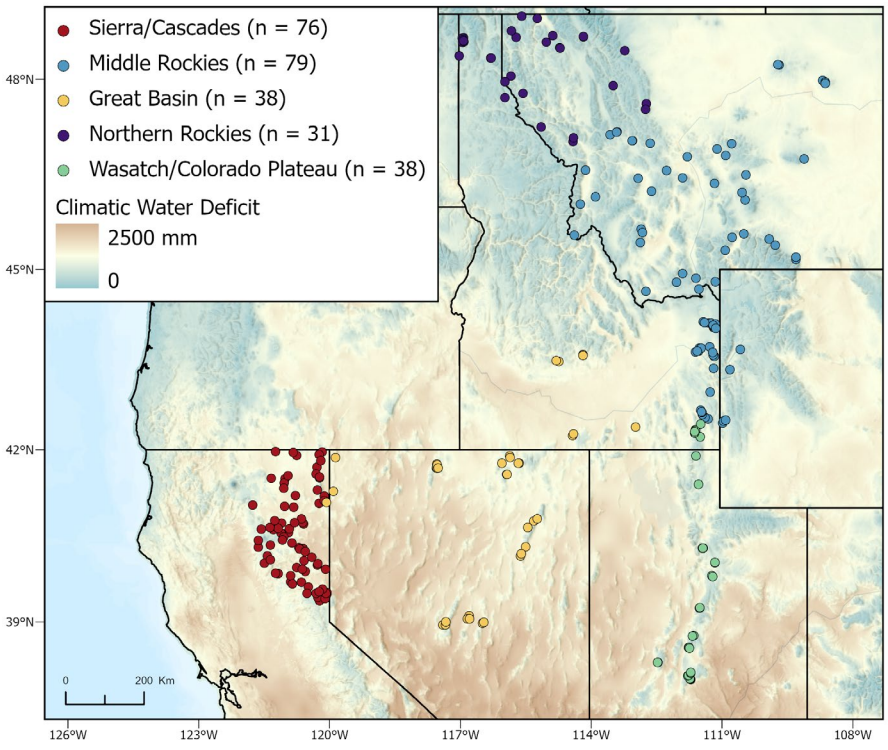

FIGURE 1 Locations of the 263 plots in the western United States used to study demographic rates of aspen. Plots are coloured according to their assigned ecoregion, adapted from the US Environmental Protection Agency (Omernik & Griffith, 2014). The base layer for this map depicts climatic water deficit.

and Colorado Plateau received 30%–40% of their precipitation during the summer (Romme et al., 2009).

Quaking aspen is a fast-growing deciduous tree species that occurred in our field plots at elevations ranging from 690 to 3155 m. Although it can reproduce sexually (Kreider & Yocom, 2021; Mock et al., 2008), aspen also propagates asexually by suckering from roots, and clones can be very large and long lived (Kemperman & Barnes, 1976). This species commonly regenerates after fire, varies in ploidy level across its range, and exists as both successional stands and relatively stable, persistent stands (Callahan et al., 2013; Shinneman et al., 2013).

At our sites in the Sierra Nevada and Cascade Mountains, aspen co-occurred with numerous conifer species including ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), lodgepole pine (*P. contorta*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), red fir (*A. magnifica*), Douglas-fir (*Pseudotsuga menziesii*) and western juniper (*Juniperus occidentalis*). In the Great Basin, aspen co-occurred with single-leaf pinyon (*P. monophylla*), limber pine (*P. flexilis*) and Douglas-fir. In the Rocky Mountains, aspen co-occurred with subalpine fir (*A. lasiocarpa*), Douglas-fir, limber pine, lodgepole pine and Utah juniper (*Juniperus osteosperma*). In the Wasatch Mountains and Colorado Plateau, aspen co-occurred with Engelman spruce (*Picea engelmannii*) and subalpine fir. In all the ecoregions where our study occurred, non-conifer tree species other than aspen were very uncommon, but included bigtooth maple (*Acer grandidentatum*), black cottonwood (*Populus trichocarpa*), willow (*Salix* spp.) and alder (*Alnus* spp.).

2.2 | Aspen plot network

We addressed our research questions with data collected from 263 long-term plots established by the US Forest Service's Forest Health Protection Program (Cluck, 2011; Guyon & Hoffman, 2011; Steed & Kearns, 2010) in mature aspen stands throughout California, Nevada, Idaho, Montana, Utah and Wyoming (Figure 1; Table 1). We assigned each plot to one of five ecoregions, adapted from Level II and III ecoregions as defined by the US Environmental Protection Agency (Omernik & Griffith, 2014): Sierra/Cascades, Great Basin, Northern Rockies, Middle Rockies and Wasatch/Colorado Plateau.

All study plots were randomly chosen among mapped aspen stands and were within a half mile of roads for ease of access. Plots had to contain at least two live mature aspen stems in California (Cluck, 2011), whereas they had at least seven mature aspen stems in Nevada, Utah, Wyoming, Idaho and Montana (Guyon & Hoffman, 2011; Steed & Kearns, 2010). We defined mature aspen stems as those with a diameter at breast height (DBH) of ≥12.7 cm. For each of our 263 plots, the average distance to their nearest plot was 11.0 km (±15.3 S.D.).

All plots were circular in shape, with an 8 m radius, with plot centres monumented with metal posts. All trees with DBHs of ≥12.7 cm were permanently marked with metal tags. The location of all plot centers was documented using GPS units with submetre accuracy.

2.3 | Field sampling

As shown in Table 1, all 263 plots were initially sampled between 2006 and 2009 and then again between 2017 and 2019 to assess mortality, growth and recruitment rates of mature aspen stems. During the first and second samplings, the DBH, species and status (alive/dead) of aspen were recorded for all mature trees (DBH ≥12.7 cm) in each plot. A tree was classified as being alive if it had green, living tissue just under the bark on the main stem, even if 100% of the branches/leaves appeared dead. In addition, during the first sampling, canopy dieback was quantified for mature aspen stems using four categories: no dead branches in crown; 1%–33% of branches in crown dead; 34–66% of branches in crown dead; and 67%–100% of branches in crown dead.

