# ARTICLE

# Effects of thinning-induced changes in structural heterogeneity on growth, ingrowth, and mortality in secondary coastal Douglas-fir forests

Christian Kuehne, Aaron R. Weiskittel, Shawn Fraver, and Klaus J. Puettmann

**Abstract:** Thinning is believed to accelerate the development of late-successional attributes, thereby enhancing stand structural heterogeneity in young, secondary forests. By making use of a large-scale experiment implemented in 40- to 60-year-old coastal Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) forests, we addressed the following objectives: (*i*) determine the effect of three thinning treatments on the temporal dynamics (first 11 years after thinning) of key forest structure measures, (*ii*) evaluate the relationships between spatially explicit structural diversity measures and spatially nonexplicit stand metrics, and (*iii*) test the relationships between stand structure and observed periodic stand volume growth, ingrowth, and mortality. Treatments consisted of high-density, moderate-density, and variable-density thinnings-from-below, as well as a control. Differences in stand structural heterogeneity between treatments were mostly nonsignificant. However, our results suggest that variable-density stands displayed structural enrichment as tree size and tree species diversity increased throughout the study period as a result of continuous ingrowth of species other than Douglas-fir. Simple spatially nonexplicit metrics could not be used to reliably model spatially explicit structural diversity measures. The inclusion of structural and species diversity measures only rarely improved accuracy of sample plot level growth, ingrowth, and mortality prediction models. Despite the short-term nature of this study, we conclude that variable-density thinning shows promise in increasing structural heterogeneity in young even-aged stands. The inclusion of structural diversity measures in growth and mortality models may be beneficial, but further work is needed to clarify the underlying relationships, particularly at the individual-tree level.

*Key words:* variable-density thinning, tree species diversity, tree size diversity, spatial tree arrangement, forest structure.

**Résumé :** L'éclaircie est censée accélérer le développement des attributs de fin de succession, améliorant ainsi l'hétérogénéité structurelle des jeunes peuplements de seconde venue. À l'aide d'une expérience à grande échelle établie dans des forêts côtières de douglas de Menzies (*Pseudotsuga menziesii* (Mirbel) Franco) âgées de 40 à 60 ans, nous avons poursuivi les objectifs suivants : (*i*) déterminer l'effet de trois traitements d'éclaircie sur la dynamique temporelle (11 premières années après l'éclaircie) des mesures clés de la structure forestière, (*ii*) évaluer les relations entre des mesures spatialement explicites de diversité structurelle et des mesures de peuplements non spatialement explicites, et (*iii*) tester la relation entre la structure du peuplement et les valeurs observées de croissance périodique du volume, du recrutement et de la mortalité dans le peuplement. Les traitements étaient des éclaircies par le bas à densités forte, modérée et variable ainsi qu'un témoin. Les différences d'hétérogénéité structurelle des peuplements entre les traitements étaient généralement non significatives. Cependant, nos résultats indiquent qu'un enrichissement structurel s'est produit dans les peuplements à densité variable puisque la diversité en taille et en espèce d'arbre a augmenté pendant la période d'étude à cause du recrutement continu d'espèces autres que le douglas de Menzies. Des mesures simples, non spatialement explicites, n'ont pu être utilisées pour modéliser de façon fiable les mesures de diversité structurelle spatialement explicites. L'inclusion de mesures de diversité structurelle et spécifique a rarement amélioré la précision des modèles de prévision de la croissance, du recrutement et de la mortalité à l'échelle de la placette échantillon. Malgré la courte échelle temporelle de cette étude, nous concluons que l'éclaircie à densité variable semble prometteuse pour augmenter l'hétérogénéité structurelle dans les jeunes peuplements équiennes. L'inclusion de mesures de diversité structurelle dans les modèles de croissance et de mortalité peut être bénéfique, mais d'autres travaux sont nécessaires pour clarifier les relations sous-jacentes, particulièrement à l'échelle de l'arbre individuel. [Traduit par la Rédaction]

*Mots-clés :* éclaircie à densité variable, diversité des espèces d'arbre, diversité de la taille des arbres, distribution spatiale des arbres, structure forestière.

## 1. Introduction

Restoring structural heterogeneity in secondary forests as a means to increasing the provision of ecosystem services has become a major objective in forest management and a much-noticed topic in forest research (Bauhus et al. 2009; Franklin et al. 2007). These services include maintaining biodiversity (Spies 2004) and enhancing resilience and adaptive capacity to climate change (D'Amato et al. 2011; Churchill et al. 2013). Silvicultural thinning has been promoted as one means of enhancing heterogeneity in secondary forests (Bauhus et al. 2009). Although traditional thinning methods result in more uniform tree spacing and a narrower distribution of crop tree sizes (Nyland 2002), more recent methods such as variable-density thinning create nonuniform tree spacing, thereby potentially increasing heterogeneity (Churchill et al.

