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Variations in tree growth provide limited evidence of species mixture effects in Interior West USA mixed-conifer forests

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Abstract

1. In mixed stands, species complementarity (e.g. facilitation and competition reduction) may enhance forest tree productivity. Although positive mixture effects have been identified in forests world-wide, the majority of studies have focused on two-species interactions in managed systems with high functional diversity. We extended this line of research to examine mixture effects on tree productivity across landscape-scale compositional and environmental gradients in the low functional diversity, fire-suppressed, mixed-conifer forests of the U.S. Interior West.
2. We investigated mixture effects on the productivity of *Pinus ponderosa*, *Pseudotsuga menziesii* and *Abies concolor*. Using region-wide forest inventory data, we created individual-tree generalized linear mixed models and examined the growth of these species across community gradients. We compared the relative influences of stand structure, age, competition and environmental stress on mixture effects using multi-model inference. We analysed growth of neighbouring tree species to infer whether a mixture effect in a single species translated to the stand-level.
3. We found support for a positive mixture effect in *P. menziesii*, although our results were equivocal in light of a weaker but still plausible alternative model. Growth of *P. menziesii* neighbouring species in mixed stands declined or held constant depending on aridity, suggesting that a positive mixture effect in *P. menziesii* does not necessarily extend to the stand level. We found no evidence for mixture effects in *P. ponderosa*, *A. concolor* or their neighbouring species.
4. Complementarity appears to have a limited influence on tree growth in the mixed-conifer systems of the U.S. Interior West, reflecting limited functional diversity. Historical changes in stand structure following fire exclusion, particularly high stand densities, may limit the potential for positive species mixture effects. The limited species pool of Interior West forests increases the risk that, without careful management, what functional diversity exists could be lost to compositional changes resulting from stand dynamics or disturbance.

KEYWORDS

environmental gradient, forest structure, individual-tree growth modelling, mixed-conifer forest, National Forest Inventory, species complementarity, species mixture, stress-gradient hypothesis

1 | INTRODUCTION

The relationship between biodiversity and productivity has long been a topic of ecological research (Tilman et al., 2014), but only recently has it gained attention in the context of forest management (Ammer, 2019). Growing evidence suggests that managing forests for tree species diversity may increase productivity (Ammer, 2019), while enhancing carbon sequestration and forest resilience to drought and other environmental fluctuations (Jucker, Bouriaud, Avacaritei, & Coomes, 2014; Ruiz-Benito et al., 2014). As predicted by ecological theory (Tilman et al., 2014), a positive relationship between forest productivity and diversity in mixed stands reflects complementary traits among species (Forrester & Pretzsch, 2015). This complementarity results in a 'positive mixture effect' in which growth of a given tree species is relatively higher in mixed stands than in a monoculture, potentially enhancing overall stand productivity (Forrester & Bauhus, 2016).

The mechanisms behind positive mixture effects are complex and system-specific but can be broadly categorized as facilitation (mutualism between species) or reduced competition (Forrester & Bauhus, 2016). For example, evergreen species may escape light competition from deciduous neighbours at the beginning and end of the growing season (Lu et al., 2018), while hydraulic lift of deep soil moisture by *Quercus* (oak) species may facilitate neighbouring species by reducing water stress (Pretzsch et al., 2013; Sousa-Silva et al., 2018). In addition to promoting overall stand productivity, competition reduction and facilitation in mixtures may translate into higher individual-tree vigour (Kane et al., 2014), which is of key importance to reducing tree mortality and enhancing carbon storage residency times (Körner, 2017).

Stand structure, stand age and site quality influence mixture effects (Forrester & Bauhus, 2016). Positive mixture effects increase with stand density as interactions between trees become more common (Forrester et al., 2013). The canopy stratification of tree species is also important, with stands composed of a shade-intolerant overstorey and shade-tolerant lower strata more likely to display positive mixture effects (Ishii & Asano, 2010). Positive mixture effects observed in younger stands may not persist as these stands age and shade-intolerant overstorey species decline in the process of forest succession (Cordonnier et al., 2018). In partial agreement with the stress-gradient hypothesis, which states that the relative importance of facilitation increases with environmental stress (Bertness & Callaway, 1994), positive mixture effects increased in harsh subalpine environments (Callaway, 1998) and on arid sites (Mina et al., 2018), although these effects were more subtle in drought-prone forests (Jactel et al., 2018; Madrigal-González et al., 2016).

While positive mixture effects have been identified in forests world-wide (Jactel et al., 2018), most research has focused on two-species interactions in managed systems with high functional diversity, where species complementarity is expected to be more pronounced (Forrester & Bauhus, 2016; Jactel et al., 2018; Pretzsch et al., 2019). Few studies to date have investigated mixture effects in the low functional diversity, fire-suppressed forests of the U.S. Interior West. In a stand-level study that examined high- versus low-quality western U.S. forest sites, Potter and Woodall (2014) found species richness and phylogenetic species clustering were positively associated with standing above-ground biomass on low-quality sites. Schuler and Smith (1988) postulated positive mixture effects in semi-arid *Pinus edulis-Juniperus* spp. (pinyon-juniper) woodlands based on stand density and leaf area. Callaway (1998) found that *Pinus albicaulis* (whitebark pine) facilitates individual-tree growth of large-diameter *Abies lasiocarpa* (subalpine fir) on harsh subalpine sites in Montana. In contrast, Long and Shaw (2010) found no diversity–productivity relationship in *Pinus ponderosa* (ponderosa pine), although their stand-level study did not investigate the nuanced patterns associated with environmental gradients (Bertness & Callaway, 1994).

With low functional diversity and disturbance regimes altered by fire suppression, Interior West mixed-conifer forests provide a unique opportunity to further extend this line of research to examine mixture effects on individual-tree productivity across landscape-scale compositional and environmental gradients (Eyre, 1980; Fulé et al., 2009; Windmuller-Campione & Long, 2016). Interior West mixed-conifer forests are dominated by phylogenetically close conifer species, including *P. ponderosa*, *Pseudotsuga menziesii* var. *glauca* (Rocky Mountain Douglas-fir) and *Abies concolor* var. *concolor* (white fir; Eyre, 1980). These species occur with occasional small populations of *Populus tremuloides* (quaking aspen), *Quercus gambelii* (Gambel oak) and other associated hardwoods in montane stands that represent a pure-to-mixed compositional gradient (Eyre, 1980), thus allowing the growth of the major species to be examined across the variety of mixtures in which they occur. The extended range of mixed-conifer forest combines with the mountainous topography of the Interior West to create a xeric to humid-subalpine environmental gradient (Windmuller-Campione & Long, 2016), ideal for testing the generality of plant community interactions (Keddy, 2001). Within these gradients, *P. ponderosa* is dominant at lower elevations and co-dominant with *P. menziesii* and *A. concolor* at mid-elevations (Eyre, 1980). Frequent fire regimes historically maintained *P. ponderosa* and *P. menziesii*, while limiting growth of *A. concolor* (Fulé et al., 2009). In recent decades, compositional shifts from fire exclusion have resulted in higher densities of deep-crowned shade-tolerant *A. concolor* (Fulé et al., 2009; Rodman et al., 2016), increasing drought-related tree mortality and fire risk (Fulé et al., 2009; Kane et al., 2014), but potentially enhancing subtle complementarity effects in these conifer-dominated systems.

