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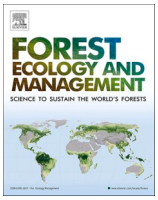

Structural-complexity effects on forest demographics and self-thinning in ponderosa pine and Douglas-fir on U.S. public lands

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ABSTRACT

Western U.S. public forest managers are applying structurally complex treatments not only to restore established mature stands, but to juvenile and reforested stands through practices such as cluster planting. Although studies suggest that structural complexity may negatively impact productivity and ecosystem services throughout stand development, findings are inconsistent. The inconsistencies may reflect a) the structural complexity attributes investigated, b) focusing on tree growth without recruitment or mortality, and/or c) unidentified site quality and stand factors that modulate structural complexity-productivity effects. We used forest inventory data to investigate how structural complexity influences productivity in western U.S. ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii)* forest types. To evaluate the responses of survivor-tree growth, recruitment, mortality, and the size-density relationship to diameter-distribution complexity (tree-size variation) vs. horizontal-structural complexity (patchiness in stocking) across gradients of stand density, mean tree size, and site quality we used multi-model inference with generalized linear models. For both forest types, structural complexity reduced survivor basal area increment on high-quality sites, with the effect decreasing as site quality declined. Structural complexity interacted with mean stand diameter to increase recruitment rates in small-diameter stands while reducing recruitment in large-diameter stands. Diameter-distribution complexity exacerbated mortality in small-diameter Douglas-fir stands while reducing mortality in large-diameter stands. Higher horizontal structural complexity lowered maximum stocking. Our findings suggest that site quality and stand structure influence structural-complexity effects and that positive complexity effects on recruitment could counter survivor growth losses. These findings have implications for management of western U.S. and potentially other forest types.

1. Introduction

In western U.S. coniferous forest types adapted to low-mixed severity fire, the challenges posed by rising abiotic stress and disturbance (Malmsheimer et al., 2009; Spies et al., 2010) are compounded by stand densification resulting from historical fire exclusion (Agee, 2003; Fulé et al., 2009; Safford and Stevens, 2017). On public lands, a silvicultural innovation for restoring these forests has been the adoption of structurally heterogeneous treatments, such as variable density thinning (Knapp et al., 2017), modified group selection management (Ritchie, 2020; York et al., 2021), and individual, clump, and openings prescriptions (Churchill et al., 2013). These treatments draw upon historical reconstructions of mature forest structure (Knapp et al., 2017; Stephens and Gill, 2005), apex predator habitat (Long and Smith, 2000), and natural disturbance regimes (Franklin et al., 2007) to promote disturbance resistance and resilience by breaking up surface and canopy fuels while providing age class diversity (Churchill et al., 2013; Knapp et al., 2012). Even where fire risk reduction is not an overriding concern, such as portions of the coastal Douglas-fir region, these structurally complex treatments can protect biological legacies, enhance wildlife habitat, and improve public acceptance (Franklin et al., 2007). A key aspect of these treatments is the manipulation of stand structure, or the vertical and horizontal distribution of components within a forest stand (Helms, 1998).

While the primary application of structurally complex treatments has been in the restoration of mature stands (but see Davis et al., 2007; O'Hara et al., 2010), there is increasing interest in adding complexity to stand structure during reforestation (North et al., 2019; Stephens et al.,

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2010). As western U.S. forest managers face not a reforestation backlog from increased acreage burned (Dobrowski et al., 2024; Williams et al., 2023) coupled with growing risk of young reforested stand reburns (Levine et al., 2022; Lyons-Tinsley and Peterson, 2012), alternative cluster planting arrangements that mimic historical mature stand structures have been proposed (North et al., 2019; Stephens et al., 2010). In contrast to traditional reforestation line planting to efficiently reestablish stands while promoting uniform tree spacing, cluster planting reforestation operations plant at locally higher densities to take advantage of microsite conditions (North et al., 2019) or train high-value crop trees (Saha et al., 2012). Spatially heterogeneous plantings may improve reburn resistance by breaking fuel continuity, while microsite selection may increase planting success (North et al., 2019). However, these planting arrangements may also potentially reduce productivity (Looney and Zhang, 2022), and thus the recovery of wood products production, carbon storage, and other ecosystem services (Zhang et al., 2008).

Studies examining the linkage between structural complexity, defined here as the number and relative abundance of different structural attributes (McElhinny et al., 2005), and productivity, defined as the rate at which biomass is produced per unit area (Helms, 1998), have yielded mixed results. In younger plantation settings, higher structural complexity, commonly quantified in terms of the tree size inequality attribute, reduces tree and stand growth (Cordonnier and Kunstler, 2015; Looney and Zhang, 2022; Luu et al., 2013; Soares et al., 2016). Comparisons of cluster vs. evenly spaced plantations are rare, although Allen et al. (2025) found evidence of more rapid growth in evenly spaced stands following precommercial thinning. Research indicates that clustered trees can maintain growth through adjustments to crown geometry (Stiell, 1982), although information is lacking on the relative ability of individual tree species to adjust crown architecture when growing in clusters. In contrast, a study of California mixed-conifer natural regeneration under a restored fire regime found higher tree growth in clusters compared to isolated trees (Fertel et al., 2022). In temperate European forests, the influences of structural complexity, quantified in terms of the inequality of tree size, on productivity shift from negative to positive as stand density increases during stand development (Zeller and Pretzsch, 2019). A study of Norway spruce (*Picea abies* L.) suggested that structural complexity, quantified in terms of variation in stem sizes, may promote complementary resource use in monocultures that is analogous, and of potentially equal strength, to species mixture effects (Pretzsch et al., 2024).

Prior studies have commonly examined structural complexity in terms of the variation or inequality in tree size distributions (e.g., Cordonnier and Kunstler, 2015; Zeller and Pretzsch, 2019). However, horizontal structural complexity, defined as within-stand variation in tree density, is arguably of equal relevance to the ecology of fire-dependent, western conifer forests (Stephens and Gill, 2005) and prescriptions to restore them following historical fire exclusion (Churchill et al., 2013; North et al., 2019). In addition, the majority of research to date has focused on tree growth, which may miss important, alternative pathways through which structural complexity can influence productivity (for an exception, see Liang et al., 2007). For example, in stands not subject to removals, net stand-level change is a complex function involving survivor-tree growth, recruitment, and mortality (Bechtold and Patterson, 2005), with these demographic processes mediating site-quality or abiotic-stress effects on the strength and direction of net stand biomass change (Astigarraga et al., 2020; Bell et al., 2014; Dupont-Leduc et al., 2024). While previous studies have commonly examined the influence of tree size diversity (or diameter-distribution complexity) on forest demographic processes (Astigarraga et al., 2020; Liang et al., 2007; Pretzsch et al., 2024), the comparative influence of horizontal complexity again has not been explored.

To help extend the understanding of how structural complexity influences productivity, as well as factors that may modulate its influence, we selected two common, western U.S. forest types, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Previous studies of structural complexity in ponderosa pine, quantified in terms of the number of age cohorts per stand, found evidence of marginally higher gross volume increment in multi-aged vs. even-aged stands (O'Hara and Nagel, 2006). However, when quantified in terms of diameter-distribution complexity, a subsequent study found no evidence of a structural-complexity effect on ponderosa pine net basal area increment (Long and Shaw, 2010). Meanwhile, a study of diameter-distribution complexity on Douglas-fir net growth and demographic processes found that survivor growth did not vary with respect to structural complexity, while a decline in recruitment amid a mild peak in mortality at intermediately complex stands contributed to a decline in net growth (Liang et al., 2007). Whether horizontal structural complexity has similar influences on forest demographic processes in these forest types and whether factors such as site quality modulate these effects is unknown.

We used U.S. Forest Inventory and Analysis data to investigate how diameter distribution and horizontal complexity affect 1) survivor growth, 2) sapling recruitment, 3) mortality, and 4) the size-density relationship (Reineke, 1933) in each of the two forest types. Our goal was to inform managers of potential tradeoffs when introducing structural complexity in contexts ranging from mature stand restoration to reforestation and across gradients of stand density, mean tree size, and site quality. Because elevated density-dependent mortality is commonly predicted using density management diagrams and relative density (Ray et al., 2023; Swann et al., 2025), we examined the allometric size-density relationship in addition to the dynamic components of forest change.

