RESEARCH ARTICLE

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Increasing rates of subalpine tree mortality linked to warmer and drier summers

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Abstract

1. Warming temperatures and rising moisture deficits are expected to increase the rates of background tree mortality–low amounts of tree mortality (~0.5%–2% year^{-1}), characterizing the forest demographic processes in the absence of abrupt, coarse-scale disturbance events (e.g. fire). When compounded over multiple decades and large areas, even minor increases in background tree mortality (e.g. <0.5% year^{-1}) can cause changes to forest communities and carbon storage potential that are comparable to or greater than those caused by disturbances.

2. We examine how temporal variability in rates of background tree mortality for four subalpine conifers reflects variability in climate and climate teleconnections using observations of tree mortality from 1982 to 2019 at Niwot Ridge, Colorado, USA. Individually marked trees (initial population 5,043) in 13 permanent plots—located across a range of site conditions, stand ages and species compositions—were censused for new mortality nine times over 37 years.

3. Background tree mortality was primarily attributed to stress from unfavourable climate and competition (71.2%) and bark beetle activity (23.3%), whereas few trees died from wind (5.3%) and wildlife impacts (0.2%). Mean annualized tree mortality attributed to tree stress and bark beetles more than tripled across all stands between initial censuses (0.26% year^{-1}, 1982–1993/1994) and recent censuses (0.82% year^{-1}, 2008–2019). Higher rates of tree mortality were related to warmer maximum summer temperatures, greater summer moisture deficits, and negative anomalies in ENSO (La Niña), with greater effects of drought in some subpopulations (tree size, age and species). For example, in older stands (>250 years), larger and older trees were more likely to die than smaller and younger trees. Differences in tree mortality rates and sensitivity to climate among subpopulations that varied by stand type may lead to unexpected shifts in stand composition and structure.

4. *Synthesis*. A strong relationship between higher rates of tree mortality and warmer, drier summer climate conditions implies that climate warming will continue to increase background mortality rates in subalpine forests. Combined with increases in disturbances and declining frequency of moist-cool years suitable for seedling establishment, increasing rates of tree mortality have the potential to drive declines in subalpine tree populations.

1 | INTRODUCTION

Rates of tree mortality are increasing in forested regions across the earth (McDowell et al., 2020; Peng et al., 2011; Senf et al., 2018). Abrupt, widespread mortality of high proportions of trees due to coarse-scale disturbance events (e.g. insect outbreaks, fire, extreme drought) has been a key focus of many studies in temperate forests (e.g. Anderegg et al., 2019; Sommerfeld et al., 2018; Stovall et al., 2019). Discrete disturbance events result in visually obvious tree mortality across large forest patches to entire regions (Cannon et al., 2019; Seidl et al., 2017). In contrast, *background tree mortality* refers to the typically low rates of tree mortality (~0.5%–2% per year), characterizing the forest demographic processes in the absence of abrupt pulses of widespread tree mortality (Das et al., 2016; Furniss et al., 2020; Taccoen et al., 2019). Background mortality is influenced by slower acting processes such as competition, endemic rather than epidemic insect pest activity, and stress related to unfavourable short-term weather as well as longer-term unfavourable climatic conditions. The importance of tree mortality and the variability in background tree mortality as a regulator of change in forest structure and function are well established (Etzold et al., 2019; Franklin et al., 1987; van Mantgem & Stephenson, 2007). Long-term and fine-scale monitoring of tree populations is required to study the processes affecting the slower dynamics of background tree mortality (Furniss et al., 2020). Slight increases in background mortality rates, such as 0.5% per year, compounded over many decades can cause similar if not greater losses of trees and carbon storage at broad spatial scales compared to the effects of coarse-scale disturbances, such as fires and outbreaks of lethal insects (Das et al., 2016). Detecting trends and sensitivity of background tree mortality rates to climate is essential for projecting broad-scale shifts in forest structure and composition that influence global carbon, energy and water cycles (Bonan, 2008; Pan et al., 2011).

Background tree mortality is often the result of a combination of multiple abiotic and biotic stressors (e.g. the 'death spiral' of Franklin et al. 1987; Manion, 1981), which complicates the identification of proximate causes of mortality. Both the direct (extreme heat, drought) and indirect (bark beetles) effects of climate can drive tree mortality (McDowell et al., 2008). The direct effects of climate often elevate tree stress, which may push trees beyond critical physiological thresholds for survival (i.e. hydraulic failure and/or carbon starvation; Adams et al., 2017; Allen et al., 2015; McDowell et al., 2008) or increase tree susceptibility to lethal forest insects, such as bark beetles (Raffa et al., 2008). Depending on the frequency and intensity of warmer and drier climate conditions, as well as the physiological status and other attributes of the tree (Allen et al., 2015), mortality may be immediate (Adams et al. 2009) or delayed (i.e. lagged effects; Bigler et al. 2007). Gradual increases in temperature

from climate warming are predicted to exacerbate the effects of warmer and drier conditions created by natural climate variability (including effects teleconnected to ocean–atmosphere oscillations) in many forest ecosystems (Slik, 2004; Villalba & Veblen, 1998). Such conditions are also expected to gradually intensify tree stress and support higher rates of bark beetle survival (Huang et al., 2020), which may increase the susceptibility of trees to bark beetle attack. Consequently, climate and bark beetles are expected to elevate the rates of background tree mortality under continued climate warming (Allen et al., 2015).

Tree and stand-scale factors mediate the effects of climate on background tree mortality (Taccoen et al., 2019), often leading to variability in mortality rates among subpopulations (e.g. different species or tree size and age classes). At the tree scale, larger (and generally older) trees are at higher risk of mortality from declines or failure of physiological functions (e.g. photosynthesis, water and nutrient transport; McDowell & Allen, 2015; Olson et al. 2018) and greater susceptibility to bark beetle attack (Das et al., 2016). At the stand scale, decadal changes in tree mortality within a stand may occur as a result of stand development processes (Oliver, 1980) that are often considered to be independent of climate (Lutz & Halpern, 2006; Thorpe & Daniels, 2012). For example, tree mortality in younger stands originating from recent stand-replacing fire is concentrated in the smaller size classes ('stem-exclusion' stage) due to competition for key resources (e.g. light). However, the degree to which climate influences the rate of stem exclusion is largely unexplored. As trees grow and stands reach later stages of development, tree mortality may eventually be balanced by recruitment of new seedlings and ingrowth into larger size classes. Depending on species composition, differences in hydraulic traits among tree species can affect their sensitivity to mortality from climate (Adams et al., 2017) which may drive gradual but important changes in stand composition under climate change. In later stages of stand development, vulnerability to biotic mortality agents that are affected by climate is expected to play a more important role in regulating mortality (McDowell et al. 2020).

The effect of climate on tree demographic processes is also mediated by topographic effects on site moisture availability (Manion, 1981). As the climate warms, tree mortality may increase more rapidly in warmer, drier site conditions near the physiological threshold for the species' (i.e. species' distribution limits; Anderegg et al., 2019) and/or in wetter, cooler site conditions where trees are less acclimated to drought (Clark et al., 2014). Moisture availability also influences the pace of stand development following disturbance (Donnegan & Rebertus, 1999; Kashian et al., 2005), and higher tree densities are often found on wetter sites relative to neighbouring drier sites (Chai et al., 2019). Greater competition for resources in stands with higher density (or basal area) may increase the risk of

tree mortality (Bradford & Bell, 2017). Despite limitations associated with assigning proximate causes of mortality ('mortality as a continuum'; Harmon & Bell, 2020), studies that examine the effects of climate on tree mortality for multiple subpopulations (e.g. size and age classes and species) at the stand scale (Etzold et al., 2019) are needed to forecast shifts in a variety of forest communities (Clark et al., 2016; McDowell et al., 2020) and ecosystem services under a warming climate (Lindenmayer et al., 2012).

