Declining tree growth resilience mediates subsequent forest mortality in the US Mountain West

Running title: Growth resilience mediates forest mortality

Authors: Antoine Cabon[1,2*], R. Justin DeRose[3], John D. Shaw[4], William R. L. Anderegg[1,2]

Affiliation: [1]Wilkes Center for Climate Science and Policy, University of Utah, Salt Lake City, Utah, USA; [2]School of Biological Sciences, University of Utah, Salt Lake City, Utah, USA; [3]Department of Wildland Resources and Ecology Center, Logan, Utah, USA; [4]USDA Forest Service, Rocky Mountain Research Station, Logan, Utah, USA

Keywords: Forest mortality; drought; insect outbreak; tree-ring; growth; resilience; Lloret indices.

Author contributions: AC and WRLA designed the study. RJDR and JDS developed the enhanced FIA core collection protocols and compiled and processed the data. AC conducted the analyses. All co-authors wrote the manuscript.

*Author for correspondence: Antoine Cabon.
antoine.cabon@wsl.ch
The University of Utah
257 South 1400 East
Aline Wilmot Skaggs Biology
Salt Lake City Utah 84112
United States

Abstract

Climate change–triggered forest die-off is an increasing threat to global forests and carbon sequestration but remains extremely challenging to predict. Tree growth resilience metrics have been proposed as measurable proxies of tree susceptibility to mortality. However, it remains unclear whether tree growth resilience can improve predictions of stand-level mortality. Here, we use an extensive tree-ring dataset collected at ~3000 permanent forest inventory plots, spanning 13 dominant species across the US Mountain West, where forests have experienced strong drought and extensive die-off has been observed in the past two decades, to test the hypothesis that tree growth resilience to drought can explain and improve predictions of observed stand-level mortality. We found substantial increases in growth variability and temporal autocorrelation as well declining drought resistance and resilience for a number of species over the second half of the 20th century. Declining resilience and low tree growth were strongly associated to cross- and within-species patterns of mortality. Resilience metrics had similar explicative power compared to climate and stand structure, but the covariance structure among predictors implied that the effect of tree resilience on mortality could partially be explained by stand and climate variables. We conclude that tree growth resilience offers highly valuable insights on tree physiology by integrating the effect of stressors on forest mortality but may have only moderate potential to improve large scale projections of forest die-off under climate change.

Introduction

Rising global temperatures due to human greenhouse gas emissions pose a threat to Earth's forests. Notably, increasing temperature has been linked to higher frequency and intensity of drought-induced forest background mortality and die-off (Breshears *et al.*, 2009; Williams *et al.*, 2012; Allen *et al.*, 2015). Large scale forest die-off is of particular concern due to its dramatic disruption of forest function, with large consequences on biodiversity (Betts *et al.*, 2017; Feng *et al.*, 2021), ecosystem goods and services and forests' prominent role in the global carbon cycle (Anderegg *et al.*, 2020a). The western US has experienced extensive drought- and insect-induced tree mortality over the past decades, associated to strong drying trends in the area (Van Mantgem *et al.*, 2009; Williams *et al.*, 2012; Zhang *et al.*, 2021). These disturbances have resulted in the decline of several major tree species in the region (Stanke *et al.*, 2021).

A large diversity of interacting drivers and pathways mediate climate-induced tree mortality. Drought-induced mortality results from the complex and interacting set of failures across the hydraulic continuum and tree carbon economy (McDowell *et al.*, 2022), which has been typically studied as hydraulic failure and depletion of carbohydrate stores (McDowell, 2011). Hydraulic failure, i.e., the accumulation of emboli in the xylem past a threshold after which water transport cannot be recovered, disrupts water supply, leading to cell death by dehydration (Sperry & Tyree, 1988). Longer term, declines in carbon balance can eventually trigger mortality through cell failure to maintain base metabolism or osmoregulation, almost always interacting with hydraulic failure and/or biotic agents. Tree radial growth is a major process integrating water and carbon processes involved in mortality (Preisler *et al.*, 2021). Previous to drought, tree growth favors carbon assimilation by sustaining photosynthesis. On the other hand, larger allocation to conducting tissues can be at the expense of allocation to osmoregulation or defense (Huot *et al.*, 2014; de la Mata *et al.*, 2017) or translate into structural overshoot rendering trees more vulnerable to drought (Jump *et al.*, 2017). After drought, new xylem growth allows trees to recover hydraulic function and may influence delayed mortality (Trugman et al. 2018).

Biotic agents, including diseases and insects can also drive large scale forest mortality, often in interaction with climate stress, to the point that disentangling their relative importance is often challenging (Anderegg *et al.*, 2015a). Notably, western US forests have been particularly prone to extensive bark beetle outbreaks in the last decades, where drought was a key predisposing factor in many species (Raffa *et al.*, 2008; Van Mantgem *et al.*, 2009;

Chapman *et al.*, 2012; Meddens *et al.*, 2015). Drought may facilitate biotic outbreaks by impairing tree defenses against attacks such as resin and defense chemicals production, hence favoring infestations and eventually mortality (Gaylord *et al.*, 2013; Kolb *et al.*, 2019). In turn, infestations can weaken trees' water and carbon economies (Frank *et al.*, 2014) through direct damage to the bark and xylem or defoliation , which may increase tree vulnerability to drought (Paine *et al.*, 1997; Anderegg & Callaway, 2012; Anderegg *et al.*, 2015a). Finally, stand factors such as host availability, density, age and size can play a substantial role in determining whether infestations reach epidemic levels and eventually lead to extensive die-off events (Raffa *et al.*, 2008). However, predisposing factors are often highly species-specific (Reed & Hood, 2021).

Climate-induced tree mortality remains challenging to predict because of the wide array of involved processes. Success of physiology-based models has been largely limited to specific context and/or small scales, where environmental variations and the number of processes are limited, in contrast to regional applications (e.g., Venturas *et al.*, 2018, 2021; see also Benito Garzón *et al.*, 2018; Trugman *et al.*, 2021). The challenge of accounting for such complexity has led to the adoption of simpler frameworks based on tree vigor proxies (Bigler & Bugmann, 2003; Lloret *et al.*, 2011). Growth-based models of mortality are one such approach, wherein, based on the empirical assertion that tree growth declines previous to tree mortality (Cailleret *et al.*, 2016), tree growth is assumed to integrate constraints on tree physiological status. Growth-based mortality models use historical tree growth observations, e.g., derived from tree-ring or forest inventory, to parameterize empirical models of tree mortality, often in combination with cofactors such as tree diameter (Bigler & Bugmann, 2003; Hülsmann *et al.*, 2018). These models have garnered relatively good success due to their simplicity and predictive power but might be limited in that they assume a static relationship between tree growth and mortality. Such assumption may allow one to simulate smooth variations in stand background mortality, but it is unclear whether tree growth can capture the effect of drought and biotic agent perturbations in a changing climate, as such events can be uncoupled from it (e.g., epidemic insect outbreak) or instead select for slower growing trees (Jump *et al.*, 2017; de la Mata *et al.*, 2017).

By acknowledging highly non-linear responses, complex system theory may provide a useful framework to predict stand-level mortality patterns across space. In this framework a system approaching a tipping point is denoted by critical slowing down that manifests in declining system resilience to perturbations, i.e., the system's capacity to remain in a reference regime (Scheffer *et al.*, 2001, 2009). Declining resilience and associated increasing state variability and autocorrelation, can hence theoretically be used as early warning signals (EWS) of impending system transition to an alternative stable state (Scheffer *et al.*, 2009; Hammond, 2020). Stand or regional-scale forest mortality can be viewed as one such tipping point, where a perturbation might induce an abrupt transition towards a fundamentally different regime (e.g., change in stand structure, species composition or transition to a different cover type) (Hammond, 2020). Consequently, a body of literature has focused on applying critical slowing down theory to forest mortality by developing EWS based on radial tree growth (Lloret *et al.*, 2011; Camarero *et al.*, 2015). Recent syntheses notably show that large tree growth variability –in the case of gymnosperms– and low resilience (Cailleret *et al.*, 2019; DeSoto *et al.*, 2020) are associated to subsequent tree-level mortality, suggesting that these could predict future forest mortality. Implications are vast given observation of widespread declining tree resilience to drought (Zheng *et al.*, 2021, 2023; Forzieri *et al.*, 2022). Several uncertainties nevertheless remain that hinder the application of EWS to predict forest mortality. First and foremost, previous studies mostly investigated the relationship between EWS and mortality at the tree level (i.e., differences among individual trees growing in the same stand), but it is unclear if such a relationship scales to the stand or landscape level. At large spatial scales, the role of covarying environmental and genetic factors (e.g., stand structure, climate, species identity) might complicate or overshadow the relationship between growth resilience and mortality observed at the individual level (Kannenberg *et al.*, 2019). Second, previous analyses typically reported qualitatively on the existence of such relationship but lacked quantification of their predictive power. Finally, because EWS metrics have often been investigated individually, it is not clear how different metrics, including tree growth, variability, autocorrelation and resilience might be complementary to or on the contrary be redundant with stand and climate predictors of mortality.

Here, in order to address the link between tree growth resilience to drought and stand-level mortality, we leverage a large tree-ring dataset comprised of over 7000 records from ~ 3000 national forest inventory plots in the US Mountain West, where extensive mortality has been reported in recent decades. Specifically, we (1) test the hypothesis that low tree growth resilience and associated metrics are related to subsequent stand-level mortality, (2) investigate the regional stand and climatic drivers of mortality and their covariation with tree growth and resilience, and finally (3) quantify the relative power of stand, climate, growth and resilience drivers to capture spatial patterns of stand mortality in explicative vs. predictive modelling contexts.

Material and methods

Forest inventory, stand structure and mortality

The USDA Forest Service Forest Inventory and Analysis (FIA) program monitors forest structure, growth and health in a systematic way based on an extensive network of permanent plots distributed across the United States (Bechtold & Scott, 2005). Here we use a subset of 3028 FIA plots from five states of the US Mountain West where tree cores were sampled in addition to the FIA standard sampling effort (DeRose *et al.*, 2017). Following the FIA sampling design, four circular subplots of a radius of 7.3 m comprise each plot, where the diameter at breast height (DBH) of all trees with a diameter superior to 12.7 cm are measured. Each subplot contains a circular microplot of 2.1 m, within which trees with a diameter inferior to 12.7 cm are measured. Plots included in this study were selected on the basis that no silvicultural treatment was applied, and that mortality was attributed either to no agent (unknown agent), insect, drought (weather), or disease.