2.4 | Response variables

We used data from our field sampling to calculate three plot-level response variables for mature aspen stems: annual percent mortality, annual percent growth rate and annual percent recruitment of mature stems. All response variables were normalized by the number of years between sampling times to account for differences in the study period among plots. Annual percent mortality was calculated as follows:

$$\text{Annual percent mortality rate} = \frac{\left(n_I - n_F\right)/n_I}{Y_F - Y_I}\,(100\,\%)$$

where n_I and n_F are the initial and final number of live mature aspen stems, respectively, and Y_I and Y_F are the initial and final year of sampling, respectively.

TABLE 1 Characteristics of the 263 plots used to assess aspen performance in this study.

Ecoregion	No. plots	First census	Second census	Elevation (m)	MAT (°C)	MAP (mm)	CWD (mm)
Sierra/Cascades	75	2009	2019	1272-2231	3.5–8.6	369–2423	242–988
Great Basin	37	2006–2009	2019	1825-2883	2.3–6.8	331–715	544–1142
Wasatch/Colorado Plateau	40	2006, 2007	2019	2037-3155	0.8–4.5	545–958	218–620
Middle Rockies	80	2006, 2007	2017–2019	2088-2450	−0.1-6.5	341–879	257–1008
Northern Rockies	31	2007, 2008	2017–2019	690–1605	3.7–7.4	408–1088	423–856

Note: See Steed and Kearns (2010), Cluck (2011) and Guyon and Hoffman (2011) for additional details.

Annual percent growth rate was calculated as follows:

$$\text{Annual percent growth rate} = \frac{\left(\sum_{i=1}^{n_F} \frac{BA_{Fi} - BA_{Ii}}{BA_{Ii}}\right)}{Y_F - Y_I}(100\%)$$

where BA_{Ii} and BA_{Fi} are the initial and final BA, respectively, of each individual mature aspen stem *i*. For all analyses, the growth rate was log-transformed to meet model assumptions of normality of residuals.

We defined annual percent recruitment as the number of live aspen stems in each plot that transitioned into the mature stem size class during the study period, normalized by the number of mature aspen stems in the plot during the initial sampling to account for differences in overall stem densities. Annual percent recruitment was calculated as follows:

$$\text{Annual percent recruitment of mature stems} = \frac{\frac{n_R}{n_I}}{Y_F - Y_I}(100\%)$$

where n_R is the number of aspen stems newly recruited into the mature size class during the study period.

2.5 | Predictor variables

To identify patterns in and drivers of three demographic rates in quaking aspen, we selected 44 initial predictor variables relating to climate, topography and stand characteristics listed in Table S1 and summarized below. We included 20 climate-related variables because many studies had shown them to have strong effects on the demographic rates of aspen (see reviews by Kulakowski et al., 2013; Singer et al., 2019; Rogers et al., 2020; Refsland & Cushman, 2021). In addition, we included 12 variables related to the initial stand characteristics in our plots because we suspected that intraspecific and interspecific competition would be strong predictors of future aspen performance (see Bell et al., 2014). We also included 12 variables related to topography because we hypothesized that they would have a strong mediating influence on water and nutrient availability for aspen (Refsland & Cushman, 2021).

2.5.1 | Climate variables

We focussed on four general climate variables (Table S1): precipitation, minimum temperature, maximum temperature and climatic water deficit (CWD). Monthly data for each of these variables were obtained from the Basin Characterization Model (BCM) for 2006–2019. The BCM is a fine-scale (270 m) hydrological model that uses downscaled 800-m PRISM data (Daly et al., 2008), interpolated using gradient and inverse distance squared weighting onto 270 m DEM, and leverages an energy-balance model to calculate CWD (Flint et al., 2013). We summarized climate variables over the years of the study, starting at plot establishment and ending at resampling (i.e. 2006, 2007 or 2009 through 2017, 2018 or 2019—depending on a plot's history; see Table 1). We summarized climate seasonally during the study period by calculating the minimum, maximum and average values for the four climate variables in the spring (March–May), summer (June–August), fall (September–November) and winter (December–February). We also calculated climate annual anomalies for temperature (minimum and maximum), precipitation and CWD, as the difference between average conditions during the study period (e.g. 2009–2019 for plots in the Sierra/Cascades; see Table 1) and the 30-year normals from PRISM for 1981–2010.

2.5.2 | Topographic variables

To evaluate the influence of topography on aspen demographic rates, we derived the following variables: elevation, slope, aspect and heat load index (McCune & Keon, 2002). We calculated several additional variables derived from ⅓ arc-second (10-m) USGS digital elevation models: topographic convergence index (Beven & Kirkby, 1979), topographic position index, curvature, profile curvature and planform curvature (Table S1). Aspect was transformed into an index of southness by folding along the north–south line. We also created a version of aspect that was folded along the northeast–southwest line since southwest-facing slopes can experience more heating than directly south-facing slopes (McCune & Keon, 2002). The topographic convergence index is a proxy for cold air drainage and run-off accumulation based on the local slope and upslope area in the watershed. The topographic position index measures the elevation of a point relative to the average elevation of the neighbourhood surrounding the point (De Reu et al., 2013). We calculated the topographic position index for 100 m, 500 m, 2.25 km and 20–km-radius neighbourhoods. Curvature describes the degree of concavity or convexity surrounding each plot, with positive values associated with convex surfaces and negative values associated with concave surfaces. The profile curvature is calculated in the direction parallel to the slope and the planform curvature is calculated in the direction perpendicular to the slope.

2.5.3 | Initial stand characteristic variables

Because stand age, stem density and individual differences in tree size all likely influence aspen performance, we calculated the following metrics for mature trees (DBH ≥12.7 cm) relating to initial stand structure and composition: total basal area (BA), stem density, and mean basal area of individual trees per plot. Each of these metrics was calculated for several different subsets of the stand (e.g. live aspen only, live conifers only; see Table S1 for a complete list). Finally, we quantified the relative abundance of aspen in the initial sampling in two ways: the ratio of aspen trees to the total number of trees and the ratio of live aspen BA to the total live BA.

To account for differences in initial stand health among our plots, we included mean canopy dieback rating of all live mature aspen

stems in each plot (described in Field Sampling) in the initial sampling as a predictor variable in our analyses.