In subalpine forests in the southern Rocky Mountains, tree mortality is increasing (Colorado State Forest Service, 2018; Lalande et al., 2020; Smith et al., 2015). Warmer temperatures and lower moisture availability have been shown to influence some demographic processes (e.g. radial growth and mortality) in many of these subalpine forest habitats (Bigler et al., 2007; Kueppers et al., 2017; Villalba et al., 1994). Warming temperatures and more frequent and extreme droughts, as well as decreasing snowpack, are expected to further increase moisture deficits in the next several decades (Rodman et al., 2020; Siler et al., 2019). The effects of a changing climate may be exacerbated or modulated by ocean–atmosphere oscillations, such as El Niño-Southern Oscillation (ENSO), that promote episodic droughts (McCabe et al., 2004) and coarse-scale disturbances (e.g. wildfire and bark beetles) in subalpine forests (Hart et al., 2014; Schoennagel et al., 2005). However, few studies examine the contribution of different causal agents as well as effects of climate variability and ocean–atmosphere oscillations on long-term rates of background tree mortality in subalpine forests. Reliable observations of individual trees from long-term (i.e. permanent) forest plots are necessary to identify proximate causes, rates and ecological consequences of tree mortality (Bakker et al., 1996). Subalpine forests located across complex topo-climatic gradients and with multiple species that vary in drought tolerance may be particularly helpful for evaluating community-level changes in subalpine forests over time (Peet, 1981; Veblen, 1986a).

Here, we investigate how the temporal variability in rates of background tree mortality for four subalpine conifers was affected by climate warming, site moisture availability and stand structure. We tracked >5,000 trees (stems >4 cm dbh) for mortality every 3 years from 1982 to 2019 in 13 permanent forest plots in the Colorado Front Range (CFR), USA. We asked (a) how are the rates of background tree mortality for four subalpine conifers affected by annual variability and decadal trends in climatic conditions and by ENSO, and how did rates vary across a series of different stand ages and range of site moisture conditions? We expected background tree mortality rates to increase over the 37-year study period and higher annualized mortality rates during 3-year census periods to be associated with negative anomalies in snowpack, cool phases of ENSO (La Niña) and positive anomalies in hotter and drier summer conditions. In older stands (>250 years old), we expected mortality rates to be higher for larger and older trees rather than smaller and younger trees, higher for less drought-tolerant species (*Abies* and *Picea*) than more drought-tolerant species (*Pinus* spp.; Pataki et al., 2000), higher in stands on xeric compared to mesic or hydric sites and higher in denser compared to less dense stands. For younger postfire stands

(<130 years) in the stem-exclusion phase, we expected climate would have minimal effects on tree mortality. Rates of bark beetle-caused tree mortality may also be responding to warming climate through higher bark beetle survival and elevated tree stress. Therefore, we also asked the following question: (b) How are the rates of tree mortality attributed to bark beetle activity changing over time during a period without punctuated beetle outbreaks? We expected tree mortality attributed to endemic bark beetle populations to increase from 1982 to 2019, primarily in the more susceptible older stands compared to younger stands in the stem-exclusion stage.

2 | MATERIALS AND METHODS

2.1 | Study area

We resurveyed permanent forest plots spanning the elevational gradient of subalpine forests (2,900–3,300 m) on the eastern slope of the CFR, USA (Figure 1). The study area has a continental climate characterized by long, snowy winters and a short, dry growing season (Kittel et al., 2015). From 1952 to 2018, the average annual temperature was 1.8°C with monthly average minimum temperatures of −11.6°C occurring in the coldest months (January and/or February) and monthly average maximum temperatures of 19.9°C occurring in the warmest month (July) at the C-1 climate station (40.0362 N, −105.5434 W, 3,048 m; Kittel et al., 2019a). Most (~70%) of the 670 ± 130 mm (*SD*) of average annual precipitation falls as snow from November to May, but convective storms during the summer months can produce intense, isolated rainfall events (Kittel et al., 2015). In the CFR subalpine zone, average annual precipitation has not significantly changed from 1978 to 2010 (Kittel et al., 2015) and snow water equivalent (SWE, April 1) has remained steady (1984–2018, Siler et al., 2019), but mean and maximum annual average temperatures increased (mean, 0.2°C per decade; maximum 0.44°C per decade) from 1953 to 2008 (McGuire et al., 2012).

Tree species composition and stand structure of subalpine forests in the CFR vary across topo-climatic gradients and with disturbance history (Peet, 1981; Veblen, 1986a). The permanent plots capture most subalpine *forest community types* in the CFR (Appendix S1: Table S1), as described by Peet (1981). Lower elevation subalpine forests on xeric sites are dominated by even-aged, monotypic stands of *Pinus contorta* var. *latifolia* Engelm. ex S. Watson (lodgepole pine) that originated following severe fire and logging in the late 1800s to early 1900s (*young postfire stands*, <130 years since stand initiation). At higher elevations and wet low-elevation sites, *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir) and *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) are the dominant species. *Picea-Abies* are expected to replace earlier seral *Pinus flexilis* E. James (limber pine) and *P. contorta* (*old seral postfire stands*, 270–400 years since stand initiation) or *Picea-Abies* forests are considered to be self-replacing in the absence of coarse-scale disturbance (*old Picea-Abies stands*, >450 years since stand
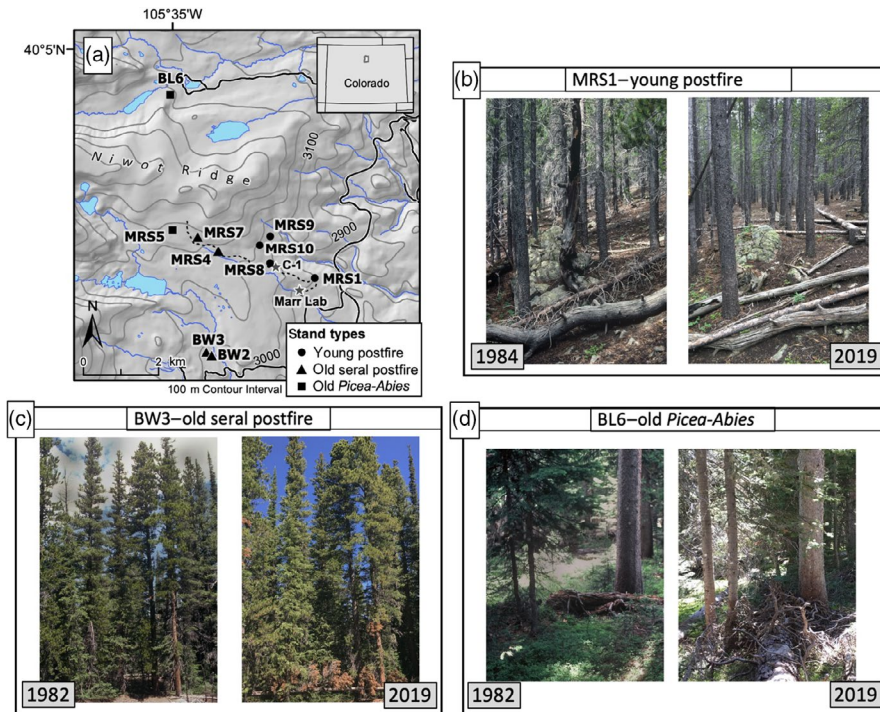
FIGURE 1 (a) Map showing location of permanent forest plots at Niwot ridge in Colorado, USA, (b–d) repeat photos from the year of permanent plot installation (1982 or 1984) and the most recent census (2019). (b) Note the fallen, burned snag from an 1880s fire and slow growth of the small diameter lodgepole in a young postfire stand; (c) the death of the fallen lodgepole pine in a mesic old postfire seral stand (BW3); (d) the growth release of the small individuals in the foreground and recently fallen snag with evidence of spruce bark beetle activity in the old *Picea-Abies* stand

initiation). Native, tree-killing bark beetles (described in Section 3) are associated with each of the four coniferous species in our study. *Populus tremuloides* Michx. (Quaking aspen) also occurs in some locations in the subalpine zone of the CFR, but population sizes in our study sites were insufficient for mortality analyses (24 trees total in all plots combined).