Trees are classified into live, recently dead and older dead based on canopy status. On repeated inventory plots (~35% of all plots), 'recent dead' is assigned to the trees that were live during the previous inventory and dead in current inventory. On first-visit plots, 'recent dead' is assigned to trees that appear to have died during the previous 5 years, assessed by the census crew based on canopy and bark status (Shaw *et al.*, 2005). This initial-visit approach has been commonly and successfully used in tree mortality research in this region (e.g., Venturas *et al.*, 2021). 'Old dead' trees are ignored in the following analysis and 'recently dead' trees are referred to as 'dead' hereafter.

We computed species-specific per hectare sum of basal area of individual trees in live and dead categories (BA). Mortality was subsequently defined at the stand level as the BA of dead in percent of total BA (live and dead). Tree density was calculated as the sum of live and dead stems per hectare. Tree species diversity was estimated based on the Shannon index where species abundance is taken as species total basal area.

Climate data

Several climatic variables have been previously shown to be closely related to tree mortality across the US (Venturas *et al.*, 2021). Monthly min and max temperature, precipitation, Palmer's drought severity index (PDSI), vapor pressure deficit and climatic water deficit were retrieved from the TerraClimate database (Abatzoglou *et al.*, 2018) for each of the plots on the period 1958 to 2019 (TerraClimate variable names: tmin, tmax, ppt, PDSI, vpd and def, respectively). Mean annual temperature (MAT, computed as the average of min and max temperature), precipitation (MAP), vapor pressure deficit and climatic water deficit were calculated on the same period. We further calculated plot-level historical temporal trends of these climatic variables by means of linear regression. Drought intensity, frequency and heat stress during the FIA census period were calculated at each plot respectively, as the minimum growing season PDSI (averaged over April through September), the number of years with growing season PDSI < -1.5, and the difference between maximum and average growing season max temperature .

FIA tree-ring collection & growth metrics

Generally, one (about 75% of the plots) but up to 16 and an average of 2.2 tree cores per plot were collected (~1.6 cores per plot and per species), yielding a total of 7281 cores. Tree cores were initially collected to determine stand age and site index, based on the average age per species within 12.7 cm diameter classes and the dominant size class, respectively. As a result, tree selection consisted exclusively of live trees and was typically skewed toward the dominant size cohort. Cores were collected during the period 2000-2022, but over 90% of the cores were collected after 2010. The cores were processed, and ring width was measured following standard dendrochronological methodology (DeRose *et al.*, 2017). Cross-dating was performed using nearby chronologies from the International Tree-Ring Data Bank (ITRDB), as well as adjacent FIA plots as the tree-ring collection grew. Past tree basal area increment (BAI) was retrieved backward from tree DBH at core collection. A detrended ring width index (RWI) was calculated by dividing RW series by splines with 50% cutoff at 30 years fitted on individual ring width series. In order to investigate the potential of past tree growth temporal patterns as early warning metrics of mortality, BAI and RWI series were used to calculate a set of six metrics to characterize average and trends in past tree growth and resilience to drought events, during the 40 years prior to the mortality census period.

Growth metrics included BAI, as well as RWI autocorrelation (1 year lag; ar) and RWI variation coefficient (VC) calculated on 10-year windows, which have been previously proposed as early warning metrics of tree mortality (Cailleret *et al.*, 2019). Resilience metrics included tree growth resilience (Rl) to past droughts and its resistance (Rs) and recovery (Rc) components. Resilience metrics were calculated for each RWI series and drought years. Drought years were defined as years for which growing season PDSI (averaged over April–September) was inferior to the 1st decile at a given plot. Rl, Rs and Rc were calculated as differences, analogous to Lloret’s ratios (Lloret *et al.*, 2011):

$$Rs = RWI_{drought} - RWI_{pre} \qquad \text{Eq. 1}$$

$$Rc = RWI_{post} - RWI_{drought} \qquad \text{Eq. 2}$$

$$Rl = RWI_{post} - RWI_{pre} = Rs + Rc \qquad \text{Eq. 3}$$

Where $RWI_{drought}$ is RWI during the drought year, RWI_{pre} is the average RWI during the 4 years prior and RWI_{post} is the average RWI during the 4 years posterior to the drought year, following (Anderegg *et al.*, 2015b). The use of differences instead of ratios was motivated by the distribution of RWI, which included zeroes and values close to zero.

In order to investigate tree-ring metric temporal variations and their effect on tree mortality, all six growth and resilience metrics were decomposed at the core level into a temporal trend and a period-independent average. To do so we fitted two sets of mixed linear models. First, each metric was modelled as a function of species identity, including one random intercept per core as well as a random effect of year per species, such that:

$$Y_{ijk} = \beta_{0,i} + u_{0,j} + u_{1,ik} + \epsilon_{ijk} \qquad \text{Eq. 4}$$

Where, Y_{ijt} is the metric value of the i^th^ species, j^th^ core and k^th^ year, $\beta_{0,i}$ is a fixed species intercept, $u_{0,j}$ is a random intercept per core, $u_{1,ik}$ is the random effect of year per species and ϵ is an error term. Based on this model we estimated period-independent mean values per core for each metric (hereafter metric name plus 'mean') such as $\beta_{0,i} + u_{0,j}$. Second, we fitted a mixed linear model which included fixed species and year per species effects, as well as a random intercept and slope per core, nested within species:

$$Y_{ij} = \beta_{0,i} + \beta_{1,i}Year + u_{0,j} + u_{1,j}Year + \epsilon_{ij} \qquad \text{Eq. 5}$$

Where, $\beta_{1,i}$ is the slope for the fixed effect of year. From this model we extracted core-level linear temporal trends for each metric (hereafter metric name plus 'trend') such as $\beta_{1,i} + u_{1,j}$. When relevant, previous to model fitting we normalized leptokurtic-distributed metrics using the Lambert W function in the R package 'LambertW'. Homoskedasticity and normality of residuals were visually checked for each model and metric.

Stand mortality models

We considered the role of a total of ~40 unique variables as predictors of stand mortality, that were classified into one of stand, climate, growth, or resilience categories. Stand structure predictors included overall and species-specific basal area, tree density, average and maximum height and diameter at breast height (DBH), as well as stand age, aspect, slope and diversity (Shannon index). Climate variables included MAT, MAP, mean annual vapor pressure and climatic water deficit, temporal trends of the previous, as well as drought intensity, frequency and heat stress during the census period. Growth variables consisted in the overall mean and temporal trends of BAI, BAI autocorrelation and BAI variation coefficient. Resilience variables consisted in overall mean and temporal trends of Rl, Rs and Rc.

In order to perform a balanced comparison between the effects of stand, climate, growth and resilience factors on stand mortality and to limit the total number of model parameters to avoid overfitting, we performed a preliminary model selection to restrict the number of predictors per category to four. To do so, for each predictor category (i.e., stand, climate, growth and resilience), we fitted logistic models of stand-level mortality with all combinations of up to four predictors per category. For each category we then identified the best model based on the Akaike information criterion (AIC) and retained the corresponding set of predictors. When the AIC difference between models was < 2, we retained the most parsimonious and biologically meaningful model (**Table S1–4**). The covariance structure of selected predictors was assessed by calculating pairwise Pearson's correlation between each predictor.

Species-specific basal area mortality occurrence, intensity (i.e., proportion of conspecific mortality basal area at plots where mortality occurred) and overall basal area mortality (hereafter 'mortality') were subsequently modelled both as a function of one predictor at a time (univariate case) and as a function of all predictors at the same time (multivariate case). In all cases, the three components of mortality were modelled using logistic regressions with binomial residual distribution in the case of mortality occurrence and overall mortality, and beta distribution in the case of intensity (generalized linear models; GLMs). FIA census repeat interval was found to have only a small effect on mortality but was nevertheless included in all models as a covariable. Species-specific tree density was similarly found to induce a positive bias on mortality occurrence detection (increased likeliness to observe at least one mortality tree with large sample size; **Fig. S1A**) as well as a negative bias on mortality intensity (increased likeliness of mortality to make up for a large proportion of species BA with low sample size; **Fig. S1B**), but these biases cancelled out in the case of overall mortality (**Fig. S1C**). Hence, we included species-specific density as a second covariable in mortality occurrence and intensity models. GLMs had the form:

$$\text{logit}(\text{M}) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_n X_n + \qquad \text{Eq. 6}$$

$$\beta_{n+1}\text{CensusPeriod} + (\beta_{n+2}\text{SpeciesDensity}) + \epsilon$$

Where, M is mortality occurrence, intensity or overall mortality β_0 is the intercept, $\beta_1, \beta_2, \ldots, \beta_n$ are the coefficient estimates for the included $X_1, X_2, \ldots, X_n$ variables, β_{n+1} is the effect of repeat census period, β_{n+2} is the effect of species density (only for mortality occurrence and intensity models) and ϵ is an error term.

In the univariate case we used generalized linear mixed models (GLMMs) that had the same general form as Eq. 6 but further included a random intercept per species, in order to account for different mortality pathways between species and evaluate the predictive power of each variable *within* in addition to *across* species. Finally, multivariate models' variance was decomposed into stand, climate, growth and resilience contributions based on the Lindeman, Merenda and Gold (LMG) and proportional marginal variance decomposition (PMVD) metrics (Grömping, 2007). Both metrics are similar in that they fully decompose total model variance into non-negative shares between predictors irrespective of their order in the model. However, by attributing equal weights to all variables, LMG informs on the explicative power of predictors ('marginal' perspective), whereas PMVD provides an estimate of variable usefulness in a predictive modelling setting by giving larger weights to variables that capture a larger proportion of the variance in combination with a smaller number of variables ('conditional' perspective). Last, we calculated the unique variance carried by each predictor category as the additional amount of explained variance by the full model compared to the model without this predictor category.