2. Methods

2.1. Datasets and study area

We queried U.S. Forest Service Forest Inventory and Analysis (FIA) data from the western continental U.S. Queried states ranged from South Dakota and New Mexico to the east to the Pacific Coast in the west (Fig. 1). This dataset provides an unbiased assessment of forested conditions across both public and private lands, with a nominal density of approximately 1 plot per 2430 ha (Bechtold and Patterson, 2005). Compared to long-term growth and yield plots which are commonly established to minimize the within-plot variation of prime interest to this study (Pretzsch, 2009), FIA data offers an extensive sample of variable forest conditions at the cost of weaker inferences regarding stand origin, disturbance, total yield, and treatment history. We consider these limitations further at the end of the Discussion.

Plot installation began in these states in 2001 (Brodie and Palmer, 2020). Plots are organized into panels for remeasurement with most plots in the western U.S. receiving a single remeasurement approximately 10 years after installation. Trees and saplings on each plot are assessed within 4 nested, circular subplots. Plots are not repositioned based on stand boundaries, and plots may straddle non-forest or multiple forested "conditions," or stands. Four 0.0013 ha microplots monitor saplings $> 2.54 <$ 12.7 cm diameter at breast height (DBH). Four 0.016 ha subplots monitor trees $\geq$ 12.7 cm DBH on 4 $\times$ 0.016 ha subplots. In California, Oregon, and Washington, four 0.101 ha macroplots monitor large trees $>$ 60.1 cm DBH (California, and eastern Oregon and Washington) or $>$ 76.2 cm DBH (western Oregon and Washington). Characteristics including terrain, stand age, site quality, treatment history, and recent disturbance are assessed at the stand level. Trees and saplings are assessed for species, DBH, height, growth, cull, damaging agents, ingrowth, and mortality.

We queried tree, plot, and stand data with the FIESTA package (Frescino et al., 2023) for R (R Core Team, 2022) using data from the most recent measurement. We also included growth, removals, and mortality tables to reconstruct initial conditions at the beginning of the

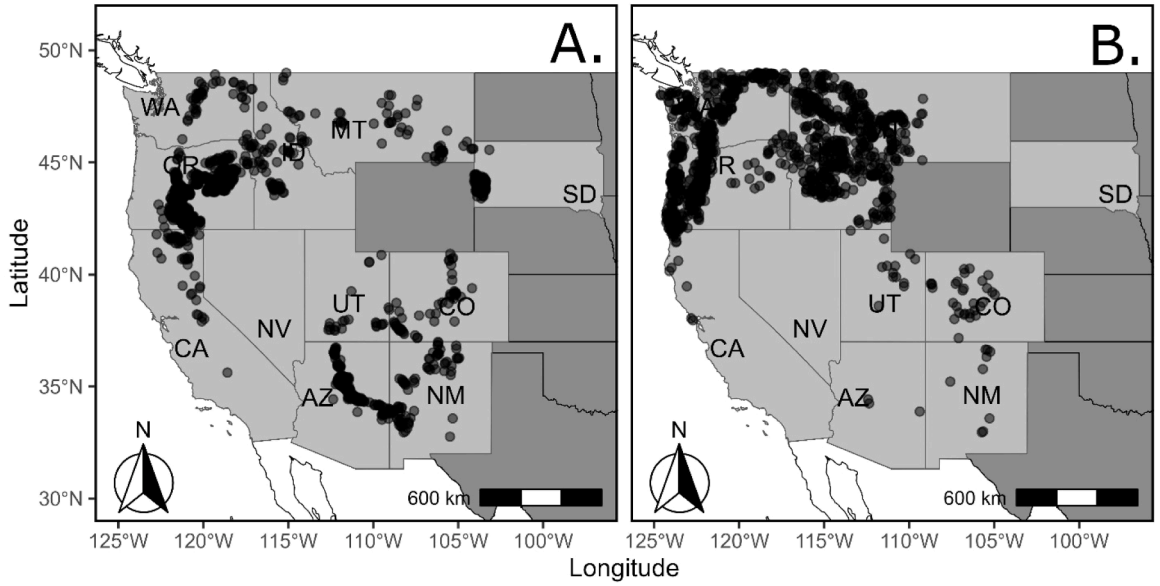

Fig. 1. Map of selected Forest Inventory and Analysis public plot coordinates for A) ponderosa pine and B) Douglas-fir. Abbreviations are provided for U.S. states intersecting selected plots.

observation period. Only plots with at least two visits were included to be able to calculate change over time. We selected only plots where the entire area overlapped a single stand, or FIA "condition", to examine within-stand variation in stand density as an attribute of structural complexity. We selected pure (>80% by relative stand density index) stands of ponderosa pine and Douglas-fir, two regionally important coniferous forest types. Selected stands had at least some established sapling trees as of the first plot visit to be able to calculate initial stand structure. We opted to focus on pure stands to avoid the potentially confounding influences of species mixtures on structural complexity (Pretzsch et al., 2024). We selected stands with no recent treatment history. We omitted plots on private lands, where the more widespread use of even-aged management and intensive forest management practices could potentially confound productivity-complexity relationships. We dropped stands with fewer than 60 trees ha^{-1} and 4 monitored stems to further avoid extreme per-area estimates. Stands were < 150 years of age to focus on juvenile-mature stands. For ponderosa pine, mean stand age was 87.0 ± 29.9 yr (mean ± S.D), while for Douglas fir mean stand age was 85.7 ± 37.1. We dropped stands falling on private lands to avoid the potentially confounding influences of intensive practices such as fertilization. Our filtered dataset consisted of 1178 ponderosa pine plots and 1365 Douglas-fir plots (Table 1, Fig. S1).

The climate of the selected plots encompasses Mediterranean, marine, temperate desert, and temperate steppe ecoregional divisions To facilitate comparison between the climate of our study systems and similar forests, we joined FIA public plot locations and elevations with the ClimateNA dataset of locally downscaled, gridded climate data (Wang et al., 2016). Mean annual temperature was 7.4 ± 1.5 °C in ponderosa pine compared to 7.2 ± 2.7 °C in Douglas-fir locations. The temperature regime was more strongly continental for ponderosa pine, with a mean January-July temperature differential of 20.5 °C ± 2.0 S.D. of mean, compared to 18.8 ± 3.8 °C for Douglas-fir. Mean annual precipitation was lower in ponderosa pine (572 ± 164 mm yr^{-1}) than in Douglas-fir locations (1350 ± 849 mm yr^{-1}), with a higher proportion of precipitation falling in the May-September range for ponderosa pine (0.33 ± 0.16 vs. 0.25 ± 0.13).

2.2. Response and predictor variables

Our modeling investigated survivor-tree growth, recruitment, mortality, as well as the allometric size-density relationship (Reineke, 1933). We modeled each of these responses individually by forest type. Growth, recruitment, and mortality were expressed in terms of basal area, which relies on more accurate diameter measurements than diameter and height-based volume (Forest Service, 2024) and thus is less subject to measurement error. For growth, we calculated the basal area increment (BAI) of survivors, or trees and saplings initially present at the first measurement, and surviving until the second measurement (Burrill et al., 2024). For recruitment, we calculated the BAI of ingrowth saplings, or saplings not present at the first measurement and growing across the FIA microplot size threshold by the second measurement (Burrill et al., 2024). For mortality, we included two components: 1) the BAI of trees and saplings that were alive and measured in the initial measurement and died by the second measurement, and 2) the BAI of saplings that crossed the microplot size measurement threshold since the previous visit and subsequently died before the most-current measurement (Burrill et al., 2024). Growth, recruitment, and mortality were divided by the plot remeasurement period to obtain annualized rate estimates. To investigate self-thinning under the size-density relationship, we used trees per hectare as of the most-recent plot measurement

Table 1
Summary of stand characteristics (mean ± (*S.D.*)) for selected FIA conditions by forest type.

Forest Type	Site class	SDI	TPH	Growth (m^2 ha^{-1} yr^{-1})	Recrt (m^2 ha^{-1} yr^{-1})	Mort. (m^2 ha^{-1} yr^{-1})	D_R (cm)	DCI	HCI
Ponderosa	5.5	367.8	609.3	0.30	0.02	0.04	25.9	0.08	57.0
	(0.7)	*(185.6)*	*(756.9)*	*(0.19)*	*(0.07)*	*(0.08)*	*(11.7)*	*(0.08)*	*(29.7)*
Douglas-fir	4.4	569.1	682.6	0.50	0.02	0.09	29.0	0.09	52.4
	(1.4)	*(313.0)*	*(685.7)*	*(0.39)*	*(0.05)*	*(0.18)*	*(14.4)*	*(0.07)*	*(32.8)*

Notes: abbreviations are as follows: SDI = stand density index, TPH = trees per hectare, PAI = periodic annual increment, Ht = height, D_R = Reineke's diameter, SCI = size complexity index, HCI = horizontal complexity index.

as our response variable (Table 2).