2.2 | Permanent forest plot installation and remeasurement protocol

Permanent forest plots (324–2,916 m^2, $n = 13$) were installed in the early- to mid-1980s (see Appendix S1: Table S1 for installation year) at sites without evidence of past logging (Veblen, 1986a). Plots were located across gradients of moisture availability that are related to topographic position and inferred from tree-growth variation to interannual climatic variability (Veblen, 1986a; Villalba et al., 1994). In the present study, we validate a soil moisture classification (xeric, mesic or hydric) for each plot with soil moisture measurements (Appendix S1: Table S1; Figure S1). Since the early 1900s, the stands where the permanent plots are located have not experienced fire, epidemic-level bark beetle outbreaks (e.g. mortality by basal area from bark beetles has been <5% per tree species) or blowdown events (Colorado State Forest Service, 2018; Smith et al., 2015). For three permanent plots (termed clustered small plots in Appendix S1: Table S1), we combined the data from 5 to 15 clustered small plots (60–336 m^2) to represent one plot. These clusters (*c.* 50 m separation) of small plots were located in natural openings in the forest adjacent to one of three larger (*c.* 50 m separation) plots. Canopy cover, basal area and stem density are generally lower in these clusters of smaller plots relative to the adjacent larger plots (Appendix S1:

Table S1), but demographic rates (including ingrowth and mortality) were similar (Andrus, Harvey, Chai, et al., 2018).

During initial plot installation, all live and dead trees were permanently tagged and measured for tree size (dbh), status (live or dead) and height class (main canopy, intermediate or subcanopy). Censuses of tree status, including the cause of death, were conducted every 3 years, except for the 1993/1994–2007 period (see Appendix S1: Table S2 for plot-specific mortality census intervals). In summers 2007 and 2016, a complete re-census of all trees >4 cm dbh, including tree size, status and height class, was conducted, and new recruitment (i.e. ingrowth) into the tree size class (>4 cm dbh) was recorded. During each census of tree status, all trees with green foliage were considered live. Dead trees were inspected for evidence identifying species of bark beetles (exit holes, pitch tubes and galleries in cambium following Furniss & Johnson, 2002) and mechanical damage (e.g. uprooted, bole snap, crushed by a fallen tree or damaged by antler rub). We attributed tree death to one of three proximate causes: (a) tree stress (direct effects of climate and climate effects on competition, no evidence of bark beetle activity or mechanical damage), (b) bark beetles (evidence of bark beetle activity) or (c) mechanical damage. We acknowledge that our ability to search for mortality agents above a bole height of 2 m was limited and that some bark beetle species, such as western balsam bark beetle (WBBB; *Dryocoetes confusus*), opportunistically attack recently dead trees (i.e. false attribution of mortality to bark beetles; Furniss & Johnson, 2002).

2.3 | Annualized tree mortality

This study builds on past work (Smith et al., 2015) by incorporating a longer temporal record of tree mortality (six additional years

and two additional censuses) and rigorous analyses of trends and drivers in mortality for multiple subpopulations using statistical methods rather than numerical and graphical interpretations. Here we analyse tree mortality at the stand scale to examine population-level changes in forests rather than individual-level changes (e.g. Hülsmann et al., 2018), which follows similar research from other geographical areas and forest types (Furniss et al., 2020; van Mantgem et al., 2009). To examine trends and variability in tree mortality within and among multiple subpopulations by stand type, we computed annualized mortality for each census period for the following (sub)populations: (a) all species combined, (b) three tree size classes for all species combined, (c) two age classes for all tree species combined and (d) each species individually. We assigned individual trees to one of three tree size classes ('subcanopy', 'intermediate' and 'main canopy') based on DBH thresholds and height class information in each plot. We classified trees into two age classes (young and old) using species-specific age thresholds because age data were not available for all trees. The age thresholds were approximately half the age of the oldest tree in the plot by species (Appendix S1: Figure S2). For trees without age data (~20% of trees by plot), we predicted the age class based on DBH at the plot level using linear discriminant analysis (MASS package in R; Venables et al., 2002); overall classification accuracy of age class was ~69%.

Annualized mortality rates were computed as $(Td/Tl)/P \times 100 = M$, where Td represents the number of trees >4 cm dbh that died (combined or by species) during time period P and Tl represents the live count of trees >4 cm dbh at the beginning of each census period (Andrus, Harvey, Chai, et al., 2018). Tree mortality cannot be accurately attributed to individual years within 3-year census periods and thus we chose to average tree mortality across census periods. Thus, our metric of tree mortality is an 'annualized' rather than a true annual mortality rate (sensu Sheil et al., 1995). All census periods were of equal length (3 years), except one census period (12 years), and this longer census period was only included in the trend analysis. A failure to incorporate recruitment into the >4 cm dbh size class during a census period has the potential to inflate mortality rates because the live tree count can only decrease over time in the absence of recruitment. However, recruitment data were only available from the 2007 and 2016 censuses (Appendix S1: Table S1). We computed an annualized recruitment (number of individuals recruiting per year) as $T_r/P = R$, where T_r represents the number of trees recruiting into the >4 cm dbh class between the initial census and 2016 and P is the number of years between the initial census and 2016. Annualized recruitment rates were multiplied by the length of the census period and added to the live tree count (Tl) during each census period. Tree death due to mechanical damage (5.5% of the total) was excluded from analyses of trends and relationships between tree mortality and climate because the focus of our study is on changes in mortality rates from direct and indirect climate effects (van Mantgem & Stephenson, 2007).

2.4 | Climate and ENSO datasets

Variability in climate and ENSO affect tree mortality by moderating the availability of moisture for tree physiological processes. Subalpine tree species depend upon soil moisture from snowmelt late in the growing season, and lower snow water equivalent (SWE) is associated with reduced net ecosystem productivity in our study area (Hu et al., 2010). As such, we obtained a long-term record (1938–2019) of SWE on 1 May from the University Camp snow course (#838, 40.03 N, 105.57 W; 3,140 m; 1.5–4.5 km from permanent plots; NRCS, 2019). The rate of decline in soil moisture following snowmelt and the variation in soil moisture throughout the summer months (June–September) are mediated by spring-summer temperatures and precipitation (Harpold et al., 2015), which both affect soil moisture deficits. To characterize the frequency of extremely hot summer days (1 June–31 September), we summed the number of days that maximum summer temperature exceeded the 90th percentile (23°C; hereafter, MT) using daily climate data from the C-1 climate station (Kittel et al., 2019a,b). To quantify the combined influence of temperature and precipitation on moisture deficits, we computed the summer climatic water deficit (CWD) for each year (modified Thornthwaite water balance model; 'CWD and AET function' in R; Redmond, 2019) using monthly average temperature and precipitation data from the C-1 climate station and an available soil water capacity (AWC) of 90 mm (representative of the study area) from POLARIS (Chaney et al., 2016). Higher CWD values are indicative of warmer and drier conditions and greater moisture stress experienced by trees. To examine the effects of ENSO, we selected average January and February MEI.v2 (Multivariate ENSO Index; ESRL, 2019; Wolter & Timlin, 2011). Winter negative (positive) MEI or La Niña (El Niño) indicates cooler (warmer) than average ocean water temperatures across the equatorial central and eastern Pacific and is a strong predictor of drought in northern Colorado (Hart et al., 2014).