**C. Kuehne, A.R. Weiskittel, and S. Fraver.** School of Forest Resources, University of Maine, 5755 Nutting Hall, Orono, ME 04469-5755, USA.
**K.J. Puettmann.** Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331, USA.
**Corresponding author:** Christian Kuehne (e-mail: christian.kuehne@maine.edu).

2013). In addition, the overall influence on tree spatial variability and vertical distribution of canopy layers further depends on the thinning method implemented (e.g., thinning from below vs thinning from above; Peck et al. 2014).

Quantifying forest structural heterogeneity, including how it changes as forests age and in response to silvicultural treatments, presents a challenge because of the wide variety of structural elements that could potentially be characterized. In general, forest structure has been defined as the spatial arrangement of the various components of a forest ecosystem, whereas forest structural heterogeneity, also referred to as forest structural complexity, refers to a measure of the variety and relative abundance of different structural attributes (Pommerening 2002; von Gadow et al. 2012; Sabatini et al. 2015). These attributes commonly include canopy cover, tree diameter, tree spacing, tree species, and deadwood abundance (McElhinny et al. 2005). Attributes that quantify variation are particularly important because only these can capture heterogeneity within stand elements (Staudhammer and LeMay 2001). Forest structural heterogeneity has been quantified based on overarching indices combining several attributes (e.g., Neumann and Starlinger 2001) or by evaluating multiple individual attributes at the same time (e.g., Bachofen and Zingg 2001). Although there seems to be consensus that various attributes need to be evaluated to interpret and compare complex forest structures (e.g., Gerzon et al. 2011), the need for detailed spatial information of tree locations appears to be open for discussion (Aguirre et al. 2003; Hui and Pommerening 2014).

Using relatively simple, spatially nonexplicit measures of forest structure (e.g., coefficient of variation of the diameter at breast height (DBH) distribution, Shannon–Weaver index), previous studies successfully distinguished forest stand structures among various silvicultural treatments (e.g., Hanewinkel 2004; Sterba and Zingg 2006). Investigating the influence of silvicultural treatments on three-dimensional forest structure, as assessed by more sophisticated, spatially explicit measures that require tree $X$ and $Y$ coordinates (e.g., DBH differentiation index, species intermingling index), has recently emerged as a research field, partly the result of more readily available stem-mapped data. However, relatively few studies describing forest structural heterogeneity based on such spatially explicit measures have been applied to various silvicultural systems and partial harvest methods to date (see Zenner 2000; Sterba and Zingg 2006; Saunders and Wagner 2008; Barbeito et al. 2009; Zenner et al. 2011, 2012; Peck et al. 2014).

Given the added field sampling effort required for the spatially explicit measures, recent investigations have asked if such measures can be predicted from simpler, spatially nonexplicit measures, including stem density and mean tree diameter derived from traditional stand inventory data. The few attempts at these predictions have yielded mixed results and reported varying prediction accuracy and hence varying potential for different spatially explicit measures (Sterba and Zingg 2006; Peck et al. 2014). Spatially nonexplicit measures of stand structure have also been used to evaluate the effects of varying forest structural heterogeneity on stand growth and mortality (Sterba and Monserud 1995; Edgar and Burk 2001; Liang et al. 2005, 2007). These studies add to the knowledge derived from semi-empirical modelling to investigate the influence of diameter distribution (or cohort structure) or spatial tree arrangement on stand volume increment (Pukkala 1988; Miina 1994; O'Hara 1996; Shao and Shugart 1997; Woodall et al. 2009; see also Hardiman et al. 2011). However, findings from these studies are often inconsistent and contradictory. The relationships between forest structure, using structural diversity measures, and stand-level forest growth thus remain poorly understood (cf. Lei et al. 2009).

Forests of the Pacific Northwest, USA, provide a promising setting in which to explore the relationships between forest structural heterogeneity, silvicultural treatments, and tree growth and mortality. Here, the majority of mature and old-growth forests have been replaced by young second-growth stands because of widespread harvesting and subsequent reforestation in the 20th century (Bolsinger and Waddell 1993; Muir et al. 2002). These stands are currently comprised of relatively homogeneous, even-aged Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) that lack the rich structural complexity typical of late-successional forests of this region (Spies and Franklin 1988; Franklin et al. 2002). Public concerns over the long-term effects of such forest practices have shifted the management focus on public lands from timber production to a complex set of objectives, including an emphasis on late-successional forest structure (Kessler et al. 1992). Consequently, enhancing and fostering structural heterogeneity in young plantations has become an important research focus (Hummel 2003; Reutebuch et al. 2004).