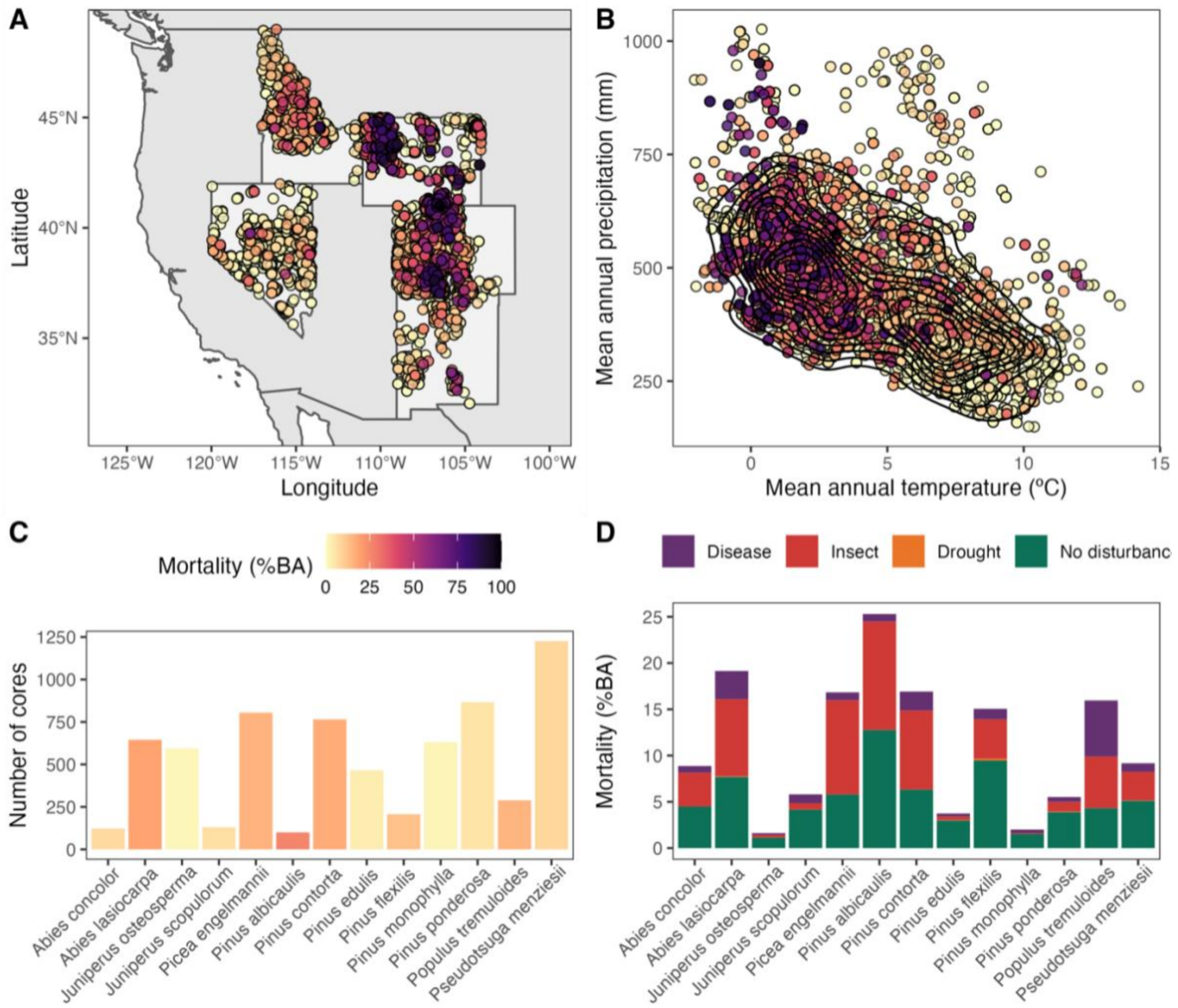

Fig. 1. (**A**) Geographic and (**B**) climatic distribution of stand-level mortality, in percent of conspecific basal area, at sampled forest inventory plots. (**C**) Number of cores collected per species. The bars color indicates species-level mortality average. (**D**) Average mortality per species and reported proximal disturbance agent based on field evidence of disease, insect or drought mortality. The absence of observable dominating disturbance agent is reported as "no disturbance". Mortality is calculated for each core as a plot-level conspecific basal area proportion.

Results

Mortality spatial distribution

About 1200 of the ~3000 FIA plots considered here exhibited some degree of mortality. In these plots, mortality affected 25±1% (mean ± SE) of basal area on average (6%, 16%, 38% for 1st, 2nd and 3rd quartiles). In the field, ~31% of observed basal area mortality was associated to insect outbreaks, 12% were associated to diseases and only 1% to drought, due to the limited field evidence and use of this disturbance code by crews. The remaining 56% of all mortality was listed as 'no disturbance' but can most likely be attributed to drought (see Discussion). Stand mortality varied widely spatially and across space and species (**Fig. 1**). Dry and warm, low elevation, pinyon-juniper dominated areas exhibited the lowest mortality levels, whereas colder and wetter subalpine areas exhibited extensive mortality, in relation with insect outbreaks, such as mountain pine beetles and spruce bark beetles. Subalpine pines, spruces and firs (*Abies lasiocarpa, Picea engelmannii, Pinus albicaulis, P. contorta* and *P. flexilis*) hence experienced mortality of ~20% basal area on average, of which 46% were associated to insect disturbance. Mortality averaged only 5% for the remaining conifer species, 20% of which were associated to insects. Quaking aspen (*Populus tremuloides*), which stands out as the only angiosperm species in our dataset, also experienced substantial mortality (16% on average). *P. tremuloides* was further unlike other species in the study in that its mortality agent was largely associated to diseases (38%) induced by pathogens such as Cytospora canker (Marchetti *et al.*, 2011), in addition to insects (35%).

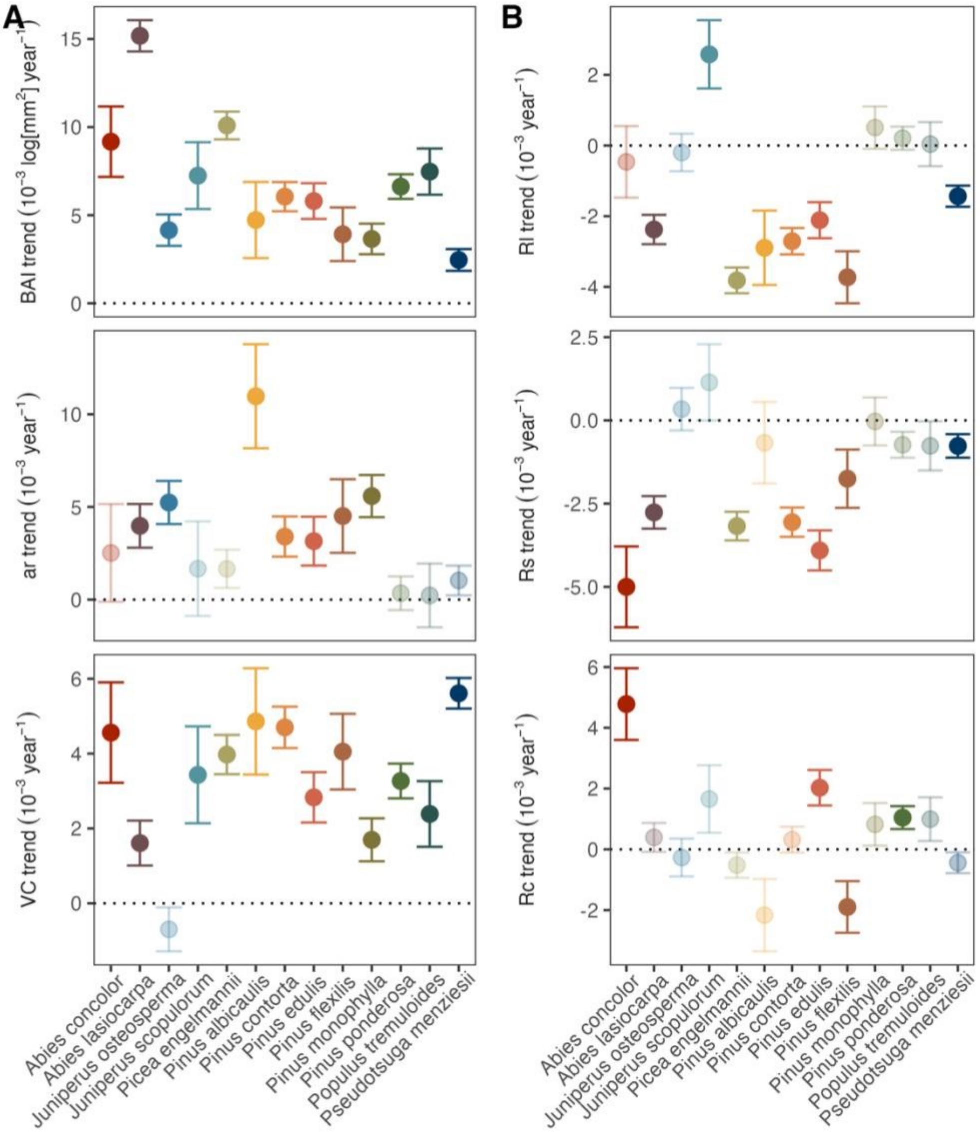

Fig. 2. Temporal trend of (**A**) tree growth and (**B**) resilience metrics. From top to bottom and left to right, basal area increment (BAI), RWI autocorrelation (ar), RWI variation coefficient (VC), growth resilience (Rl), resistance (Rs) and

recovery (Rc). Temporal trends were estimated from mixed linear models including a random intercept and slope per core. Variables were transformed to approximate a gaussian distribution when necessary. Solid and transparent dots represent significant and unsignificant species-level temporal trends, respectively ($\alpha = 0.05$).

Tree growth resilience decline

We observed that tree-level BAI of all species significantly increased between 1958–2010 (**Fig. 2A**). Tree-ring based BAI estimates were found to be representative of FIA plot-level BAI on the same period ($r = 0.68$, $p < 0.0001$). We found that this temporal increase in BAI was matched for most species by an increase in growth variability (11 out of 13 species with a significantly positive trend) and, to a lower extent, autocorrelation (5 out of 13 species with a significantly positive trend). We further observed a general tendency of growth drought resilience to decline over time (**Fig. 2B**; overall mean ± SE: $-1.40 \pm 0.52\ 10^{-3}$ year^{-1}, $p < 0.05$), with 7 out of 13 species that exhibited a significant decline, and only one species with a significant increase (*Juniperus scopulorum*), although this last result should be interpreted cautiously due to lower sample size for *J. scopulorum*. The resilience decline appeared to be driven overall by a decrease in drought resistance (on average $-1.26 \pm 0.42\ 10^{-3}$ year^{-1}, $p < 0.05$), whereas trends in drought recovery were inconsistent across species and overall did not compensate for decreased resistance ($p = 0.84$).