2.6 | Data analyses

2.6.1 | Comparison of aspen and conifer performance

To compare the demographic trends of aspen and co-occurring conifers across the different regions, we calculated the plot-level annual percent change in live BA of mature stems over the study period. This captured the combined effects of mortality, adult recruitment, and growth rates in a single metric. We analysed these data using a Bayesian model, with annual percent change in live BA predicted by tree group (aspen versus conifers) and ecoregion. Change in annual percent BA was modelled as a normal distribution. We used relatively vague priors for all coefficients, with means drawn from a normal distribution (mean = 0, SD = 10) and precision drawn from a gamma distribution (rate = 2, shape = 0.1). Pairwise comparisons between all groups were performed by sampling from the posterior distributions and estimating the probability that points drawn from one distribution were higher or lower than another. Groups were considered distinct when this probability exceeded 95%. Given that the comparison of trends among aspen and co-occurring conifers required plots to contain at least one mature conifer in the initial sampling, our analysis was restricted to a subset ($n = 234$) of the total number of plots ($n = 263$), none of which were in the Great Basin region. Analyses were performed using the jagUI package in R (Kellner & Meredith, 2019).

2.6.2 | Variation in demographic rates among ecoregions

To assess the degree to which mortality, growth and recruitment rates of mature aspen varied among our five ecoregions, we used Bayesian models where each of these variables was predicted by ecoregion. Mortality, growth (log-transformed) and recruitment rates (log-transformed) were modelled as normally distributed. We used relatively vague priors for all coefficients, with means drawn from a normal distribution (mean = 0, SD = 10) and precision drawn from a gamma distribution (rate = 2, shape = 0.1). Differences among groups were determined using the same pairwise posterior distribution method described previously. Analyses were performed using the jagUI package in R (Kellner & Meredith, 2019).

2.6.3 | Variable reduction of predictor variables

The complete set of 44 potential predictor variables—grouped into climate, climate anomalies, topography and initial stand characteristics—was too large for standard linear models (Table S1). We elected to reduce the dimensionality of this set of potential variables using principal component analysis (PCA), which created new composite variables that reflected underlying correlational structures among potential explanatory variables, and then became the predictor variables used in linear models. This procedure was achieved by performing four separate PCAs in the R statistics package (R Core Team, 2023), which reduced the number of predictor variables from 44 to eight. PCAs were generated for climate, climate anomalies, topography and initial stand conditions. All data were centred and *z*-transformed before performing each PCA. We then extracted the first few axes from each PCA (depending on the explained variance and the interpretation). Although PCA axes within an analysis are orthogonal, between different analyses, they can be correlated. Despite this, we did not find high correlations among composite variables and thus all were retained for analyses (Figure S1).

2.6.4 | Predicting aspen performance

To quantify the relationships between the composite predictor variables and each of our response variables, we used a Bayesian linear model with an error structure that incorporated geographic distances between plots. All composite predictor variables were z-transformed to compare the relative strength of effect sizes. Since preliminary analyses indicated that aspen canopy dieback rating at the start of the study was often an important predictor variable, we included it as a covariate in each model.

Annual percent mortality and relative growth rate of mature stems (log-transformed) were modelled as normally distributed variables. They were predicted using multiple regression models that included each of the composite predictor variables from PCA, aspen canopy dieback rating at the start of the study and a spatial error structure calculated from the coordinates of each plot. This was done in R using the spLM function in the SpBayes package (Finley et al., 2007). We used vague priors with means drawn from a normal distribution (mean = 0, SD = 10). Models were run with four chains, each consisting of 5000 iterations and a 1000 burn-in period. Model convergence was assessed by examining trace plots and the Gelman-Rubin convergence diagnostic associated with each parameter. For each model, we calculated an R^2 using the mean of the predictive distribution for each data point to calculate the mean squared error of the residuals.

Ideally, we would have modelled adult aspen recruitment rate employing the same approach that we used for adult mortality and growth rates. However, a substantial number of our plots did not exhibit any adult recruitment during the study period, which resulted in a response variable that was zero-inflated and did not meet the assumptions of a linear model. To address this issue, we modelled adult recruitment as a two-step process. First, we included all 263 plots and modelled whether any recruitment occurred as a binary response variable. Second, we restricted our analysis to those plots

with some adult recruitment and used the amount of adult recruitment as the focal response variable.

The annual percent recruitment of mature stems was modelled as a binary process using a generalized linear model with a binomial distribution and spatial error structure. Whether a site saw any recruitment was predicted using a multiple regression model that included each composite predictor variable (from PCA) and a spatial error structure calculated from the coordinates of each plot. This was done in R using the spGLM function from the SpBayes package (Finley et al., 2007). This model was run with four chains, each consisting of 10,000 iterations and a 1000 burn-in period. Model convergence was assessed by examining trace plots and the Gelman-Rubin convergence diagnostic associated with each parameter. For this model, we calculated a McFadden R^2 value by comparing the ratio of log likelihood from the full model to the log likelihood of an intercept-only model. We then modelled the amount of recruitment by removing all zeros from the dataset and log-transforming the data. The amount of recruitment (log-transformed) was modelled in the same way as mortality and growth as described above.

3 | RESULTS

3.1 | Comparison of aspen and conifer performance

The annual proportion change in live basal area (BA) was different for aspen and conifers inhabiting the same plots across three of the four geographic regions included in this analysis—Sierra/Cascades, Middle Rockies and Wasatch/Colorado Plateau (Figure 2, Table S2). Live BA of conifers increased over time in these regions, with mean values per plot ranging from 2.5% to 6.5% per year, whereas live BA of aspen decreased over time by 1.3% to 2.6% per year. In contrast, the annual proportion change in live basal area (BA) did not differ between aspen and conifers in the Northern Rockies (Figure 2).

3.2 | Variation in demographic rates among ecoregions

We found a median annual mortality of 3.5% (IQR 1.7%–5.7%) for mature aspen stems in our plots. These rates differed among the five regions, with mortality being highest in the Great Basin and the Wasatch/Colorado Plateau, lowest in the Northern Rockies and intermediate in the Middle Rockies and Sierra/Cascades (Figure 3a, Table S3). The growth rate of mature aspen stems increased by a median of 1.9% (IQR 1.2%–3.0%) per year but did not differ among the five regions (Figure 3b, Table S3). No recruitment was observed in 58% of the plots, but in plots with recruitment, mature aspen stems increased by a median of 1.5% (IQR 0.8%–3.8%) per year, with these rates also not differing among the five regions (Figure 3c, Table S3).