Observations that old-growth forests in this region initiated at lower densities than in current plantations (Tappeiner et al. 1997) have led to suggestions that thinning may be used to accelerate the development of structural heterogeneity in young Douglas-fir stands (Carey 2003). As a consequence, several replicated, large-scale management experiments, including the Density Management Study (Cissel et al. 2006), were established to gauge the effects of various thinning prescriptions on stand dynamics and the provision of ecosystem services (e.g., Monserud 2002; Peterson and Anderson 2009). Early results suggest that thinning operations promote the establishment of several late-successional stand attributes (Thysell and Carey 2001; Davis et al. 2007; Root et al. 2010; Dodson et al. 2012); however, an evaluation of thinning effects on stand structural heterogeneity and its relationship to stand development has yet to be conducted.

To address the identified research needs above, we used the Density Management Study to address the following specific questions. (*i*) How have various thinning treatments altered stand structural heterogeneity over the first 11 years after harvest? (*ii*) Can spatially nonexplicit stand inventory metrics be used to predict spatially explicit structural diversity measures? (*iii*) To what extent does stand structure (determined from both spatially explicit and spatially nonexplicit measures) influence stand volume growth, ingrowth, and mortality? Here we focus on stand dynamics to address the operational management scope of the Density Management Study. We therefore quantified structural heterogeneity, calculated forest growth and mortality, and analyzed the relationships at the stand level because this is the spatial scale at which the majority of silvicultural decisions are made and interpretation of the findings is less confounded by other factors. The working hypotheses were that the thinning treatments increased stand structural heterogeneity and the spatially explicit structural diversity measures would be effective predictors of the observed stand dynamics.

## 2. Material and methods

### 2.1. Study sites and data collection

The Density Management Study was initiated in 1994 in 40- to 60-year-old, commercially unthinned Douglas-fir dominated stands, and it contained four thinning treatments, replicated once on each of seven sites, located up to 300 km apart (Chan et al. 2004; Anderson and Poage 2014). The seven study sites, located in three ecoregions in Oregon (Coast Range, Willamette Valley, and Cascades) and covering a range of conditions typical for the region, are described in detail by Cissel et al. (2006). Forest stands of six of the seven study sites established naturally after clearcutting with or without residuals (seed trees), whereas the remaining site was artificially regenerated after clearcutting following wildfire (Cissel et al. 2006). Precommercial thinning had been conducted in four sites. Homogeneous stand conditions within each site, as well as a low probability of significant wind damage, were important initial site selection criteria to avoid confounding site effects within treatment units (Cissel et al. 2006). Treatments of each site

consisted of an unthinned control (CON, ~600 trees·ha⁻¹), a high-density retention (HD, ~300 trees·ha⁻¹), a moderate-density retention (MD, ~200 trees·ha⁻¹), and a variable-density retention (VD, ~100–300 trees·ha⁻¹). Circular retention tree islands (0.1, 0.2, or 0.4 ha) were included in all of the thinning treatments, whereas circular patch cuts (canopy openings of 0.1, 0.2, or 0.4 ha) were created in the MD and the VD treatments only. Because retention islands and patch cuts each covered 10% of the treated stands, their number differed across the treatment units, which substantially varied in size (14–69 ha).

All thinning treatments focused on removing intermediate and suppressed trees (i.e., thinning from below) of major species (primarily Douglas-fir), while retaining minor species such as western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), bigleaf maple (*Acer macrophyllum* Pursh), and red alder (*Alnus rubra* Bong.), among others, which usually made up less than 10% of the overstory. Remaining old retention trees were also preferentially reserved. Within the CON, HD, and MD treatments, nine 0.4 ha areas were underplanted with western hemlock and western redcedar. Western hemlock, Douglas-fir, western redcedar, and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) were planted in all patch openings and in the 100 trees·ha⁻¹ areas of the VD treatment.

Permanent circular sample plots (0.1 ha) were installed within all 28 treatment units (four treatment stands on each of the seven sites including controls).