We investigated the effects of interspecific relative density on the productivity of the three focal species, *P. ponderosa*, inland *P. menziesii*, and *A. concolor*, across compositional and environmental gradients in Interior West mixed-conifer forests. To accomplish this, we took advantage of a landscape-level forest inventory dataset to model individual-tree growth as a function of stand structure, forest community, and site quality to provide a flexible analysis framework. Our objectives were to examine (a) the extent to which stand structure, site quality, community composition and relative density

influence the growth of each focal species; (b) whether tree canopy position, competition, abiotic stress and stand age interact with relative density to influence productivity; and (c) whether a mixture effect observed in a focal tree species extends to neighbouring tree species, suggesting that species mixtures may influence total stand productivity. The overarching goal of our research was to provide a more complete scientific basis for efforts to manage Interior West mixed-conifer forests for long-term sustainability and carbon sequestration under an uncertain climate.

2 | MATERIALS AND METHODS

2.1 | Study data, area and plot selection

We used data collected by the USDA Forest Service Forest Inventory and Analysis Program, Interior West Region, which encompasses the U.S. mountain states of Arizona, Colorado, Idaho, Montana, Nevada and Utah (Figure 1). Although formally part of the region, we omitted New Mexico and Wyoming due to the unavailability of plot remeasurements required for tree growth estimates. Plots range in elevation from 490 m to 3,300 m above sea level, in latitude from 32.13°N to 48.99°N, and in longitude from 104.6°W to 119.9°W. For the 1971–2010 period, mean annual temperatures ranged from 0 to 14.3°C (PRISM Climate Group, 2019) and mean annual precipitation ranged from 271 mm to 1,863 mm/year. The climate is continental with topography strongly influencing both temperature and precipitation (Wise, 2012). Winter and spring precipitation form an increasing fraction of annual totals towards the west and north of the region, with mountainous areas tending to experience greater total precipitation (Wise, 2012). Topography further controls forest community composition by influencing water limitation (Copenhaver-Parry & Cannon, 2016).

We queried data from forested FIA plots (at least 10% forest cover; Bechtold & Patterson, 2005) lacking recent treatment or other major disturbance. To simplify interpretation, we excluded plots that were coded as split among multiple stands (via the joined FIA database 'COND' table, where the CONDPROP_UNADJ field = 1), thereby making FIA plot synonymous with stand (Woudenberg et al., 2010). We queried only methodologically consistent annual FIA program plots (Bechtold & Patterson, 2005), each of which consists of 4 × 0.016 ha subplots for assessing overstorey trees [>12.7 cm diameter at breast height (DBH)]. A single microplot within each subplot (0.0013 ha) assesses saplings (>2.54 cm DBH < 12.7 cm). Interior West annual plot measurements began in 2003, with individual sample plots targeted for remeasurement every 10 years (Goeking, 2015). To maintain a consistent interval for growth comparisons, we excluded plots with measurement intervals <8 and >12 years. We selected plots ranging from >0 to <100% of plot relative density for each of the three focal species: *P. ponderosa*, *P. menziesii* and *A. concolor*. Plots were non-exclusive (i.e. the same plot could be selected for more than one focal species). We quantified stand density in terms of stand density index (calculated via the summation method; Long & Daniel, 1990), which

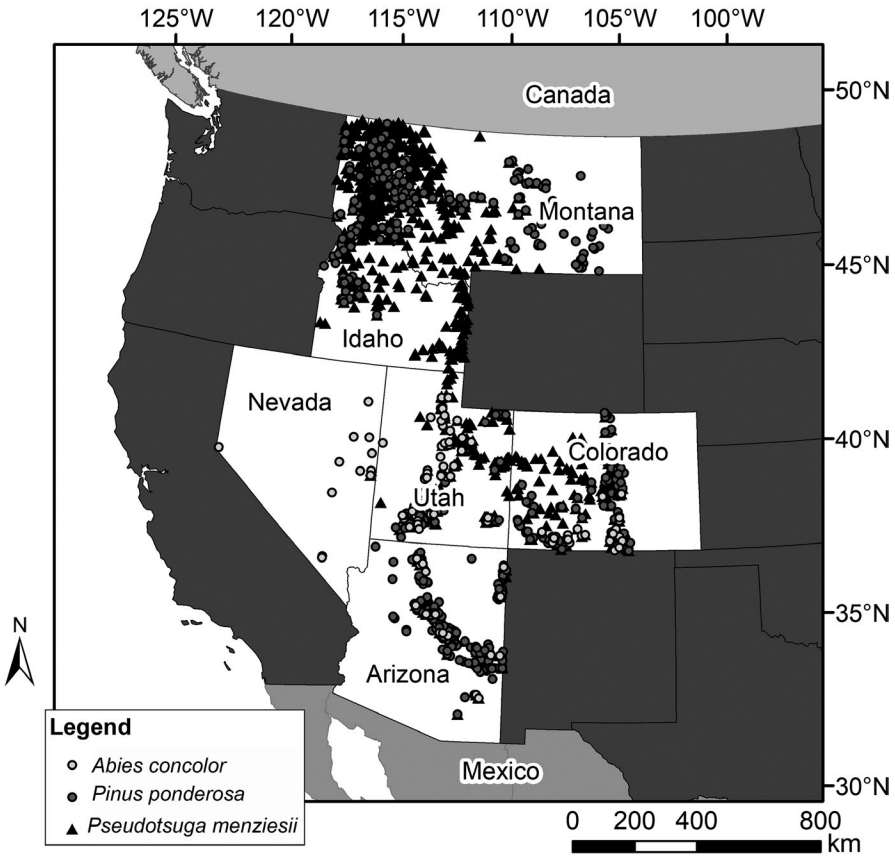

FIGURE 1 Map showing queried Forest Inventory and Analysis (FIA) *Pinus ponderosa*, *Pseudotsuga menziesii* and *Abies concolor* sample plots in six states of the Interior West, USA. Remeasurement data were available for all sample plots, which contained >0%–99% relative plot stand density index of the focal species and lacked major recent disturbance. Plots were not mutually exclusive by species

combines information about tree size and number to more accurately represent stocking compared to basal area or stems/ha. This metric of stand density applies the −3/2 power law between stem size and number to describe stand-level competition in terms of the number of 25 cm tree-equivalents per ha (Shaw & Long, 2010).