Because stand dynamics are tied to site-quality factors such as soil and climate (Pretzsch, 2005), we used the FIA site class variable (Dunning and Reineke, 1933) to represent site quality. Site class is a widely adopted proxy of site quality used in both research and management that integrates soil, terrain, and climate factors (Skovsgaard and Vanclay, 2008), whereas detailed soil data cannot be obtained for public FIA plot locations. FIA site class is an ordinal variable ranging from 1 (highest, potential productivity $\geq$15.74 m^3 ha^{-1} yr^{-1}) to 7 (lowest, potential productivity $\leq$ 1.33 m^3 ha^{-1} yr^{-1}). The FIA site class variable is derived via mean annual increment models, which in turn, use site index as their primary input (Hanson et al., 2003). Typically, 3–10 site trees are assessed for each condition, sometimes using trees adjacent to the FIA plots when no appropriate site trees can be located on-plot (Hanson et al., 2003). Site trees were preferably at least 50 years old, occupied dominant crown classes, and had normally formed tops (Hanson et al., 2003). Using the FIA site class variable to represent site quality simplified the process of standardizing site index from the numerous site index curves and base ages used across the range of ponderosa pine and Douglas-fir (Hanson et al., 2003).

We modeled growth, recruitment, and mortality individually for each forest type, based on the most-recent (T2) plot measurement, using predictor variables representing stand structure at the time of initial measurement (T1). We used the same general model form for each of these three forest change components. To account for initial stand density, we incorporated stand density index, calculated using the additive method (ASDI; Long and Daniel, 1990) into all forest change models. We included Reineke's diameter (Zeide, 2001) as an indicator of stand maturity (Pretzsch, 2005):

$$Reineke's diameter = \left[(1/N)\sum d_i^b\right]^{1/b}$$

Where N is trees ha^{-1}, d is the diameter of tree i, and b is the absolute value of the slope coefficient of the self-thinning line. We used the traditional exponent of −1.605 for b (Shaw and Long, 2010). Using Reineke's diameter in place of quadratic mean diameter (QMD) in Reineke's original SDI formula will yield identical estimates of ASDI as summing the individual-tree contributions to ASDI. Reineke's diameter offers a more representative indicator of mean stand diameter than QMD in irregular stands (Andrews et al., 2018; Zeide, 1983).

We focused on two aspects of structural complexity that could be derived from public FIA plot data: diameter-distribution complexity and the patchiness of biomass across the stand. We calculated a distribution complexity index (DCI) based on the ratio of ASDI vs. Reineke's SDI (Ducey, 2009). In stands with normal diameter distributions, the ratio of these two variables is equal. In stands with right-skewed, uniform, or particularly multi-modal distributions, ASDI will be lower than Reineke's SDI (Ducey, 2009). Once rescaled by subtracting this ratio from 1, higher DCI values indicate more complex diameter distributions. For a horizontal structural complexity index (HCI), we calculated the coefficient of variation among FIA subplots within an FIA condition, or stand. Although FIA plots do not intentionally sample individual stands, our filtering of plots to focus on those intersecting a single stand allowed us to examine within-stand variation. Higher values signify greater patchiness in stocking. By taking the coefficient of variation rather than the standard deviation of within-stand ASDI, our intent was to remove scaling effects introduced by variation in total ASDI. These structural complexity metrics had the advantage of: a) being based on more precise diameter measurements, as opposed to tree height (Forest Service, 2024), b) avoiding issues with small sample sizes that affect metrics such as the Gini coefficient (Deltas, 2003), and c) relative simplicity of calculation based on stand summary data, which better supports potential application to management.

For our analysis of the size-density relationship, we focused on both response and predictor variables calculated only for the most-recent (T2) plot visit. This approach simplified modeling, allowing us to avoid issues with temporal autocorrelation. We used Reineke's diameter as the basic predictor of trees ha^{-1} in self-thinning models.

Table 2
Details of response and predictor variables used in analyses.

Category	Abbreviation	Description	Interpretation	Units
Response	Growth	Annualized basal area growth of survivor trees	Higher = faster rate	m^2 ha^{-1} yr^{-1}
Response	Recruit.	Annualized sapling recruitment rate by basal area	Higher = faster rate	m^2 ha^{-1} yr^{-1}
Response	Mort.	Annualized tree and sapling mortality rate by basal area	Higher = faster rate	m^2 ha^{-1} yr^{-1}
Response	Trees ha^{-1}	Combined density of trees and saplings per hectare	Higher = denser stocking	Stems ha^{-1}
Predictor	Site class	FIA site class code	Higher = less productive	Ordinal scale of 1 (most productive) to 7 (non-forest)
Predictor	ASDI	Additive stand density index	Higher = greater relative stand density	#25.4 cm tree-equivalents ha^{-1}
Predictor	Reineke's diameter	Mean stand diameter derived as a function of trees ha-1 and additive SDI	Higher = larger mean tree size	cm
Predictor	DCI	Diameter complexity index	Higher = more complex diameter distribution	Rescaled ratio
Predictor	HCI	Coefficient of variation in within-stand ASDI	Higher = more horizontal complexity	Percent

2.3. Modeling procedures

We created sets of competing alternative hypothesis models (Table 3). We used the information-theoretic approach (Burnham and Anderson, 2002) with corrected Akaike's Information Criterion (Sugiura, 1978) to evaluate the relative support for each hypothesis model. In addition to selecting the model that minimized AIC, we applied several criteria to consider models plausible and warranting inclusion in inference: 1) were within 6 AICc units of the best-approximating model, 2) each added parameter reduced AICc by at least 2 relative to simpler, nested models, and 3) added parameters increased log-likelihood relative to simpler models (Richards, 2008). We created a null (intercept-only) hypothesis model for each response.

We used the same general set of hypothesis models for growth, recruitment, and mortality. Our basic model form followed Pretzsch's (2009) model of the periodic annual volume increment-density relationship, incorporating ASDI to account for initial stand density, Reineke's diameter to account for biological maturity, and site class to represent site quality. We opted to use Reineke's diameter to represent biological maturity rather than investigate age-related trends, given the inherent uncertainty in a single point estimate of age in complex stands (Stevens et al., 2016). Our first alternative model included these three

Table 3
Hypothesis models used in the three analyses.

Hypothesis	Response	Varies as a function of
0	G, R, M	intercept-only
1	G, R, M	ASDI, site class, D_R
2	G, R, M	ASDI, site class, D_R, DCI
3	G, R, M	ASDI, site class, D_R, HCI
4	G, R, M	ASDI, site class, D_R, DCI, DCI x SDI
5	G, R, M	ASDI, site class, D_R, HCI, HCI x SDI
6	R, M*	ASDI, site class, D_R, DCI, DCI x D_R
7	R, M*	ASDI, site class, D_R, HCI, HCI x D_R
8	G, R, M	ASDI, site class, D_R, DCI, DCI x site class
9	G, R, M	ASDI, site class, D_R, HCI, HCI x site class
0	Trees ha^{-1}	Intercept-only
1	Trees ha^{-1}	D_R, site class
2	Trees ha^{-1}	D_R, DCI, site class
3	Trees ha^{-1}	D_R, HCI, site class
4	Trees ha^{-1}	D_R, site class, DCI, D_R x DCI
5	Trees ha^{-1}	D_R, site class, HCI, D_R x HCI
6	Trees ha^{-1}	D_R, quad. DCI, site class
7	Trees ha^{-1}	D_R, quad. HCI, site class
8	Trees ha^{-1}	D_R, site class, quad. DCI, D_R x quad. DCI
9	Trees ha^{-1}	D_R, site class, quad. HCI, D_R x quad. HCI

Note: Abbreviations are as follows: ASDI = additive stand density index, D_R = Reineke's diameter, SCI = structural complexity index, HCI = horizontal complexity index, G = survivor growth, R = sapling recruitment, M = mortality, N = net change.
* excluded from survivor growth modeling due to collinearity.

main effects. Alternatives 2 and 3 included the same terms as #1 but added DCI and HCI terms, respectively. Alternatives 4 and 5 examined interactions between ASDI and DCI and SDI and HCI, respectively. By examining the interaction between density and structural complexity, Alternatives 4 and 5 allowed us to investigate whether the strength of structural-complexity effects varied with stand density, as has been commonly observed in species-mixture effects on growth (Bauhus et al., 2017) and the influence of size inequality on the periodic annual volume increment of Norway spruce (Pretzsch et al., 2024). Alternatives 6 and 7 examined whether diameter-distribution complexity or horizontal complexity interacted with Reineke's diameter to examine whether structural-complexity effects were contingent on stand biological maturity, given previous findings that species-mixture effects on individual-tree growth were contingent on tree size (Madrigal-González et al., 2016). Lastly, Alternatives 8 and 9 examined whether diameter-distribution complexity or horizontal complexity interacted with site class, given previous findings that species-mixture effects are contingent on site quality (Toïgo et al., 2015).