For the current study, we used a subset of 792 of these sample plots that included stem-mapping of all trees. One set of these sample plots was established by the U.S. Department of the Interior Bureau of Land Management (BLM, 306 plots: CON = 68, HD = 54, MD = 63, VD = 121) 1–3 years (initial sampling varied among sites) following thinning; these sample plots were resampled twice, 6 and 11 years following thinning. Another set was established by Oregon State University (OSU, 486 plots: CON = 90, HD = 138, MD = 128, VD = 130) 6 years following thinning; these sample plots were resampled once, 11 years following thinning (for additional details, see Dodson et al. 2014). The number of combined BLM and OSU sample plots within each treatment unit ranged between 19 and 26 for CON, 25 and 31 for HD, 21 and 32 for MD, and 34 and 39 for VD. Prethinning data were not available, and sample plots were randomly located within treatments units, meaning that they could be located within the thinned matrix, within retention islands, or within patch cuts. As such, the sample plots were intended to capture the stand-level response to treatment.

At plot establishment, the species, location with regard to plot center (distance and azimuth), and DBH of all live trees with a DBH > 5.1 cm (2 inches) were collected. Total tree height was measured on a subsample of trees, that is, 10 conifers and six hardwoods, if present, per sample plot. During resampling, trees that had died were noted, and ingrowth (newly recruited stems achieving 5.1 cm DBH) was measured and mapped. Measurements from all three inventories of each of the seven study sites were used in this study.

## 2.2. Data analysis

### 2.2.1. Structural diversity measures

To quantify forest stand structure, we calculated a total of 11 structural diversity measures at the sample-plot level. It is worth noting that each of the analyzed measures represents only one specific attribute of forest structural heterogeneity. Although this approach allows for the evaluation of change among different aspects or attributes of forest structure, it does not reflect forest diversity in its entirety. For example, given the focus on the forest overstory in this study, our structural diversity measures do not reflect understory vegetation and deadwood characteristics. However, we deliberately did not use structural complexity measures

collectively as suggested by McElhinny et al. (2005) to avoid confusion with some of the individual metrics and indices calculated. Because this study aimed at comparing various spatially nonexplicit and spatially explicit structural diversity measures, we selected several metrics and indices with and without spatial reference. All selected measures are comprehensively described in Motz et al. (2010) and Peck et al. (2014), and a detailed overview of the spatially explicit indices is provided in Table 1.

Classical spatially nonexplicit measures are easily deducible from traditional stand inventory data and generally represent variation in tree size, which have included the standard deviation of tree diameters (DBHsd, cm) and the number of 4 cm diameter classes (DBHclass). As a potential spatially explicit counterpart, we calculated the mean DBH differentiation index (TDM; Füldner 1995), which is a measure of tree size interspersion. Stocking and spatial arrangement of trees were represented by tree density (*N*, number of trees per hectare) as well as the relative stand density index (RD; Reineke 1933; Curtis 2010) and the spatially explicit mean directional index (MDI; Corral-Rivas 2006), respectively. Tree size inequality was represented by the spatially nonexplicit tree basal area based Gini coefficient (GC; Gini 1921), whereas the tree diameter based structural complexity index (SCI; Zenner and Hibbs 2000) served as the spatially explicit counterpart. Tree species diversity and interspersion were quantified based on the spatially nonexplicit stem number based Shannon–Weaver index (*H*; Shannon and Weaver 1949) and the spatially explicit species intermingling index (*M*; von Gadow 1993), respectively. Finally, we calculated mean tree diameter (DBHm, cm) as a spatially nonexplicit metric. All selected measures are comprehensively described in Motz et al. (2010) and Peck et al. (2014).

Because TDM, *M*, and MDI describe forest structure at the tree-neighborhood level (here the four nearest neighbors of a focal tree), we averaged the retrieved individual-tree values at the sample-plot level to make them comparable to the other structural diversity measures. We did not apply an edge correction technique, e.g., establishing an internal buffer, because of the relatively small plot size and the resulting loss of information due to an eventually very small number of remaining trees, particularly in the MD and VD treatments (Gignoux et al. 1999; Barbeito et al. 2009).