Mortality predictors selection

Preliminary category-wise variable selection yielded 3 to 4 best predictors of forest mortality per predictor category. The best stand structure predictors were conspecific and other species basal area, species maximum tree height and overall maximum DBH. Selected climate predictors were MAT, MAP, drought intensity and heat stress. Growth predictors comprised mean BAI, mean and temporal trend of BAI variation coefficient and mean BAI autocorrelation. Resilience predictors were mean Rl, Rs trend and Rt trend. Rl trend was not selected, likely due to its high correlation to Rs and Rt trends but was nevertheless included in univariate analyses for comparison.

Univariate models of stand mortality

When considering the relationship between individual predictors and stand mortality *across* species (generalized linear models, black lines in **Fig. 3**), we found a significant effect of all predictors, except Rl mean and max DBH. Best individual predictors of stand mortality were MAT, Rl trend, heat stress and species max height, in that order. We found a negative relationship between MAT or drought frequency and mortality, which was consistent with observed geographical distribution of mortality that was strongly skewed towards high mountain areas of Colorado and Wyoming (**Fig. 1**). However, the positive effect of heat stress during the census interval, indicated that given MAT, positive temperature anomalies were associated to higher mortality. Finally, rather than absolute tree growth resilience to drought, its decline over time was most strongly associated with mortality across species. The association between mortality and resilience decline across species appeared to be carried mostly by its resistance component.

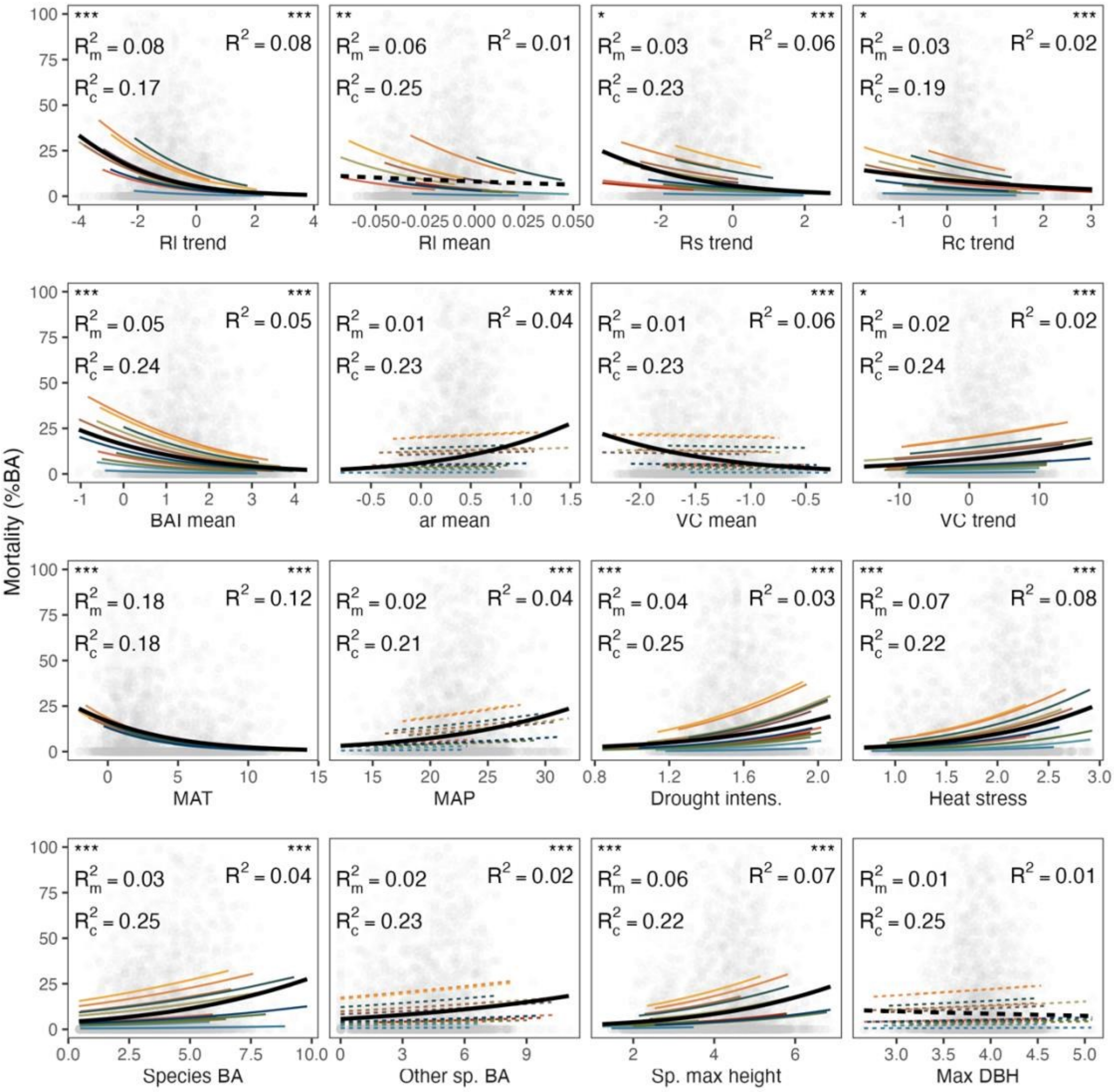

Fig. 3. Univariate logistic models of stand mortality (in percent of conspecific basal area). Both generalized (thick black lines) and mixed linear models including a random species intercept (thin colored lines) were fitted to the data. All models include the effect of census period duration. Predictors are transformed to approximate a normal distribution but its contribution to model variance is little (< 1%). Corresponding model marginal or conditional R^2 (GLMMs: R^2_m, R^2_c) and R^2 (GLMs) and significance ($p < 0.05$: * – $p < 0.01$: ** – $p < 0.001$: ***) are indicated on the top left and right corner of each panel, respectively. Significant effect of x-axis variable is further denoted by solid lines ($p < 0.05$). Note that Rl trend is included here to illustrate its effect on mortality but has been discarded from multivariate analyses in favor of its resistance and recovery components.

When looking at *within* species relationships (colored lines in **Fig. 3**, GLMMs) we found similar effects of MAT, heat stress, max species height and Rl trend compared to *cross*-species patterns. The effect of some variables which was significant cross-species was found to fade or disappear within species, showing that some or most of the cross-species effect was driven by between-species variations. This was the case of mean growth variation coefficient and growth autocorrelation, and to some extent, that of other species BA and MAP. By contrast, we found a stronger effect of Rl mean on mortality at the within-species level, which indicated that species-specific differences in resilience blurred the cross-species pattern. Individual predictors of mortality intensity were somewhat similar to overall mortality (**Fig. S2 & S3**), whereas the drivers of mortality occurrence more largely differed. Most strikingly, mortality intensity was most strongly related to resilience and growth metrics, whereas mortality occurrence was best described by stand structure metrics.

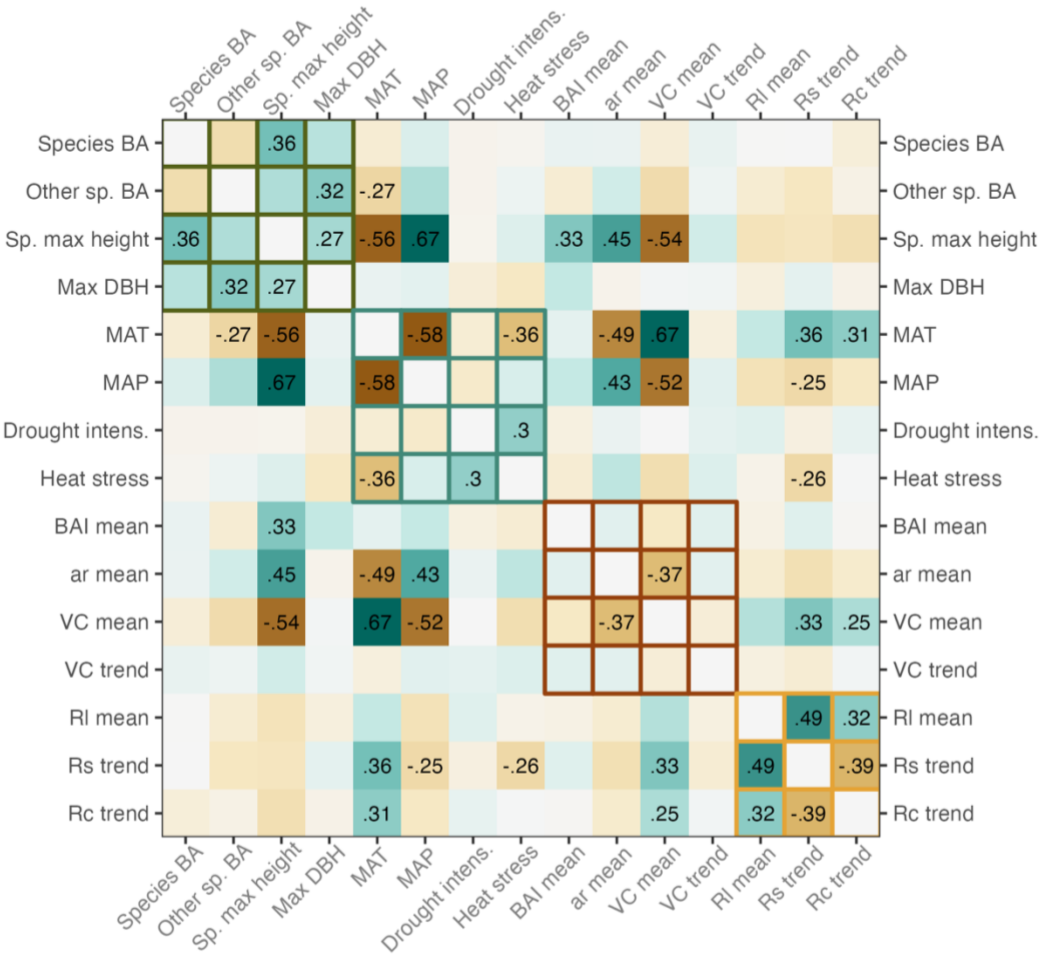

Fig. 4. Pearson's correlation matrix of the selected mortality predictors. Correlations which absolute value is > 0.25 ($p < 0.0001$) are displayed on top of the corresponding cells. Outlined cells denote correlations between variables of a same group: i.e., stand (green), climate (blue), tree growth (brown) and resilience variables (yellow).

Covariation of stand mortality drivers

Substantial covariation was observed between the predictors of mortality considered here (**Fig. 4**). Notably MAT and MAP were strongly correlated to each other and to a range of other variables, including species max height, mean growth variation coefficient and autocorrelation, as well as to a lesser extent, trends in resistance and recovery. Namely, colder- and wetter-than average climates, were associated to lower tree growth variation coefficient and higher autocorrelation, as well as stronger declines in drought resistance and recovery.