In null model of the size-density relationship, trees ha^{-1} varied as a simple function of the intercept. Under our first alternative model, log-transformed trees ha^{-1} varied with the main effect of log-transformed Reineke's diameter site class, which accounted for potential site-dependence of maximum stocking (Andrews et al., 2018). Alternatives 2 and 3 added the main effects of DCI and HCI, respectively. Alternative 4 included the main effects of Reineke's diameter, site class, DCI, and the Reineke's diameter x DCI interaction, respectively. Alternative 5 included the main effects of Reineke's diameter, site class, HCI, and Reineke's diameter x site class interaction. Alternatives 6 and 7 included the effects of Reineke's diameter and site class as well as both linear and quadratic DCI or HCI terms, respectively, to account for a potential peak in maximum stocking at intermediate levels of structural complexity reported in Norway spruce (Pretzsch et al., 2024). Alternatives 8 and 9 added interactions between Reineke's diameter and polynomial quadratic DCI or HCI effects, respectively, to account for potential nonlinear structural-complexity effects on the slope of the self-thinning line. We used the quantreg package (Koenker et al., 2018) for quantile regression modeling.

All growth, recruitment, and mortality modeling was performed using generalized linear models in the glmmTMB package (Brooks et al., 2025) for R (R Core Team, 2022). We opted to use generalized linear modeling because this approach was more amenable to analyzing potential interactions and inference through model selection compared to more automated alternatives such as random forests (e.g., Dupont-Leduc et al., 2024). We modeled survivor growth with a normal distribution. For recruitment and mortality data, which ranged from zero to positive, right-skewed, and included abundant zero values, we used the log link to the Tweedie error distribution (Foster and Bravington, 2013). The streamlined implementation of the Tweedie distribution in the glmmTMB package motivated this choice of analysis software despite our lack of random effects.

Quantile regression, stochastic frontiers analysis, and quantile mixed modeling are three contemporary methods of fitting the self-thinning line (Chivhenge et al., 2024). We selected quantile regression (Koenker and Bassett, 1978) as this method allowed us to make inferences between forest types at a consistent quantile of the data, while the effective quantile may otherwise vary under stochastic frontiers analysis (Tian et al., 2021). Our focus on data from the most recent plot visit and desire to make direct inferences about the slope and intercept of the self-thinning line, as opposed to derived maximum SDI, prompted us to select quantile regression vs. linear quantile mixed modeling. We selected the 0.95 quantile due to a balance between insensitivity to outliers and realistic maximum stocking thresholds (Andrews et al., 2018).

We used simulated residuals plots (Hartig, 2018) to check model assumptions of linearity, the appropriateness of error distributions, and homoscedasticity. We chose simulated residuals, as opposed to traditional residuals, because these allowed us to perform equivalent diagnostics for both Gaussian and Tweedie GLMs. Transformations of the typically right-skewed increment response and predictor stand density and mean stand diameter variables are common used to represent asymptotic growth curves in stand-level increment models (Pretzsch, 2009). Our diagnostics supported transforming survivor growth by taking the square root after converting a small number of negative observations (N = 1 for ponderosa pine, N = 4 for Douglas-fir) to 0, assuming trees on these plots had diameter increments low enough to be within measurement error. We log-transformed ASDI in growth, recruitment, and mortality models. We included both log-transformed and squared terms of Reineke's diameter in growth models to account for nonlinearity. For mortality, we included both linear and quadratic log-transformations of Reineke's diameter. For recruitment and self-thinning models, we only included a log-transformed Reineke's diameter term. We used untransformed DCI for mortality and trees ha^{-1} and square-root transformed DCI for the other responses. We square-root transformed HCI for all responses except trees ha^{-1}. After log-transforming the response variable, trees ha^{-1}, in self-thinning models, we did not consider further response variable transformations given the robustness of quantile regression to violations of the normality assumption of residuals (Hao and Naiman, 2007).

Severe collinearity may prevent accurately estimating the coefficients, and sometimes even the sign, of individual model parameters (James et al., 2021). To address potential collinearity, we centered and scaled predictors to reduce apparent collinearity among variables on widely different measurement scales while also promoting model convergence. We used variance inflation factors in the "performance" package (Lüdecke et al., 2021) as a collinearity diagnostic, setting a threshold of VIF > 5 as signifying models had problematic levels of collinearity and should be dropped from consideration (James et al., 2021). We dropped Alternatives 6 and 7 (examining DCI or HCI interactions with Reineke's diameter, respectively) from survivor growth modeling due to collinearity. We calculated R^2 or pseudo R^2-statistics for plausible models for descriptive purposes but relied on AICc scores for inference. In the event of multiple plausible models, we used model averaging based on AICc weights to interpret results. We interpreted interactions at the 25th and 75th percentile values of the covariate involved, as these values were representative of the main range of the

data rather than outliers. We calculated estimated marginal means and confidence intervals, which allowed us to examine the main effects and interactions of primary interest while holding other covariates constant at their means (Lüdecke and Schwemmer, 2017).

3. Results

3.1. Survivor growth

In the best-supported model, ponderosa pine survivor basal area increment (BAI) varied with the interaction between site class and distribution complexity index (H8, DCI; Table 4; Fig. 2A). Under this interaction, the survivor BAI of stands with complex diameter distributions was generally lower than that of stands with simple distributions. However, differences between complex and simple stands weakened with declining site quality (increasing site class) such that the two groups overlapped in survivor BAI on the poorest sites. It should be noted that relationships between survivor growth and site class were primarily driven by site classes 2–6, given relatively few stands at extremes of site quality. Survivor growth increased asymptotically with initial additive stand density index (ASDI), increasing more steeply at low densities vs in dense stands. Survivor growth initially declined steeply with Reineke's diameters up to about 10 cm, declined at a slower, linear rate up to about 80 cm, and plateaued in the largest diameter stands. No other survivor growth model was plausible for ponderosa pine. Please see Table S2 for the full sets of survivor BAI model comparisons.

Under the best-supported survivor BAI model for Douglas-fir, BAI varied with the site class x horizontal complexity index (HCI) interaction (H9, Table 4, Fig. 2B). Under this interaction, the survivor BAI of stands with patchy stocking (high HCI) was generally lower than that of stands with uniform stocking (low HCI). However, differences between complex and simple stands weakened as site quality declined, with both uniform and patchily-stocked stands exhibiting equivalent survivor BAI on the poorest sites. In terms of other covariates, survivor BAI increased curvilinearly with initial ASDI, increasing most rapidly between 0 and 300 ASDI above which this relationship became more gradual. Survivor BAI declined sharply with Reineke's diameter in the smallest-diameter stands, while declining at a more gradual, consistent rate as Reineke's diameter increased beyond 5 cm. No other survivor BAI model was plausible for Douglas-fir (Table S2).

3.2. Sapling recruitment

The best-approximating model of ponderosa pine sapling recruitment basal area included the interaction between Reineke's diameter and horizontal complexity index (HCI; H7, Table 4, Fig. 2C). In stands with uniform stocking (low HCI), recruitment rates were comparable to stands with patchy stocking (high HCI) as Reineke's diameter increased up to approximately 15 cm. Above this threshold, recruitment declined more gradually with Reineke's diameter in patchy vs. uniform stands. Recruitment rates fell to negligible as Reineke's diameter increased above 20 cm in uniformly stocked stands and above 40 cm in patchily stocked stands. In terms of other covariates, sapling recruitment declined steeply between 0 and 200 ASDI, essentially falling to zero at higher stand densities. Recruitment showed a similar relationship with initial Reineke's diameter, declining steeply up to approximately 20 cm, which did not change substantially as Reineke's diameter increased beyond this point. Recruitment weakly declined with declining site quality. No other sapling recruitment model was plausible for ponderosa pine. Please see Table S3 for the full sets of recruitment model comparisons.

