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Species mixture effects and climate influence growth, recruitment and mortality in Interior West USA *Populus tremuloides*-conifer communities

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Abstract

1. Tree-species mixture effects (e.g. complementarity and facilitation) have been found to increase individual-tree productivity, lessen mortality and improve recruitment in forests worldwide. By promoting more efficient and complete resource use, mixture effects may also lessen individual-tree-level water stress, thus improving drought resistance. We investigated the influence of mixture effects on tree productivity, mortality and recruitment across broad compositional and moisture gradients in high-elevation Interior West US mixed-conifer communities, where *Populus tremuloides* (trembling aspen) is the major contributor to functional diversity. Our goal was to provide a more complete scientific foundation for managing these drought-prone, fire-excluded systems under an uncertain climate.
2. We used landscape-scale national forest inventory data to examine mixture effects on *P. tremuloides* and the major associated conifer species, *Pseudotsuga menziesii*, *Pinus contorta*, *Abies lasiocarpa* and *Picea engelmannii*. Using generalized linear mixed modelling, we isolated the influences of *P. tremuloides* relative density and climate on tree-level (stems ≥ 12.7 cm DBH) growth, mortality and stand-level recruitment (presence/absence of new trees). Cold-season precipitation (PPT) and warm-season vapour pressure deficit (VPD) served to represent soil moisture supply and demand, respectively.
3. *Populus tremuloides* growth declined as interspecific density increased. In contrast, *Pinus contorta* and *A. lasiocarpa* growth increased with *P. tremuloides* density. For all species except *A. lasiocarpa* and *P. menziesii*, growth increased under higher PPT and VPD. *Populus tremuloides* mortality increased under high VPD but not with interspecific relative density. We found limited evidence that *A. lasiocarpa* mortality decreased as *P. tremuloides* density increased. *Populus tremuloides* recruitment declined steeply above 25% interspecific relative density. We found a decline in conifer recruitment odds as *P. tremuloides* density increased, ranging from strong in *P. contorta* to insubstantial in *P. engelmannii*.
4. *Synthesis*. Our findings have implications for sustaining mixed-conifer communities impacted by climate change and historical fire exclusion. Mixtures of *P. tremuloides* and conifers may improve conifer growth while adversely impacting *P. tremuloides*

growth relative to pure stands. Higher conifer productivity combined with lower *P. tremuloides* recruitment at high conifer relative density may accelerate succession.

KEYWORDS

Abies lasiocarpa, drought stress, forest dynamics, *Picea engelmannii*, *Pinus contorta*, plant–climate interactions, *Pseudotsuga menziesii*, Rocky Mountain mixed-conifer

1 | INTRODUCTION

Promoting tree-species diversity is a key strategy for enhancing forest adaptative capacity under an uncertain climate (Ammer, 2019). In addition to providing insurance against loss of individual species (Yachi & Loreau, 1999), species mixtures may enhance productivity (Ammer, 2019). A positive relationship between productivity and tree-species diversity occurs when growth of one or more tree species is higher in a mixture than in a monoculture (Forrester & Bauhus, 2016). Positive mixture effects may reflect niche complementarity (contrasting functional traits among species that promote competition reduction through more efficient resource use; Forrester & Pretzsch, 2015) or facilitation (mutualism primarily reflecting stress reduction processes; Callaway, 1995). Increased productivity resulting from positive tree-species mixture effects may enhance forest carbon sequestration and potentially improve tree resistance to climate change and related disturbances (Griess & Knoke, 2011; Malmsheimer et al., 2009).

The stress-gradient hypothesis predicts that facilitation will increase with stress (Bertness & Callaway, 1994), suggesting that species mixture effects may sustain growth in the face of drought and longer-term changes in aridity (Jucker et al., 2016). Depending on the traits of the focal species, niche complementarity has also been found to lessen individual-tree water stress, thus improving drought resistance (Anderegg et al., 2018). For example, studies of European forests found that conifer-hardwood mixtures may reduce drought-related growth loss relative to monocultures (Mina et al., 2018; Pretzsch et al., 2013; Thurm & Pretzsch, 2016). Asynchrony, or differences in species' responses to disturbance and natural environmental fluctuations, may further stabilize growth in drought-affected mixed-species stands relative to pure stands (Jucker, Bouriaud, Avacaritei, & Coomes, 2014). However, a global literature review reported that tree-species mixtures do not have a consistently positive influence on drought resilience based on studies that predominantly examined tree growth rates (Grossiord, 2020).

Species mixture effects, alone or in combination with climate, may also influence tree mortality and recruitment, important components of forest population dynamics (Archambeau et al., 2020; Condés & del Río, 2015; Liang et al., 2007). As with growth, mixture effects on mortality vary by species. Whereas mortality of both *Pinus sylvestris* L. (Scots pine) and *Fagus sylvatica* L. (European beech) increases with drought, *P. sylvestris* mortality is higher and *F. sylvatica* mortality is lower in mixed stands (Archambeau et al., 2020; Condés & del Río, 2015). The composition of tree recruitment ultimately determines the stability of positive mixture effects in forests, as the early seral species often critical to functional diversity experience demographic decline through forest succession (Cordonnier et al., 2018). Under high abiotic stress, facilitation can enhance both tree establishment and subsequent growth (Callaway, 1998) while intraspecific competition reduction may promote recruitment under the spatial segregation hypothesis (Pacala & Levin, 1997). In *Pseudotsuga menziesii* (Douglas-fir)/*Tsuga heterophylla* (western hemlock) and mixed-conifer forests in California, Oregon, and Washington, USA, seedling recruitment increases with species diversity, although diversity does not influence the growth or mortality of surviving trees (Liang et al., 2007).

In the predominantly coniferous, high-elevation forests of the Interior West, USA, *Populus tremuloides* Michx. (quaking aspen), is an important contributor to functional diversity (St. Clair et al., 2013). *Populus tremuloides* occurs in the Rocky Mountain region along an environmental gradient ranging from semi-arid high desert to the subalpine zone (Jones, 1985). Within this gradient, *P. tremuloides* grows in pure-to-mixed stands with associated conifer species. As the most widespread deciduous tree species in the region (Peet, 2000), *P. tremuloides* promotes conifer growth by altering microclimate, litter quality and light portioning (Calder & St. Clair, 2012) while enhancing wildlife habitat, increasing watershed yield and reducing fire risk (LaMalfa & Ryle, 2008; Shepperd et al., 2006). Fire history, herbivory and increasingly severe droughts associated with climate change have contributed to a sharp rise in *P. tremuloides* mortality and unsustainably low *P. tremuloides* recruitment in many Interior West stands (Binkley et al., 2014; Brodie et al., 2012; Worrall et al., 2013), particularly within conifer mixtures (Kaye et al., 2005). Understanding how mixture effects and climate combine to impact growth, mortality and tree recruitment in Interior West *P. tremuloides* communities is necessary for predicting longer-term changes to these systems (Cordonnier et al., 2018; Liang et al., 2007).