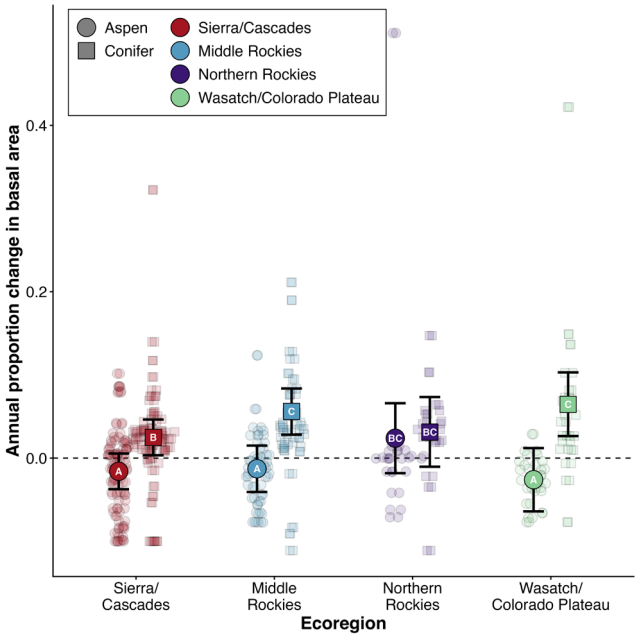

FIGURE 2 Proportional change in live basal area of mature aspen and conifer stems over the 9- to 13-year study period. Shapes indicate tree species and points are coloured by region. Only four of the five study regions are shown due to the lack of conifers in the Great Basin plots. The larger centre point denotes the mean of the posterior distribution of each group, and the error bars show 95% credible intervals. Letters in graph groups where less than 95% of the posterior distribution overlaps with groups of a different letter.

3.3 | Modelling mature aspen performance

3.3.1 | Variable reduction of predictor variables

For the stand characteristics PCA, the first three principal component axes explained 79% of the variation in initial conditions at the beginning of our study. The first axis represented the initial dominance of conifers in our plots, the second axis corresponded to the initial aspen dominance, and the third axis described the initial basal area of dead aspen (Figure 4a, Table S4). For each axis, higher values indicated greater dominance or amount.

For climate anomalies PCA, the first principal component axis explained 50% of the variation, so we elected to use only one composite variable. This axis described plots that experienced hotter and drier conditions during the study period (Table 1), relative to 30-year normals for 1981–2010 (Figure 4b, Table S4).

For the climate PCA, the first two principal component axes explained 70% of the variation and were used as predictor variables in our analyses of demographic rates. The first axis loaded variables relating to temperature and the timing of precipitation, with higher values associated with increased temperature and precipitation that falls primarily during the winter and lower values indicating sites that were cooler and received more precipitation in the summer (Figure 4c,

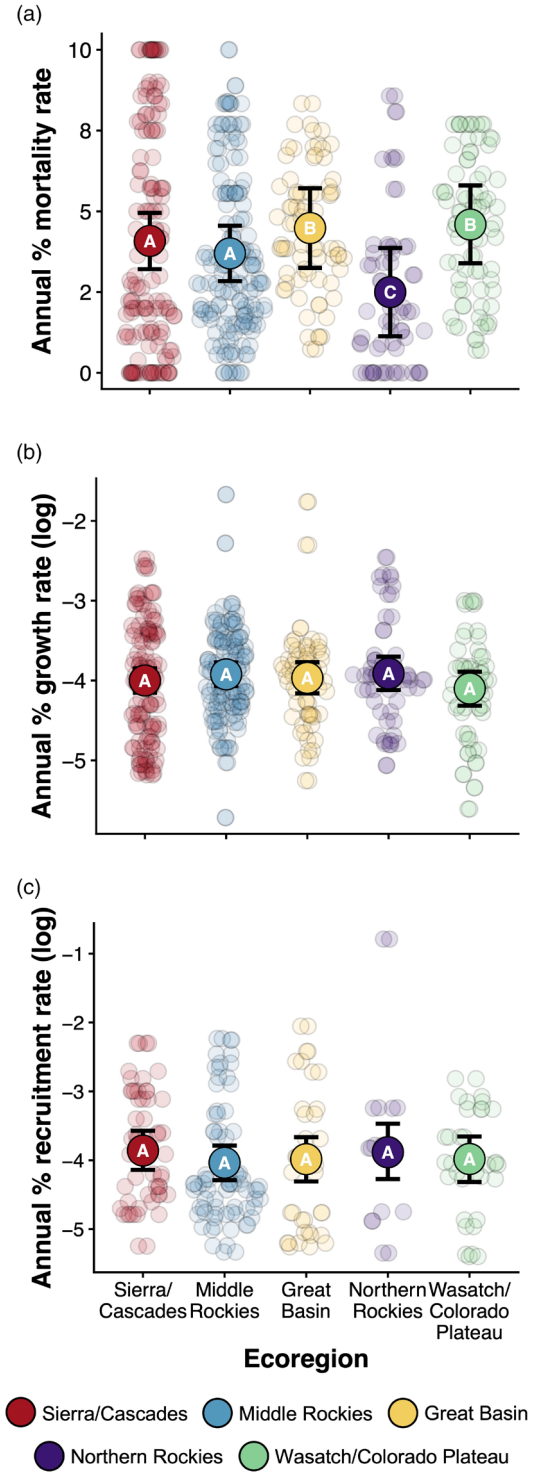

FIGURE 3 Variation in mortality (a), growth (b), and recruitment rate (c) across the five ecoregions in the study area. The larger centre point denotes the mean of the posterior distribution of each group, and the error bars show 95% credible intervals. Letters in graph groups where less than 95% of the posterior distribution overlaps with groups of a different letter.

Table S4). The second axis represented variation in water availability, with higher values corresponding to increased precipitation, especially in non-summer months, and decreased aridity (Figure 4c, Table S4).