### 2.2.2. Treatment effects on forest structural heterogeneity

To evaluate the effects of the various thinning treatments on the structural diversity measures (here the response variables) at the sample-plot level over time, we used linear mixed-effects models with a specified error correlation structure to account for the repeated measures of each sample plot and with a nested random effects structure on the intercept of sample plots within treatment units within study sites to account for the hierarchical study design (Zuur et al. 2009). An additional level of nesting of study sites within ecoregions did not improve the models. These models, conducted separately for each of the 11 structural diversity measures, were evaluated using the "nlme" package (Pinheiro et al. 2014) in R (version 3.0.3; R Core Team 2014). Generalized $R^2$ were calculated with ($R^2_{\text{fixed\&random}}$) and without ($R^2_{\text{fixed}}$) the inclusion of the random effects for each of the model. The function "lsmeans" of the R package "lsmeans" (Lenth 2014) was used to calculate least squares means and respective standard errors. The derived statistics were graphed to visually evaluate differences between treatments and time after thinning. Treatment effects within inventories were deemed to be statistically different ($\alpha < 0.05$) if a gap of at least one average standard error separated treatment error bars (Cumming et al. 2007).

### 2.2.3. Relationships between structural diversity measures

Relationships between spatially nonexplicit and spatially explicit structural diversity measures were first explored with a correlation matrix using data from the initial and second inven-

**Table 1.** Overview of spatially explicit structural diversity measures used in this study.

| Measure | Formula | Explanation | Range and meaning |
|---|---|---|---|
| Mean DBH differentiation index ($TDM_i$) | $1 - \dfrac{1}{n}\sum_{j=1}^{n}\dfrac{\min(DBH_i, DBH_j)}{\max(DBH_i, DBH_j)}$ | $i$, focal tree; $n$, number of neighbor trees | $TDM_i \in [0,1]$; values of 0 reflect similar tree sizes of focal tree and neighbors, whereas increasing values refer to increasing tree size differences |
| Mean directional index ($MDI_i$) | $\sqrt{\left(\sum_{j=1}^{n}\cos\alpha_{ij}\right)^2 + \left(\sum_{j=1}^{n}\sin\alpha_{ij}\right)^2}$ | $i$, focal tree; $n$, number of neighbor trees; $\alpha_{ij}$, angle between a line pointing away from the focal tree $i$ to neighbor $j$ and the reference bearing north | $MDI_i \in [0,4]$; values of 0 refer to a spatial arrangement in a square lattice, whereas increasing values represent a more clustered aggregation |
| Structural complexity index ($SCI_p$) | $\dfrac{SCI_p^*}{AT_p}$ where $SCI_p^* = \sum_{k=1}^{N}\dfrac{1}{2}\lvert a_k \times b_k \rvert$ | $AT_p$, sum of the projected areas of all triangles of sample plot $p$; $N$, number of triangles of sample plot $p$; $a_k \times b_k$, absolute value of vector product forming triangle $k$ | $SCI_p \in [1.0, 5.3]^a$; values of 1 reflect similar tree sizes within the sample plot, whereas increasing values refer to increasing tree size differences |
| Mingling index ($M_i$) | $\dfrac{1}{n}\sum_{j=1}^{n}m_{ij}$ where $m_{ij} = \begin{Bmatrix} 1, & species_i \neq species_j \\ 0, & \text{otherwise} \end{Bmatrix}$ | $i$, focal tree; $n$, number of neighbor trees | $M_i \in [0,1]$; values of 0 refer to no intermingling, whereas values of 1 mean that every neighbor belongs to a different species than the focal tree |

[a]This study. Values may vary based on stand conditions.

tories, 1–3 and 6 years after thinning, respectively. We then followed a procedure modified from Peck et al. (2014) in which all four spatially explicit structural diversity measures (TDM, MDI, SCI, and $M$) were regressed against all spatially nonexplicit structural diversity measures ($N$, RD, DBHm, DBHsd, DBHclass, GC, and H) using linear regression and data from the first two inventories. Only significant explanatory variables at the $\alpha < 0.05$ level with variance inflation factors less than 1.6 were retained in the regression models (function "vif" in R package "car"; Fox et al. 2014). The Akaike information criterion (AIC) was used for final model selection. Each final calibration model was then used to predict spatially explicit structural diversity measures for the final inventory conducted 11 years after thinning. To evaluate model performance and calibration and prediction accuracy, we calculated relative residual errors of the predicted values (% residual error) and root mean square errors (RMSE).