Relatively, few studies have examined species-mixture effects on Interior West aspen-conifer forests. Positive mixture effects were found to increase stand-level growth in cold, temperature-limited Canadian *P. tremuloides*-conifer mixtures (Calder & Clair, 2012; Kweon & Comeau, 2019), with mixture effects decreasing along with stress in warmer growing seasons (Cortini et al., 2012; Kweon & Comeau, 2019). To our knowledge, however, no research has similarly examined the influence of tree-species mixtures and climate in Interior West *P. tremuloides*-conifer mixtures, where climate change-related drought and secondary insect damage increasingly jeopardize forest carbon balance (Anderegg et al., 2013; Kane & Kolb, 2014). Three studies that investigated mixture effects on mortality in Interior West *P. tremuloides* communities arrived at conflicting results. Whereas Kaye et al. (2005) found no relationship between conifer density and *P. tremuloides* mortality in northern Colorado, USA, two landscape-level studies of Interior West forests found *P. tremuloides* mortality increases with conifer relative density (Bell et al., 2014, 2015). Young et al. (2011) found that total sapling recruitment increased with increasing species diversity in Alaskan *P. tremuloides/Populus balsamifera* (balsam poplar) forests, but did not distinguish among species. Calder and St. Clair (2012) found that *P. tremuloides* overstories promote establishment, recruitment and survival in *Abies lasiocarpa* (subalpine fir; Calder & St. Clair, 2012). Other studies suggest that *P. tremuloides* tree recruitment strongly declines with increasing conifer dominance (Berrill & Dagley, 2014; Kaye et al., 2005). The combined influences of composition and climate on tree mortality and recruitment have not been simultaneously compared among species within *P. tremuloides*-conifer communities.

To fill these knowledge gaps, we used permanent plot remeasurement data from the USDA Forest Service Forest Inventory and Analysis (FIA) programme to examine individual-tree growth, mortality and tree recruitment in *P. tremuloides* communities across the Interior West, USA. Trends in tree recruitment have rarely been examined in studies of tree-species mixture effects on forest productivity, but may be critical to the long-term stability of species mixtures (Cordonnier et al., 2018). Our goals were to determine (a) how the relative proportion of *P. tremuloides* in high-elevation forests of the Rocky Mountain region affects the growth and mortality of *P. tremuloides* and the most frequently co-occurring conifer species, *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir; syn. *Abies bifolia* A. Murray), *Picea engelmannii* Parry ex. Engelm. (Engelmann spruce), *Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco (interior Douglas-fir) and *Pinus contorta* Douglas ex Loudon (lodgepole pine); (b) whether tree-species mixture effects interact with climate to ameliorate drought impacts on growth and mortality and (c) whether species mixture effects, alone or in combination with climate, influences tree recruitment and, thereby, the sustainability of *P. tremuloides* species mixtures.

2 | MATERIALS AND METHODS

2.1 | Study area and plot selection

This study was based on national inventory data collected for the USDA Forest Service Forest Inventory and Analysis (FIA) program. We selected data from the Interior West region of the FIA for the states of Idaho, Montana, Utah, Colorado, Nevada and Arizona (Figure 1). We omitted New Mexico and Wyoming because, although formally part of the region, plot remeasurement data required to estimate tree growth were unavailable. The Interior West region uses a common FIA sampling protocol (Bell et al., 2014). Climate is continental, with winter precipitation increasing to the northwest and summer precipitation increasing to the southeast (Wise, 2012).

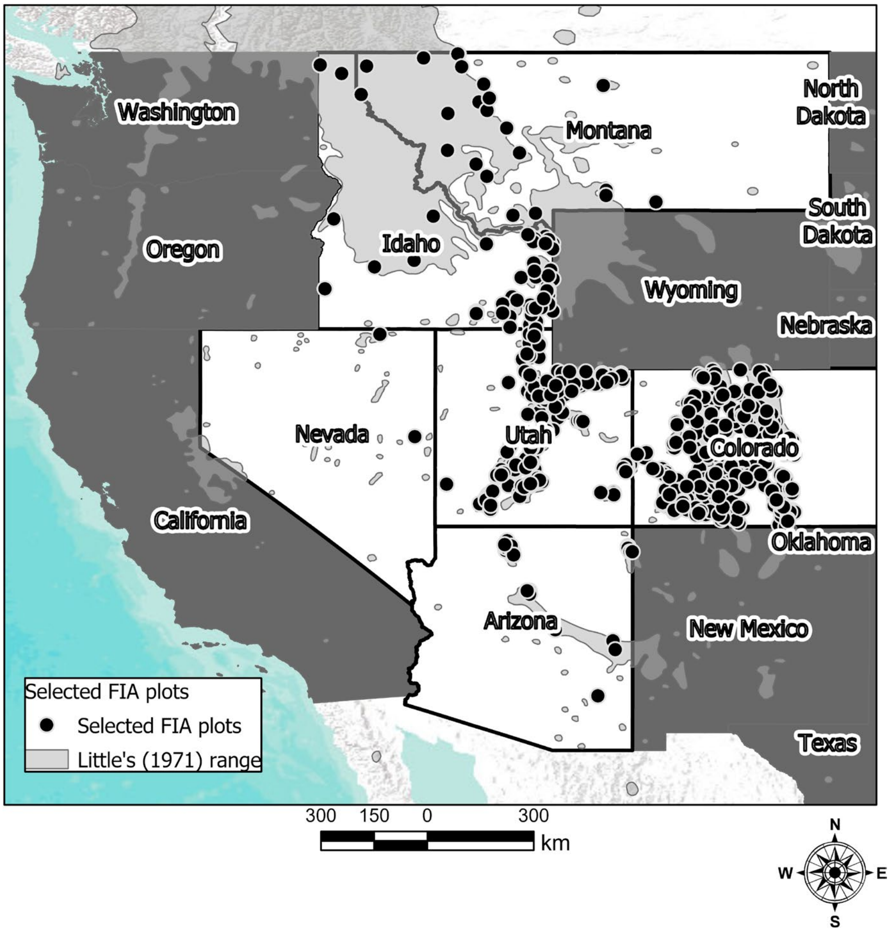

FIGURE 1 Map of study area showing states and plots within the FIA Interior West region selected for analysis based on condition, stand age and composition criteria

The elevation of queried plots ranged from 720 to 3,600 m. Publicly available plot coordinates, fuzzed by ~800 m (Bechtold & Patterson, 2005), ranged from 32.73° to 48.96° latitude and from −104.9° to −117.0° longitude. Mean plot precipitation over the 1981–2010 period ranged from 283.0 to 1,329.6 mm/year. Mean annual temperature for the same period ranged from −0.7 to 9.4°C (PRISM Climate Group, 2019).

Database queries focused on forested plots (≥10% canopy cover), with each FIA plot selected representing conditions within a single stand (Woudenberg et al., 2010). We selected plots without disturbance besides insects, disease, drought or competition (≥25% of trees impacted; Woudenberg et al., 2010). We restricted queries to the current annual inventory plot design of 4 × 0.016 ha subplots for trees >12.7 cm diameter at breast height (DBH), plus 4 microplots (0.0013 ha) for assessing saplings >2.54 DBH < 12.7 cm. These plots are targeted for remeasurement every 10 years, and we only included plots with 8 year < remeasurement period < 12 years for unbiased growth estimates. At the time of querying (9/23/2019), plots ranged in sampling dates from first measurements in 2000 to second measurements in 2018. To identify the fullest possible gradient of *P. tremuloides* density, we queried all plots entering the study with ≥1 living *P. tremuloides* stem ≥12.7 cm DBH.

We used *P. tremuloides* relative live tree stand density index (SDI; calculated via the summation method with stems ≥2.54 cm DBH; Long & Daniel, 1990) to represent relative density in all analyses. For consistency of interpretation, we used the inverse of *P. tremuloides* relative density to represent interspecific relative density in *P. tremuloides* models. We excluded plots with stand ages <40 years, dropping a total of 56 of 528 plots, because preliminary analysis of plots with younger stand ages introduced nonlinearity (Bell et al., 2014). Per Interior West FIA measurement protocols, stand age reflects the mean counts of tree rings obtained at breast height (1.37 m) in the predominant diameter class (Stevens et al., 2016). We focused on species that co-occurred with *P. tremuloides* on ≥100 plots and dropped trees entering the study as dead, open-grown or sapling for a remainder of 34,938 trees. Of the remaining trees, major species included *P. tremuloides* (13,632 trees/446 plots), *A. lasiocarpa* (4,018 trees/188 plots), *P. engelmannii* (4,016 trees/182 plots), *P. menziesii* (3,842 trees/207 plots) and *P. contorta* (3,804 trees/114 plots).