2.2 | Tree growth models

Mixture effects can be investigated by modelling either stand-level aggregate growth or individual-tree growth (Forrester & Pretzsch, 2015). Forest inventory data are representative of regional forest conditions and management practices, yet is commonly confounded by uncertain plot-level disturbance history (Pretzsch et al., 2019). Recent Interior West tree mortality, largely related to drought and insect attack (Goeking, 2015), also confounds stand-level estimates of aggregate growth (Bechtold & Patterson, 2005). To better control for diverse growing conditions, disturbance legacies and ongoing tree mortality across the FIA dataset, we opted to investigate mixture effects from an individual-tree perspective. To accomplish this, we used linear mixed modelling of individual-tree growth, which permits flexibly incorporating tree, neighbourhood and stand-level information (Table 1) while avoiding pseudoreplication (Bolker et al., 2009). We modelled the growth of each of the three focal species in support of objectives 1 and 2 and the growth of neighbouring trees in support of objective 3.

We performed growth modelling on a subset of trees and plots meeting minimum size thresholds (initial tree diameter ≥12.7 cm DBH) and possessing values for all requisite data fields. We excluded open-grown trees (crown class code = 1), as the relatively few trees in this crown class were assumed to have no neighbours with which to interact. Plots spanned the study area for *P. ponderosa* and *P. menziesii*, but *A. concolor* did not occur in Idaho or Montana (Figure 1). Growth model sample sizes were largest for *P. menziesii* (n = 6,125 trees/644 plots), followed by *P. ponderosa* (3,102 trees/318 plots) and *A. concolor* (587 trees/61 plots). Neighbouring-species model sample sizes were largest for *P. menziesii* (n = 9,509 trees/642 plots), followed by *P. ponderosa* (n = 3,507 trees/306 plots) and *A. concolor* (n = 1,137 trees/64 plots).

2.2.1 | Model response, structure and site quality variables

Because tree height and diameter growth may vary independently in species mixtures when these mixtures alter the forest light environment (Lu et al., 2016), we selected net annual sound volume increment as our response variable (Table 1). Net annual sound volume

TABLE 1 Variables used in volume increment modelling

ID	Variable	Category	Description	Level
1	growcfal	Response	Annual net sound cubic volume increment	Tree
2	plot id	Sample strata	Random effect, synonymous with stand	Stand
3	subplot	Sample strata	Random effect, nested overstorey subplot	Subplot
4	Dia	Stand structure	Initial DBH	Tree
5	cclcd	Stand structure	Initial tree crown class[b]	Tree
6	CI	Stand structure	Average squared size ratio[a]	Neighbourhood
7	stdage	Stand structure	Estimated stand establishment	Stand
8	corr. elev	Site quality	Plot elevation correcting for latitude	Stand
9	p/pet	Site quality	Total precipitation/potential evapotranspiration	Stand
10	siteclcd	Site quality	FIA site class code (1 = high, 7 = poor)	Stand
11	nms axis 1	Forest community	Ordination score based on live trees[a]	Stand
12	nms axis 2	Forest community	Ordination score based on live trees[a]	Stand
13	nms axis 3	Forest community	Ordination score based on live trees[a]	Stand
14	rel. density	Species mixture	Proportion of plot SDI by focal species[a]	Stand

Abbreviations: SDI, stand density index.

[a]Mean value calculated across remeasurement period.

[b]Ordinal variable treated as continuous.

increment (GROWCFAL in FIA database) is the annualized change in cubic volume of a given tree between consecutive inventories (calculated as $(V_2 - V_1)/(t_2 - t_1)$), which, as a net value, may be negative due to volume loss from mortality or live-tree damage, rot and other causes (Woudenberg et al., 2010).

To account for stand structural influences on individual-tree growth, we included tree initial diameter, crown class (i.e. canopy position; Schomaker et al., 2007), neighbourhood competition and stand age in our modelling (Table 1; Schomaker et al., 2007). Crown class is an ordinal indicator of tree social status ranging from open-grown (crown class = 1) to suppressed (crown class = 5). For neighbourhood competition, we used distance-independent indices that represented competition as a function of the size of competitors sharing the same 0.016 ha subplot relative to the focal tree (Larocque et al., 2012). We examined three competition indices for each species. CI-1 was Glover and Hool's (1979) index:

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

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 index:

$$\mathrm{CI}_i = \sum_{j=1}^{n} \frac{d_j}{d_i},$$

where CI_i is the competition index (CI) for the individual target tree (i); d_j is the diameter (d) of a given competitor (j) and d_i is the diameter of target tree (i). CI-3 consisted of a variant of Lorimer's index that squared the size ratio between competitor and focal tree (Looney et al., 2018):

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

where symbols are as per the equations above. These indices model competition as size-symmetric, size-asymmetric and highly size-asymmetric, respectively (Larocque et al., 2012). Preliminary analyses indicated that CI-3 had greatest support relative to the two alternative indices for all three focal species (ΔAICc > 6; Richards, 2008). Therefore, only CI-3 (hereafter referred to as CI) was used in subsequent modelling.

We selected a set of variables to serve as indicators of site quality, which can otherwise confound productivity–diversity relationships (Forrester & Bauhus, 2016). We avoided site index due to issues with interpretability in mixed-species stands, instead incorporating FIA site class code (1–7 scale; 1 = potential wood-volume production > 15.7 $m^3\ ha^{-1}\ year^{-1}$; 7 = potential wood-volume production < 1.3 $m^3\ ha^{-1}\ year^{-1}$) as a continuous fixed-effect indicator of site potential. We supplemented these site quality indicators with two indicators of environmental stress. We extracted 800-m resolution PRISM climate norms for the 1981–2010 period (PRISM Climate Group, 2019) for each fuzzed (~800 m) publicly available FIA plot location to calculate the ratio of annual precipitation to potential evapotranspiration (P/PET) as a site aridity index. Lower values of P/PET (e.g. <1) correspond with greater evapotranspiration demand relative to precipitation, indicating greater aridity. We calculated P/PET using the Thornthwaite method (Thornthwaite, 1948). Given elevational influences on tree growth (Coomes & Allen, 2007), we calculated latitude-corrected elevation for each sample plot (Windmuller-Campione & Long, 2016). See Table S1 for a summary of both predictor and response variables for each species group.