Trees that experienced increasing resistance and recovery to drought also tended to exhibit higher resilience overall. We found a negative association between Rs and Rc trends, suggesting that at the tree level, decline in growth resistance to drought was partially mitigated by increased recovery. We did not find that fast-growing trees were more resilient to drought. However, resistance and recovery trends were positively associated to mean growth variability, which was in turn negatively correlated to growth autocorrelation.

Multivariate stand mortality models

Full models (including all 15 predictors and 1-2 covariables –census return time and species density when applicable) explained 40%, 20% and 24% percent of observed mortality occurrence, intensity and overall mortality, respectively (**Fig. 5A**). Variance decomposition showed that the weight of the different predictors strongly differed between models. Mortality occurrence appeared to be mostly driven by stand structure, followed by climate and denoted little relative importance of growth and resilience metrics. Mortality intensity displayed an opposite pattern, where growth and resilience metrics had the largest relative importance overall, followed by climate and a small contribution of stand structure. These effects balanced each other when considering overall mortality, leading to a roughly similar relative importance of the different predictor categories. Variance decomposition nevertheless gave somewhat different results depending on the perspective. Notably, from the marginal perspective (LMG), variance decomposition gave substantially higher importance to resilience and lower importance to stand and climate overall, compared to the conditional perspective (PMVD). This result was related to the fact that predictors shared a substantial amount of variance, depending on the model. Predictor unique variance in occurrence model averaged about 68% of overall predictor explained variance (unique/marginal variance), but that number fell under half for intensity and overall mortality.

Coefficient estimates showed substantial consistency across occurrence, intensity and mortality models (**Fig. 5B**). This was mostly true for climate, growth and resilience coefficients, although less so in the case of stand coefficients. Namely, we found a strong positive effect of conspecific BA and max height on occurrence and overall mortality, but all stand coefficients were non-significant in the intensity model. Max DBH had no effect in all models. In contrast, we found consistently strong negative effect of resistance and recovery trends, as well as a positive effect of mean resilience on the three components of mortality. We also found a consistent negative effect of mean BAI across models, but other growth variables had small and inconsistent effect. Last, the effect of all climate variables was found to be positive across models, except MAT which was insignificant in the case of overall mortality.

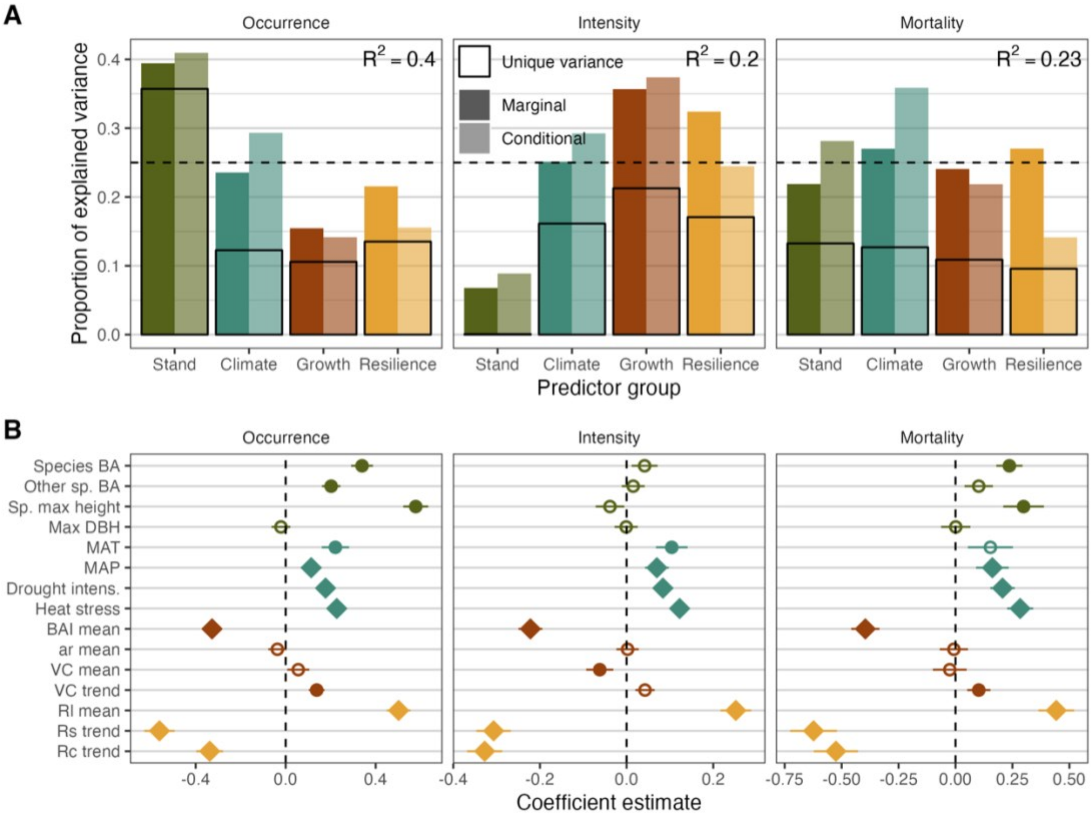

Fig. 5. Multivariate models of stand mortality occurrence, intensity and overall mortality (‘mortality’). (**A**) Variance decomposition analysis. Variance is partitioned between four previously defined predictor groups (stand, climate, growth and resilience variables) based on the LMG (dark colors) and PMVD (light colors) metrics (Grömping, 2007). LMG gives an estimate of each predictor contribution to explain observed variance, whereas PMVD is a metric of the usefulness of each variable for predictive purposes. Marginal and conditional R^2 of corresponding models are indicated on the top-left of each panel. The dashed line indicates the theoretical metric value if all variables equally participated to model variance (0.25) (**B**) Model coefficient estimates. Coefficients are standardized. Points and intervals indicate mean and standard error. Significant ($p < 0.05$) coefficients are denoted by filled points. Diamonds indicate consistent coefficient sign and significance across models. Colors indicate variable groups: stand (green), climate (blue), growth (brown) and resilience (yellow).

Discussion

Drought and biotic imprint on widespread Mountain West stand mortality

We report widespread elevated mortality rates, though highly variable, across many taxa and five states of the US Mountain West in the past two decades, consistent with previous reports in the region (McNellis *et al.*, 2021; Stanke *et al.*, 2021). Mortality was most pronounced in species found in high mountain regions of the Rockies, in Colorado and Wyoming. This clear distribution towards cool and moist forests contrasts with previous large scale pinyon pine die-off in warm and dry lowlands of the region during the 2000's, where climate-change type drought had been identified as a primary triggering factor (Breshears *et al.*, 2005; Shaw *et al.*, 2005; Greenwood & Weisberg, 2008). Pathogens and insects –notably bark beetles–, have been found to be a primary disturbance for a third of mortality reported here (**Fig. 1D**), while about half of the time no disturbance was reported. Our results nevertheless suggest a strong contribution of drought and heat to observed mortality (**Fig. 3** & **5**). Attribution of mortality to drought by the crews in the field is notoriously challenging because of the lack of clear diagnosis elements (Anderegg *et al.*, 2015a), but a broad body of literature in this region reveals that most of observed mortality is primarily driven by drought and with frequent insect interactions (Breshears *et al.*, 2005; Shaw *et al.*, 2005; Worrall *et al.*, 2010; Williams *et al.*, 2012; Stanke *et al.*, 2021). Overall, biotic and climate factors may interact through various processes and it is often challenging to disentangle the two as mortality drivers. For example, droughted trees are much more likely to suffer and succumb to biotic attacks, e.g., because of reduced production of resin and defense compounds against biotic agents (Turtola *et al.*, 2003; Rissanen *et al.*, 2020). On the other hand, insects and pathogens may cause direct damage to trees' vascular system and thus compromise trees' drought resistance (Anderegg *et al.*, 2015a). Such interactions make it difficult in many cases to identify the primary agent of mortality, and blur the role climate and biotic factors in shaping the spatial distribution of mortality.

Our results revealed that the observed decreased probability of mortality *occurrence* with temperature was essentially driven by between-species variations, whereas within species, this probability on the contrary tended to increase with temperature (**Fig S2**). This reflects larger susceptibility of high elevation species to perturbations. Pronounced increase of *overall* mortality with colder temperature within-species (**Fig. 3**) nevertheless shows that despite lower probability of mortality occurrence, cold vs warm populations of a given species were considerably more susceptible to mortality events reaching high intensity (**Fig.**

S3). Multivariate analyses revealed that the negative effect of temperature on was underlaid by several covarying variables. Notably, cool forests in the region, which also tend to be wetter and more productive, generally exhibit larger basal area and maximum tree height under colder climates. Tall trees –because of their hydraulic architecture– may be particularly sensitive to drought, which might be exacerbated by important competition for resources, including water, in stands with large basal area (McDowell & Allen, 2015; Grote *et al.*, 2016). On the other hand, lower stand basal area might reflect competition release or enhanced microsite suitability in areas previously affected by mortality, such as lowland pinyon-juniper communities (Greenwood & Weisberg, 2008). Finally, biomass availability and the presence of large trees is critical for insect infestations to develop sufficiently to reach epidemic levels (Raffa *et al.*, 2008). Consistently with all these potential processes, here we find strong positive effects of both species basal area and max height on overall mortality and occurrence. Surprisingly though, we did not find any effect of stand factors on mortality intensity. This is odd considering that higher drought and insect sensitivity conferred by a given stand structure would be expected to similarly drive mortality occurrence and intensity, but this result might be explained by the contrasting properties entailed by stand structure. For example, large basal area and max tree height may also reflect large competition asymmetry, whereby dominated individuals may be more vulnerable to mortality, while dominant trees, which make up for most of plot basal area, benefit from large resource availability (Pretzsch & Biber, 2010).

Cool forests also tended to experience more relative heat stress (i.e., larger summer temperature anomaly). Heat stress together with drought intensity were found to be strongly related to mortality, hence suggesting an important role of recent hotter droughts in triggering mortality (Hammond *et al.*, 2022). Positive temperature anomalies also favor bark beetle population development and outbreaks (Raffa *et al.*, 2008), especially at cold species boundaries where warming might allow biotic agents to infest new tree populations (Deutsch *et al.*, 2008; McDowell *et al.*, 2020). Hence, species vulnerability, stand history and current structure, as well as recent climate extremes all help explain why cool forests were found to be more susceptible to tree mortality than their warm counterparts. We further observed higher growth autocorrelation, as well as stronger declines in growth resistance and recovery to drought in cool forests, suggesting deteriorating tree physiology and a role in mediating observed mortality patterns along the temperature gradient.