2.2 | Tree volume increment models

We fit generalized linear mixed growth models for each of the five study species. We followed an individual-tree modelling approach to detect tree-species mixture effects in terms of individual-tree growth over compositional gradients (Condés & del Río, 2015; Forrester & Pretzsch, 2015), which can flexibly incorporate tree, stand and site-level information (Table 1). As our growth response variable, we selected net sound volume increment (Table 1), the annualized change in cubic volume of a given tree between consecutive

TABLE 1 Variables used in volume increment, mortality and recruitment modelling

ID	Variable	Category	Description	Level	Analysis
1	Increment	Response	Annual net sound cubic volume increment	Tree	G
2	Status	Response	Tree status code: 0 = live tree, 1 = mortality tree	Tree	M
3	Recruitment	Response	Binary absence (0)/presence (1) code for tree (≥12.7 cm DBH) recruitment[a]	Tree	R
4	Rem. period	Time covariate	FIA plot remeasurement period	Stand	M, R
5	Plot ID	Sample strata	Random effect, synonymous with stand	Stand	G, M
6	Subplot	Sample strata	Random FIA subplot effect	Subplot	G, M
7	DBH	Stand structure	Initial diameter at breast height	Tree	G, M
8	CI	Stand structure	Mean squared size ratio[b]	Tree	G, M
9	SDI	Stand structure	Stand Density Index[c]	Stand	R
10	Stand age	Stand structure	Estimated stand age	Stand	G, M, R
11	Site class	Site quality	FIA site class code (1 = high, 7 = poor)	Stand	G, M, R
12	Heat load	Site quality	Estimated plot heat exposure	Stand	G, M, R
13	Cold-season PPT	Climate	Mean cold-season precipitation	Stand	G, M, R
14	Warm season VPD	Climate	Mean warm-season vapour pressure deficit	Stand	G, M, R
15	RD	Species mixture	Relative density[a,d]	Stand	G, M, R

Abbreviations: CI, competition index; G, growth; M, mortality; PPT, precipitation; R, recruitment; SDI, stand density index; VPD, vapour pressure deficit.

[a] Mean value calculated across remeasurement period.

[b] CI was consistently CI-3.

[c] Calculated using the summation formula for irregular stands.

[d] Relative density = proportion of plot stand density index comprised of *P. tremuloides* for conifer models and proportion of plot stand density index not comprised of *P. tremuloides* for *P. tremuloides* models.

inventories (calculated as $(V_2 - V_1)/(t_2 - t_1)$) of which the net value may be negative due to volume loss from mortality or live-tree damage, rot and other causes (Woudenberg et al., 2010). For growth modelling, we dropped trees without detectable (non-zero) volume increment. We modelled these strongly right-skewed growth data using a log-gamma error distribution (Lindsey, 1997).

We followed a common individual-tree growth modelling approach to construct a null hypothesis of growth as a function of tree size, vigour, site quality and competition (Biging & Dobbertin, 1992; Crookston & Dixon, 2005). We also included stand age as a term, given demonstrated growth declines in *P. menziesii*, *P. contorta* and *A. lasiocarpa* with age (Buechling et al., 2017). We included heat load, which incorporates plot slope, aspect and latitude, to control for topographic variation in solar radiation (McCune, 2007). Site class code, an ordinal variable of potential site productivity ranging from 1 (>15.7 m^3 ha^{-1} $year^{-1}$) to 7 (<1.3 m^3 ha^{-1} $year^{-1}$), represented site quality. This variable is derived from site index of individual species (Bechtold & Patterson, 2005), which is, in turn, not typically influenced by mixture effects (Pretzsch & Biber, 2016), with the caveat of reduced accuracy and utility in structurally complex stands (Dănescu et al., 2017). We used initial tree diameter to represent tree size. We excluded live crown ratio, a common term signifying vigour in tree growth models that mediates complementarity effects (Jucker, Bouriaud, Avacaritei, Dănilă, et al., 2014).

We used neighbourhood competition indices to represent the competitive environment for individual trees (Crookston & Dixon, 2005; Larocque et al., 2012). We selected three indices based on the sizes of competitors within the same 0.016 ha subplot relative to the focal tree. CI-1 was Glover and Hool's (1979) index, which represents tree competition as proportional to competitor size (Larocque et al., 2012):

$$\mathrm{CI} = \left(D_i^2 / \overline{D}^2 \right),$$

where CI is the competition index, D is the diameter of target tree i and $\overline{D}$ is the mean diameter of all sampled trees in the subplot. CI-2 was Lorimer's (1983) size-asymmetric index (trees larger than the focal tree are weighed more heavily), although we substituted tree heights for Lorimer's relative tree diameters to avoid collinearity and improve prediction based on preliminary modelling:

$$\mathrm{CI}_i = \sum_{j=1}^{n} \frac{h_j}{h_i},$$

where h is the tree height, i is the subject tree and j is a competitor tree, and other symbols are as per the equations above. CI-3 represented competition as strongly size-asymmetric:

$$\mathrm{CI}_i = \sum_{j=1}^{n} \left(\frac{h_j}{h_i} \right)^2,$$

where symbols are as per the equations above. Preliminary analysis (Table S1) indicated CI-3 had higher performance than other CI for all species, and we used this index for subsequent growth modelling. We averaged both CI and *P. tremuloides* relative density between measurements to better account for intervening tree mortality resulting in competition and compositional change.

Recent research suggests seasonal water supply and demand provide strong, interpretable indicators of drought in the Interior West, capturing the sub-annual variation in water balance most critical to tree growth and survival (Bell et al., 2014; Williams et al., 2012; Truettner et al., 2018; Venturas et al., 2020). In terms of supply, cold-season (previous November to growth-year March) precipitation (PPT) is most critical to forest vegetation given correspondingly low evapotranspiration demands (Williams et al., 2012). Warm season (previous August-previous October and growth year May–July) vapour pressure deficit (VPD) effectively captures the peak period of temperature-driven, regional forest water demand (Williams et al., 2012). Bell et al. (2014) recently demonstrated the sensitivity of stand-level aspen mortality to these climate variables. We used these seasonal climate variables to examine for niche differentiation in moisture use or facilitation under drought conditions as a driver of potential species mixture effects (Forrester & Bauhus, 2016). We joined monthly PPT and VPD records for each FIA plot location, based on bilinear interpolation of 4-km resolution gridded climate data (PRISM Climate Group, 2019) in GIS (Quantum GIS Development Team, 2018). We consolidated climate variables as periodic averages corresponding with measurement intervals for each FIA plot. We also calculated annual average PPT and VPD, but found these variables to be inferior in preliminary data analysis. Recent studies have also demonstrated the utility of the climate water deficit (CWD) for predicting tree mortality (Koontz et al., 2021; Venturas et al., 2020). Our comparison of both sets of climate indicators found generally comparable predictive value (See Supp. Inf. Appendix S1), and we opted to use VPD and PPT for ease of ecological interpretation.