2.2.2 | Relative density and community gradient variables

We represented relative-density gradients in terms of relative live plot focal species (trees and saplings ≥2.54 cm DBH) stand density index (SDI). In addition to relative density, we characterized the tree/sapling community of each set of focal species plots through non-metric multi-dimensional scaling (NMS) ordination (Kruskal, 1964). We based the ordination on queried FIA plots that met our basic selection criteria. Plots were not mutually exclusive among focal species, with 510 plots for *P. ponderosa*, 882 for *P. menziesii* and 108 plots for *A. concolor*. The main goal of ordination was to produce NMS scores to represent variation in plot communities for growth modelling. We were also interested in examining compositional gradients in the event that modelling found important community effects on growth. We performed NMS ordination based on proportional live species SDI by plot totals, with Bray–Curtis distances. Preliminary NMS ordinations were run in Autopilot mode in PC-ORD v. 7.04 (McCune & Medford, 2016), using a stress improvement criterion of 5 for axis number determination and a Monte Carlo test of 250 iterations to verify axis significance. After verifying stability, dimensionality and significance, we reran ordinations with the suggested configuration based on 500 iterations with real data (McCune et al., 2002). To facilitate interpretation, we rotated NMS ordinations to orthogonal principle axes (Peck, 2010), and reflected axes so focal species consistently increased with each axis. We accounted for temporal variation in competition and composition (such as ingrowth and tree mortality) by calculating neighbourhood CI, relative density and NMS scores for each time period. We averaged these values for each plot to represent mean growing conditions over time.

2.3 | Statistical analysis

We used the Information-Theoretic approach to perform multimodel inference (Burnham & Anderson, 2002) with corrected Akaike's information criterion (Sugiura, 1978). This approach to model building and statistical inference considers each model to represent a distinct hypothesis (Burnham & Anderson, 2002).

The best approximating model therefore represents a broadly applicable hypothesis rather than necessarily maximizing fit with the current dataset (Burnham & Anderson, 2002). Due to the large number of potential fixed effects, we developed 14 distinct hypothesis models (Table 2) in place of stepwise selection or exhaustive model building. Random effects common to all models included the nested effects of subplots within FIA plots. We considered models that were within ΔAICc ≤ 6 of the best-approximating model to be plausible and thus warranting inclusion when making inferences (Richards, 2008). As further precautions against overfitting, we excluded models that failed to achieve lower AICc values than simpler nested alternatives (Richards, 2008). We excluded models that were within AICc = 2 of simpler nested models due to the strong possibility of overfitting (Burnham & Anderson, 2002).

TABLE 2 Hypothesis models with constituent indicator variables and associated research objectives

Hypothesis	Volume increment varies as a function of:	Research objectives
1	Stand structure (null model)	1, 3
2	Site quality	1, 3
3	Stand structure and site quality	1, 3
4	Stand structure, site quality, community	1, 3
5	Relative density*stand structure, site quality, community	2, 3
6	Relative density, stand structure, site quality	2, 3
7	Stand structure, site quality, community, relative density, rel. density × competition[a]	2, 3
8	Stand structure, site quality, community, relative density, rel. density × crown class (stratification)[a,b]	2, 3
9	Stand structure, site quality, community, relative density, rel. density × *P*/PET (aridity)[a]	2, 3
10	Stand structure, site quality, community, relative density, rel. density × stand age[b]	2, 3
11	Stand structure, site quality, relative density, rel. density × competition	2, 3
12	Stand structure, site quality, relative density, rel. density × crown class (stratification)	2, 3
13	Stand structure, site quality, relative density, rel. density × *P*/PET (moisture stress)	2, 3
14	Stand structure, site quality, relative density, rel. density × stand age	2, 3

Note: Stand structure includes the terms diameter, crown class, CI and stand age. Site quality includes the terms elevation, *P*/PET and site class. Community includes NMS axes 1, 2 and 3. See Table 1 for description of terms.

Hypotheses 1–4 are simpler alternative hypotheses that tree growth varies as a function of stand structure, alone and in combination with site quality and/or community indicators. Hypothesis 5 evaluates the main effect of focal species relative density on growth, in combination with stand structure, site quality and community, whereas Hypothesis 6 omits community. Hypothesis models 7–10 evaluate interactions between relative density and crown class (i.e. canopy position), relative density and CI, relative density and stand age or relative density and *P*/PET (i.e. water-stress from aridity), assuming substantial community gradient effects. Hypothesis models 11–14 are equivalent to models 7–10, except in assuming that associated forest community did not substantially influence growth.

[a]Hypothesis models excluded for *Pinus ponderosa* and *P. ponderosa* neighbours due to multicollinearity.

[b]Hypothesis models excluded for *Abies concolor* due to multicollinearity.

We built a series of nested models ranging from basic (growth as a function of stand structure and/or site quality terms) to complex (growth as a function of stand structure, site quality, community and relative density; Table 2). Following widely used individual-tree growth models (Crookston & Dixon, 2005), our null model considered tree growth to be solely a function of stand structure indicators, a second modelled growth as a function of site quality indicators and a third as a function of stand structure and site quality. We used this combined stand structure and site quality model as the basis for isolating mixture effects. Simple mixture effects models evaluated the main effect of relative density, with and without forest community terms. Interactive mixture effect models iteratively examined the interaction between relative density and crown class (i.e. canopy position), relative density and CI, relative density and stand age or relative density and *P*/PET. We did not build models that included multiple interaction terms or higher order interactions for the sake of interpretability and to avoid multicollinearity (variance inflation factors <10 for main effects; Quinn & Keough, 2003). Given the potentially confounding influences of stand structure and site quality on complementarity (Forrester & Bauhus, 2016), we did not evaluate the influence of relative density or community in isolation from stand structure and site quality.

We performed generalized linear mixed modelling in the GLMMTMB package (Magnusson et al., 2018) for R (R Core Team, 2018), using maximum likelihood estimation. We graphically confirmed model assumptions of linearity and confirmed the normality and homogeneity of residual variance using simulated residuals plots (Hartig, 2018). Tree volume increment showed a pronounced right-skew for all six species groups (three focal species/neighbouring tree pairs). Based on inspection of simulated residuals plots (Hartig, 2018), we chose log-gamma error distribution over log-normal or Gaussian alternatives (Lindsey, 1997). Log-gamma models have been previously applied to studies of Interior West conifer basal area increment with similar distributional properties (Contreras et al., 2011). We log-transformed CI, initial diameter, and *P*/PET to meet assumptions of linearity. We confined the analysis to trees with initial diameters ≥12.7 cm DBH that ranged from dominant to suppressed (crown class = 2–5). We fit models using maximum likelihood estimation. Given high correlations between some variables (see Table S2), we verified that variance inflation factors did not exceed 10 for model main effects (Quinn & Keough, 2003). Based on this criterion, we dropped *P. ponderosa* and

P. ponderosa neighbouring species models incorporating both community and relative density, and a single *P. menziesii* model (Table 2). We used the MuMIn package (Bartoń, 2017) to perform multi-model inference with AICc. To provide a more intuitive measure of model support, we used model weights to calculate the evidence ratio, which shows the likelihood of the best-approximating model being true compared to competing models (Burnham & Anderson, 2002). We back-transformed log-gamma model coefficients for ease of visualization.