2.5 | Statistical analysis

2.5.1 | Multi-decadal trends in tree mortality, bark beetle-caused mortality and climate

To examine trends in annualized tree mortality, tree mortality attributed to bark beetles and climate conditions, we used least-squares linear regression analysis to examine the rate of change (slope) and tested for statistically significant trends in annualized tree mortality (averaged across stand type by census) with nonparametric, Mann–Kendall trend tests with variance correction (MODIFIEDMK package in R; Patakamuri & O'Brien, 2019). The Mann–Kendall trend test with variance correction is robust to temporal autocorrelation in time-series data (Blain, 2013). To minimize type II error (i.e. a failure to detect meaningful trends in tree mortality) and to account for sample size limitations (i.e.

eight or nine census periods/plot), we evaluated statistical significance with $\alpha = 0.10$. We graphically interpreted the effect of stand structure and site moisture availability on trends and annualized tree mortality due to insufficient replication for statistical tests.

2.5.2 | Testing the influence of climate variability on tree mortality

To test whether annualized tree mortality during each 3-year census period (excluding the one 12-year census period) was related to variability in climate and MEI, we used generalized linear mixed models with a binomial error structure ('glmer' in R; Bates et al., 2015). Separate models of tree mortality (response variable) were constructed for each subpopulation. Subpopulations included the following: all species combined, individual tree species (one model each for *A. lasiocarpa*, *P. engelmannii*, *P. contorta* and *P. flexilis*), size classes (one model each for subcanopy, intermediate and main canopy) and age classes (one model each for young and old). While climate data were available at annual and sub-annual time periods, tree mortality was assessed at longer time intervals. To better capture extreme climatic events that are known to play an important role in forest demographics (Law et al., 2019), we summarized climate and MEI predictor variables using minimum or maximum values over a 3-year period from 1 year prior to the beginning and end of each census period. Predictor variables included the following: (a) SWE (minimum), (b) MT (maximum), (c) CWD (maximum) and (d) MEI (minimum). Models were fit for each climate variable independently (to account for collinearity between MT and CWD; Spearman's rho 0.59, $p < 0.001$) with stand type as an interaction and covariate. Climate and stand type predictor variables were considered statistically significant if they were an improvement on the null model ($\alpha = 0.05$, likelihood ratio test; Rousset & Ferdy, 2014). Predictor variables were standardized (i.e. converted to z-scores) to allow comparison of model coefficients by subtracting the mean and dividing by the standard deviation. To account for dependence in repeated measurements, we included a random intercept term for permanent plot. Final model residuals were assessed for dispersion, homogeneity of variance and temporal independence (DHARMa package in R, Hartig, 2018).

3 | RESULTS

3.1 | Attributing mortality to causal agents

From 1982 to 2019, a total of 908 trees (of an initial population of 5,043 trees) died in the permanent forest plots, and more than half (52.6%) of dead trees died during the most recent 30% of the record (2008 to 2019). The majority (71.2%) of mortality was attributed to tree stress (i.e. direct effects of climate and climate effects on competition, no evidence of bark beetle activity; Appendix S1: Table S5). We attributed 23.3% of all tree deaths to bark beetles (211 trees,

evidence of bark beetle activity), 5.3% to mechanical damage by wind (48 trees, see Appendix S1: Table S8) and 0.2% to mechanical damage by wildlife (2 trees).

3.2 | Trends in annualized tree mortality from 1982 to 2019

The annualized rate of tree mortality attributed to the direct or indirect effects of climate was 0.43% per year for all species and stand types combined over the 37-year study period (Figure 2; Appendix S1: Table S7). Mean annualized tree mortality varied among census periods but increased (positive slope) over time in all subpopulations (stand type, size and age classes, and species; Figure 2a–w) and plots (Appendix S1: Figure S3a–c). Among stand types, mean annualized tree mortality increased more rapidly in old *Picea-Abies* stands (0.33% decade^{-1}, Figure 2c) than in young postfire (0.10% decade^{-1}; Figure 2a) or old seral postfire stands (0.13% decade^{-1}; Figure 2b).

Comparing mortality among tree size classes within stand types, in young postfire stands annualized tree mortality increased more rapidly for subcanopy and intermediate trees (0.06% decade^{-1}; Figure 2j,g) than for main canopy trees (0.01% decade^{-1}; Figure 2d). In contrast, annualized mortality in older stands (i.e. old seral postfire and old *Picea-Abies*) increased more rapidly in main canopy trees (0.12% decade^{-1}; Figure 2e,f) than in subcanopy trees (0.04% decade^{-1}, Figure 2k,l). Similarly, increases in annualized mortality were greater for older trees (old postfire 0.10% decade^{-1}, old *Picea-Abies* 0.18% decade^{-1}; Figure 2m,n) than younger trees (old postfire 0.01% decade^{-1}, old *Picea-Abies* 0.14% decade^{-1}; Figure 2o,p) by stand type.

Among species within stand types, tree mortality increased more rapidly for *A. lasiocarpa* (old postfire, 0.06% decade^{-1}; old *Picea-Abies* 0.25% decade^{-1}) than *P. engelmannii* (old postfire, 0.04% decade^{-1}; old *Picea-Abies* 0.07% decade^{-1}) in older stands (Figure 2r–w). In old postfire stands, annualized mortality of *P. engelmannii* and *A. lasiocarpa* increased more rapidly than *P. contorta* and especially *P. flexilis* (Figure 2r,s,u,w). When annualized rates of mortality were computed over the 37-year study period (rather than 3-year census periods), annualized mortality rates for each species followed a similar hierarchy by stand type (Appendix S1: Table S7).