2.3 | Tree mortality models

We evaluated mortality for all trees that were alive at first measurement. We modelled mortality using generalized linear mixed modelling with a binomial error distribution and logit link function. We opted to use the equivalent null model structure as for growth modelling (Table 2), except that we added remeasurement period to account for variation in observation time in all models. Although initial tree growth is a strong indicator of vigour (Crookston & Dixon, 2005; Das et al., 2008), these data were not included as they were both largely unavailable and had potential to obscure mortality–composition relationships through mediation. We included tree size in mortality models, as larger trees are commonly at greater risk of stem insects or drought (Das et al., 2008). We included site class to account for higher productivity potentially driving more rapid increases in competition (Crookston & Dixon, 2005) and stand age based on findings that stand-level *P. tremuloides* mortality is higher in older stands (Bell et al., 2014; Kaye et al., 2005). Preliminary analysis showed that CI-3 was the best performing predictor of mortality across all

TABLE 2 Hypothesis models with constituent indicator variables

Analysis	Hypothesis	Response varies as a function of:	Variable IDs
G, M	1	Null model (stand structure, site quality)	5–8, 10–12
G, M	2	Null model, climate	5–8, 10–14
G, M	3	Null model, climate, PPT × VPD	5–8, 10–14
G, M	4	Null model, POTR RD	5–8, 10–12, 15
G, M	5	Null model, POTR RD, climate	5–8, 10–15
G, M	6	Null model, POTR RD, climate, PPT × VPD	5–8, 10–15
G, M	7	Null model, POTR RD, climate, POTR RD × PPT	5–8, 10–15
G, M	8	Null model, POTR RD, climate, POTR RD × VPD	5–8, 10–15
G, M	9	Null model, POTR RD, climate, PPT × VPD, POTR RD × PPT	5–8, 10–15
G, M	10	Null model, POTR RD, climate, PPT × VPD, POTR RD × VPD	5–8, 10–15
G, M	11	Null model, POTR RD, climate, POTR RD × PPT × VPD	5–8, 10–15
R	1	Null model, (stand structure, site quality)	5–7, 9–12
R	2	Null model, climate	5–7, 9–14
R	3	Null model, linear POTR RD	5–7, 9–12, 15
R	4	Null model, quadratic POTR RD	5–7, 9–15
R	5	Null model, climate, linear POTR RD	5–7, 9–15
R	6	Null model, climate, quadratic POTR RD	5–7, 9–15
R	7	Null model, climate, linear POTR RD, POTR RD × PPT	5–7, 9–15
R	8	Null model, climate, linear POTR RD, POTR RD × VPD	5–7, 9–15
R	9	Null model, climate, quadratic POTR RD, POTR RD × PPT	5–7, 9–15
R	10	Null model, climate, quadratic POTR RD, POTR RD × VPD	5–7, 9–15

Note: Please see Table 1 for details of model main effects corresponding to the 'Variable ID' column.

Abbreviations: G, tree-level growth, M, tree-level mortality, R, plot-level tree recruitment, PPT, precipitation, VPD, vapour pressure deficit, POTR RD, *Populus tremuloides* relative density.

species (Appendix S1), and we used this CI in all subsequent mortality modelling. We included cold-season PPT and warm-season VPD as recent climate indicators.

2.4 | Plot-level tree recruitment models

We define tree recruitment as the transition to a larger size class by at least one stem between inventories from sapling (2.54 cm < DBH < 12.7 cm) to tree (>12.7 cm DBH). Large saplings represent the nearest-term replacements for trees lost to mortality, providing insights into near-term compositional changes based on the supply of new trees. In contrast, the regeneration layer (stems < 2.54 cm DBH) may take several decades to achieve tree stature in the absence of disturbance, depending on species.

We modelled tree recruitment as a plot-level process, as most stems are not tracked prior to achieving tree size under FIA nested sapling plot design (Bechtold & Patterson, 2005). We reclassified tree recruitment as presence/absence data modelled with a binomial error distribution. Our null model expressed mortality as a function of SDI, site class, stand age, heat load and remeasurement period. Because Kaye et al. (2005) found a nonlinear decline in *P. tremuloides* recruitment with conifer density, we considered both linear and quadratic *P. tremuloides* relative density terms. Warm-season VPD and cold-season PPT served as recent climate indicators, but we omitted the VPD × PPT interaction due to the complexity of quadratic *P. tremuloides* models.

2.5 | Statistical analysis

We built sets of growth, mortality and tree recruitment models for use in multi-model inference with corrected Akaike's Information Criterion (Burnham & Anderson, 2002; Sugiura, 1978). Based on the null models of growth or mortality as functions of tree characteristics, stand age and site quality, we built alternative models to examine the effects of *P. tremuloides* relative density and climate indicators (Table 2). We examined whether climate modified the effect of *P. tremuloides* relative density through interaction terms. For growth and mortality models containing climate variables, we also included alternatives examining the interaction between cold-season PPT and warm-season VPD, which may more strongly impact growth in certain species than either main effect (Truettner et al., 2018). Our most complex models included a three-way interaction between *P. tremuloides* relative density, cold-season PPT and warm-season VPD. We followed the same model building and comparison approach for recruitment, examining *P. tremuloides* relative density in isolation and in interaction with climate. We considered models for a given species with ΔAICc < 6 of the best-approximating model that did not contain simpler nested models with stronger AICc support to be plausible (Richards, 2008). We also excluded more complex models (i.e. models containing more parameters) that were within 2 AICc of simpler nested alternatives (Burnham & Anderson, 2002). We considered all models meeting these criteria to warrant inclusion in inference.

We used the GLMMTMB package (Magnusson et al., 2018) in R (R Core Team, 2018) for all modelling. We included the random effects of plot in all growth and mortality models to correctly stratify tree and stand-level variables. We also included the random effect of subplot in growth models to account for spatially autocorrelated growth estimates, but omitted this subplot effect in mortality models due to the frequently low number of dead trees per subplot (Bell et al., 2015). We omitted both random effects in analysis of recruitment due to the lack of sample strata. We graphically verified model assumptions of linearity and the suitability of error distributions using simulated residuals plots (Hartig, 2018). We log-transformed initial tree diameter, cold-season precipitation, CI-3 and SDI based on these diagnostics. Based on residual diagnostics indicating nonlinearity, we included quadratic SDI terms in recruitment models for *P. menziesii*, *P. contorta* and *P. engelmannii*. Variance inflation factors did not exceed 3 for any model term, indicating low to moderate collinearity (James et al., 2013).

We calculated the marginal and conditional (fixed factors-only and combined fixed and random effects, respectively) pseudo-R^2 for each tree growth model with substantial AICc support for descriptive purposes. For plausible tree mortality and recruitment models, we calculated the area under the receiver operating curve (AUC). We calculated AUC for both the original mixed-effect tree mortality models as well as fixed-effect-only versions to better isolate the predictive value of the fixed effects. We used the MUMIN package (Bartoń, 2017) to perform multi-model inference and calculate R^2 statistics. All predictor variables were converted to *Z*-scores to facilitate interpretation and model convergence. We back-transformed logit-binomial model coefficients for ease of visualization in graphics.

We interpreted AIC support for a relative density effect on growth, mortality or tree recruitment in several ways. A positive relative density term signified a positive mixture effect, defined as enhanced performance of a given tree species in functionally diverse mixtures compared to monocultures. A negative relative density term indicated a negative mixture effect resulting in reduced performance of a given tree species in functionally diverse mixtures compared to monocultures. In the event of significant relative density interactions with climate, we interpreted positive or negative mixture effects as contingent on climate variables.

3 | RESULTS

3.1 | Individual-tree volume increment

The growth of each of the five species responded similarly to the null model terms of diameter, competition, stand age, site class and heat load (Table 3). Growth of all species also showed similar responses to the null model terms of diameter, stand age, competition and site class, although the magnitude of response varied by species (Figure S1). Growth increased with initial diameter while declining with site class (1 = high, 7 = poor), stand age and competition (Figure S1). The null model had greatest AICc support for *P. menziesii*. For transformed predictor variables (diameter, competition and PPT), the relationships described were curvilinear rather than linear once the results were back-transformed.