For the three focal species, we define a positive mixture effect as a positive growth- interspecific relative density relationship, indicating that growth of a given species is higher in a mixture versus a monoculture. A negative mixture effect is defined as a negative growth-interspecific relative density relationship, indicating greater tree growth in a monoculture. For the three groups of neighbouring tree species, these definitions are the same except that neighbouring-species growth is regressed against focal-species relative density for consistent interpretation. In the context of log-gamma growth models with back-transformed coefficients, a positive mixture effect would have a relative density slope >1, while a negative mixture effect would have a slope value >1. We did not set effect size or significance criteria, instead deferring to model selection results.

3 | RESULTS

3.1 | Focal-species growth models

The best-approximating model of *P. ponderosa* volume increment included stand structure and site quality, while excluding the relative density term (Table 3). Under this model, *P. ponderosa* volume increment increased with initial tree diameter and *P*/PET (Figure 2). Growth declined with stand age, subordinate crown class (back-transformed slope ± *SE* vs. dominant trees: codominant = 1.02 ± 0.07, intermediate = 0.52 ± 0.10, suppressed = 0.16 ± 0.20), CI, elevation and site class. Other *P. ponderosa* models were implausible due either to low support or greater complexity relative to this simpler nested model (ΔAICc < 6; Richards, 2008).

The best-approximating model of *P. menziesii* volume increment included the effects of stand structure, site quality, community, and relative density (Table 3). *Pseudotsuga menziesii* volume increment increased with initial diameter and *P*/PET (Figure 2). *Pseudotsuga menziesii* volume increment decreased with subordinate crown class (back-transformed slope ± *SE* vs. dominant: codominant = 1.04 ± 0.05, intermediate = 0.71 ± 0.05, suppressed = 0.55 ± 0.07), CI, stand age, site class, elevation and NMS axis 1 (i.e. growth was higher on plots associated with more drought-tolerant species such as *P. ponderosa*, *Quercus gambellii* (Gambel oak) and *Juniperus* (juniper) spp.; see Figure S1 with Interpretation of Results in Supporting Information for the complete ordination results). Volume growth did not vary with NMS axes 2 or 3. *Pseudotsuga menziesii* volume growth increased with interspecific relative density (Figure 3). The second and third plausible models included only main effects, dropping the community (ΔAICc = 3.49) and relative density terms (ΔAICc = 4.08) respectively.

The best approximating model of *A. concolor* volume increment included the main effects of stand structure, site quality and community, while excluding relative density (Table 3). Growth increased with DBH, NMS axis 1, and NMS axis 3. Growth declined with CI, stand age, elevation and NMS axis 2. Growth did not substantially vary with crown class, stand age or site class.

TABLE 3 Plausible models based on corrected Akaike's information criterion (AICc) for *Pinus ponderosa* (PIPO), *Pseudotsuga menziesii* (PSME), *Abies concolor* (ABCO), and neighbouring tree species

		Model														
		Stand structure				Site quality			Community							
Species	Hypos	dia	cclcd	CI	stdage	elev	*P*/PET	site clcd	NMS axis 1	NMS axis 2	NMS axis 3	rd	rd × *P*/PET	logLik	ΔAICc	RelLik
PIPO	3	x	x	x	x	x	x	x						4,975.62	0.00	1.00
PSME	5	x	x	x	x	x	x	x	x	x	x	x		4,975.62	0.00	1.00
PSME	6	x	x	x	x	x	x	x				x		4,970.86	3.49	5.72
PSME	4	x	x	x	x	x	x	x	x	x	x			4,972.57	4.08	7.67
ABCO	4	x	x	x	x	x	x	x	x	x	x			567.13	0.00	1.00
PIPO nbr	4	x	x	x	x	x	x	x	x	x	x			3,377.93	0.00	1.00
PSME nbr	9	x	x	x	x	x	x	x	x	x	x	x	x	6,587.95	0.00	1.00
ABCO nbr	3	x	x	x	x	x	x	x						1,384.95	0.00	1.00

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

Abbreviations: Hypos, hypothesis; logLik, log likelihood; ΔAICc, difference compared to best-approximating model; RelLik, relative likelihood of the best-approximating model being true compared to competing models; diam, diameter at breast height; cclcd, crown class; CI, competition index; stdage, stand age; elev, plot elevation corrected for latitude; *P*/PET, total precipitation/potential evapotranspiration (proxy for aridity); site clcd, site quality; rd, relative density; rd × *P*/PET, relative density × aridity; nbr, neighbours.