For the topography PCA, the first two principal component axes explained 41% of the variation. The first axis largely explained topographic position, with higher values corresponding to plots in upland areas, such as hill tops, and lower values indicating plots in valleys (Figure 4d, Table S4). The second topography axis explained variation in the heat load index, where higher values indicated hotter, more south-facing slopes (Figure 4d, Table S4).

3.3.2 | Annual percent mortality rate for aspen

All parameters of the mortality model converged and collectively explained 49% of the variation in aspen mortality over the study period, where our predictor variables explained 34% and an additional 15% was due to the spatial error structure (Figure S2, Table S5). The strongest predictor of mortality was the level of aspen canopy dieback at the beginning of our study, a positive relationship three times stronger than any other predictor in the model (1.00 probability of direction [pd], Figure 5a, Table S5). Mortality was also related to each of the composite variables representing initial stand conditions. Increasing levels of initial conifer and aspen dominance were associated with lower annual mortality (0.98 and 0.95 pd, respectively). Plots with greater initial dead aspen also experienced elevated mortality during the study period, an effect twice as strong as that for initial aspen or conifer dominance (0.99 pd). Finally, we found a relationship between aspen mortality rate and water availability, where increased precipitation and reduced aridity was associated with reduced aspen mortality (0.94 pd). We did not find a relationship between mortality and climate anomalies, upland position, or heat load (Table S5).

3.3.3 | Annual percent growth rate for aspen

All parameters of the growth model converged, collectively explaining 33% of the variation in aspen growth rates, with 25% due to our predictor variables and an additional 8% due to the spatial error structure (Figures S4 and S5, Table S6). All four biotic predictor variables showed a negative relationship with aspen growth rate, with greater initial aspen dieback, initial dead aspen, and initial aspen and conifer dominance associated with reduced aspen growth (1.0 pd for all variables, Figure 5b, Table S6). Both climate predictor variables in the model were important, with greater aspen growth associated with increased temperature and greater winter precipitation (1.0 pd) and reduced growth associated with reduced water availability (0.89 pd). Climate anomalies were also important, with plots characterized by hotter and drier conditions relative to the historic baseline experiencing lower growth rates (0.95 pd). Finally, we found plots with more upland and south-facing locations (with higher heat loads) experiencing increased aspen growth (0.87 and 0.97 pd, respectively).

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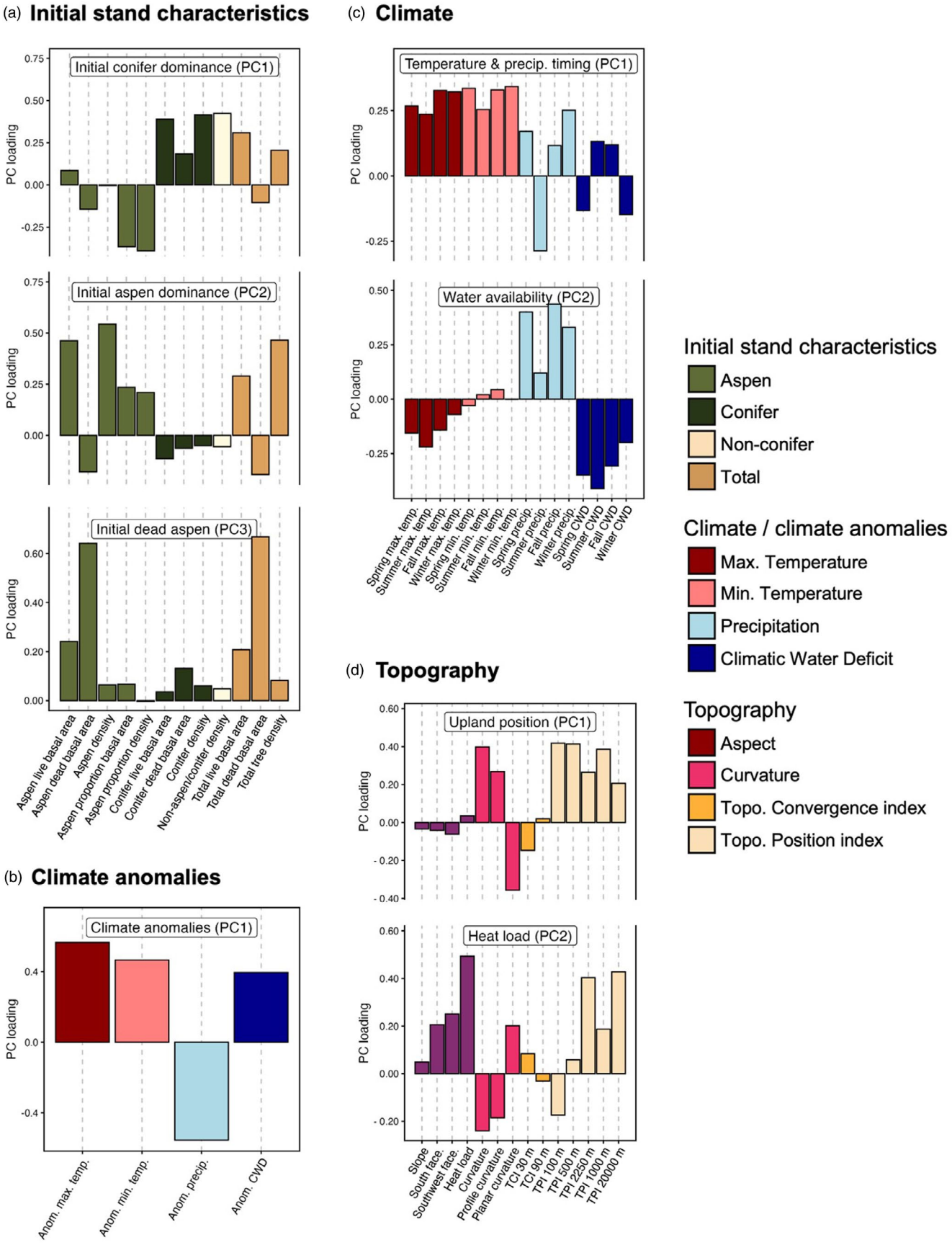

FIGURE 4 Loadings from principal components analysis of original predictor variables onto new composite axes. Each panel shows the results of a separate PCA where the original variables were (a) stand characteristics, (b) climate anomalies, (c) climate and (d) topography.