We found a single plausible model for *P. tremuloides* growth, which included relative density and climate, in addition to the null model terms. Growth increased with increasing PPT and VPD, and decreased with increasing interspecific relative density. For *P. contorta*, the best-approximating model included relative density, climate main effects and the PPT × VPD interaction. *Pinus contorta* growth increased with PPT, VPD and *P. tremuloides* relative density (Table 3). Under the PPT × VPD interaction, growth remained neutral with increasing PPT under low VPD conditions while increasing under high VPD conditions (Figure 2). For *P. engelmannii*, the best-approximating model included both relative density and climate terms. Growth increased with *P. tremuloides* relative density and PPT, as well as marginally with VPD. A plausible alternative model omitted *P. tremuloides* relative density (ΔAICc = 2.29).

3.2 | Individual-tree mortality

In terms of mortality, species showed differing responses to the null model terms of site class, stand age, heat load, initial diameter, competition and remeasurement period (Table 3; Figure S2). As with growth, mortality relationships involving diameter, competition and cold-season PPT were nonlinear due to predictor transformations. Competition and DBH were the most consistently strong mortality predictors across the five species. Mortality odds increased with competition in all species except *P. contorta*, where CI had a neutral influence. Mortality odds increased with DBH for the conifers, most strongly for *P. contorta* where a 1 standard deviation increase in DBH

TABLE 3 Plausible growth and mortality models based on corrected Akaike's Information Criterion (AICc) for *Populus tremuloides* (POTR), *Pseudotsuga menziesii* (PSME), *Pinus contorta* (PICO), *Abies lasiocarpa* (ABLA) and *Picea engelmannii* (PIEN)

			Model terms[a]							
Response	**Species**	**Hypos**	**Null**	**Clim M.E.**	**RD**	**VPD × PPT**	**logLik**	**ΔAICc**	**R^2**	**AUC**
Growth	POTR	5	x	x	x		122,247.6	0.00	0.35/0.65	
	PSME	1	x				2,739.5	0.00	0.51/0.78	
	PICO	6	x	x	x	x	2,622.3	0.00	0.29/0.46	
	PICO	5	x	x	x		2,619.4	3.80	0.29/0.46	
	ABLA	4	x		x		2,480.78	0.00	0.35/0.71	
	PIEN	2	x	x			2,351.2	0.00	0.42/0.76	
Mortality	POTR	2	x	x			−5,912.51	0.00		0.63/0.81
	PSME	1	x				−528	0.00		0.59/0.93
	PICO	1	x				−1,212.7	0.00		0.69/0.92
	ABLA	4	x		x		−1,292.8	0.00		0.60/0.84
	ABLA	1	x				−1,295.5	3.35		0.60/0.84
	PIEN	1	x				−1,009.4	0.00		0.74/0.96

Abbreviations: logLik, log likelihood, AICc, corrected Akaike's information criterion, ΔAICc, difference compared to best-approximating model, ER, evidence ratio (ratio of best-approximating model weights vs. alternative models), clim M.E., climate main effects, RD, relative density, VPD × PPT, warm-season vapour pressure deficit × cold-season PPT interaction (not fitted without also including the main effects of these variables). Models with ΔAICc < 6 of the best-approximating model and which do not contain simpler nested models with greater AICc support are considered plausible.

[a] At a minimum, all models included the null model terms of stand age, site class, competition and diameter at breast height.

increased mortality odds by approximately 10. In contrast, mortality odds in *P. tremuloides* declined with DBH. Of stand age, site class, remeasurement period and heat load, only stand age for *A. lasiocarpa* and site class for *P. engelmannii* were evident factors in mortality. The null model had greatest AICc support for *P. menziesii*, *P. contorta* and *P. engelmannii*.

In addition to the null model terms, the only plausible model for *P. tremuloides* included climate terms. Mortality odds declined with PPT and increased under high VPD (Figure 3). There was no support for a relative density main effect. The best-approximating model for *A. lasiocarpa* included *P. tremuloides* relative density as a main effect, suggesting that composition influenced mortality odds for this species. Mortality odds declined with increasing *P. tremuloides* relative density. The null model without the *P. tremuloides* relative density term was also plausible (ΔAICc = 3.35).

3.3 | Plot-level tree recruitment

Recruitment–SDI relationships were nonlinear due to log-transformation of SDI and use of both linear and quadratic SDI terms in *P. menziesii* and *P. contorta* models. Tree recruitment odds varied weakly for the five species with the null model, which included stand age, site class and remeasurement period (Table 4; Figure S3). Recruitment odds varied strongly with SDI in species other than *P. tremuloides*. For *P. menziesii* and *P. contorta*, recruitment was highest at intermediate SDI while *A. lasiocarpa* and *P. engelmannii* recruitment continued to increase across the range of SDI. The null model was most plausible for *P. engelmannii* tree recruitment.

In addition to the null model terms, the most plausible model of *P. tremuloides* tree recruitment included both climate terms and a quadratic relationship with interspecific relative density, with recruitment steeply declining above 25% non-*P. tremuloides* relative density (Figure 4). Recruitment odds of *P. tremuloides* increased with both VPD and PPD, but a plausible competing model omitted these climate terms. The best-approximating model for *P. menziesii* included a linear *P. tremuloides* relative density effect, although the null model was also plausible. Recruitment odds decreased with increasing *P. tremuloides* relative density. The best-approximating model for *P. contorta* included the null model terms and a linear *P. tremuloides* relative density effect. For *A. lasiocarpa*, the most plausible model included the null model terms and a linear *P. tremuloides* relative density main effect. Recruitment odds declined with *P. tremuloides* relative density, although the null model dropping this relative density term was also plausible. For *Picea engelmannii*, the sole plausible model included climate effects. Recruitment odds strongly declined with VPD while not varying with PPT.

4 | DISCUSSION

Species mixtures have been shown to enhance forest productivity worldwide (Jactel et al., 2018; Mina et al., 2018), offering potentially greater growth stability and enhanced carbon sequestration under climatic fluctuations (Ammer, 2019; Malmsheimer et al., 2009).