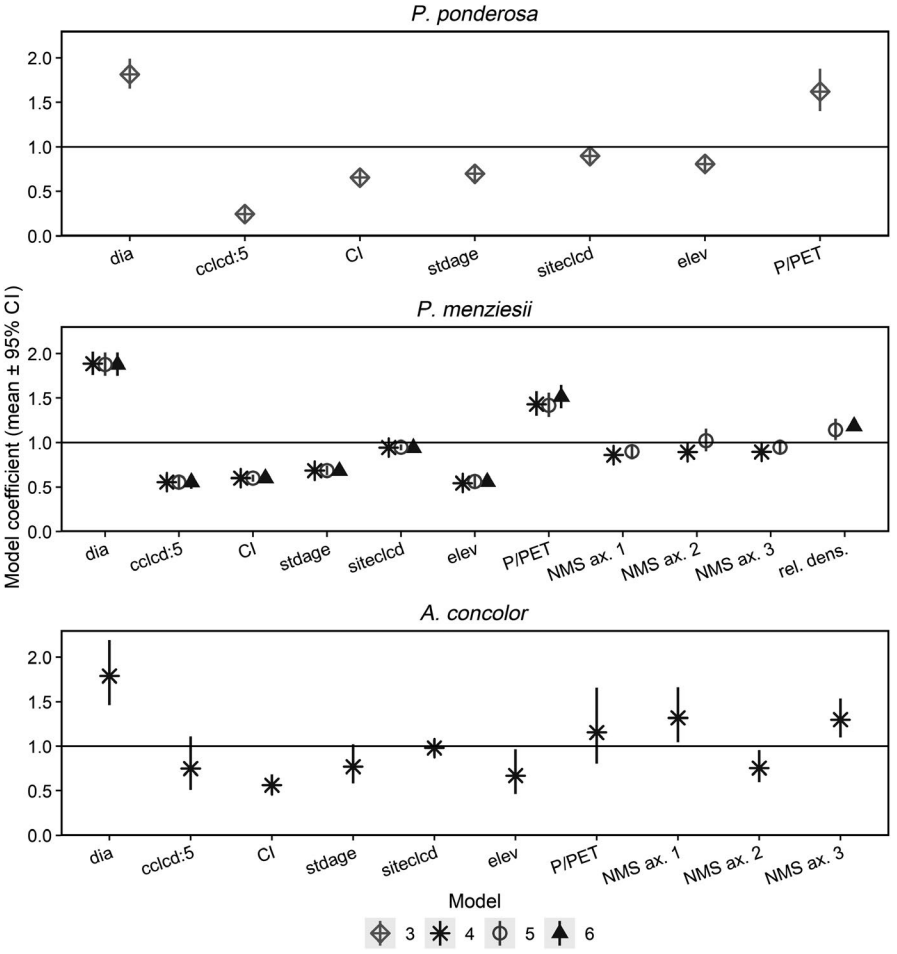

FIGURE 2 Interaction plots of marginal effects of relative stand density index (SDI; *Z*-scores) on individual-tree, sound cubic volume increment (*y*-axis, m^3/year). Species mixture effects are plotted based on best approximating model results for *Pinus ponderosa* (PIPO), *Pseudotsuga menziesii* (PSME) and *Abies concolor* (ABCO), as well as for *P. menziesii* neighbouring tree species. Predictor variables are displayed as *Z*-scores unless specified. Crown class represents categorical crown position (2–5–dominant-to-suppressed–scale), CI is competition index, and *P*/PET is the ratio of precipitation to potential evapotranspiration

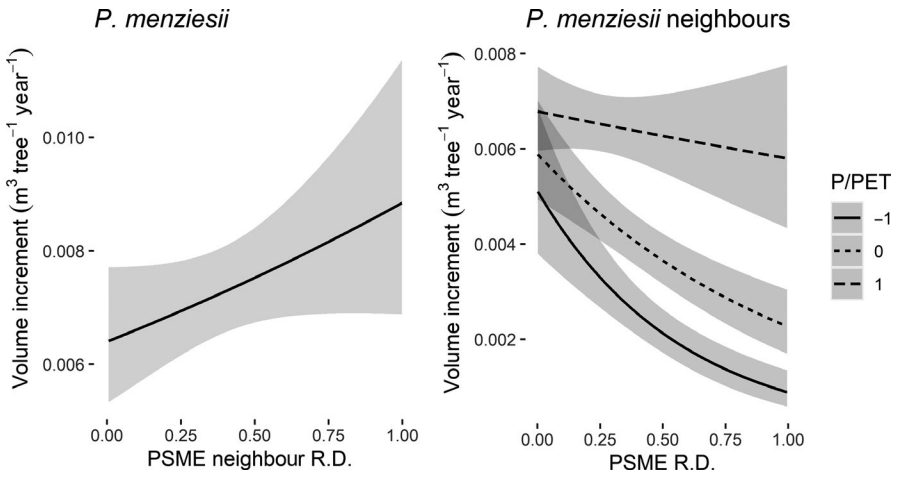

FIGURE 3 Interaction plots of marginal effects of relative stand density index (SDI; *Z*-scores) on individual-tree, sound cubic volume increment (*y*-axis, m^3/year) based on best-approximating model results for *Pseudotsuga menziesii* (PSME) and *P. menziesii* neighbouring tree species. Predictor variables are displayed as *Z*-scores

3.2 | Neighbouring-tree growth models

We found a single plausible model of *P. ponderosa* neighbouring-tree volume increment (Table 3), which included the stand structure, site quality and community terms. Volume increment increased with initial diameter, *P*/PET and NMS axis 2 (higher growth on plots with lower densities of xeric *Pinus edulis* (pinyon pine), *Quercus arizonica* (Arizona white oak), and/or *J. osteosperma*; Figure 4). Growth decreased with stand age, CI, crown class (back-transformed slope ± *SE* vs. dominant: codominant = 1.02 ± 0.07, intermediate = 0.70 ± 0.08, suppressed = 0.61 ± 0.11) and NMS axis 1. Growth did not substantially vary with NMS axis 3. The single plausible model of *P. menziesii* neighbouring-tree volume increment included stand structure, site quality, community, relative density, and a relative density × *P*/PET Interaction (Table 3; Figure 4). Growth of *P. menziesii* neighbours increased with initial diameter, *P*/PET and NMS axis 2 (i.e. higher growth on plots associated with *J. osteosperma and P. edulis*, as well as *A. concolor*; Figure 4). Growth decreased with crown class, CI, stand age, site class, elevation,