### 2.2.4. Relationships between stand growth and forest structure

To characterize forest growth at the sample-plot level, we first calculated individual-tree volume using Kozak's (2004) model 02 equation and species-specific parameters from southwestern Oregon (Hann and Weiskittel 2010). Missing tree heights were estimated using existing height measurements, Curtis' (1967) height–diameter equation with $\alpha_1 = 1$, and nonlinear mixed-effects modeling (R package "nlme"). The mixed-effects model had a variance structure to account for the increasing residual spread along the explanatory variable DBH and a nested random structure component on the intercept of plots within treatment units within study sites. Area-based annual net stand volume growth at the sample-plot level (PAI) was then calculated as the annual volume growth of survivor trees (accretion, $PAI_S$) plus the annual volume of ingrowth minus the annual volume lost to mortality. Given the zero-inflated structure of our ingrowth and mortality volume data, we used and subsequently analyzed count data instead of semi-continuous volume data (Affleck 2006; Li et al. 2011). We therefore calculated hectare-based annualized number of ingrowth trees ($COUNT_I$) and annualized number of dead trees (annual mortality, $COUNT_M$) at the sample-plot level. We annualized

the response variables PAI, $PAI_S$, $COUNT_I$, and $COUNT_M$ to account for uneven period lengths in the data (Table 2).

To evaluate the effects of forest structural heterogeneity (here the explanatory variable) on PAI, $PAI_S$, $COUNT_I$, and $COUNT_M$, we used a two-stage approach, which is described below in detail. The first stage compared the influence of site variables with the effect of structural diversity measures on volume growth and mortality. The second stage tested if adding structural diversity measures — in addition to site and stand variables — improved model predictions of volume growth, ingrowth, and mortality.

For the first stage, we used generalized boosted regression tree models to identify the most influential site variables and structural diversity measures. A generalized boosted regression tree model is a nonparametric technique that allows identification of key covariates and their relationship with the dependent variable while avoiding many of the shortcomings of forward or backward regression selection techniques (Elith et al. 2008). Generalized boosted regression tree models estimate the relative influence of explanatory variables. The measures are based on the number of times that a variable is selected for splitting (Friedman and Meulman 2003).

Using the R package "dismo" (Hijmans et al. 2013), we implemented generalized boosted regression tree models following procedures described in Elith et al. (2008) with a tree complexity of 5 and a bag fraction of 0.5, while increasing the learning rate from an initial 0.1 until the final model contained at least 1000 trees.

The site- and stand-related explanatory variables included initial (time of sample plot establishment) stand volume at the sample-plot level ($m^3 \cdot ha^{-1}$), non-Douglas-fir volume percentage (%), initial stand age (years), initial stand density (trees·$ha^{-1}$ at the sample-plot level), time since thinning (years), sample-plot elevation (metres above sea level), a topographic index (cosine of sample-plot aspect (in degrees) multiplied by sample-plot slope (in percent); Stage 1976), site index (site potential tree height (in metres) at the study-site level; Cissel et al. 2006), sample-plot mean annual temperature (°C), sample-plot mean annual precipitation

**Table 2.** Mean ± standard deviation (minimum–maximum) of stand metrics, environmental variables, and structural diversity measures at the sample plot level 6 years after thinning (PAI, PAIs, COUNT$_I$, COUNT$_M$ 6–11 years after thinning) by treatment.