Historic decline of tree growth resilience to drought

Over the study period, we found that BAI of sampled trees increased over time, and this held for all species. Because increment core sampling was biased towards dominant crown class trees, this result is likely inflated (Duchesne *et al.*, 2019). Positive tree growth trends were nevertheless largely confined to relatively young stands (<100 years, **Fig. S4**), consistent with expected stand development. We further observed that tree growth tended to increase faster in cool and moist high-elevation forests, which hinted that besides stand development positive tree growth trends could be partly explained by alleviation of cold-limitation (Gao *et al.*, 2022).

Despite positive growth trends, we observed parallel increases in growth autocorrelation and variability for a majority of the study species. On the theoretical basis that system state autocorrelation and variability should increase close to a tipping point (Scheffer *et al.*, 2009), these metrics have been proposed as early warning signals of mortality (Hereş *et al.*, 2012; Camarero *et al.*, 2015; Cailleret *et al.*, 2019). This expectation relies on the common hypothesis that tree growth is a reliable proxy of system state, i.e., tree physiological status. However, growth autocorrelation and variability might integrate other signals on top of tree physiology. Notably, autocorrelation and variability of tree growth are partly driven by that of climate and hydrology (Bowers *et al.*, 2013; Coulthard *et al.*, 2020). For example, PDSI is a strong determinant of tree growth in the region and was substantially more autocorrelated at colder sites ($r = –0.45$, $p < 0.001$), hence potentially explaining the strong negative correlation observed between MAT and growth autocorrelation. Autocorrelation can further be determined by species functional traits such as leaf or carbon reserves lifespan (Zweifel & Sterck, 2018) and tree ontogeny (Zweifel *et al.*, 2006). Here, we find strong association between stand structure (tree height), climate and tree growth autocorrelation and variability. Such dependences might thus substantially blur potential relationships between tree growth autocorrelation, variability and mortality, which could explain inconsistent reports (Cailleret *et al.*, 2019; Tai *et al.*, 2022).

In parallel to increasing growth autocorrelation and variability, we observed declining growth resilience to drought across several species. Despite mathematical connection between growth variability, autocorrelation and resilience, these metrics were only weakly correlated, suggesting that they encoded different signals. Decline in tree growth resilience to drought has been previously reported at the local scale (Gazol *et al.*, 2018) and across temperate and boreal forests (Zheng *et al.*, 2021, 2023). The decline observed here was primarily a result of decreasing resistance, which was not compensated for by increasing recovery (**Fig. 2**). Declining drought resistance is often symptomatic of increasing drought intensity and/or competition (Gazol *et al.*, 2018; Castagneri *et al.*, 2021). Though increasing temperature and drought intensity over part of the study area (Andreadis & Lettenmaier, 2006), as well as increasing stand density due to fire suppression (Noss *et al.*, 2006) reflected in current stand structure, could indeed explain some of the decline in tree growth resilience, most of the spatial variability in Rl decline was nevertheless related to annual temperature, which was ultimately related to species distribution (**Fig. S5-6**, **Table S5**). Like mortality, species-dependence of observed Rl decline suggests either species-specific variation in drought vulnerability and/or host-biotic agent interactions. Notably, increasing temperatures may have allowed insect infestation of naive species at higher latitude and elevations (Raffa *et al.*, 2008), causing decline in tree growth resilience to subsequent droughts in these populations. Overall, several factors, including increasing stand competition, drought and insect outbreaks, are likely responsible for the observed decline in tree growth resilience to drought. In this regard, temporal resilience trends most likely carry information on past stand history and tree physiological damage, which could influence stand vulnerability to subsequent perturbations.

Despite their differences, temporal trends of tree growth autocorrelation, variability and resilience to drought converge to suggest tree physiological decline in the US Mountain West during the second half of the 20th century. This result contrasts with a context of increasing basal area growth and highlight a divergence between tree productivity and physiological status. Further, while tall, productive forests located in moist and cool environments exhibited the largest temporal growth trends, they were also the most exposed to physiological weakening denoted by declining growth resilience. Progressive lifting of cold limitation might thus benefit tree growth while at the same time exposing trees to larger vulnerability to drought and insect outbreaks, e.g., because of structural overshoot and insect population development (Raffa *et al.*, 2008; Jump *et al.*, 2017).

Declining resilience mediates stand mortality

Our results reveal strong association between stand-level mortality and tree growth resilience to drought. Long-term average resilience was negatively associated with mortality, but only within-species. While difference in mean resilience between species might reflect different exposition to drought, it may not reflect different susceptibility to mortality. Resilience levels are in fact in large part dependent on growth temporal autocorrelation (Klesse *et al.*, 2022), which is notably related to species functional traits such as leaf and carbon lifespan (Zweifel & Sterck, 2018; Zweifel *et al.*, 2020; Song *et al.*, 2022) or wood density (Serra-Maluquer *et al.*, 2022). Unexpectedly, we found a positive effect of mean resilience on mortality in multivariate models, indicating that all else being equal, trees with higher resilience level were associated with higher stand mortality, similar to a previous remote-sensing study (Tai *et al.*, 2022). This likely reflects larger vulnerability of trees historically little exposed to drought, e.g., because of structural overshoot (Jump *et al.*, 2017).

Univariate and multivariate models both indicated that resilience trends were strong predictors of stand mortality, superior to resilience means in that regard. This indicates that trends in resilience successfully capture the integrated effect of past stresses on tree physiological status and susceptibility to mortality. Hence in refinement of previous report on the potential of growth resilience to drought as early warning metric (DeSoto *et al.*, 2020), we propose that declining resilience, rather than absolute resilience, is indicative of unhealthy stands, which are likely more vulnerable to perturbations, regardless of the agent. The observed relationship between declining resilience and mortality further suggests that damage build up induced by repeat perturbations may be an important component of observed stand mortality patterns, consistent with regional and global analyses (Anderegg *et al.*, 2013, 2020b). For example, declining resilience might be indicative of drought-induced cavitation fatigue, i.e., larger hydraulic vulnerability of the xylem induced by previous drought, which is a major factor of subsequent *Populus tremuloides* mortality following drought in the region (Anderegg *et al.*, 2013). More generally, by hindering trees' capacity to regrow functional vascular tissue, declining growth resilience to drought might fundamentally alter trees' water and carbon economies. Processes include reduced hydraulic conductance and increased vulnerability to embolism, reduced carbon assimilation and shifting C allocation away from resin and defense molecule production, which may compromise tree vulnerability to subsequent biotic and abiotic perturbations (Raffa *et al.*, 2008; McDowell, 2011; Rissanen *et al.*, 2020). At the forest scale, the processes that underlie loss of resilience likely destabilize the system and increase the likelihood that future perturbations may lead forests to transition to an alternate stable state (Hammond, 2020; Johnson *et al.*, 2022).

On the other hand, the capacity to grow new xylem rapidly would confer trees reduced vulnerability to following droughts. Despite resilience level being a weak predictor of mortality, we found that rapid tree growth overall was associated with lower stand mortality rates, consistent with a widely observed pattern (Bigler & Bugmann, 2003; Hülsmann *et al.*, 2018). Hence, rather than the capacity to quickly resume baseline wood growth as denoted by average resilience the ability to maintain resilience to drought and rapid overall tree growth appears as a key factor to mitigate mortality (Anderegg *et al.*, 2015b), despite rapid tree growth might come at the expense of allocation to drought resistance and pathogen defense (Huot *et al.*, 2014; de la Mata *et al.*, 2017). Multivariate models show that decomposing resilience into resistance and recovery components improved predictions, and further indicate similar importance of growth resistance and recovery components of resilience trends in mediating stand mortality (**Fig. 5**, **Table S4**). This suggests that stress avoidance and tolerance strategies (Oliveira *et al.*, 2021) can both be successful in mitigating mortality. Our results illustrate the role of resilience in denoting past physiological decline and mediating subsequent stand mortality. The loss of growth resilience to drought following past perturbations, due to either declining resistance or recovery,

Modelling stand mortality

Here, we assess the relative importance of stand, climate, growth and resilience factors to model stand-level mortality. We make the distinction between explicative (i.e., how much variance can a variable explain overall) and predictive power (i.e., how much does a model improve by adding a new variable) denoted by the marginal and conditional decomposition of model variance, respectively (Grömping, 2007). Moderate model performance overall was expected on the basis of the complexity of processes involved and variability between species, but was within the range of previous studies (Trugman *et al.*, 2021; Venturas *et al.*, 2021). As expected from longstanding literature on the topic, stand and climate factors played an important role in explaining stand mortality (Dietze & Moorcroft, 2011; Ruiz-Benito *et al.*, 2013; Neumann *et al.*, 2017). Stand variables notably most largely contributed to explain the occurrence of mortality observations, related to stand basal area and tree height, but had strikingly little effect on mortality intensity. This is likely related to stand dynamics, where mature stands are more likely to exhibit low intensity mortality (Franklin, 2002). Tree growth and resilience to drought nevertheless had similarly large importance, explaining together about half of observed spatial variations in overall stand-level mortality. Tree growth and resilience performed particularly well to explain mortality intensity, explaining over two thirds of the observed variance. These results upscale previous tree-level evidence (Bigler & Bugmann, 2003; Cailleret *et al.*, 2016; DeSoto *et al.*, 2020), and demonstrate the potential of growth and resilience metrics to encapsulate tree physiological status and help explain mortality over broad scales, despite large complexity diversity of pathways across species (Lloret *et al.*, 2011).

On the other hand, covariation between tree growth and resilience, climate and stand factors (Lloret *et al.*, 2011; Serra-Maluquer *et al.*, 2022) is important to take into account as it may partially underlie their respective effect on mortality. This is particularly the case for tree growth variation coefficient and autocorrelation, which despite showing a strong effect on mortality across species, is mostly driven by other climate and stand variables, hence yielding non-significant parameters in multivariate models (**Fig 5B**). To a lesser extent, the difference between the conditional and marginal decomposition of variance (**Fig. 5A**) also suggests that part of the resilience effect on mortality could be explained by other variables in the multivariate model, notably stand and climate factors. This view is supported by the fact that resilience exhibited limited unique model variance. Although this result does not necessarily imply non-causality between resilience and mortality, it does suggest modest gains from adding resilience in a model for prediction purposes. The relative importance of tree growth on the other hand appeared to be robust to the adopted perspective, indicating limited redundancy with other variables in the model. The potential of past tree growth to predict future mortality that we observe here is consistent with its common use in vegetation models (Hülsmann *et al.*, 2018). The existence of a survivorship and dominance bias in our dataset (mostly live and often dominant trees were sampled (DeRose *et al.*, 2017)) might have led to underestimating the growth- and resilience-mortality relationships. Analyses based on a more representative sampling design might thus conclude to a larger relative importance of these metrics to explain and predict stand mortality.