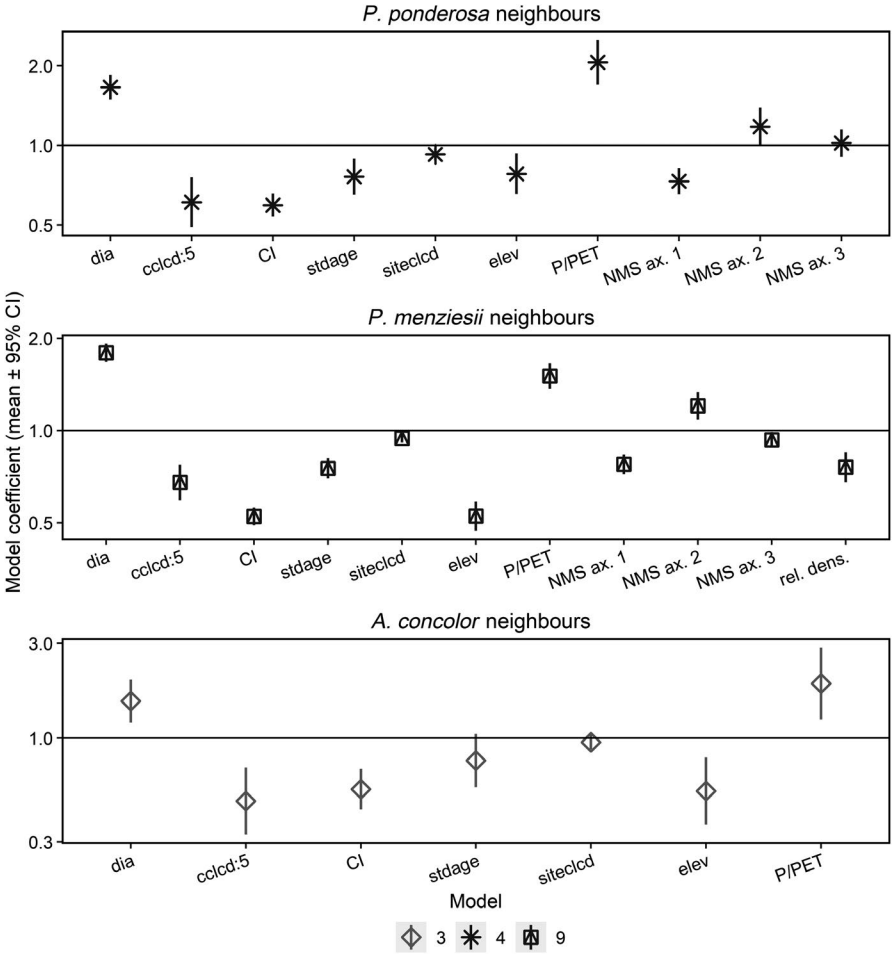

FIGURE 4 Model coefficients for the best-approximating log-gamma mixed model of individual tree, sound cubic volume increment for neighbouring tree species of *Pinus ponderosa* (PIPO), *Pseudotsuga menziesii* (PSME) and *Abies concolor* (ABCO). Predictor variables (*x*-axis) are displayed as *Z*-scores, with the exception of the categorical crown class code for which the contrast of suppressed (cclcd:5) versus dominant (cclcd:2) is shown. The *y*-axis depicts means ±95% confidence intervals of predictor effects on volume increment (m^3/year). These coefficients are back-transformed from the log scale. Relative density (rel. dens). = interspecific (nonfocal species) relative density. See Table 1 for model term abbreviations and descriptions. See Figure S1 for a description of NMS axes 1, 2 and 3

NMS axis 1 (higher growth on plots with greater *P. tremuloides* density) and NMS axis 3 (higher growth on plots with greater *Q. gambelii* and *A. grandidentatum density*) and relative density. Neighbouring-tree growth declined more steeply under increasing *P. menziesii* relative density on arid sites than on moist sites (Figure 3).

The best-approximating model of *A. concolor* neighbouring-tree volume increment included the main effects of stand structure and site quality (Table 3). Growth of *A. concolor* neighbours increased with DBH and *P*/PET (Figure 4). Growth declined with crown class, CI and elevation, while remaining neutral with changing stand age and site class. The model indicated that *A. concolor* relative density did not influence neighbouring species growth.

4 | DISCUSSION

Our study took advantage of a regional dataset encompassing a broad range of stand structure, site quality and species composition. Using this dataset, we were able not only to investigate mixture effects in common Interior West forest species, but to test multiple hypotheses (Table 2) that may explain these effects. We found that, as a main effect, relative density had a plausible influence only on the growth of *P. menziesii* and neighbouring species. Furthermore, we found that whether growth of *P. menziesii* neighbouring species declined or held constant depended on site aridity. In the discussion below, we consider the implications of this evidence for and against mixture effects in Interior West mixed conifer forests. We divide the discussion into two parts: The first examines the influence of more fundamental site quality, stand structure and community gradient indicators on species' growth, while the second focuses on the growth implications of mixture effects as indicated by relative density.

4.1 | Focal-species growth models

4.1.1 | Stand structure, site quality and focal-species growth

Our results indicated that stand structure terms (tree diameter, crown class, CI and stand age) had a strong positive influence on the volume growth of *P. ponderosa*, *P. menziesii* and *A. concolor*. Tree diameter was a strong predictor of growth for all three species, as in previous studies of regional mixed-conifer species (Buechling et al., 2017; Contreras et al., 2011). Crown class had a substantial influence on the growth of shade-intolerant *P. ponderosa* and intermediate shade-tolerant *P. menziesii*, but not shade-tolerant *A. concolor*. In partial disagreement with previous findings that intermediate *P. menziesii* and similar species are less responsive to competition

than *P. ponderosa* (Buechling et al., 2017; Contreras et al., 2011; Copenhaver-Parry & Cannon, 2016), CI reduced growth in all three species. Tree growth declined with stand age, paralleling common age-related declines in stand growth (Smith & Long, 2001).

Two site quality terms, *P*/PET and elevation, had a similarly strong influence on focal-species growth. In contrast, site class was only a weak predictor of growth, suggesting that the strong *P*/PET and elevation effects may have captured the most important influences on site quality with the exception of soil characteristics, which were beyond the study's scope. Higher values of *P*/PET, indicating lower aridity, were associated with higher *P. menziesii* and *P. ponderosa* growth. In contrast, Buechling et al. (2017), who examined interannual variation in growth within locations rather than mean tree growth across the landscape, found that high precipitation can limit the growth of *P. menziesii*, but not *P. ponderosa*, on Interior West sites. Previous research found the response of mixture effects to interannual climatic fluctuations varies by study system, with climatic fluctuations enhancing positive mixture effects in *Quercus* spp.–*Fagus sylvatica* forests (del Río et al., 2014), while lessening the strength of these effects in Iberian *Pinus*–*Quercus* spp. forests (Jucker, Bouriaud, Avacaritei, Dănilă, et al., 2014). Consistent with previous research (Coomes & Allen, 2007), growth of all three species declined with increased elevation, which is associated with lower temperatures (Copenhaver-Parry & Cannon, 2016), greater wind stress and reduced nutrient cycling (Coomes & Allen, 2007).

4.1.2 | Relative density: Implications for productivity

In agreement with Long and Shaw (2010), the best approximating model for *P. ponderosa* excluded relative density, while including basic stand structure and site quality terms. Lack of a main effect or interactions with relative density suggests this non-result was not driven by factors such as stand age, site moisture, competition or aridity. One possibility is that any positive influence of species mixtures on *P. ponderosa* growth was counteracted by soil nutrient effects, which we did not model. Late-seral *P. ponderosa* associated species, such as *P. menziesii*, have been hypothesized to adversely impact soil nutrient availability through lower litter quality and slower decomposition rates (DeLuca & Sala, 2006). The shade-intolerance and excurrent crown architecture of *P. ponderosa* may also antagonize light partitioning with associated tree species (Ishii & Asano, 2010; Lu et al., 2018).

Our analysis yielded a diverse set of plausible growth models for *P. menziesii*, providing moderate support for a positive mixture effect on growth of this species. In agreement with previous research in mixed-species forests in the Netherlands (Lu et al., 2018), both the best-approximating model and a simpler alternative that dropped community terms yielded evidence of a positive mixture effect. The magnitude of this effect in these two models was 14% and 18%, respectively, with a 1 standard deviation change in interspecific relative density. Compared to the other species examined, *P. menziesi*linear had the largest sample size of plots and trees, and greater statistical power may have made species mixture effects evident. Previous research also suggests that *P. menziesii* has broader ecological amplitude, well-represented across a broader range of communities and site conditions compared to the other focal species in this study (Windmuller-Campione & Long, 2016). A third model omitted relative density entirely, suggesting that evidence for this mixture effect should be considered equivocal compared to predictors like stand structure. Species-mixture effects are often more pronounced in conifer-hardwood mixtures, where functional diversity in light use may promote high stand-level efficiency (Ishii & Asano, 2010; Lu et al., 2018). The relatively low diversity of the conifer-dominated forests of the Interior West may support only limited niche separation between species, lessening opportunities for complementary resource use.