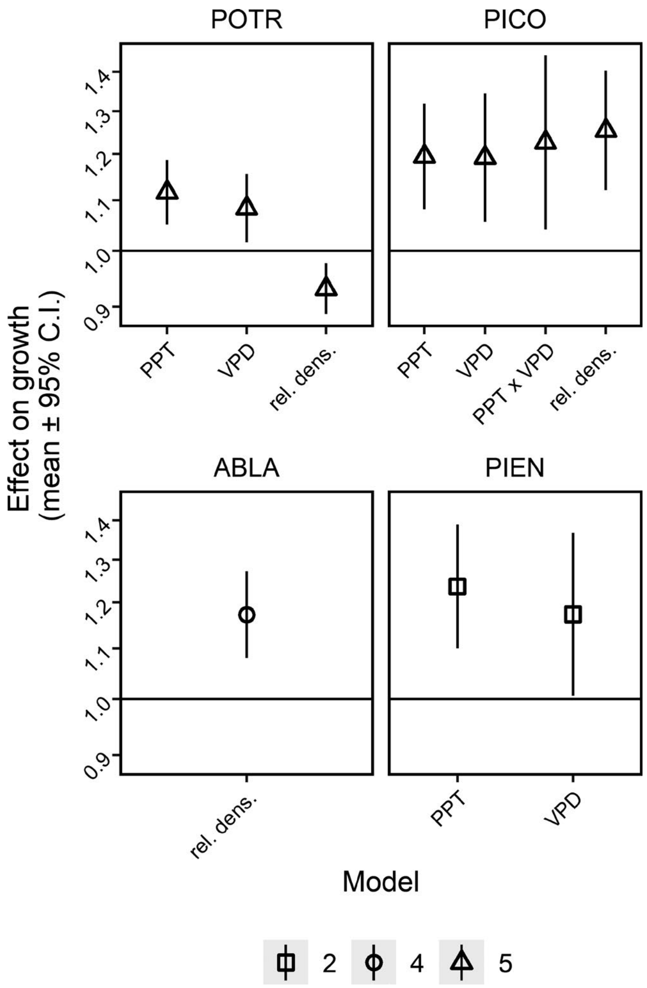

FIGURE 2 Model coefficients for the best-approximating log-gamma mixed model of individual tree, sound cubic volume increment for *Populus tremuloides* (POTR), *Pseudotsuga menziesii* (PSME), *Pinus contorta* (PICO), *Abies lasiocarpa* (ABLA) and *Picea engelmannii* (PIEN). PPT, cold-season precipitation, VPD, warm-season vapour pressure deficit, POTR rd, relative density (proportion *P. tremuloides* for conifer models, inverse for *P. tremuloides* models). Predictor variable (*x*-axis) coefficients are displayed as *Z*-scores. The *y*-axis depicts means (as symbols) ± 95% confidence intervals of predictor effects on volume increment (m^3/year). See Table 1 for details on variables and Table 3 for other terms included in each model

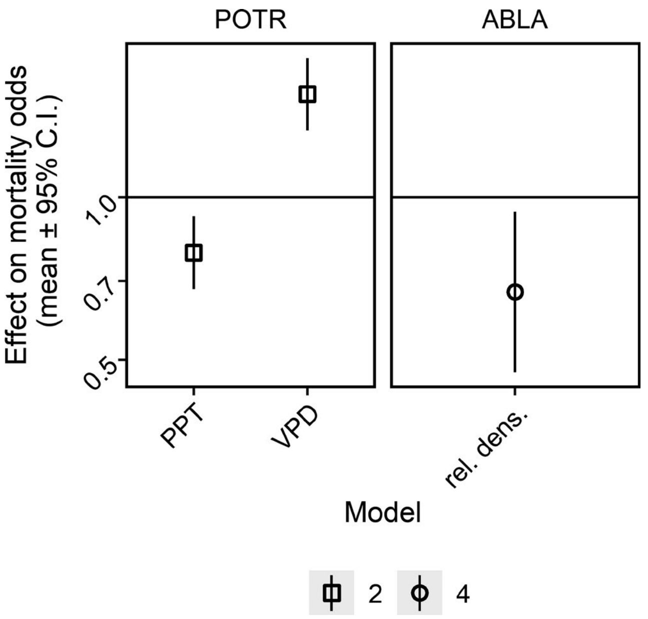

FIGURE 3 Model coefficients for the best-approximating binomial mixed model of individual-tree mortality odds. Coefficients are derived from the best-approximating models for *Populus tremuloides* (POTR), and *Abies lasiocarpa* (ABLA). Abbreviations are as follows: PPT, cold-season precipitation, VPD, warm-season vapour pressure deficit, POTR rd, relative density (proportion *P. tremuloides* for conifer models, inverse for *P. tremuloides* models). Predictor variable (*x*-axis) coefficients are displayed as *Z*-scores. The *y*-axis depicts means (as symbols) ± 95% confidence intervals of predictor effects on mortality odds. See Table 1 for details on variables and Table 3 for other terms included in each model

However, to our knowledge, only a single study has comprehensively examined the influence of composition on growth, mortality and tree recruitment (Liang et al., 2007), which together are the major demographic drivers of forest population dynamics (Bechtold & Patterson, 2005). We applied recently available, regional forest inventory data to quantify forest change in *P. tremuloides* ecosystems spanning broad compositional and climatic gradients. Through generalized linear modelling with this large dataset, we isolated compositional and climatic variables of major interest to this study from factors of only peripheral interest, such as stand structure and site quality. Our examination of composition–climate interactions allowed us to investigate both the contemporary role of complementarity as modified by abiotic stress and to infer the dynamics of *P. tremuloides* species mixtures under future climate.

It should be noted, however, that our use of forest inventory and gridded climate data may have constrained our ability to fully identify compositional and climate effects. First, the small radius of each FIA subplot increases the influence of unmeasured neighbours on sampled trees, relative to a single plot of the same area. To minimize this constraint, we selected only plots in which a single stand was sampled to assure greater within-plot consistency of species composition, forest structure and site quality. Next, tree death may occur anytime between FIA remeasurement periods, and studies have found high noise in tree mortality analysis using FIA data (Venturas et al., 2020), which could reduce the robustness of the cause-and-effect relationships our analysis found between mortality and climate. Lastly, our use of 4-km resolution, gridded climate data and publicly available, 800 m resolution plot coordinates may not have captured important variations in microclimate. Precipitation is particularly difficult to model in mountainous terrain with limited field instrumentation (Henn et al., 2018). Imprecise climate data or other unmeasured environmental variation may have introduced covariation between tree performance and composition, although our geographically broad landscape-level dataset was selected specifically to address these concerns through high site replication.

TABLE 4 Plausible tree recruitment models based on corrected Akaike's Information Criterion (AICc) for *Populus tremuloides* (POTR), *Pseudotsuga menziesii* (PSME), *Pinus contorta* (PICO), *Abies lasiocarpa* (ABLA) and *Picea engelmannii* (PIEN)

Species	Hypos	Description Null[a]	 Climate	 Quadratic RD	 Linear RD	logLik	ΔAICc	AUC
POTR	R-6	x	x	x	x	−576.73	0	0.70
POTR	R-4	x		x	x	−581.42	5.31	0.70
PSME	R-3	x			x	−284.40	0	0.65
PSME	R-1	x				−287.60	4.38	0.64
PICO	R-6	x	x		x	−129.77	0	0.79
ABLA	R-6	x	x		x	−178.80	0	0.69
ABLA	R-1	x				−195.56	5.64	0.67
PIEN	R-1	x	x			−258.27	0	0.69

Note: Models with ΔAICc < 6 of the best-approximating model and which do not contain simpler nested models with greater AICc support are considered plausible.

Abbreviations: clim, climate, quad, quadratic, rd, relative density (proportion *P. tremuloides* by plot stand density index for conifer models; Hypos, hypothesis, logLik, log likelihood, AICc, corrected Akaike's information criterion, ΔAICc, difference compared to best-approximating model, ER, evidence ratio (AICc weights of best-approximating model/plausible model set alternative); proportion non-*P. tremuloides* for *P. tremuloides* models).

[a] All models contained the null model terms of stand density index, stand age, site class and remeasurement period.