| Variable or measure | Treatment | | | |
| --- | --- | --- | --- | --- |
| | CON | HD | MD | VD |
| No. of sample plots | 158 | 192 | 191 | 251 |
| $N$ (number of trees·ha$^{-1}$) | 564±232 (150–1510) | 332±138 (100–1120) | 274±193 (60–1770) | 241±119 (50–740) |
| Basal area (m$^2$·ha$^{-1}$) | 59.9±14.1 (21.9–89.5) | 43.3±12.3 (18.3–84.9) | 34.9±11.3 (6.0–81.7) | 33.2±13.7 (0.4–81.7) |
| % Douglas-fir | 73.9±30.0 (0–100) | 80.8±23.4 (16.8–100) | 79.8±26.9 (7.9–100) | 69.7±31.8 (0–100) |
| VOL (m$^3$·ha$^{-1}$) | 653±198 (198–1231) | 452±153 (173–1188) | 366±148 (42–963) | 352±153 (2–873) |
| PAI (m$^3$·ha$^{-1}$·year$^{-1}$) | 6.9±9.0 (−40.5–46.2) | 8.3±7.6 (−38.3–30.2) | 7.0±7.0 (−32.9–25.7) | 7.7±6.5 (−16.1–24.6) |
| PAIs (m$^3$·ha$^{-1}$·year$^{-1}$) | 14.0±5.1 (3.6–48.7) | 12.5±4.4 (4.0–39.1) | 10.8±4.0 (1.1–32.0) | 10.5±4.3 (0.3–24.6) |
| COUNT$_I$ (trees·ha$^{-1}$·year$^{-1}$) | 0.1±0.4 (0–2) | 0.4±1.2 (0–8) | 0.6±2.3 (0–22) | 1.5±4.5 (0–32) |
| COUNT$_M$ (trees·ha$^{-1}$·year$^{-1}$) | 16.2±20.5 (0–166) | 9.3±14.6 (0–114) | 9.2±18.6 (0–146) | 4.8±8.4 (0–72) |
| Elevation (m above sea level) | 520±179 (186–797) | 555±142 (200–789) | 550±171 (132–809) | 506±144 (207–773) |
| Topographic index | 6.4±28.7 (−86.6–76.6) | 2.1±27.5 (−66.0–78.8) | 3.1±24.8 (−88.6–108) | 3.7±23.9 (−113–62.6) |
| Temperature (°C)[a] | 9.7±1.0 (8.5–11.0) | 9.5±0.9 (8.3–10.8) | 9.6±0.9 (8.4–11.0) | 9.7±0.9 (8.5–10.9) |
| Annual precipitation (mm)[a] | 1865±377 (1330–2254) | 1892±352 (1428–2231) | 1880±378 (1340–2232) | 1846±355 (1389–2224) |
| GS precipitation (mm)[a] | 388±98 (277–524) | 393±92 (277–523) | 394±96 (281–526) | 388±96 (260–526) |
| Total AWC (mm)[a] | 220±37 (145–269) | 203±46 (122–269) | 202±60 (118–305) | 238±67 (145–380) |
| Site index (m)[b] | 63.1±5.8 (54.9–73.2) | 63.1±5.8 (54.9–73.2) | 63.1±5.8 (54.9–73.2) | 63.1±5.8 (54.9–73.2) |
| RD | 0.67±0.15 (0.26–1.00) | 0.46±0.12 (0.20–0.82) | 0.37±0.12 (0.07–0.88) | 0.35±0.14 (0.01–0.83) |
| DBHm | 36.0±6.8 (19.6–54.9) | 39.2±8.2 (21.6–60.1) | 40.7±9.6 (16.3–64.9) | 40.5±9.2 (6.9–62.2) |
| DBHsd | 12.8±3.7 (6.6–24.9) | 14.3±4.9 (5.9–35.7) | 13.3±4.6 (4.6–31.2) | 13.7±4.9 (1.5–28.2) |
| DBHclass | 12.8±2.2 (9–18) | 11.4±2.7 (5–17) | 9.8±2.7 (3–18) | 9.6±2.9 (2–19) |
| GC | 0.35±0.09 (0.19–0.61) | 0.35±0.13 (0.14–0.71) | 0.31±0.13 (0.10–0.69) | 0.32±0.13 (0.09–0.65) |
| $H$ | 0.49±0.32 (0–1.22) | 0.54±0.38 (0–1.42) | 0.50±0.38 (0–1.39) | 0.57±0.34 (0–1.49) |
| TDM | 0.31±0.07 (0.17–0.52) | 0.32±0.10 (0.14–0.56) | 0.30±0.11 (0.11–0.62) | 0.31±0.12 (0.08–0.62) |
| MDI | 1.93±0.20 (1.56–2.39) | 2.04±0.19 (1.63–2.70) | 2.08±0.20 (1.62–2.71) | 2.13±0.28 (1.53–3.35) |
| SCI | 2.58±0.57 (1.75–4.84) | 2.36±0.75 (1.27–5.27) | 2.06±0.63 (1.12–4.18) | 2.08±0.71 (1.08–4.89) |
| $M$ | 0.26±0.18 (0–0.63) | 0.29±0.21 (0–0.74) | 0.28±0.22 (0–0.73) | 0.33±0.20 (0–0.80) |

**Note:** % Douglas-fir, percentage of basal area in Douglas-fir; VOL, total standing volume; PAI, annual net volume growth; PAIs, annual volume growth of survivor trees; COUNT$_I$, annual number of ingrowth trees; COUNT$_M$, annual number of dead trees (mortality); GS precipitation, growing season precipitation; total AWC, total available water capacity; RD, relative density; DBHm, mean stand diameter (cm); DBHsd, standard deviation of tree diameters (cm); DBHclass, number of 4 cm diameter classes; GC, Gini coefficient; $H$, Shannon–Weaver index; TDM, mean DBH differentiation index; MDI, mean directional index; SCI, structural complexity index; $M$, mingling index.

[a]Calculated at the treatment unit level.

[b]Calculated at the site level.