In the best-supported model of Douglas-fir sapling recruitment, DCI interacted with Reineke's diameter (Table 4). Under this interaction, recruitment in stands with simple diameter- distributions declined less steeply with Reineke's diameter compared to complex stands up to approximately 25 cm (H6, Fig. 2D). Above this diameter threshold, recruitment fell more quickly in structurally complex stands as Reineke's diameter continued to increase. However, recruitment was essentially negligible above Reineke's diameters of 25 cm regardless of structural complexity. This interaction was also weak enough so that recruitment rates in complex vs. simple stands largely overlapped across the ranges of Reineke's diameter except at extremes of DCI. In terms of other covariates, recruitment declined with initial ASDI, becoming asymptotic once ASDI increased above 300. At first recruitment steeply declined with Reineke's diameter, with the decline becoming asymptotic above about 25 cm. Recruitment weakly declined with declining site quality, as indicated by higher values of site class. No other recruitment model had substantial AICc support for Douglas-fir (Table S3).

3.3. Tree and sapling mortality

For ponderosa pine tree and sapling mortality basal area, we found no support for main effects of DCI or HCI, nor support for interactions with stand structure or site quality (Table 5). Mortality rates increased

Table 4
Model comparison results for the analyses of survivor growth, sapling recruitment, and mortality.

Forest type	Response	Varies as a function of	Loglik	AICc	ΔAICc	w_i	R^2
Ponderosa	Growth	ASDI + site class + D_R + DCI + site class x DCI	809.1	-1602.0	0	0.99	0.49
Ponderosa	Growth	Intercept-only (null)	408.2	-812.3	789.7	0.0	0
Douglas-fir	Growth	ASDI + site class + D_R + HCI + site class x HCI	527.8	-1039.6	0	0.99	0.62
Douglas-fir	Growth	Intercept-only (null)	-718.3	-138.54	1320.7	0	0
Ponderosa	Recruit.	ASDI + site class + D_R + HCI + HCI x D_R	-108.2	232.52	0	0.96	0.14
Ponderosa	Recruit.	Intercept-only (null)	-204.4	414.9	182.4	0	0
Douglas-fir	Recruit.	ASDI + site class + D_R + DCI + DCI x D_R	-131.9	279.9	0	0.97	0.10
Douglas-fir	Recruit.	Intercept-only (null)	-208.9	423.9	144.0	0	0
Ponderosa	Mortality	ASDI + site class + D_R	-97.3	208.7	0	1	0.09
Ponderosa	Mortality	Intercept-only (null)	-156.9	319.7	111.0	0	0
Douglas-fir	Mortality	ASDI, site class, D_R, DCI, DCI x D_R	53.2	-86.2	0	1	0.16
Douglas-fir	Mortality	intercept-only	-66.1	138.1	224.3	0	0
Ponderosa	Trees ha^{-1}	D_R + site class + quad. HCI	-936.6	1883.2	0	0.93	0.83
Ponderosa	Trees ha^{-1}	D_R + site class + lin. HCI	-940.2	1888.4	5.2	0.07	0.83
Ponderosa	Trees ha^{-1}	Intercept-only (null)	-1957.2	3916.5	2034.3	0	0
Douglas-fir	Trees ha^{-1}	D_R + site class + quad. HCI	-1106.6	2223.2	0	0.99	0.78
Douglas-fir	Trees ha^{-1}	Intercept-only (null)	-2093.3	4188.5	1967.4	0	0

Note: Please see Table 2 for interpretation of response and predictor variable abbreviations. s() denotes use of smoothed term in general additive modeling. Other abbreviations are as follows: AICc=corrected Akaike's information criterion, Loglik=log-likelihood, w_i=Akaike weights, R^2 = coefficient of determination, quad. = includes linear and quadratic polynomial terms.

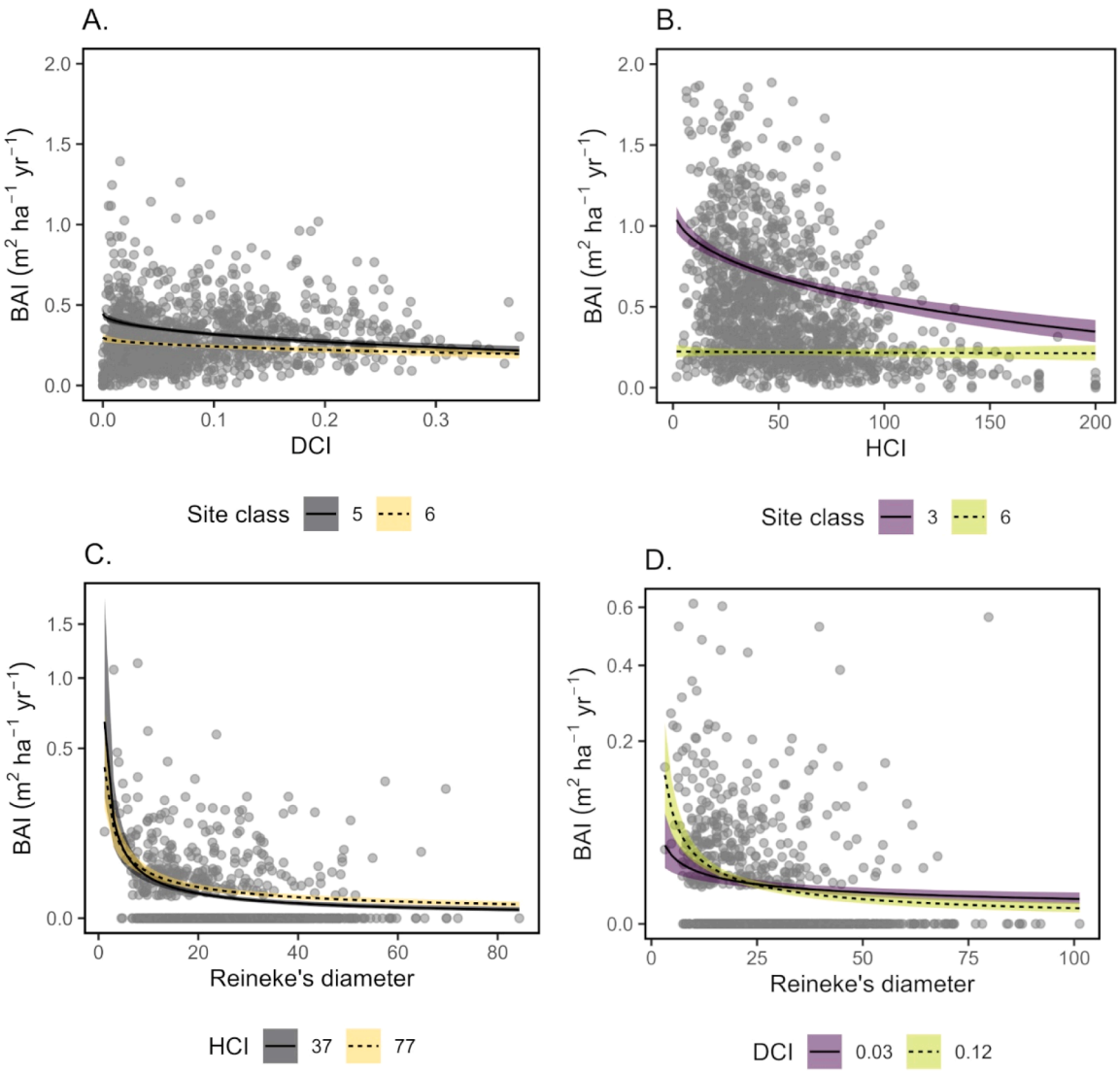

Fig. 2. Line and scatterplots illustrating the results of the survivor growth and sapling recruitment analyses. Panels A illustrates the effect of the site class (1–7 scale; low values = better site quality) x horizontal complexity index (HCI) interaction on combined tree and sapling basal area increment (BAI) for ponderosa pine. Panel B illustrates the effect of the interaction between site class and diameter complexity index (DCI) on Douglas-fir survivor BAI. Panel C illustrates the effect of the interaction between Reineke's diameter and horizontal complexity index (HCI) on sapling recruitment BAI in ponderosa pine. Panel D illustrates the effects of the interaction between Reineke's diameter and distribution complexity index (DCI) on Douglas-fir recruitment BAI. Lines and error bands show means ± 95% confidence intervals. Please note the recruitment y-axes have been square root-transformed for visibility, with zero values clustered along the bottom of the axis.