Our results highlight the strengths but also some of the limitations of tree-growth based resilience as early warning signal of stand mortality. Models, including that of forest mortality, need to strike a balance between predictive power *versus* the number of parameters and associated costs (Bentler & Mooijaart, 1989). Though model selection criterion (AIC) suggested that the benefits of including resilience outweighs statistical costs, further costs associated with enabling resilience-based forest mortality models need to be considered. Notably, such a model would require extensive and annually resolved tree growth monitoring. Existing national forest inventory programs generally lack temporal resolution and though adding core sampling to inventories would provide necessary resolution (DeRose *et al.*, 2017; Evans *et al.*, 2022), repeat sampling and processing to enable updated predictions might reveal costly. Finding a way around this issue would require lower costs and/or higher benefits of including resilience metrics in mortality models. Remote sensing of canopy status thus seems a promising avenue in this regard, although mortality inferences have been restricted in time so far, which limits the capacity to take action (Rogers *et al.*, 2018; Liu *et al.*, 2019). Automated tree growth measurement networks such as TreeNet (Zweifel *et al.*, 2021) could also show potential, in that they might enable exploring new proxies of tree physiological status in addition to reducing the return-time to forest plots. Spatial and temporal limitations to such networks yet currently hinders testing these applications. Despite limitations, tree-ring based estimates of forest resilience hold great value for retrospective analysis of past mortality events and to gain insights on underlying mechanisms. Tree-ring based resilience proved to be a reliable proxy of tree physiological status and forest vulnerability to perturbations. In that sense, widespread decline in tree growth resilience to drought (Zheng *et al.*, 2021) adds to the growing evidence of increasing risk of pervasive forest mortality at the global scale (Allen *et al.*, 2015; Hammond *et al.*, 2022).

Acknowledgments

We acknowledge funding from USDA National Institute of Food and Agriculture, Agricultural and Food Research Initiative Competitive Programme, Ecosystem Services and Agro-Ecosystem Management, grant no. 2018-67019-27850. WA acknowledges support from the David and Lucille Packard Foundation and US National Science Foundation grants no. 1714972, 1802880, 2044937, 2003017, and the Alan T. Waterman Award, IOS-2325700. This research was supported by the Utah Agricultural Experiment Station, Utah State University, and approved as journal paper number 9651.

Conflict of interest statement

The author declare that they have no conflict of interest.

References

Abatzoglou JT, Dobrowski SZ, Parks SA, Hegewisch KC. **2018**. TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015. *Scientific Data* **5**: 1–12.

Allen CD, Breshears DD, McDowell NG. **2015**. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**: art129–art129.

Anderegg WRL, Callaway ES. **2012**. Infestation and hydraulic consequences of induced carbon starvation. *Plant Physiology* **159**: 1866–1874.

Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK, McDowell N, *et al.* 2015a. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist* **208**: 674–683.

Anderegg WRL, Plavcová L, Anderegg LDL, Hacke UG, Berry JA, Field CB. **2013**. Drought's legacy: Multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Global Change Biology* **19**: 1188–1196.

Anderegg WRLL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD, Shevliakova E, Williams AP, *et al.* 2015b. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* **349**: 528–532.

Anderegg WRL, Trugman AT, Badgley G, Anderson CM, Bartuska A, Ciais P, Cullenward D, Field CB, Freeman J, Goetz SJ, *et al.* 2020a. Climate-driven risks to the climate mitigation potential of forests. *Science* **368**: eaaz7005–eaaz7005.

Anderegg WRL, Trugman AT, Badgley G, Konings AG, Shaw J. **2020b**. Divergent forest sensitivity to repeated extreme droughts. *Nature Climate Change*.

Andreadis KM, Lettenmaier DP. **2006**. Trends in 20th century drought over the continental united states: U.S. drought trends. *Geophysical Research Letters* **33**: n/a-n/a.

Bechtold WA, Scott CT. **2005**. The Forest Inventory and Analysis plot design. *The Enhanced Forest Inventory and Analysis Program: National sampling design and estimation procedures* **1**: 27–67.

Benito Garzón M, González Muñoz N, Wigneron JP, Moisy C, Fernández-Manjarrés J,

Delzon S. **2018**. The legacy of water deficit on populations having experienced negative hydraulic safety margin. *Global Ecology and Biogeography* **27**: 346–356.

Bentler PM, Mooijaart A. **1989**. Choice of structural model via parsimony: A rationale based on precision. *Psychological Bulletin* **106**: 315–317.

Betts MG, Wolf C, Ripple WJ, Phalan B, Millers KA, Duarte A, Butchart SHM, Levi T. **2017**. Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* **547**: 441–444.

Bigler C, Bugmann H. **2003**. Growth-dependent tree mortality models based on tree rings. *Canadian Journal of Forest Research* **33**: 210–221.

Bowers MC, Gao JB, Tung WW. **2013**. Long range correlations in tree ring chronologies of the USA: Variation within and across species. *Geophysical Research Letters* **40**: 568–572.

Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J, *et al.* 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 15144–8.

Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, McDowell NG, Pockman WT. **2009**. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* **7**: 185–189.

Cailleret M, Dakos V, Jansen S, Robert EMRR, Aakala T, Amoroso MM, Antos JA, Bigler C, Bugmann H, Caccianaga M, *et al.* 2019. Early-Warning Signals of Individual Tree Mortality Based on Annual Radial Growth. *Frontiers in Plant Science* **9**: 1–14.

Cailleret M, Jansen S, Robert EMR, Desoto L, Aakala T, Antos JA, Beikircher B, Bigler C, Bugmann H, Caccianiga M, *et al.* 2016. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology* **23**: 1–16.

Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM. **2015**. To die or not to die: Early warnings of tree dieback in response to a severe drought. *Journal of Ecology* **103**: 44–57.

Castagneri D, Vacchiano G, Hacket-Pain A, DeRose RJ, Klein T, Bottero A. **2021**. Meta-analysis Reveals Different Competition Effects on Tree Growth Resistance and Resilience to Drought. *Ecosystems*.

Chapman TB, Veblen TT, Schoennagel T. **2012**. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* **93**: 11.

Coulthard BL, St. George S, Meko DM. **2020**. The limits of freely-available tree-ring chronologies. *Quaternary Science Reviews* **234**: 106264.

DeRose RJ, Shaw JD, Long JN. **2017**. Building the forest inventory and analysis tree-ring data set. *Journal of Forestry* **115**: 283–291.

DeSoto L, Cailleret M, Sterck F, Jansen S, Kramer K, Robert EMR, Aakala T, Amoroso MM, Bigler C, Camarero JJ, *et al.* 2020. Low growth resilience to drought is related to future mortality risk in trees. *Nature Communications* **11**: 545–545.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. **2008**. Impacts of climate warming on terrestrial ectotherms across latitude.

Proceedings of the National Academy of Sciences **105**: 6668–6672.

Dietze MC, Moorcroft PR. **2011**. Tree mortality in the eastern and central United States: patterns and drivers. *Global Change Biology* **17**: 3312–3326.

Duchesne L, Houle D, Ouimet R, Caldwell L, Gloor M, Brienen R. **2019**. Large apparent growth increases in boreal forests inferred from tree-rings are an artefact of sampling biases. *Scientific Reports* **9**.

Evans MEK, DeRose RJ, Klesse S, Girardin MP, Heilman KA, Alexander MR, Arsenault A, Babst F, Bouchard M, Cahoon SMP, *et al.* 2022. Adding Tree Rings to North America's National Forest Inventories: An Essential Tool to Guide Drawdown of Atmospheric CO2. *BioScience* **72**: 233–246.

Feng X, Merow C, Liu Z, Park DS, Roehrdanz PR, Maitner B, Newman EA, Boyle BL, Lien A, Burger JR, *et al.* 2021. How deregulation, drought and increasing fire impact Amazonian biodiversity. *Nature* **597**: 516–521.

Forzieri G, Dakos V, McDowell NG, Ramdane A, Cescatti A. **2022**. Emerging signals of declining forest resilience under climate change. *Nature* **608**: 534–539.

Frank JM, Massman WJ, Ewers BE, Huckaby LS, Negrón JF. **2014**. Ecosystem CO_2/H_2O fluxes are explained by hydraulically limited gas exchange during tree mortality from spruce bark beetles. *Journal of Geophysical Research: Biogeosciences* **119**: 1195–1215.

Franklin J. **2002**. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* **155**: 399–423.

Gao S, Liang E, Liu R, Babst F, Camarero JJ, Fu YH, Piao S, Rossi S, Shen M, Wang T, *et al.* 2022. An earlier start of the thermal growing season enhances tree growth in cold humid areas but not in dry areas. *Nature Ecology and Evolution*.

Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yepez EA, Macalady AK, Pangle RE, McDowell NG. **2013**. Drought predisposes piñon–juniper woodlands to insect attacks and mortality. *New Phytologist* **198**: 567–578.

Gazol A, Camarero JJ, Vicente-Serrano SM, Sánchez-Salguero R, Gutiérrez E, de Luis M, Sangüesa-Barreda G, Novak K, Rozas V, Tíscar PA, *et al.* 2018. Forest resilience to drought varies across biomes. *Global Change Biology*: 1–16.

Greenwood DL, Weisberg PJ. **2008**. Density-dependent tree mortality in pinyon-juniper woodlands. *Forest Ecology and Management* **255**: 2129–2137.

Grömping U. **2007**. Estimators of relative importance in linear regression based on variance decomposition. *American Statistician* **61**: 139–147.

Grote R, Gessler A, Hommel R, Poschenrieder W, Priesack E. **2016**. Importance of tree height and social position for drought-related stress on tree growth and mortality. *Trees* **30**: 1467–1482.

Hammond WM. **2020**. A Matter of Life and Death: Alternative Stable States in Trees, From Xylem to Ecosystems. *Frontiers in Forests and Global Change* **3**: 560409.

Hammond WM, Williams AP, Abatzoglou JT, Adams HD, Klein T, López R, Sáenz-Romero C, Hartmann H, Breshears DD, Allen CD. **2022**. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications* **13**: 1761–1761.