When comparing adjacent plots that differed in density (i.e. collections of aggregated small plots adjacent to large plots), annualized mortality was higher over the 37-year period and increased more rapidly from 1982 to 2019 in higher-density stands (graphical and numerical interpretation of trends in tree mortality, Appendix S1: Figure S3; Table S6). As expected, site moisture conditions also appeared to play an important role in patterns of mortality. In young postfire stands at lower elevations, tree mortality increased more rapidly in xeric (0.24% decade^{-1}) than in mesic sites (<0.18% decade^{-1}; Appendix S1: Figure S3). In higher elevations, old seral postfire (*P. engelmannii-A. lasiocarpa-Pinus* spp.) and old *Picea-Abies* stands, tree mortality was higher and increased more rapidly in mesic (rate of increase, >0.15% decade^{-1}; mortality over 37 years, >0.39% year^{-1}) sites, as compared to
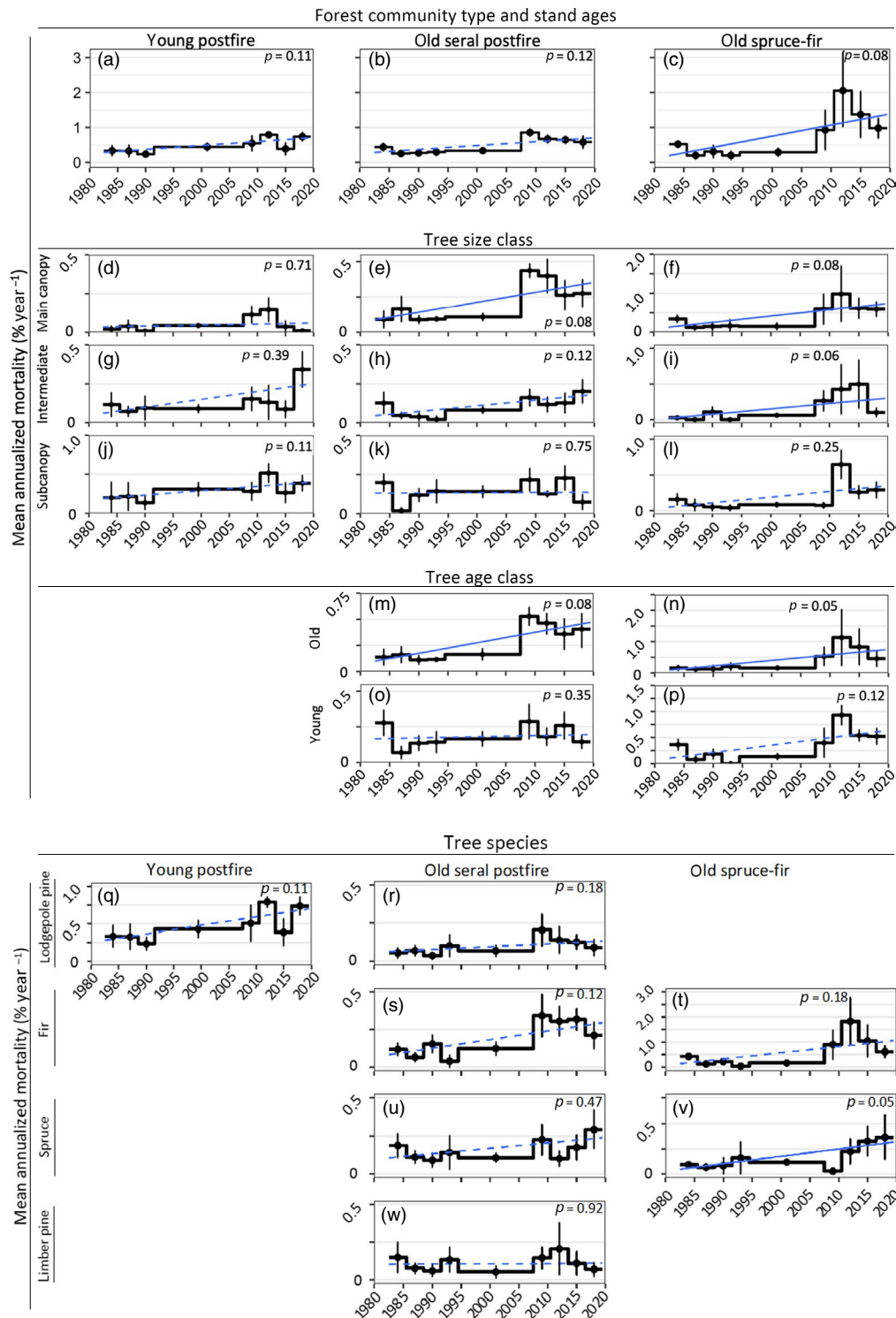
FIGURE 2 Mean annualized tree mortality from direct and indirect climate causes (tree stress and bark beetles) during each census period (black line and dot [±1 *SE*]) for (a–c) all conifer species combined, (d–l) three dbh size classes, (m–p) two stand age classes and (q–w) four subalpine tree species by forest community type (columns). Blue lines show linear trend in mean annualized tree mortality from 1982 to 2019 with a solid (dashed) line indicating a significant (non-significant) trend (Mann–Kendall trend test with variance correction, significance level, $p < 0.10$). Forest community types and stand ages are grouped by the estimated time since stand initiation into the following stand types: young postfire (YPF, <130 years old, $n = 1,849$), old seral postfire (OSPF, 250–400 years old, $n = 2,063$) and old spruce–fir (OSF, >400 years old, $n = 1,118$). Tree size classes are main canopy (>10 cm dbh, YPF; >20 cm dbh, OSPF; >22 dbh OSF), intermediate (≤10 to >6 cm dbh, YPF; ≤20 to <10 cm dbh, OSPF and OSF) and subcanopy (≤6 cm dbh, YPF; ≤10 cm dbh, OSPF and OSF). Tree age classes are young (≤150 [200] years old for fir, lodgepole pine [spruce, limber pine]) and old (opposite of young). YPF stands are even-aged (i.e. originating from one cohort following fire) and thus annualized mortality rates for age were not computed. Note that y-axis scale varies in d–w for the purpose of interpretability

xeric (<0.11% decade^{-1}; 0.30% year^{-1}) or hydric sites (0.09% decade^{-1}; 0.30% year^{-1}; Appendix S1: Figure S3; Appendix S1: Table S6).

During the 37-year study period, mortality (all causes combined) generally exceeded ingrowth (number of trees recruiting into the >4 cm dbh size class; see Appendix S1: Table S2 for population sizes). Consequently, tree density declined in all young postfire stands (5 of 5), most old postfire stands (3 of 5) and most old *Picea-Abies* stands (2 of 3). The only stands to increase in density were two, less dense old postfire stands on xeric sites (BW2, MRS7) and one old *Picea-Abies* stand on a hydric site (MRS5). Despite population declines, total stand basal area increased in all stands, except MRS4 and BL6, from the initial measurement period to 2019 (Appendix S1: Table S4).

3.3 | Trends in snowpack and summer climate conditions

Snow water equivalent (SWE; 1 May) was highly variable from 1952 to 2019 and did not show a significant trend during this time ($p = 0.42$; Figure 3a). In contrast, summer (1 June to 31 Sept) climate conditions exhibited significantly more hot days (MT, $p < 0.01$; Figure 3b) and greater summer climatic water deficits (CWD, $p < 0.01$; Figure 3c) from 1952 to 2019. For example, MT increased from 1982–1994 (8.3 days ± 2.3 *SE*) to 2008–2018 (19.4 days ± 2.1 *SE*; Figure 3b), and rates of warming also appear

to have accelerated relative to the 31-year period prior to installation of the permanent plots (1952–1982, mean 3.0 days, ±0.6 *SE*; Figure 3b). The average January–February MEI exhibited strong negative anomalies (i.e. La Niña events) in 1989, 1999–2001, 2008 and 2011.