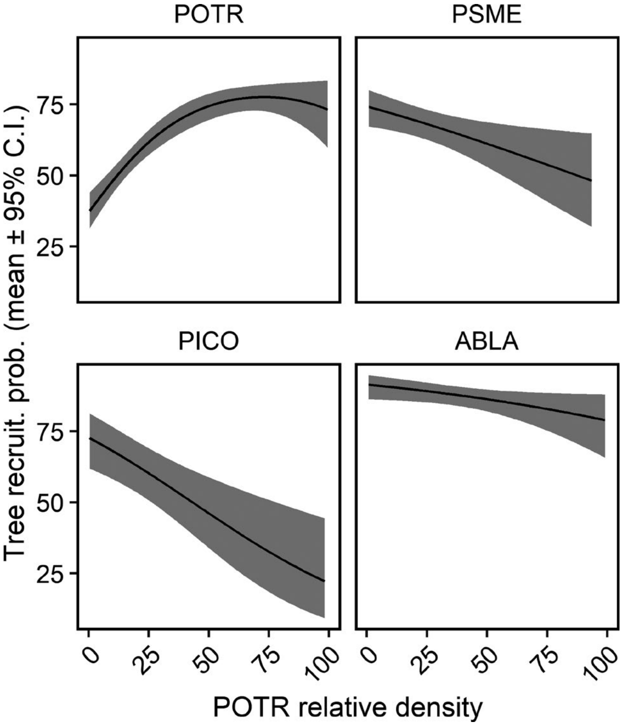

FIGURE 4 Predicted tree recruitment presence–absence for *Populus tremuloides* (POTR), *Pseudotsuga menziesii* (PSME), *Pinus contorta* (PICO) and *Abies lasiocarpa* (ABLA). For *P. tremuloides*, recruitment varies as a function of non-*P. tremuloides* relative density index; for conifers, recruitment varies as a function of *P. tremuloides* relative stand density index. The *y*-axis depicts recruitment back-transformed from the logit scale (means ±95% confidence intervals), the *x*-axis displays *P. tremuloides* relative stand density index (SDI, %). Recruitment is modelled over the study window ($\bar{x}$ = 9.6 yr for individual plots). Predictions are based on the best-approximating models for each species. See Table 4 for a full list of model covariates

4.1 | Effects of species mixture and climate on growth

Species mixtures commonly do not enhance growth of all species, but rather benefit certain species at the expense of others (Pretzsch, 2005). In our study, we found that *P. tremuloides* growth declined under high non-*P. tremuloides* relative density, providing evidence of a negative mixture effect. In contrast, we found strong evidence that higher *P. tremuloides* relative densities enhanced the growth of *P. contorta* and *A. lasiocarpa* while not affecting the growth of *P. engelmannii* or *P. menziesii*. In plantation settings in Western Canada, Kweon and Comeau (2019) found that species mixtures primarily benefit the growth of the conifer species, *Picea glauca* (white spruce), with growth of associated *P. tremuloides* largely unaffected. Our finding that mixtures with a deciduous, clonal hardwood may benefit conifer growth supports earlier findings that functional diversity is an important factor in determining whether mixture effects are positive (Lu et al., 2018). The lack of evidence for a *P. tremuloides* mixture effect on *P. menziesii* growth contrasted with the results of a previous study that found *P. menziesii* growth increased with relative density of phylogenetically similar conifers in Interior West stands impacted by fire exclusion (Looney et al., 2020). The low shade tolerance of *P. tremuloides*, coupled with high potential height growth in *P. menziesii*, may limit canopy stratification and complementarity in light use in *P. tremuloides*-*P. menziesii* mixtures. Given the lack of substantial climate effects on *P. menziesii* growth, species mixture effects on growth of this species may also have been confounded by unmeasured environmental variables or microclimate variations not captured by the use of gridded climate data and fuzzed FIA plot coordinates.

Several non-exclusive hypotheses may account for the contrasting performances of *P. tremuloides* and conifers. *Populus tremuloides* is the least shade tolerant of the species examined (Niinemets & Valladares, 2006), and diversity in traits related to light use, such as shade tolerance and crown shape, can drive positive mixture effects (Ishii & Asano, 2010; Lu et al., 2018). Deciduous *P. tremuloides* may enhance conifer growth by helping to sustain photosynthesis both within and without the growing season. The typically greater structural heterogeneity and evapotranspiration in mixed stands can reduce summer temperature stress (Ehbrecht et al., 2019) while seasonal leaf loss in deciduous hardwoods temporarily reduces light competition and promotes conifer photosynthesis (Forrester et al., 2018). Studies in Colorado, USA have confirmed that *P. menziesii*, *P. engelmannii* and *A. lasiocarpa* maintain limited photosynthetic capacity in winter and spring (Koh et al., 2009; Zarter et al., 2006), offsetting respiration costs outside the growing season (Albert et al., 2017). Finally, *P. tremuloides* may facilitate conifers by enhancing soil nutrient availability, moisture content and microbial activity (Buck & St. Clair, 2012).

Climate was also an important predictor of *P. tremuloides*, *P. contorta* and *P. engelmannii* growth, with growth–PPT relationships, suggesting that growth of all three species was water limited. A positive growth–VPD relationship suggested that low temperatures also limited the growth of the three species, particularly *P. contorta* in which growth only responded positively to PPT under high VPD conditions. Differential responses to moisture stress may have implications for the stability of growth under climate change (Jucker, Bouriaud, Avacaritei, & Coomes, 2014). Under drought conditions, total stand growth could be stabilized in mixtures of these species with climate-insensitive *P. menziesii* and *A. lasiocarpa*. Compensatory growth in *P. tremuloides* systems under stress has been reported in the Midwestern USA, where Reinikainen et al. (2013) found that increased growth of associated conifers offset stand growth losses due to defoliation of *P. tremuloides*. It is important to note, however, that space-for-time substitution of climate is problematic for making inferences regarding tree growth under future climate. Klesse et al. (2020) found that periodic growth in *P. menziesii* commonly increases with temperature across sites, whereas interannual increases in temperature within sites are instead associated with growth declines. Future studies should compare the sensitivity of periodic and tree-ring growth to climate among *P. tremuloides* community species to establish whether similar discrepancies exist in this study system.

Previous studies suggest climate commonly alters the strength of species mixture effects, sometimes even shifting growth performances relative to monocultures from positive to negative (Jactel et al., 2018; Mina et al., 2018). Yet, we did not find evidence of substantial interactions between *P. tremuloides* density and climate for the growth of any species. This finding was unexpected given that stands of *P. tremuloides* have distinct water-balance dynamics relative to conifer-dominated stands, with higher snow water equivalent from lower interception offsetting higher summer evapotranspiration (LaMalfa & Ryle, 2008). More substantial winter snowpack in *P. tremuloides*-dominated stands could also conceivably enhance the stabilizing effects of winter snowpack on soil temperatures (Decker et al., 2003). Worrall et al. (2013) also hypothesized that limited snowpack could expose *P. tremuloides* root systems to cold, perhaps contributing to the steep decline in *P. tremuloides* recruitment observed at higher conifer relative densities. Lack of support in growth models for interactions between *P. tremuloides* relative density and climate variables is consistent with the finding of a previous study that high functional diversity does not necessarily translate to reduced drought stress (Grossiord, 2020). A stable isotope study along an elevational gradient in Arizona found no evidence of variation in soil moisture source (deep winter, intermediate or shallow summer moisture) among *P. tremuloides* and associated conifers, suggesting a general lack of niche differentiation in water use in high-elevation montane forests (Guo et al., 2018). In western Canadian boreal forests, Brown et al. (2014) found the well-developed clonal root system of *P. tremuloides* enhances shallow soil moisture through hydraulic lift. However, under drought in the same ecoregion, Cardoso (2020) found that *Picea glauca* Muench (white spruce) growth and sap flow were reduced in mixtures with *P. tremuloides* and other hardwoods, which she attributed to a combination of greater shading, soil water competition and growing season soil water depletion compared to pure conifer stands.