Hereş A-M, Martínez-Vilalta J, Claramunt López B. **2012**. Growth patterns in relation to drought-induced mortality at two Scots pine (Pinus sylvestris L.) sites in NE Iberian Peninsula. *Trees* **26**: 621–630.

Hülsmann L, Bugmann H, Cailleret M, Brang P. **2018**. How to kill a tree: empirical mortality models for 18 species and their performance in a dynamic forest model. *Ecological Applications* **28**: 522–540.

Huot B, Yao J, Montgomery BL, He SY. **2014**. Growth–Defense Tradeoffs in Plants: A Balancing Act to Optimize Fitness. *Molecular Plant* **7**: 1267–1287.

Johnson DM, Katul G, Domec J-C. **2022**. Catastrophic hydraulic failure and tipping points in plants. *Plant, Cell & Environment* **45**: 2231–2266.

Jump AS, Ruiz-Benito P, Greenwood S, Allen CD, Kitzberger T, Fensham R, Martínez-Vilalta J, Lloret F. **2017**. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Global Change Biology* **23**: 3742–3757.

Kannenberg SA, Novick KA, Alexander MR, Maxwell JT, Moore DJP, Phillips RP, Anderegg WRL. **2019**. Linking drought legacy effects across scales: From leaves to tree rings to ecosystems. *Global Change Biology* **25**: 2978–2992.

Klesse S, Babst F, Evans MEK, Hurley A, Pappas C, Peters RL. **2022**. Legacy effects in radial tree growth are rarely significant after accounting for biological memory. *Journal of Ecology*: 1365-2745.14045.

Kolb T, Keefover-Ring K, Burr SJ, Hofstetter R, Gaylord M, Raffa KF. **2019**. Drought-Mediated Changes in Tree Physiological Processes Weaken Tree Defenses to Bark Beetle Attack. *Journal of Chemical Ecology* **45**: 888–900.

Liu Y, Kumar M, Katul GG, Porporato A. **2019**. Reduced resilience as an early warning signal of forest mortality. *Nature Climate Change* **9**: 880–885.

Lloret F, Keeling EG, Sala A. **2011**. Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* **120**: 1909–1920.

Marchetti SB, Worrall JJ, Eager T. **2011**. Secondary insects and diseases contribute to sudden aspen decline in southwestern Colorado, USA. *Canadian Journal of Forest Research* **41**: 2315–2325.

de la Mata R, Hood S, Sala A. **2017**. Insect outbreak shifts the direction of selection from fast to slow growth rates in the long-lived conifer *Pinus ponderosa*. *Proceedings of the National Academy of Sciences* **114**: 7391–7396.

McDowell NG. **2011**. Mechanisms Linking Drought, Hydraulics, Carbon Metabolism, and Vegetation Mortality. *Plant Physiology* **155**: 1051–1059.

McDowell NG, Allen CD. **2015**. Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change* **5**: 669–672.

McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, Chini L, Clark JS, Dietze M, Grossiord C, Hanbury-Brown A, *et al.* **2020**. Pervasive shifts in forest dynamics in a changing world. *Science* **368**.

McDowell NG, Sapes G, Pivovaroff A, Adams HD, Allen CD, Anderegg WRL, Arend M, Breshears DD, Brodribb T, Choat B, *et al.* **2022**. Mechanisms of woody-plant mortality under rising drought, CO2 and vapour pressure deficit. *Nature Reviews Earth & Environment* **3**: 294–308.

McNellis BE, Smith AMS, Hudak AT, Strand EK. **2021**. Tree mortality in western U.S. forests forecasted using forest inventory and Random Forest classification. *Ecosphere* **12**.

Meddens AJH, Hicke JA, Macalady AK, Buotte PC, Cowles TR, Allen CD. **2015**. Patterns and causes of observed piñon pine mortality in the southwestern United States. *New Phytologist* **206**: 91–97.

Neumann M, Mues V, Moreno A, Hasenauer H, Seidl R. **2017**. Climate variability drives recent tree mortality in Europe. *Global Change Biology* **23**: 4788–4797.

Noss RF, Franklin JF, Baker WL, Schoennagel T, Moyle PB. **2006**. Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment* **4**: 481–487.

Oliveira RS, Eller CB, Barros F de V, Hirota M, Brum M, Bittencourt P. **2021**. Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. *New Phytologist* **230**: 904–923.

Paine TD, Raffa KF, Harrington TC. **1997**. Interactions Among Scolytid Bark Beetles, Their Associated Fungi, and Live Host Conifers. *Annual Review of Entomology* **42**: 179–206.

Preisler Y, Tatarinov F, Grünzweig JM, Yakir D. **2021**. Seeking the "point of no return" in the sequence of events leading to mortality of mature trees. *Plant, Cell & Environment* **44**: 1315–1328.

Pretzsch H, Biber P. **2010**. Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. *Canadian Journal of Forest Research* **40**: 370–384.

Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. **2008**. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. *BioScience* **58**: 501–517.

Reed CC, Hood SM. **2021**. Few generalizable patterns of tree-level mortality during extreme drought and concurrent bark beetle outbreaks. *Science of The Total Environment* **750**: 141306.

Rissanen K, Vanhatalo A, Salmon Y, Bäck J, Hölttä T. **2020**. Stem emissions of monoterpenes, acetaldehyde and methanol from Scots pine (Pinus sylvestris L.) affected by tree–water relations and cambial growth. *Plant Cell and Environment* **43**: 1751–1765.

Rogers BM, Solvik K, Hogg EH, Ju J, Masek JG, Michaelian M, Berner LT, Goetz SJ. **2018**. *Detecting early warning signals of tree mortality in boreal North America using multiscale satellite data*.

Ruiz-Benito P, Lines ER, Gómez-Aparicio L, Zavala MA, Coomes DA. **2013**. Patterns and Drivers of Tree Mortality in Iberian Forests: Climatic Effects Are Modified by Competition (A Hector, Ed.). *PLoS ONE* **8**: e56843.

Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G. **2009**. Early-warning signals for critical transitions. *Nature* **461**: 53–59.

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. **2001**. Catastrophic shifts in ecosystems. *Nature* **413**: 591–596.

Serra-Maluquer X, Gazol A, Anderegg WRL, Martínez-Vilalta J, Mencuccini M, Camarero JJ. **2022**. Wood density and hydraulic traits influence species' growth response to drought across biomes. *Global Change Biology*: 0–2.

Shaw JD, Steed BE, DeBlander LT. **2005**. Forest Inventory and Analysis (FIA) Annual Inventory Answers the Question: What Is Happening to Pinyon-Juniper Woodlands? *Journal of Forestry*.

Song Y, Sterck F, Zhou X, Liu Q, Kruijt B, Poorter L. **2022**. Drought resilience of conifer species is driven by leaf lifespan but not by hydraulic traits. *New Phytologist*.

Sperry JS, Tyree MT. **1988**. Mechanism of water stress-induced xylem embolism. *Plant physiology* **88**: 581–587.

Stanke H, Finley AO, Domke GM, Weed AS, MacFarlane DW. **2021**. Over half of western United States' most abundant tree species in decline. *Nature Communications* **12**.

Tai X, Trugman AT, Anderegg WRL. **2022**. Linking remotely sensed ecosystem resilience with forest mortality across the continental United States. *Global Change Biology*: gcb.16529.

Trugman AT, Anderegg LDL, Anderegg WRL, Das AJ, Stephenson NL. **2021**. Why is Tree Drought Mortality so Hard to Predict? *Trends in Ecology and Evolution* **36**: 520–532.

Turtola S, Manninen A-M, Rikala R, Kainulainen P. **2003**. Drought Stress Alters the Concentration of Wood Terpenoids in Scots Pine and Norway Spruce Seedlings. *Journal of Chemical Ecology*.

Van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fulé PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, *et al.* **2009**. Widespread increase of tree mortality rates in the Western United States. *Science* **323**: 521–524.

Venturas MD, Sperry JS, Love DM, Frehner EH, Allred MG, Wang Y, Anderegg WRL. **2018**. A stomatal control model based on optimization of carbon gain versus hydraulic risk predicts aspen sapling responses to drought. *New Phytologist* **220**: 836–850.

Venturas MD, Todd HN, Trugman AT, Anderegg WRL. **2021**. Understanding and predicting forest mortality in the western United States using long-term forest inventory data and modeled hydraulic damage. *New Phytologist* **230**: 1896–1910.

Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse C a., Meko DM, Swetnam TW, Rauscher S a., Seager R, Grissino-Mayer HD, *et al.* **2012**. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* **3**: 292–297.

Worrall JJ, Marchetti SB, Egeland L, Mask RA, Eager T, Howell B. **2010**. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *Forest Ecology and Management* **260**: 638–648.

Zhang F, Biederman JA, Dannenberg MP, Yan D, Reed SC, Smith WK. **2021**. Five Decades of Observed Daily Precipitation Reveal Longer and More Variable Drought Events Across Much of the Western United States. *Geophysical Research Letters* **48**: 1–11.

Zheng T, Martínez-Vilalta J, García-Valdés R, Gazol A, Camarero JJ, Mencuccini M. **2021**. Disentangling biology from mathematical necessity in twentieth-century gymnosperm resilience trends. *Nature Ecology and Evolution* **5**: 733–735.

Zheng T, Martínez-Vilalta J, García-Valdés R, Gazol A, Camarero JJ, Mu C, Mencuccini M. **2023**. Growth plasticity of conifers did not avoid declining resilience to soil and atmospheric droughts during the 20th century. *Forest Ecosystems* **10**: 100107.

Zweifel R, Etzold S, Basler D, Bischoff R, Braun S, Buchmann N, Conedera M, Fonti P, Gessler A, Haeni M, *et al.* 2021. TreeNet–The Biological Drought and Growth Indicator Network. *Frontiers in Forests and Global Change* **4**: 1–14.

Zweifel R, Etzold S, Sterck F, Gessler A, Anfodillo T, Mencuccini M, von Arx G, Lazzarin M, Haeni M, Feichtinger L, *et al.* 2020. Determinants of legacy effects in pine trees - implications from an irrigation-stop experiment. *New Phytologist*: 1081–1096.

Zweifel R, Sterck F. **2018**. A Conceptual Tree Model Explaining Legacy Effects on Stem Growth. *Frontiers in Forests and Global Change* **1**: 1–9.

Zweifel R, Zimmermann L, Zeugin F, Newbery DM. **2006**. Intra-annual radial growth and water relations of trees: Implications towards a growth mechanism. *Journal of Experimental Botany* **57**: 1445–1459.