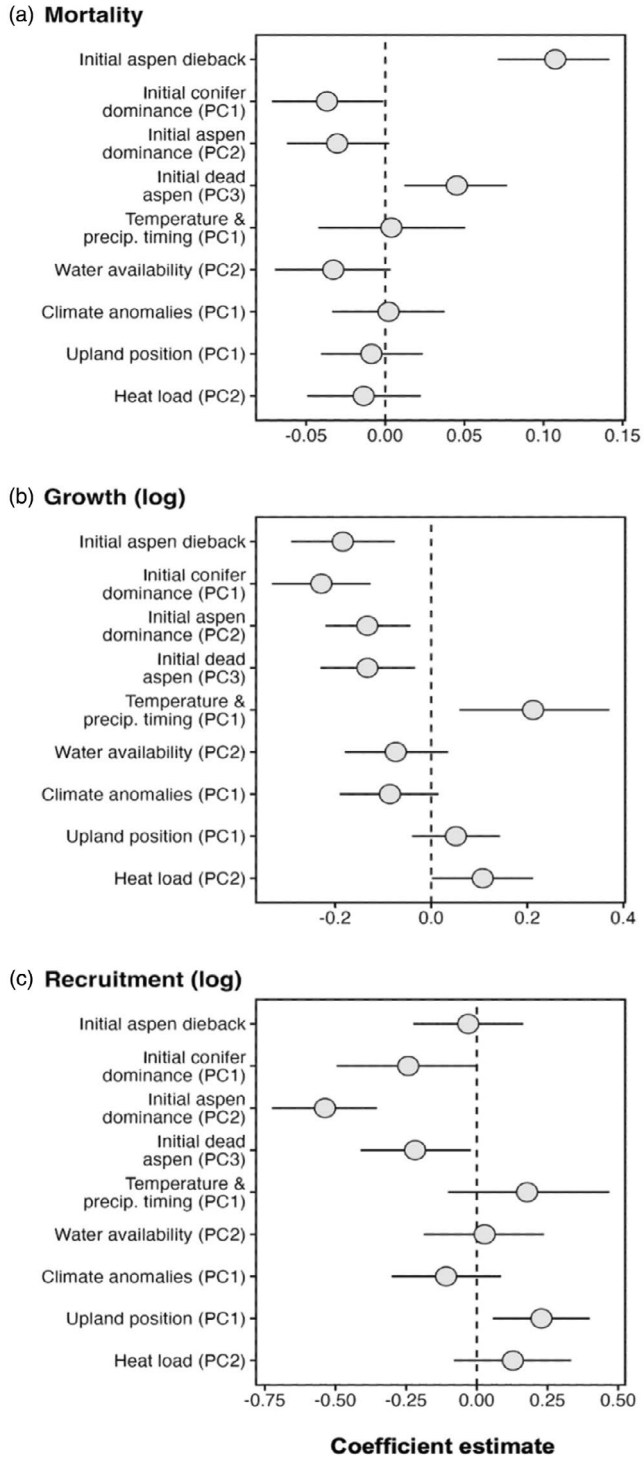

FIGURE 5 The relationship between composite predictor variables and aspen demographic rates in the western United States. Relationships are shown as posterior distributions with separate facets for each measured response variable: (a) mortality rate, (b) growth rate, and (c) recruitment rate. All coefficient estimates are standardized to facilitate comparison of the relative strength across response variables. The dotted line represents no effect and a distribution that is removed from this line shows strong evidence of a directional effect. The binary recruitment model is not shown as it lacked explanatory power.

3.3.4 | Annual percent recruitment rate for aspen

All parameters in the binary recruitment model (some recruitment versus no recruitment) converged, but they only explained 3.5% of the variation in aspen recruitment (Figure S6, Table S7). Because this model explained little variation in whether any recruitment occurred, we did not interpret it further.

All parameters of the recruitment amount model converged, and they collectively explained 48% of the variation in aspen recruitment (after excluding sites where no recruitment occurred), where 35% was due to the predictor variables and an additional 13% was due to the spatial error structure (Figures S7 and S8, Table S8). Reduced adult recruitment was associated with higher initial aspen and conifer dominance (0.95 and 1.0 pd, respectively), greater amounts of initial dead aspen (0.99 pd), and hotter and drier conditions relative to the historic baseline (0.86 pd, Figure 5c, Table S8). Greater amounts of adult recruitment were associated with higher temperatures and increased winter precipitation (0.86 pd) as well as occurring in more upslope (0.99 pd) and south-facing locations (0.85 pd).

4 | DISCUSSION

In this paper, we evaluated the role of climate, topography and forest structure in predicting the mortality, growth and recruitment rates of quaking aspen over a 9- to 13-year period in 263 plots distributed across six states in the western United States (Figure 1; Table 1). Aspen experienced substantial mortality during our study—4% of the mature trees in plots died each year on average—which was three times greater than the recruitment of new adults (1.3%). In addition, aspen performed differently from co-occurring conifers, with the dominance of aspen declining during the study period while conifers increased. As summarized in Figure 6, our study detected a wealth of legacy effects, where variables relating to tree health and dominance at the start of our study were strong predictors of mortality, growth and recruitment rates of aspen during the following decade. In addition, lower mortality rates for aspen were associated with higher precipitation and reduced aridity, whereas increased growth and recruitment rates were associated with higher temperatures and winter precipitation, as well as cooler and wetter conditions relative to historic baselines.