3.4 | Trends and variability in climate and tree mortality

The multi-decadal increase in tree mortality (Figure 2) coincided with the multi-decadal trend towards warmer (Figure 3b) and drier (Figure 3c) summer climate conditions. For most subpopulations, the highest annualized tree mortality occurred during warmer and drier periods (census periods 2008–2010 or 2011–2013), whereas lower annualized tree mortality was associated with cooler and wetter periods (Figures 2 and 3). Statistical models (GLMMs) confirmed that higher annualized tree mortality rates for all trees combined during 3-year census periods were strongly related to the higher MT, greater summer CWD and negative anomalies in MEI (La Niña), but not lower SWE (May 1st; Table 1). Among stand types, higher rates of tree mortality were more strongly related to higher MT and summer CWD in old *Picea-Abies* stands than in young postfire or old seral postfire stands (Table 1). Among species, higher rates of tree mortality for *A. lasiocarpa* and *P. contorta*
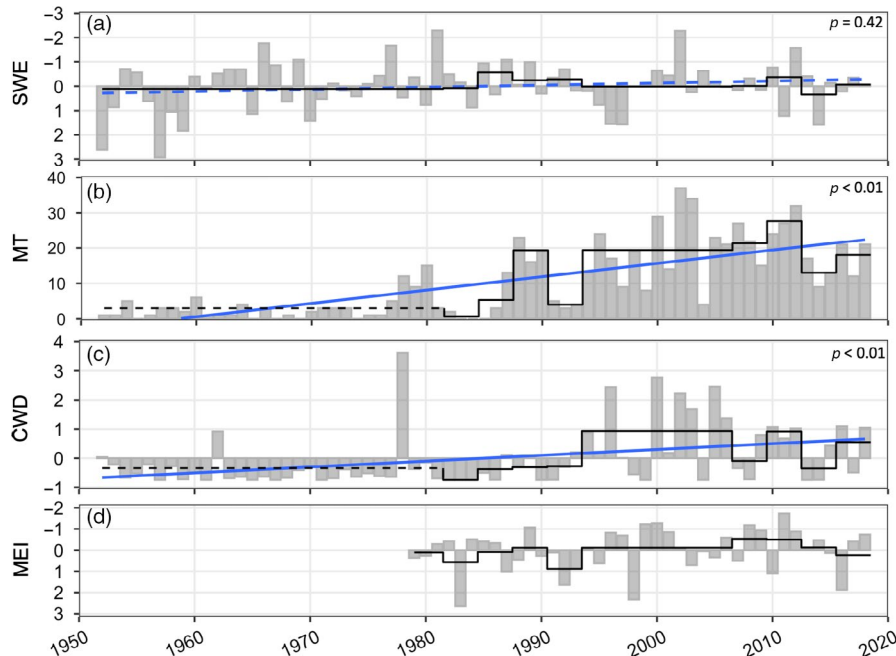

FIGURE 3 Time series of (a) snow water equivalent (SWE) in mm (1 May) from 1938 to 2019, (b) number of days maximum summer (1 June–31 September) temperature (MT) exceeded 90th percentile (23°C) from 1952 to 2018, (c) summer climatic water deficit (CWD, 1 June–31 September) and (d) average January and February Multivariate ENSO Index (MEI). In (a, d), the *y*-axis is inverted because greater negative departures were expected to increase tree mortality. Higher (lower) CWD values indicate warmer and drier (cooler and wetter) conditions. The grey bars are the annual values and the black line is the average by census period. Census periods were shifted 1 year earlier (see Section 2). The blue lines show the linear trend with a solid (dashed) line indicating a significant (non-significant) trend (Mann–Kendall trend test with variance correction, significance level, $p < 0.10$). Negative values of MEI are associated with drought in northern Colorado

TABLE 1 Standardized coefficients from generalized linear mixed models predicting annualized rates of tree mortality for all trees, each individual species, size classes and age classes (excludes even-aged, young postfire stands) at the plot level (n = 13) during 3-year census intervals (n = 8). Separate models were fit for each climate variable (Snow water equivalent [SWE], number of days maximum summer [1 June–31 September) temperature exceeded the 90th percentile [MT], summer climate water deficit [CWD] and Multivariate ENSO index [MEI]) and stand type was tested as a predictor (covariate and interaction [:]). Bold indicates that the climate variable improved model fit (p < 0.05, likelihood ratio test). In species models, plots with populations <40 individuals were excluded (see Appendix S1: Table S2 for population sizes). The reference stand type for model slope and intercept is old spruce–fir (OSF) for all models, except lodgepole pine and limber pine models where reference stand type is old postfire (OPF). Young postfire (YPF) originated from one cohort following fire and thus were not included in the 'age class' models

|		Tree species				Size class			Age class	
	All trees	**Spruce**	**Fir**	**Lodgepole pine**	**Limber pine**	**Subcanopy**	**Intermediate**	**Main canopy**	**Young**	**Old**
SWE model										
SWE (min)	−0.007	**1.1489**	−0.143	0.091	−0.352	−0.436	0.554	−0.142	−0.171	−0.023
MT model										
MT (max)	**0.564**	−0.289	**0.668**	**1.300**	0.181	0.572	0.475	**0.796**	0.282	**0.512**
MT (max):OSPF	**−0.356**									
MT (max):YPF	**−0.182**			**−0.954**						
OSPF	**−0.385**		**−1.433**					**−0.425**		
YPF	**−0.492**			**2.55**				**−2.172**		
Summer CWD model										
CWD (max)	**0.605**	0.116	**0.636**	**0.969**	0.105	0.451	**1.044**	**0.826**	0.253	**0.540**
CWD (max):OSPF	**−0.387**		0.228							
CWD (max):YPF	**−0.139**			**−0.505**						
OSPF	**−0.382**		**−1.556**					**−0.432**		
YPF	**−0.506**			**2.445**				**−2.161**		
MEI (ENSO)										
MEI (min)	**−0.307**	0.408	**−0.677**	−0.234	−0.340	−0.371	−0.048	**−0.539**	−0.471	−0.346
OSPF			**−1.422**					**−0.408**	**−1.002**	
YPF				**2.247**				**−2.090**		
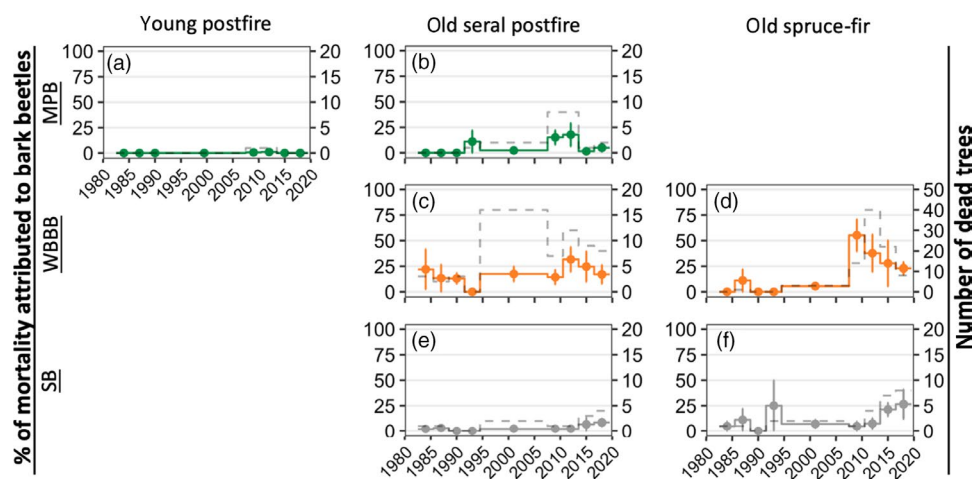
FIGURE 4 Mean percent (solid line) of total (all species combined) annualized mortality attributed to bark beetles and number of dead trees (dashed line) for (a) young postfire (<130 years old), (b, c, e) old seral postfire (250–400 years old) and (d, f) old spruce–fir (>400 years old) stands and the mean (dot) and standard error (±1 standard error) of annualized mortality during each census period. Mountain pine beetle (MPB, *Dendroctonus ponderosae*) affects limber pine *Pinus flexilis* and lodgepole pine *Pinus contorta*. Western balsam bark beetle (WBBB, *Dryocoetes confusus*) affects subalpine fir *Abies lasiocarpa*. Spruce bark beetle (SB, *Dendroctonus rufipennis*) affects Engelmann spruce *Picea engelmannii*. Trees killed by mechanical damage were not included

were associated with higher MT, higher CWD and lower MEI, whereas *P. engelmannii* or *P. flexilis* were relatively unaffected by climate and MEI variability (Table 1). Tree mortality of main canopy trees and older trees also increased under higher MT, higher CWD and lower MEI in older stands, whereas young postfire stands were less affected (Table 1).