The best-approximating model for *A. concolor* growth included the stand structure, site quality and community terms, but excluded relative density. The omission of relative density was unanticipated given *A. concolor's* high shade tolerance and conical crown shape, which theoretically should allow for more efficient light partitioning and use of growing space in mixed stands (Forrester & Bauhus, 2016; Ishii & Asano, 2010). *Abies concolor* tends to regenerate around historical fire refugia and moist microsites and, therefore, more commonly occurs in single-species groups than *P. ponderosa* or *P. menziesii*, (Rodman et al., 2016), potentially limiting its interspecific interactions. The inclusion of the community terms suggests that compositional gradients may more meaningfully represent the effects of variation in tree neighbourhoods on *A. concolor* growth than relative density. The NMS ordination results indicated that *P. tremuloides* and *Q. gambelii*, deciduous tree species that occur in occasional small populations in our study region, contribute to mixture effects by enhancing functional diversity through both light and soil resource use (Guo et al., 2018; St. Clair et al., 2013). Due to large sample sizes, future studies using FIA data might investigate pairs of species, particularly *P. menziesii*. Relative density can be a strong predictor of conifer mortality (Das et al., 2007), but specific species groups with strongly contrasting traits (e.g. Mina et al., 2018) or an index of functional dissimilarity (e.g. Madrigal-González et al., 2016) may serve as more meaningful summaries of species mixtures.

Species mixture effects showed no evidence of mediation by stand age. Cordonnier et al. (2018) observed that shade-intolerant overstorey species, often major contributors to functional diversity, are commonly ephemeral components of mixed-species stands, potentially limiting the longevity of overyielding in forests. Because our analysis approach controlled for community variation, stand age represented autogenetic changes in tree and stand characteristics rather than forest succession. Species mixture effects could potentially impact other components of forest change, such as mortality and recruitment (Liang et al., 2007), but high stand densities in fire-excluded mixed-conifer forests commonly restrict recent tree regeneration (Korb et al., 2012; Rodman et al., 2016).

The high stand densities and historical compositional shifts following fire exclusion in Interior West forests may also account for the lack of interactions between relative density and crown class or competition. The unresponsiveness of species mixture effects to

canopy position may reflect the fact that older ponderosa pine are commonly limited to the upper canopy, while mid-tolerant *P. menziesii* and shade-tolerant *A. concolor* increasingly dominate lower canopy layers (Rodman et al., 2016; Sakulich & Taylor, 2007). Species may therefore be fairly restricted in canopy position within Interior West mixed conifer stands. High competition can also negate positive species mixture effects (Mina et al., 2018), and the prevalence of dense stands in our study may have obscured any mixture effects on rarer, low-density plots.

Our results indicated that aridity did not influence mixture effects, in contrast with a study of Swiss forests, which found mixture effects were often strongly contingent on climate (Mina et al., 2018). Although positive mixture effects are commonly stronger under wetter conditions based on global datasets (Jactel et al., 2018), they may become neutral or antagonistic under drought (Jucker, Bouriaud, Avacaritei, Dănilă, et al., 2014). Long-lasting severe droughts that impacted Interior West forests in recent decades (Anderegg et al., 2015) may have negated any positive interactions prior to the sampling window.

4.2 | Neighbouring-tree responses to focal species relative density

We examined whether overyielding effects extended to neighbouring tree species. As with focal species, neighbouring tree species' growth generally increased with tree diameter and declined with crown class, CI, stand age, aridity and site class. Community composition had a substantial influence on growth, with slower growth of neighbouring tree species on plots with higher abundance of small-statured species.

We found that *P. ponderosa* relative density did not influence the growth of neighbouring tree species. The lack of a substantial main effect for relative density on tree-level growth in *P. ponderosa* communities is consistent with the stand-level findings of Long and Shaw (2010). In contrast, higher relative density of *P. menziesii* was associated with a negative mixture effect in neighbouring species. This finding is similar to that of an experimental study, which found *Tsuga heterophylla* (Raf.) Sarg. growth declines in mixtures with *P. menziesii*, limiting the potential for stand-level overyielding (Amoroso & Turnblom, 2006). Underyielding in *P. menziesii* neighbouring species was more severe in species mixtures on arid plots, as indicated by a site moisture × relative density interaction. This interaction is consistent with previous studies that found complementarity often declines with aridity (Holmgren & Scheffer, 2010; Jactel et al., 2018). On arid sites, higher leaf areas often associated with species mixtures could offset facilitation through greater canopy interception of rainfall while also increasing soil moisture demand (Holmgren & Scheffer, 2010). *Abies concolor* relative density had no effect on neighbouring-species growth, which again may reflect the tendency of *A. concolor* to occur in single-species groups (Rodman et al., 2016).

Although we found evidence for a positive mixture effect in *P. menziesii*, evidence was stronger for a negative mixture effect in *P. menziesii* neighbouring species. Our results suggest that the positive interactions among tree species commonly observed worldwide (Jactel et al., 2018; Pretzsch et al., 2019) may not necessarily translate to systems with low functional diversity. Fire regime disruption might have further reduced the potential for positive mixture effects due to increases in stand density homogenizing forest structure (Heinlein et al., 2005).

4.3 | Management implications

Our findings have implications for managing Interior West mixed-conifer forests under an uncertain climate. Management prescriptions for mixed-conifer systems presently advocate for enhancing structural diversity while reducing fire-intolerant conifer species, especially *A. concolor* (Nagel et al., 2017), the density of which has increased markedly following fire regime disruption (Korb et al., 2012). Careful monitoring of thinning treatments may establish whether mixtures of these species impact growth under lower stand densities. Without careful management, the limited species pool of Interior West forests increases the risk that what functional diversity is present could be lost to compositional changes resulting from stand dynamics or disturbance (Messier et al., 2019). A more ecologically comprehensive, functional approach to adaptive management could ultimately be more effective in fostering resilience in Interior West mixed-conifer systems under climate change.

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AUTHORS' CONTRIBUTIONS

C.E.L. conceived the research idea, which W.J.P. 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. and L.M.N., wrote 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/10.1111/1365-2745.13523.

DATA AVAILABILITY STATEMENT

Data are publicly available online via the United States Forest Service Forest Inventory and Analysis Data Mart https://apps.fs.usda.gov/fia/datamart/. The SQL query and R script used to query and prepare these data are available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.0vt4b8gx2 (Looney, Nagel, & Previant, 2020).

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SUPPORTING INFORMATION

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

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