4.1 | Patterns in aspen performance

Mortality rates for aspen in our study ranged from 2.5% to 4.6% per year, with highest levels observed in the Great Basin, the most arid ecoregion included in our study. These results are similar to those reported for North America by Refsland and Cushman (2021) based on forest inventory data from the United States (USDA Forest Service) and Canada (Canadian Forest Service). Although they could not address the drivers of these patterns (due to blurred plot locations),

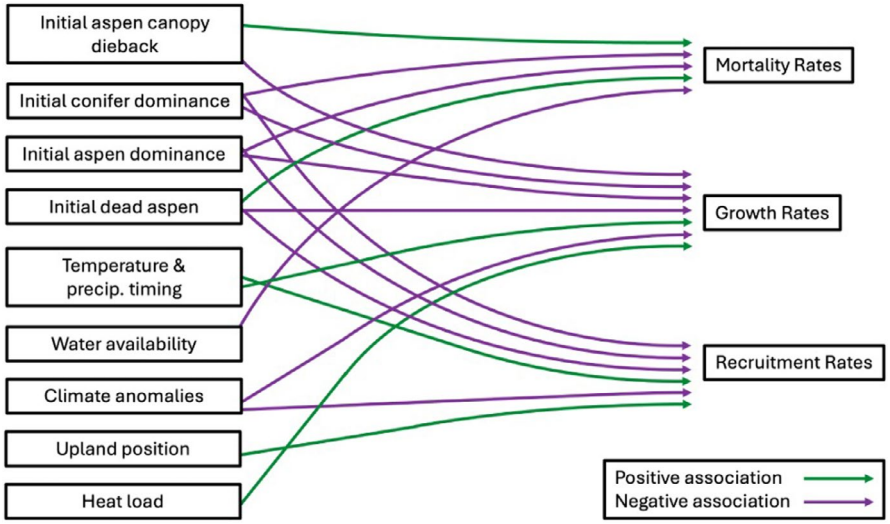

FIGURE 6 A schematic diagram summarizing the biotic and abiotic factors that best predict variation in mortality, growth and recruitment rates for mature aspen stems in the western United States. Only effects with a probability of direction greater than 0.90 are shown.

Between 1985 and 2018 in 3962 plots distributed across five biomes in North America, Refsland and Cushman (2021) found that the mean annual mortality rates for mature aspen stems increased significantly over time. Annual mortality rates ranged from 2.0% to 4.5%, with levels again being greatest in the most arid biome, montane coniferous forests. The findings from both studies suggest that aspen mortality is greatest in the drier portions of its range.

When aspen and conifers co-occurred in plots, we found that their performance was markedly different from each other. For this analysis, we focused on changes in live BA of trees in plots during the study period because it captured the combined effects of mortality, adult recruitment, and growth rates in a single variable. Live BA of conifers *increased* by 2.5%–6.5% per year whereas live BA of aspen *decreased* by 1.3%–2.6% each year in three of the four ecoregions where this comparison was possible (Figure 2). Numerous factors may explain these findings and here we discuss four possibilities. Given that temperatures and aridity have been increasing in the western United States over the past few decades (Cook et al., 2004; Overpeck & Udall, 2020), one possibility is that aspen and conifers responded to these environmental changes in opposite ways. However, this seems unlikely given that a wide range of studies have shown that *both* broadleaf deciduous trees and conifers have been adversely affected by increasing temperature and aridity associated with anthropogenic climate change (see Allen et al., 2010, 2015; Cohen et al., 2016; Hartmann et al., 2022; Van Mantgem et al., 2009). A second possibility is that levels of ungulate herbivory may have increased during our study period, with herbivores preferentially feeding on aspen over conifers. Although ungulates do indeed prefer aspen over conifers (Crouch et al., 2023), and there is a wealth of evidence indicating that herbivores adversely affect aspen (e.g. Reikowski et al., 2022; Rhodes et al., 2018; Rogers & Mittanck, 2014), we are not aware of studies showing that herbivore abundance increased in the western United States over the 9- to 13-year period during which our study occurred. A third possibility is that successional processes explain the temporal shift from aspen to conifer dominance that we observed in our study. Aspen is an early successional and relatively shade-intolerant species and is often replaced by conifers over time when the two groups co-occur (Callahan et al., 2013; Kulakowski et al., 2004; Shinneman et al., 2013). Another related possibility is that, due to long-term fire suppression, conifers have been expanding their dominance into aspen stands throughout the western United States, leading to increased competition with aspen and reductions in the latter's performance and dominance. Although we do not have data to evaluate it, we hypothesize that this is the most plausible explanation for the observed increases in BA of conifers and decreased BA of aspen shown in Figure 2. Many studies have documented that, in the absence of fire, extensive encroachment of conifers regularly occurs in aspen stands, leading to reductions in the latter's dominance, if not its outright replacement by conifers (e.g. Calder et al., 2011; Crouch et al., 2023; Krasnow et al., 2012; Kulakowski et al., 2013; Singer et al., 2019; Zegler et al., 2012).

4.2 | Drivers of aspen performance

Although our statistical models included a wide range of topographic and climatic variables (Table S1), which were often influential and are discussed below, we consistently found that factors related to stand structure at the beginning of our study were the best predictors of aspen demographic rates during the ensuing decade. For example, aspen stands that experienced elevated canopy dieback and mortality at the outset of our study continued this downward trajectory over the next decade (Figure 5a). The direction of these kinds of relationships was sometimes reversed, as sites that had high dominance of aspen and conifers at the beginning of our study experienced less mortality during the ensuing decade. Initial conditions also emerged as being important predictors of growth and recruitment rates, which typically decreased with greater levels of initial canopy dieback, dead aspen, and aspen and conifer dominance. These findings may suggest that legacy effects existed in our system. Anderegg et al. (2013), Anderegg et al. (2015) and

Kannenberg et al. (2020) have discussed the existence of such effects for trees that have experienced pronounced water stress associated with drought. They report that the adverse effects of these events—decreased growth and increased mortality—can persist long after the water stress has been alleviated and lead to lagged responses. These kinds of legacy effects may occur at smaller spatial scales, in addition to regional ones linked to large-scale drought events. Alternatively, our results may suggest that the same environmental conditions that drove mortality, growth and recruitment at the outset of our study continued to do so during the ensuing decade—challenging locations for aspen may continue to be challenging, and optimal locations may continue to be optimal well into the future. Working in southwestern Colorado, Worrall et al. (2015) reported similar findings for aspen, where high-mortality areas and low-mortality areas persisted for many years. In addition, Kane et al. (2014) and Rogers et al. (2018) documented lagged response of aspen mortality to environmental stress. Zegler et al. (2012) also found that canopy dieback was correlated with the amount of dead aspen.