Table 5
Model comparison results for the analyses of net change and the size-density relationship.

Forest type	Response	Varies as a function of	Loglik	AICc	ΔAICc	w_i	R^2
Ponderosa	Net change	ASDI + site class + D_R + DCI + site class x DCI	-3109.9	6233.8	0	0.64	0.09
Ponderosa	Net change	ASDI + site class + D_R + DCI	-3119.9	6238.4	4.6	0.33	0.09
Ponderosa	Net change	Intercept-only (null)	-3165.7	6335.3	101.5	0	0.0
Douglas-fir	Net change	ASDI, site class, D_R, HCI, HCI x site class	-4441.7	8897.5	0	0.64	0.22
Douglas-fir	Net change	ASDI, site class, D_R, HCI	-4444.0	8900.0	2.5	0.18	0.22
Douglas-fir	Net change	Intercept-only	-4627.2	9258.4	361.0	0	0
Ponderosa	Trees ha^{-1}	D_R, quad. HCI, site class	-936.6	1883.2	0	0.93	0.84
Ponderosa	Trees ha^{-1}	D_R, HCI, site class	-940.2	1888.4	5.2	0.07	0.84
Ponderosa	Trees ha^{-1}	Intercept-only	-1957.3	3916.5	2033.3	1	0
Douglas-fir	Trees ha^{-1}	D_R, quad. HCI, site class	-1219.4	2223.2	0	1	0.73
Douglas-fir	Trees ha^{-1}	Intercept-only	-2093.3	4188.5	1967.4	0	0

linearly with initial ASDI (H1, data not shown). Mortality increased with initial Reineke's diameter up to approximately 25 cm before plateauing at larger mean stand diameters. Mortality rates declined weakly with declining site quality or increasing site class. We found no substantial AICc support for any other alternative ponderosa pine mortality model. Please see Table S4 for complete sets of mortality model comparisons.

In the best-supported model of Douglas-fir tree and sapling mortality basal area, DCI interacted with Reineke's diameter (H6, Table 5, Fig. 3).

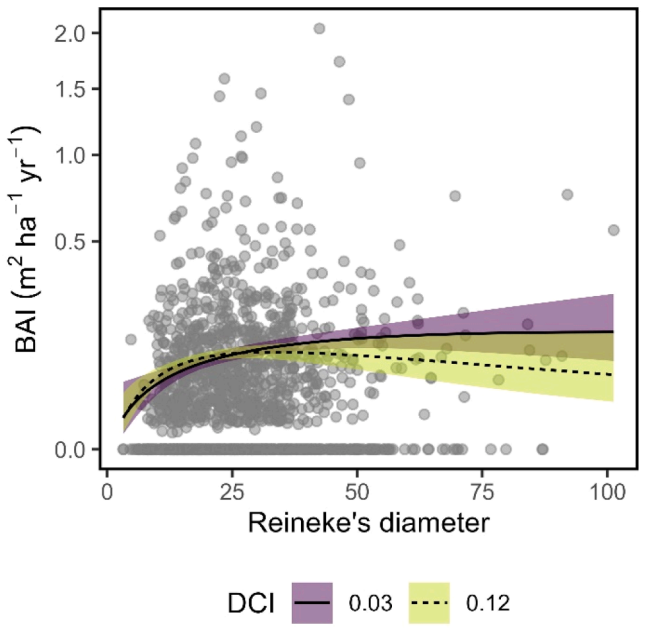

Fig. 3. Line and scatterplot illustrating the interaction between Reineke's diameter and distribution complexity index (DCI) on Douglas-fir mortality, expressed as annualized basal area increment (BAI). Lines and error bands show means ± 95% confidence intervals. Please note the y-axis has been square root-transformed for visibility, with zero values clustered along the bottom of the axis. Results are not displayed for ponderosa pine due to the lack of evidence for influences of structural complexity on this forest type.

In stands with low diameter-distribution complexity, mortality increased asymptotically with increasing Reineke's diameter. In stands with complex diameter distributions, mortality strongly increased with Reineke's diameter up to approximately 20 cm, above which mortality plateaued or reversed. However, this relationship was sufficiently noisy that mortality-diameter relationships still had substantial overlap between extremes of diameter-distribution complexity. In terms of covariates, mortality rates increased with ASDI and site class. No other mortality model had substantial support for Douglas-fir (Table S4).

3.4. Size-density relationship

The best-supported model of ponderosa pine self-thinning included the main effects of Reineke's diameter, site class, and polynomial quadratic HCI (H7; Table 5). Support for a nonlinear HCI effect was equivocal, and a second model with substantial support (ΔAICc=4.6) contained a linear HCI effect (H3). Under the main effect of HCI in the best-supported model, maximum log-trees ha^{-1} declined as stocking became increasingly patchy (Fig. 4A). When translating from the steeper observed 1.74 slope of the maximum size-density line to SDI based on the traditional 1.605 slope value, predicted maximum SDI declined asymptotically with increasing Reineke's diameter regardless of HCI (Fig. 4C). In terms of other covariates, log-trees ha^{-1} strongly declined with Reineke's diameter but did not vary with site class. Please see Table S5 for full sets of self-thinning model comparisons.

The only plausible model of Douglas-fir self-thinning included the main effects of Reineke's diameter, site class, and polynomial quadratic HCI (H7; Table 4). Under the quadratic HCI effect, log-trees ha^{-1} declined progressively more steeply with increasing HCI (Fig. 4A). When translating from the shallower, mean observed 1.49 slope of the maximum size-density line to SDI using the traditional 1.605 slope value, predicted maximum SDI increased with Reineke's diameter (Fig. 4D). Maximum stocking declined with declining site quality (higher site class). No other Douglas-fir self-thinning model had substantial AICc support (Table S5).

4. Discussion

The relationship between structural complexity and productivity has been of growing interest to both fundamental forest ecology and applications to management. Complicating factors in previous studies have been a typically narrow focus on diameter distribution complexity or tree size variation and focus on net stand growth or individual-tree growth, which can obscure potentially important patterns involving recruitment or mortality. We addressed these shortfalls by investigating large datasets of two common, single-species forest types, examining both diameter distribution and horizontal aspects of structural complexity, while breaking down net stand growth into growth, recruitment, and mortality components. We found that where present, effects of structural complexity on the survivor growth, sapling recruitment, and mortality were often modulated by other facets of stand structure or site quality.

4.1. Survivor growth

Previous studies of individual-tree growth have found generally lower ponderosa pine growth in plantation stands with higher diameter-distribution complexity (Looney and Zhang, 2022). Long and Shaw (2010) did not find evidence for an effect of diameter-distribution complexity on ponderosa pine PAI. Liang et al. (2007) found diameter-distribution complexity was negatively correlated with survivor growth in Douglas-fir. Distinct cohorts creating multimodal diameter distributions lead to higher values of our diameter-distribution complexity index (Ducey, 2009), and gross stand volume increment does not appear to strongly vary with the number of age cohorts in this forest type (O'Hara and Nagel, 2006). In terms of horizontal structural complexity, a study of naturally regenerated ponderosa pine found accelerated growth with spatially aggregated clumps in natural stands subject to a restored fire regime (Fertel et al., 2022). Studies of structural complexity in Douglas-fir found evidence of minimal short-term (5 yr) treatment effects on growth among uniform thinning vs small gaps (Davis et al., 2007), while suggesting modest, but insignificant declines in projected growth when 20% of stand area consisted of 0.07–0.2 ha gaps (Newton and Cole, 2015).

Our findings generally support a negative role of structural complexity in ponderosa and Douglas-fir survivor growth, with important nuances across site-quality gradients and between forest types. Higher structural complexity can promote survivor-tree growth in mature stands of more shade-tolerant species (Lei et al., 2009; Zeller and Pretzsch, 2019). However, for ponderosa pine and Douglas-fir, which are relatively intolerant or mid-tolerant, shading effects in more complex stands may be generally deleterious. Trees in upper canopy positions are generally best positioned to intercept light, a process which favors large-tree performance (Forrester, 2019). Our diameter complexity index, generally a strong negative predictor of Douglas-fir survivor growth, reaches its highest values in bimodal diameter distributions (Ducey, 2009). Under these conditions, the upper canopy layer can effectively intercept direct overstory light and cause rapid light extinction through the canopy (Gersonde et al., 2004). Meanwhile, shade-intolerant ponderosa pine typically requires large gap sizes before the relative growth losses of regenerating cohorts vs. open-grown conditions become asymptotic (York et al., 2004).