3.5 | Trends in mortality attributed to bark beetles

Of the mortality attributed to bark beetles (dead trees with evidence of bark beetle activity), 80.5% occurred in recent census periods (2008–2019; Figure 4). Among bark beetle-tree host associations, the mortality of *A. lasiocarpa* from western balsam bark beetle (WBBB) was the most common insect–host association over the 37-year study (62.4% [73.8%] of total tree deaths in old postfire stands [old *Picea-Abies*]). In contrast, mortality of *P. engelmannii* from spruce beetle (SB, *Dendroctonus rufipennis*) and *P. flexilis* or *P. contorta* from mountain pine beetle (MPB, *Dendroctonus ponderosae*) were much lower (<26.1% of total tree mortality). Among stand types, tree mortality from bark beetles was much greater in older stands (27.1% in old postfire, 47.3% in old *Picea-Abies* stands) than young postfire stands (<1%; Figure 4) and was concentrated in main canopy trees in all stand types (>80% in main canopy trees). Over the 37-year study period, SB-caused mortality of *P. engelmannii* was the only bark beetle-tree host association that significantly increased (*p* < 0.05, Figure 4e,f).

4 | DISCUSSION

We detected increases in background tree mortality from 1982 to 2019 in subalpine forests in the southern Rocky Mountains. As expected, higher annualized tree mortality rates (from tree stress and bark beetles only) were related to warmer and drier summer conditions and the negative phase of MEI (i.e. La Niña). However, we found variability in the strength of the relationship between climate and annualized tree mortality among subpopulations (tree size classes, age classes and species) that may have important implications for future subalpine forest dynamics.

Greater increases in tree mortality and stronger relationships between higher rates of tree mortality and warmer, drier climate in old *Picea-Abies* stands compared to young postfire stands in the stem-exclusion phase supports the expectation that older stands are more vulnerable to climate-related mortality (Table 1; Figure 2; Smith et al., 2015; van Mantgem & Stephenson, 2007). Older stands were composed of more trees in larger (>~20 cm dbh) and older size classes that were more susceptible to the direct (warmer, drier conditions) and indirect (bark beetles) effects of climate than younger stands. Climate-driven losses of large, dominant trees have occurred in many other forest types across the earth (Bennett et al., 2015; Lutz et al., 2018; Stovall et al., 2019), and we show that similar processes are occurring in subalpine forests that cover ~2.6 Mha in Colorado (Thompson et al., 2017). Increases in tree mortality also

tended to occur during the cool phase of ENSO (La Niña), which are the same conditions linked to increases in wildfire activity and bark beetle outbreaks in the southern Rockies (Hart et al., 2014; Schoennagel et al., 2005). By linking La Niña conditions to rates of background tree mortality, our findings address uncertainty about the implications of ENSO for tree mortality in the absence of coarse-scale disturbances (wildfire or SB outbreak) and help predict periods of elevated background tree mortality.

Although climate had a stronger effect on older stands, we also found that periods of higher rates, but not trends (Figure 2), of mortality in young postfire stands were associated with warmer and drier summer conditions (Table 1). This result is thus counter to our expectation that stands in the stem-exclusion stage, experiencing steady self-thinning of trees in the smallest size class, would exhibit no detectable influence of climatic variability on mortality rates. As competition for resources (e.g. light, moisture, nutrients) is a primary driver of mortality in the stem-exclusion stage of stand development, warmer and drier conditions that increase resource limitations may compound the effects of competition, potentially causing mortality earlier than would be expected under favourable climate conditions. In our study, young postfire stands were almost exclusively composed of *P. contorta*, which close stomata in response to drought to increase water use efficiency (Adams et al., 2014). Smaller trees have shallower roots than larger trees and thus may lose access to water and close their stomata earlier (Sapes et al., 2019), potentially causing earlier mortality of smaller trees from carbon starvation and hydraulic failure (Hammond & Adams, 2019). Although tree mortality in younger postfire stands in the stem-exclusion stage may result from the direct effects of competition, we show that climate is likely influencing the competitive environment.

Differences among subalpine species in their annualized mortality rates in our study reflected their expected tolerance to drought. In older stands, annualized rates and increases in tree mortality over the 37-year study were greater for *A. lasiocarpa* than *P. engelmannii*. This finding is consistent with the lower water use efficiency for *A. lasiocarpa* (Brodersen et al., 2006), higher vulnerability of *A. lasiocarpa* to cavitation during moisture stress (Sperry et al., 1994), high susceptibility of *A. lasiocarpa* to root fungi (e.g. *Armillaria* spp.; Lalande et al., 2020) and the documented sensitivity of *A. lasiocarpa* to mortality during annual and multi-year droughts (Bigler et al., 2007). In agreement with patterns in tree mortality inferred from tree-ring data (Mast & Veblen, 1994; Smith, 2012), our results highlight relatively continuous mortality of *A. lasiocarpa* as opposed to infrequent pulses of mortality for the longer-lived *P. engelmannii*. The higher mortality rate of *A. lasiocarpa* relative to *P. engelmannii* allows the less abundant *P. engelmannii* to persist in the main canopy and *Picea-Abies* forests to maintain similar structure and composition for centuries, despite much higher abundances of *A. lasiocarpa* seedlings and saplings (Andrus, Harvey, Chai, et al., 2018; Oosting & Reed, 1952; Veblen, 1986b). In the context of warming temperatures and future stand dynamics, the greater climate sensitivity for *A. lasiocarpa* than *P. engelmannii* in older stands implies that *P. engelmannii* may further increase in relative dominance in the main canopy in the absence of coarse-scale disturbance.

In old seral postfire stands, rates of mortality for *A. lasiocarpa* and *P. engelmannii* were higher and increased more rapidly than *Pinus* spp. over the 37-year study period (Figure 2; Appendix S1: Table S6). However, tree mortality for *P. contorta* and *A. lasiocarpa* was considerably more sensitive to interannual climate variability than *P. engelmannii* and especially *P. flexilis* (Table 1). In old seral postfire stands, shifts in tree densities across age and size classes indicate that *A. lasiocarpa* and *P. engelmannii* are on a trajectory to replace the *Pinus* spp., which exist primarily in the largest size classes (Chai et al., 2019; Veblen, 1986a). The high sensitivity of *P. contorta* to climate variability, and their currently low population sizes, may result in more rapid losses of *P. contorta* than expected in the absence of warming and drying climate conditions. In contrast, the low rates of mortality (consistent with its potential longevity >1,000 years; Donnegan et al., 2001) and high tolerance of *P. flexilis* to climate variability, even under extremely dry site conditions (BW2), may signal longer persistence of *P. flexilis* in the main canopy relative to *A. lasiocarpa* and *P. engelmannii* (Conlisk et al., 2017). Different sensitivities of tree mortality among species to long-term trends and variability in climate may affect the rate of successional loss of *Pinus* spp., but the scarcity of *Pinus* spp. in the smaller size classes implies that *A. lasiocarpa* and *P. engelmannii* are still expected to successionally replace *Pinus* spp.