Our composite variables indicate that precipitation and water availability were important predictors of aspen demographic rates. Increased water availability (greater precipitation, especially in non-summer months, and reduced aridity; PC2) was associated with decreased mortality rates (Figure 5a), and higher temperatures with increased winter precipitation (PC1) were associated with increased growth and recruitment rates (Figure 5b,c). Given that aspen is a fast-growing species with high water demand (Singer et al., 2019), it is not surprising that this species experienced lower mortality in areas receiving greater precipitation. Indeed, many studies have reported that aspen has exhibited pronounced mortality levels at sites experiencing water shortages associated with drought (see Anderegg et al., 2013; Bell et al., 2014, 2015; Hanna & Kulakowski, 2012; Kulakowski et al., 2013; Michaelian et al., 2011; Refsland & Cushman, 2021; Singer et al., 2019). In addition, Clement et al. (2019) reported that drought adversely influenced aspen recruitment in Arizona.

Our results provide further support for the hypothesis that both intraspecific and interspecific competition have been important and long-lasting forces limiting aspen performance. Aspen in plots with greater dominance of both conifers and aspen at the beginning of the study experienced reduced growth and recruitment rates (Figure 5b,c). Given that aspen is highly shade intolerant, its growth may have been light limited in stands with relatively high density of aspen and conifers. Our results are consistent with other studies in the western United States, which have reported a negative relationship between the rates of aspen growth and the density of co-occurring trees (e.g. Berrill & Dagley, 2012; Bretfeld et al., 2016; Brown et al., 2006; Pierce & Taylor, 2010).

Our analyses indicated that aspen growth and recruitment rates decreased with increasing climate anomalies (Figure 5b,c). As anomalies increased, plots during our 9- to 13-year study period became hotter and drier than they had been between 1981 and 2010 (Figure 4b). This result is especially informative when combined with our finding that increased aspen growth and recruitment occurred in sites experiencing warmer temperatures combined with drier summers and wetter winters (Figure 4c). They suggest that, while aspen may benefit from relatively warm conditions and drier summers that may prolong the growing season, additional warming and drying beyond historical norms had negative consequences. Given that the western United States has become hotter and drier over the past few decades (e.g. Dannenberg et al., 2022; McKinnon et al., 2021; Zhang et al., 2021), it makes sense that the growth and recruitment rates of aspen would decrease with increasing climate anomalies. These findings, coupled with our findings of mortality being highest in the driest ecoregions, suggest that aspen, in addition to being influenced by climate per say, were also adversely responding to climate change, with areas experiencing the greatest warming having the largest declines.

At first glance, the increased growth and recruitment of aspen on upland sites (PC1) and south-facing aspect (PC2) may appear counterintuitive. South-facing aspects and upland topographic positions should be associated with fewer resources, and hence, we might expect lower growth and recruitment rates based on resource availability alone. However, it is possible that these positive relationships represent conditions that favour aspen more than co-occurring conifers. Topography has the potential to influence demographic rates of aspen directly, by increasing or decreasing resource availability, and indirectly by altering interactions with potential competing tree species. For example, in southwestern Idaho, Strand et al. (2009) found that aspen was relatively free from competition with conifers on south-facing slopes because the latter could not thrive there.

5 | CONCLUSIONS

In one of the most geographically expansive field-based studies of quaking aspen to date, we have assessed the importance of climate, topography, and forest structure as drivers of mortality, growth, and recruitment rates in six western US states over a 9-13-year period. We have documented that mortality rates for aspen substantially exceeded recruitment of new adults, and as such the dominance of this tree species declined over the course of our study. In addition, we show that declining growth and recruitment rates of aspen have intensified due to climate change and have detected a range of long-lasting effects whereby aspens stands that were struggling or thriving at the outset of our study continued on these same trajectories over the next decade. Given our results and those of other studies, combined with the reality that climate change is projected to intensify in the coming decades, we suspect that the dominance of aspen, at least in the more arid parts of its range in western North America, will continue to decline in the future. If true, such changes would likely result in reductions in the many ecosystem services that aspen have historically provided.

AUTHOR CONTRIBUTIONS

J. Hall Cushman—Conceptualization, funding acquisition, project administration, supervision, methodology, visualization, writing—original

draft. Jacob A. Macdonald—Methodology, investigation, writing—original draft. Christopher A. Halsch—Formal analysis, visualization, writing—original draft. Tyler K. Refsland—Methodology, writing—review and editing. Brytten E. Steed—Methodology, investigation, writing—review and editing. Thomas E. Dilts—Methodology, writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

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

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70367.

DATA AVAILABILITY STATEMENT

All data and code used in this manuscript have been published on Dryad: https://doi.org/10.5061/dryad.s4mw6m9md (Cushman et al., 2026).

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SUPPORTING INFORMATION

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

Table S1. Description of all 44 predictor variables used to model mortality, growth, and recruitment rates of mature aspen in 263 plots across six states in the western United States.

Table S2. Summary statistics for a Bayesian model examining regional differences in change in live basal area of mature trees.

Table S3. Summary statistics for a Bayesian model examining differences among ecoregional with respect to mortality, growth and recruitment rates for mature aspen.

Table S4. Loadings from four principal components analyses (performed within each variable type) for the first four axes.

Table S5. Summary statistics for the Bayesian hierarchical model predicting mortality rate of mature aspen stems. The 2.5, 50 and 97.5 quantiles are for standardized effect sizes.

Table S6. Summary statistics for the Bayesian hierarchical model predicting relative annual growth rate of mature aspen stems (log-transformed). The 2.5, 50 and 97.5 quantiles are for standardized effect sizes.

Table S7. Summary statistics for the Bayesian hierarchical model predicting recruitment rate (binary) of mature aspen stems. The 2.5, 50 and 97.5 quantiles are for standardized effect sizes.

Table S8. Summary statistics for the Bayesian hierarchical model predicting recruitment rate (log-transformed) of mature aspen stems. The 2.5, 50 and 97.5 quantiles are for standardized effect sizes.

Figure S1. Correlations between all predictor variables in linear models. All correlations are less than 0.5.

Figure S2. Trace plots for each parameter in the mortality rate model.

Figure S3. Fitted versus observed values generated from the mortality rate model.

Figure S4. Trace plots for each parameter in the growth rate model.

Figure S5. Fitted versus observed values generated from the growth rate model.

Figure S6. Trace plots for each parameter in the recruitment (binomial) model.

Figure S7. Trace plots for each parameter in the recruitment rate (log-transformed) model.

Figure S8. Fitted versus observed values generated from the recruitment rate (log-transformed) model.

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