A fundamental question in silviculture is whether there is an optimal stand density that maximizes increment (Assmann, 1970; Zeide, 2001). Various authors have suggested that the shape of this relationship is consistent across a range of stand densities (Wiedemann, 1951), increases to an optimum at moderate-to-high stand densities (Assmann, 1970; Pretzsch, 2005), or asymptotically increases with density (Curtis et al., 1997). Pretzsch et al. (2024) established that the density-growth relationship is more accurately a density-structure-growth relationship in Norway spruce, where diameter-distribution complexity modulates the role of density. We found that rather than modulating the

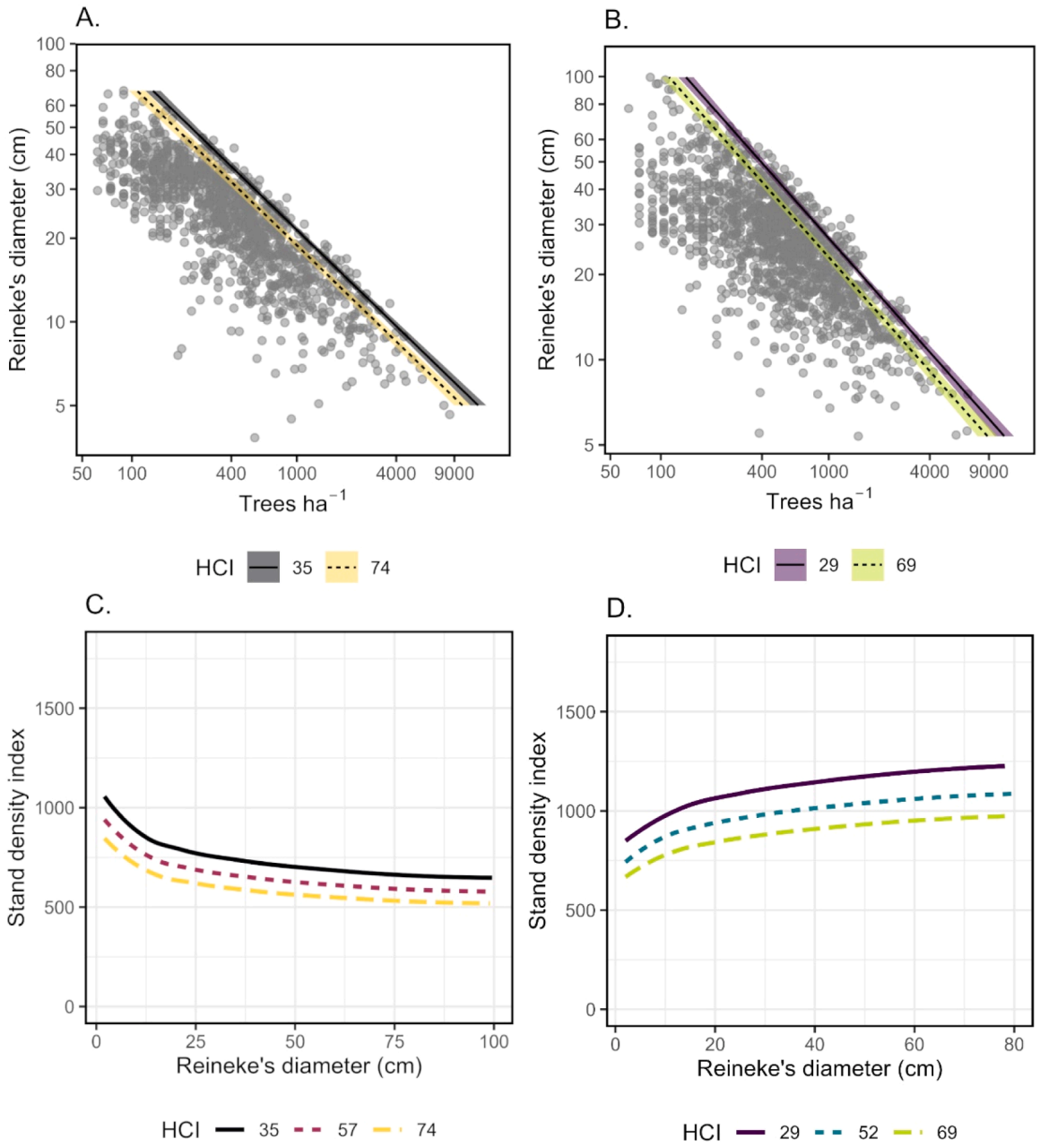

Fig. 4. Line and scatterplots illustrating the results of the size-density relationship analysis. Panels A and B illustrate the effect of horizontal complexity index (HCI) on the intercept of the size-density line for A) ponderosa pine and B) Douglas-fir. Lines and error bands show means ± 95% confidence intervals. Please note both the x and y-axes have been log-transformed. Panels C and D illustrate how predicted maximum SDI varies nonlinearly with Reineke's diameter at three discrete levels of HCI for ponderosa pine and Douglas-fir, respectively.

growth-density relationship, structural complexity instead played a stronger role in modulating the growth-site quality relationship in stands of these relatively less shade-tolerant forest types. Lower horizontal complexity, or uniformity of stocking, generally promoted ponderosa pine survivor-tree increment while lower diameter-distribution complexity promoted Douglas-fir increment. However, in both cases site quality, as indicated by FIA site class, more strongly modulated structural-complexity effects than stand density. Whereas stands with low structural complexity supported higher survivor BAI under high site quality, the BAI of structurally simple and complex stands converged on poor sites.

Complex arrangement of trees and plants within the stand can result in interactions such as competition and facilitation that influence resource-use efficiency (Murphy et al., 2022), with facilitative effects expected to become stronger with increasing abiotic stress (Callaway, 2007, 1995). Our finding that poor site quality moderated the generally negative influence of structural complexity on survivor growth in both forest types appears to be consistent with this stress-gradient hypothesis. Our finding echoes that of a study of French national forest inventory which found that the overyielding of mixed stands vs. monocultures increased on low-quality sites (Toïgo et al., 2015), supporting assertions that species-mixture and structural-complexity effects on forest growth may operate through similar mechanisms (Pretzsch et al., 2024). Theoretically, patchy stocking in ponderosa pine might counter abiotic stress on poor sites through greater sharing among mycorrhizal networks (Simard et al., 2012), a justification presented for cluster planting (North et al., 2019). Greater variation in tree sizes, which appears to be particularly influential for Douglas-fir, could potentially promote

greater belowground resource partitioning (Biondi, 1996; Niinemets, 2010). However, given the limitations of our observational, non-spatial dataset, additional research is needed to establish the specific mechanisms driving the interactions.

4.2. Sapling recruitment

Recruitment is a key component of forest change, and, in previous studies, may be at least as strong a mediator of the effects of stand structural complexity on net stand growth as survivor-tree growth (Astigarraga et al., 2020; Dupont-Leduc et al., 2024; Liang et al., 2007). From the perspective of forest management, the presence of recruitment may be a key criterion of the viability of uneven-aged silvicultural systems in regenerating a stand (Matthews, 1989; Nyland, 2016). Conversely, recruitment may be negative from the perspective of hazardous fuel treatments by contributing to ladder fuels (Fialko et al., 2020), thereby limiting treatment durability (Francis et al., 2018). For this study, we investigated only the recruitment of saplings, which, while constituting a smaller part of net growth than ingrowth trees on pole-sized or sawtimber plots, allowed us to make stronger inferences between the effects of current forest structure on recent regeneration dynamics.

We found that higher structural complexity generally promoted recruitment, but that there were important nuances between forest types and complexity effects weakened with mean stand diameter. For ponderosa pine, greater patchiness in stocking generally promoted higher sapling recruitment rates. This finding is consistent with the regeneration ecology of ponderosa pine, which typically requires large gap size to promote light environments conducive to sapling establishment and performance (York et al., 2004). Mean stand diameter is an important indicator of the availability of trees of seed-bearing size, and thus an important predictor of natural regeneration potential (Swann et al., 2025; Vandendriesche, 2010). When raising mean tree size while holding gap size constant, the light environment within gaps will be increasingly dominated by indirect light at temperate latitudes (Canham et al., 1990; Gersonde et al., 2004). The duration of sun flecks in mature Douglas-fir-hemlock (*Tsuga heterophylla*) forests is notably fleeting due to relatively extreme tree heights (Canham et al., 1990), which may account for the weaker evidence for horizontal complexity effects on both growth and recruitment in this forest type.