Our results show that the sites at the greatest risk of ecological change as climate warms are stands in lower elevation xeric sites and higher elevation mesic sites with higher tree densities due to the direct effects of climate and to the combined effects of climate and bark beetles, respectively (Appendix S1: Figure S3; Table S6). Warming temperatures are exacerbating drought effects on tree populations at drier sites (Clark et al., 2016), and our finding that rates of mortality increased more rapidly in xeric than mesic sites in young postfire stands is consistent with this expectation. In older stands at higher elevations, tree mortality increased more rapidly and was higher in mesic than xeric or hydric sites, which may reflect the lower water use efficiency in mesic sites or the confounding effects of species composition and stage of stand development. For example, comparing mesic old seral postfire stands (BW3, MRS4) to their xeric counterparts (BW2, MRS7), mesic stands have species compositions with higher abundances of more drought-sensitive species (*P. engelmannii* and *A. lasiocarpa* vs. *Pinus* spp.), higher densities of large, susceptible host trees for bark beetle attack (Hart et al., 2014) and higher biomasses (Chai et al. 2019). Despite the important variability in factors explaining tree mortality across gradients of site moisture availability, we consistently found that tree mortality rates were higher and increased more rapidly in denser stands relative to adjacent less dense stands with similar site moisture availability, implying that lower competition for resources may reduce the risk of mortality in subalpine forests.

Similar to studies in subalpine forests in the maritime climate of the Sierra Nevada (Das et al., 2013, Furniss et al., 2020), we found that bark beetles (indirect climate effect) were an important cause (23.3% of dead trees with evidence of bark beetle activity) of background tree mortality in our study. Although increasing

trends were only detected for SB, higher rates of beetle-caused mortality (SB and WBBB) occurred during a warmer and drier period in older stands (2008–2019). In contrast, young postfire stands were relatively unaffected by bark beetle activity. Warmer and drier conditions, the same conditions that initiate broad-scale bark beetle outbreaks (Chapman et al., 2012; Hart et al., 2014; Lalande et al., 2020), appear to be increasing the susceptibility of *A. lasiocarpa* and *P. engelmannii* to higher rates of bark beetle-caused mortality in older stands with endemic beetle populations. In contrast, very low levels of beetle-caused mortality were observed in younger postfire stands, which is consistent with the lower susceptibility of younger *P. contorta* stands (<125 years old) to bark beetle outbreaks (Kulakowski et al., 2012). As the warming climate continues to increase tree stress and increase survival rates of bark beetles (Huang et al., 2020), bark beetle-caused mortality may play an increasingly important role in background tree mortality with endemic beetle populations.

4.1 | Implications of a warmer, drier future for tree mortality

Strong links between higher tree mortality and warmer, drier summer climate conditions imply that climate warming will continue to increase the rates of background tree mortality. Summer temperatures in high elevation areas of the Southern Rocky Mountains are expected to warm by 1°–2.7°C under low-medium emissions scenarios (RCP 4.5) and 2°–3.6°C under high emissions scenarios (RCP 8.5) by mid-century (Lukas et al., 2014). Relatively, stable levels of total annual precipitation but greater variability in timing and intensity for the eastern slope of the CFR is expected to further increase soil moisture deficits during the growing season with more extreme moisture deficits anticipated under higher emissions scenarios (e.g. RCP 8.5; Knowles et al., 2018). The climate conditions that lead to marked increases in tree mortality in our long-term plots are the same conditions projected to become increasingly common by mid-century (Lukas et al., 2014). Climate warming, in combination with interannual to multi-decadal climate variability (i.e. ENSO and PDO), has also led to earlier snow disappearance over the last 30 years (Lukas et al., 2014). However, in our study, we did not detect an effect of snowpack (SWE, May 1st) on adult tree mortality. Although low snowpack limits *P. engelmannii* and *A. lasiocarpa* seedling establishment (Andrus, Harvey, Rodman, et al., 2018), the current study shows that mortality of adult trees depended primarily on summer climate conditions, which is consistent with the greater sensitivity of gross primary productivity to summer rather than winter precipitation in the southern Rocky Mountains (Berkelhammer et al., 2017).

Our results highlight two implications of increasing tree mortality for stand structure that may have long-term effects on the capacity for subalpine forests to store and fix carbon. First, subalpine tree populations may be slowly declining as a result of unfavourable climate conditions for seedling establishment (Andrus, Harvey, Rodman, et al., 2018; Kueppers et al., 2017) and increasing

tree mortality documented in all stand types in the current study. Second, larger and older trees that store and fix carbon at higher rates than smaller and younger trees (Stephenson et al., 2014) are dying at faster rates in older stands. Despite these early warning signs, from 1982 to 2016 tree growth offset losses in above-ground live biomass (AGB, an indicator of carbon storage) to mortality, and AGB increased in most (80%) of the permanent plots (Chai et al., 2019). Similarly, subalpine forests near the young postfire stands in the present study, in which mortality was concentrated in smaller size classes, have functioned as a steady carbon sink since the inception of eddy covariance measurements in 1998 (Barnard et al., 2018; Blanken et al., 2020). However, carbon sequestration in the southern Rocky Mountains may be increasingly vulnerable to drought (Knowles et al., 2018), and gradual changes in background tree mortality rates compounded over decades may have important implications for carbon sequestration and storage.

Although we show strong relationships between annualized tree mortality and climate conditions, causation of mortality should be considered in the context of two limitations. First, tree mortality was averaged over 3-year census periods, whereas climate variation was quantified at an interannual resolution. To account for this limitation, we selected the climate conditions most likely to result in tree mortality during each census period (e.g. maximum CWD), but we did not account for potential lagged effects of prior climate (both prior extreme events or gradually intensifying moisture deficits) that previously have been shown to affect mortality of the study species (Bigler et al., 2007). Second, in the absence of long-term physiological measurements, our assessment of the proximate cause of death is based on the best available evidence (e.g. bark beetle galleries). We acknowledge that climate may have predisposed trees to lethal bark beetle attack, thus making it difficult to fully disentangle abiotic and biotic agents of mortality. Despite these limitations, our data represent a robust assessment of the causal agents of mortality.

5 | SUMMARY

Our findings highlight that the direct and indirect effects of climate have important effects on the rates of background tree mortality. Across a range of stand types in subalpine forests in the southern Rockies, we found that increasing trends and higher rates of background tree mortality were occurring in conjunction with hotter summer temperatures and greater summer moisture deficits as well as with the warm–dry conditions during La Niña events. Strong links between tree mortality and warmer, drier climate conditions imply that climate warming will likely continue to increase the rates of background tree mortality in subalpine forests. However, we observed key differences in tree mortality rates and sensitivity to climate among stand types, tree age and size classes, and species that collectively may lead to unexpected shifts in stand composition and structure. Although the direct effects of warmer, drier climate conditions had the greatest effect on tree mortality in our study, we detected elevated rates of bark beetle-caused mortality (i.e. indirect effect of climate) during a warmer and drier period. Thus, understanding both the direct effects of climate and indirect implications of elevated tree stress for susceptibility to bark beetle attack is critical to forecasting the effects of climate warming on tree mortality. The persistence of subalpine forest cover will depend on the net outcome of the responses of demographic processes—including reproduction, growth and mortality—to climate warming. In combination with recent findings of a declining frequency in years suitable for tree seedling establishment, our finding of increased rates of background tree mortality is potentially an early warning sign of climate warming effects on ecosystem services that depend on the maintenance of current forest structure in the subalpine forests of the Southern Rocky Mountains.

AUTHORS' CONTRIBUTIONS

Authors 2–5 are ranked alphabetically rather than in order of contribution; R.A.A. and T.T.V. designed the study; R.A.A., R.K.C., B.J.H., K.C.R. and T.T.V. assisted with field work; R.A.A. performed the statistical analyses with input from co-authors; R.A.A. led the writing of the manuscript. All authors helped revise the manuscript and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

Data are available through the Environmental Data Initiative, https://doi.org/10.6073/pasta/48fa11a8f5bc6541b0472bc3fd4c0c71 (Veblen et al., 2021).

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SUPPORTING INFORMATION

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

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