4.2 | Effects of species mixture and climate on tree mortality

We did not detect a substantial influence of *P. tremuloides* relative density on *P. tremuloides* mortality, in contrast to the stand-level and tree-level results of Bell et al. (2014, 2015). Compared to these studies, we had the benefit of longitudinal data (Bell et al., 2014) over a larger geographical expanse (Bell et al., 2015) due to the expanding number of re-inventoried plots. The severe drought events of the late 1990s and early 2000s may have removed many vulnerable trees from mixed stands prior to our 2000–2018 study window while increased pathogen and insect activity may counter otherwise lower *P. tremuloides* mortality in purer stands (Bell et al., 2015). In contrast to conifer species and in keeping with the findings of previous research (Worrall et al., 2010), mortality risk declined with increasing *P. tremuloides* diameter, perhaps reflecting increased drought-related mortality in marginal aspen stands or stands with younger clonal roots. In the mixed stands common under historical fire exclusion and browse pressure, younger *P. tremuloides* are often subject to heavy conifer competition in lower size classes (Binkley et al., 2014; Kaye et al., 2005). Tree size can strongly influence whether the growth of a species responds positively or negatively to mixture effects (Madrigal-González et al., 2016; Mina et al., 2018), and future studies should investigate this possibility given the potential importance for forest stand development.

Consistent with previous research, we found that *P. tremuloides* mortality odds increased under warmer temperatures and/or lower precipitation (Anderegg et al., 2013; Rehfeldt et al., 2009; Worrall et al., 2013) and higher warm-season VPD (Anderegg et al., 2013; Bell et al., 2014), relationships demonstrated for many other tree species around the world (Allen et al., 2015; McDowell et al., 2016). The higher mortality of *P. tremuloides* relative to conifers, especially under high VPD conditions indicative of temperature-driven drought, suggests that droughts likely have differential impacts on mortality in *P. tremuloides* communities (Worrall et al., 2013). Mixtures of *P. tremuloides* with conifers may be less susceptible to tree mortality overall but unless offset by recruitment, mortality events would diminish the benefits of positive mixture effects in these systems in terms of conifer growth as *P. tremuloides* mortality accelerates forest succession.

We found mixed support for reduced *A. lasiocarpa* mortality in mixtures with *P. tremuloides*, a finding consistent with St. Clair et al.'s (2013) finding of facilitation between these species. Of the species examined, *A. lasiocarpa* is not only the most drought sensitive but also the most shade tolerant. Shade tolerance is often associated with reduced tree mortality, rather than necessarily faster growth (Kobe et al., 1995). Besides reflecting lower shade tolerance, the lack of *P. tremuloides* density effects on the mortality of other conifer species may indicate trade-offs between stand productivity and mortality risk. Enhanced forest productivity can accelerate leaf area accretion (Crookston & Dixon, 2005), which, in turn, may drive more frequent mortality in diverse forests despite their higher overall productivity (Morin et al., 2011). In addition, productive stands reach critical stocking-related mortality thresholds more quickly (Long et al., 2004), although stocking thresholds for tree mortality may be higher in mixed versus pure stands, particularly for shade-intolerant species (Kimsey et al., 2019).

Rapid diameter growth is commonly associated with reduced risk of tree mortality (Cailleret et al., 2017; Kane & Kolb, 2014). Yet, enhanced individual-tree growth rates under higher *P. tremuloides* relative densities did not correspond with lower mortality odds for conifer species other than *A. lasiocarpa*. Given that increased volume in mixed stands reflects diameter rather than height growth (Pretzsch & Biber, 2016), faster growth rates over the study period would have contributed to larger tree diameters, a key risk factor for bark beetle infestation (Bakaj et al., 2016). Although we controlled for initial tree diameter in our analysis, rapid conifer growth in *P. tremuloides* mixtures may also have increased neighbourhood stand density, another factor associated with bark beetle risk (Bakaj et al., 2016; Das et al., 2008). For tree species susceptible to aggregating bark beetles, mixed stands may reduce mortality by reducing host-tree density (Das et al., 2008; Koontz et al., 2021). Previous studies have found non-host tree species relative density is associated with reduced *Dendroctonus* beetle infestation in *P. contorta* (Negron & Klutsch, 2017), *P. engelmannii* (Bakaj et al., 2016) and *P. menziesii* (McMillin et al., 2003). However, individual-tree diameter and age are more consequential for bark beetle risk than neighbourhood characteristics (Bakaj et al., 2016).

4.3 | Effects of climate and species mixture on tree recruitment

Tree recruitment is rarely examined in the context of species mixture effects on forest productivity, yet it is key to understanding the long-term viability of species mixtures in the absence of severe disturbance (Cordonnier et al., 2018). Although shade-intolerant species such as *P. tremuloides* often provide the critical contribution to functional diversity needed to drive complementarity or facilitation, they are also the most subject to forest succession (Cordonnier et al., 2018). *Populus tremuloides* recruitment odds plateaued at low intraspecific relative densities, consistent with hormonal suppression of root suckers by overstorey stems (Doucet, 1989). Steep declines in *P. tremuloides* recruitment odds under higher proportions of associated conifers are consistent with previous studies in Colorado (Binkley et al., 2014; Kaye et al., 2005) and California, USA (Berrill & Dagley, 2014). *Populus tremuloides* displays a strong ability for self-replacement under severe disturbances, particularly under compound events such as fire followed by windthrow (Kulakowski et al., 2013). Our findings confirm the results of previous studies highlighting a role of disturbance in maintaining *P. tremuloides* in stands with more tolerant conifers (Kaye et al., 2005; Lieffers et al., 1996).

In the absence of species interactions, we would have expected conifer recruitment to decline as conifer seed sources became scarce at high *P. tremuloides* relative densities. We observed a strong decline in recruitment of *P. contorta* while the recruitment odds of the more shade-tolerant conifer species ranged from weak to insubstantial. Our findings are consistent with secondary successional dynamics widely documented in *P. tremuloides* stands (Binkley et al., 2014; Kaye et al., 2005; Lieffers et al., 1996). In the absence of composition–climate interactions that would suggest processes such as complementarity or facilitation, we cannot infer among the potential mechanisms driving forest succession (Connell & Slatyer, 1977). However, the stronger decline in *P. contorta* recruitment odds relative to the more shade-tolerant conifer species would be more consistent with inhibition than facilitation. A realistic null model is needed to more definitively discern the influence of conifer seed source limitation from species interactions (Hubbell, 2005).

In the context of global change, overstorey species adapted to current conditions may help to ameliorate microclimate effects in the lower canopy, sustaining existing species while aiding the transition to future climate adapted communities (Muller et al., 2019; Nagel et al., 2017). Cortini et al. (2012) found that *P. tremuloides* exacerbates temperature limitations on the growth of juvenile (14–16 years) *Picea glauca* in Canadian boreal mixedwood forests. We found no evidence, however, that climate interacted with composition to alter either *P. tremuloides* or associated conifer recruitment odds in Interior West mixed-conifer forests. Our findings suggest that under climate change, anticipated increases in temperature-driven VPD in the region are more likely to contribute to forest succession through the higher growth of certain conifer species and increased odds of *P. tremuloides* tree mortality (Rehfeldt et al., 2009) rather than through tree recruitment.

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AUTHORS' CONTRIBUTIONS

C.E.L. and W.J.P. conceived the research idea, which J.B.B. and L.M.N. helped to refine; C.E.L. queried the FIA database, with support from W.J.P., and performed the statistical analysis; C.E.L., with contributions from W.J.P., J.B.B. and L.M.N., wrote and revised the paper. All authors discussed the results, commented on the manuscript and participated in the revision.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13709.

DATA AVAILABILITY STATEMENT

Forest inventory data are publicly available online via the United States Forest Service Forest Inventory and Analysis Data Mart: https://apps.fs.usda.gov/fia/datamart/. Climate data are available via PRISM https://prism.oregonstate.edu/recent/ and Terraclim http://www.climatologylab.org/terraclimate.html. An SQL query code and r that can be used to reconstruct the primary data query and derived data, as well as final derived data files used analyses, are available through Dryad Digital Repository https://doi.org/10.5061/dryad.h9w0vt4hv (Looney 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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