Douglas-fir recruitment has previously been linked to higher diameter-distribution complexity (Liang et al., 2007). Liang et al. (2007) hypothesized that higher Douglas-fir recruitment in stands with complex diameter distributions might reflect a role of facilitation on sapling survival. Our results showed a more nuanced pattern where mean stand diameter modulated this relationship so that diameter distribution complexity was associated with relatively higher recruitment in small-diameter stands. An empirical model of natural regeneration similarly predicted that the relationship between small sapling abundance and canopy cover reversed as mean stand diameter increased, with closed stands supporting relatively higher regeneration at small mean stand diameters and relatively lower regeneration in large-diameter stands (Vandendriesche, 2010). More complex canopies can reduce the rate of light attenuation downward through the crown profile (Gersonde et al., 2004), and potentially moderate microclimates (Ehbrecht et al., 2017). Again, this is a topic for future research as our relatively simple structural complexity indices based on non-spatial tree diameter data do not support making direct inferences as to the distribution of leaf area through the canopy profile. For Douglas-fir, it is also important to note that the effect sizes of DCI were comparatively minor compared to other stand structure and site main effects.

4.3. Sapling and tree mortality

Compared to growth and recruitment, we found less evidence for roles of either diameter distribution complexity or horizontal complexity on mortality rates. For ponderosa pine, we found no evidence that mortality varied with either aspect of structural complexity. Studies of experiments manipulating structural complexity in ponderosa pine/mixed conifer stands have found that overall stocking levels are more important for mortality compared to tree spatial arrangements (Knapp et al., 2021; Looney et al., 2024). A key aspect of ponderosa pine disturbance ecology is its susceptibility to aggregating bark beetle species, with risk of successful attacks strongly linked to stand density and large mean tree size (Fettig, 2016; Koontz et al., 2021).

For Douglas-fir, we found evidence that mean stand diameter modulated the effect of diameter distribution complexity on mortality rates. In small-diameter stands (<25 cm) with complex diameter distributions, mortality rates were slightly elevated relative to small-diameter stands with simple distributions. This relationship reversed in large-diameter stands, where mortality rates declined in stands with more complex diameter distributions. This behavior may reflect a shift in the mode of competition during biological maturation (Larson et al., 2015). In small-diameter stands, this behavior may reflect elevated self-thinning mortality, a result previously reported for Norway spruce (Pretzsch et al., 2024). Recent Douglas-fir mortality in the Pacific Northwest is concentrated in small-diameter trees in large-diameter stands (Andrus et al., 2026). Lower mortality under more diverse diameter distributions could potentially reflect mitigation of Douglas-fir beetle, which preferentially targets large-diameter trees (Andrus et al., 2026).

4.4. Size-density relationship

The log-log size-density relationship (Reineke, 1933), or self-thinning rule, has been proposed as one of the few near-universal relationships in plant ecology (Keddy, 2001; Long et al., 2004). This relationship describes the tradeoff between tree size and number in fully stocked stands, which becomes roughly linear when plotted on logarithmic scales (Reineke, 1933; Yoda, 1963) and forms the basis of many stocking guidelines worldwide (Chivhenge et al., 2024). Recent research has identified circumstances in which stand structure alters this relationship, thereby limiting stocking levels below the potential maximum for a given forest type (Forrester et al., 2021; Pretzsch et al., 2024). Once breaking stands into distinct size cohorts, Forrester et al. (2021) found that self-thinning declines in several forest types as individual cohorts become more dominant. Pretzsch et al. (2024) found a more nuanced complexity effect, where intermediate levels of diameter-distribution structural complexity optimize maximum stocking in Norway spruce. Our study confirmed that structural complexity altered the size-density relationship and clarified that horizontal complexity is more important to the forest types examined here than diameter-distribution complexity. The consistently negative effect of structural complexity on maximum stocking in these two forest types may reflect greater sensitivity to shading compared to shade-tolerant Norway spruce.

We found that patchiness lowered overall maximum stocking but did not affect the slope of the self-thinning line. The tradeoff between maximum tree size and density reflects the allometric relationship between stem diameter and crown size, which may in turn vary depending on local environmental conditions (Vanclay and Sands, 2009). Variation in allometric crown-stem diameter relationships are expected to alter the slope of the self-thinning line (Vanclay and Sands, 2009), whereas we found patchiness only affected the intercept. We found no difference in mortality rates between patchy and uniform stands once adjusting for stand density and mean stand diameter, suggesting lower maximum stocking in patchy stands may reflect poor microsites or areas of disturbance rather than accelerated self-thinning. Theoretically, patchy stands should not automatically have lower maximum stocking as tree crowns and boles can adjust to exploit openings and reduce apparent competition below that indicated based on stem positions alone (Adams et al., 2013; Stiell, 1982). In practice, unmanaged stands commonly struggle to reoccupy growing space opened through mortality,

potentially limiting maximum stocking below that of previously thinned stands (Ray et al., 2023). Given the lack of spatial, soils, and longer-term disturbance data in our FIA dataset, additional research is needed to determine the mechanisms driving our finding of lower stocking in patchy stands. It should also be noted that drawing conclusions from allometric relationships such as the size-density relationship introduces additional uncertainty compared to focusing solely on short-term forest demographics.

In addition to those previously stated, our study had several research limitations that constrain inference and generalization, while at the time suggesting directions for future research. Due to limited observations on the best and worst sites, our survivor growth-site class results are primarily driven by stands of intermediate site quality. Although necessary for translating across the various site index curves and base ages in these data, these results should ideally be verified with datasets using traditional site index or other more continuous indicators of site quality. While we dropped stands on private lands or with recent histories of treatment, defined as occurring within the last 5 years for new plots or since the last plot measurement (Burrill et al., 2024), we cannot discount that stands with patchy stocking were still recovering from either natural disturbance or older treatment. On National Forest System lands, which comprised the majority of our data, the annual area disturbed through mechanical treatment or wildfire averaged 1.9% during the 2008–2012 period alone (Vaillant and Reinhardt, 2017). Some of the relationships in our results may reflect regional, rather than study-wide patterns, given a peak in ASDI, site quality, and survivor growth in the Pacific Northwest (Fig. S1). Although forest inventory can provide insights into potential trends, long-term forest growth and yield plots are irreplaceable for robust inferences regarding stand origin, disturbance, and management history (Pretzsch et al., 2019). Pending published information quantifying the impacts of cluster planting on structural complexity, our results should be applied cautiously to assess the tradeoffs of this technique. Finally, we looked at just two attributes of structural complexity. Future studies should consider more comprehensive indices integrating multiple attributes, including components such as deadwood, tree height diversity, and canopy evenness (McElhinny et al., 2005).

5. Conclusions

Our study of how diameter distribution and horizontal structural complexity altered survivor growth, sapling recruitment, mortality, and size-density relationships had four main conclusions. Structural complexity interacted with site class to generally reduce survivor BAI compared to uniform stands. Structural complexity interacted with mean stand diameter to increase recruitment rates in small-diameter stands while reducing recruitment in large-diameter stands. Linkages between structural complexity and mortality were weaker, with evidence that diameter-distribution complexity exacerbated mortality in small-diameter Douglas-fir while reducing mortality in large-diameter stands. Finally, higher horizontal structural complexity lowered maximum stocking compared to structurally homogeneous stands.

Our findings have nuanced implications for managing stands for ecosystem management objectives on public lands. Promoting structural complexity in treatments may come at a cost in productivity driven primarily by survivor tree growth, although effects on net growth may be largely offset by higher recruitment in structurally complex stands (Astigarraga et al., 2020). Given the value of both early and late successional stands for biodiversity conservation and non-timber ecosystem services (Swanson et al., 2011), tradeoffs in terms of timber and carbon sequestration must be considered in light of other management objectives. From a fuels-reduction perspective, lower recruitment in structurally simple stands would improve treatment durability. However, fostering recruitment in structurally complex stands could be a positive outcome from the perspective of forest restoration, particularly if it consisted of desired shade-intolerant, fire-tolerant species (Stephens et al., 2021). Finally, managers should anticipate potentially lower maximum stocking in stands with high horizontal complexity, but this does not necessarily reflect exacerbated competition problems.

CRediT authorship contribution statement

W. Keith Moser: Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Christopher E. Looney:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Christopher Looney reports financial support was provided by USDA Forest Service Pacific Southwest Research Station. W. Keith Moser reports financial support was provided by USDA Forest Service Rocky Mountain Research Station. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123941.

Data Availability

Data will be made available on request.

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