(mm) and growing season precipitation (April to September, mm), sample-plot available water capacity (mm; Osborne 2013), and the presence or absence of precommercial thinning (Cissel et al. 2006; Dodson et al. 2012; Table 2). Climate data (average from 1961 to 1990) were obtained as custom data request from the Moscow Forestry Sciences Laboratory. Significant factors were deemed those with relative influence greater than expected from random variation, that is, relative influence > (total influence / number of factors) (Müller et al. 2013).

For the second stage of this analysis, we used mixed-effects models to test the degree of improvement achieved by adding structural and species diversity measures to growth- and mortality-prediction models based on the significant site and stand variables determined from the first stage. Analyses were run at various times using the hectare-based response variables PAI, PAI$_S$, COUNT$_I$, and COUNT$_M$ calculated for the two time periods 1–3 to 6 and 6 to 11 years following thinning. Using published literature (Liang et al. 2007; Lei et al. 2009), as well as the results from the generalized boosted regression tree models, we identified initial stand age, elevation, topographic index, initial stand volume, and non-Douglas-fir volume percentage as initial explanatory variables in the prediction models. Because of findings in previous studies and the outcome of the respective generalized boosted regression tree model, we replaced initial stand volume by initial stand density in the set of potential explanatory variables for the COUNT$_M$ dataset (Álvarez González et al. 2004; Affleck 2006).

Interactions between the most influential explanatory variable initial stand volume or initial stand density, respectively, and the remaining explanatory variables were tested but not included in the models because preliminary analysis indicated they had a limited influence and a more parsimonious model was desired. A base model that included no structural diversity measure was first calibrated for each response variable and served as a reference. The base models were derived by iteratively excluding insignificant explanatory variables in a stepwise procedure from each full growth-, ingrowth-, and mortality-prediction model until only significant predictors remained.

The continuous response variables PAI and PAI$_S$ were analyzed using linear mixed-effects models (R package "nlme") with a specified error correlation structure to account for the repeated measurements of each sample plot, a variance structure to account for the variability in stand volume at the beginning of the growth period, and a nested random effects structure on the intercept of sample plots within treatment units within study sites to account for site variation (Zuur et al. 2009). As above, an additional level of nesting of study sites within ecoregions did not improve the accuracy of the models. Based on (i) the visual examination of the model's underlying relationships between stand volume growth the initial hectare-based sample plot volume (data not shown) and (ii) the outcome of the above-described procedure to reduce the number of initial predictor variables, the following model forms were applied:

$$(1) \quad \text{PAI} = b_0 + b_1\text{AGE} + b_2\text{TI} + b_3\text{PercVOLnoDgl} + b_4\text{VOL} + b_5\text{VOL}^2 + b_6\text{SDM}$$

(2) $\quad \mathrm{PAI_S} = b_0 + b_1\mathrm{AGE} + b_2\mathrm{TI} + b_3\mathrm{PercVOLnoDgl} + b_4\mathrm{VOL}$
$$+ b_5\ln(\mathrm{VOL}) + b_6\mathrm{SDM}$$

where AGE is initial stand age (years), TI is topographic index, PercVOLnoDgl is non-Douglas-fir volume percentage, VOL is a hectare-based sample plot volume (m³·ha⁻¹) at the beginning of the growth period, and SDM represents one of several structural diversity measures; all other variables have been defined above. Here we used all four spatially explicit structural diversity measures (TDM, MDI, SCI, or $M$) and potential corresponding spatially nonexplicit counterparts (DBHsd, RD, GC, or $H$, respectively). Pairing the spatially nonexplicit and spatially explicit measures in parallel analyses allowed us to assess the added benefit, if any, of spatially explicit measures when predicting growth, ingrowth, or mortality, respectively.

We used zero-inflated generalized linear mixed-effects models (ZIGLMM) with a negative binomial error structure to analyze the overdispersed count datasets of $\mathrm{COUNT_I}$ and $\mathrm{COUNT_M}$ (Affleck 2006; Li et al. 2011). Using the R package "glmmADMB" (Skaug et al. 2013) allowed for the inclusion of the same nested random-effects structure as implemented in the PAI and $\mathrm{PAI_S}$ models. The systematic linear predictors of the generalized linear mixed-effects ingrowth and mortality models ($X\beta$; Zuur et al. 2009; Li et al. 2011) had the following forms:

(3) $\quad \mathrm{COUNT_I} = b_0 + b_1\mathrm{AGE} + b_2\mathrm{VOL} + b_3\mathrm{SDM}$

(4) $\quad \mathrm{COUNT_M} = b_0 + b_1\mathrm{AGE} + b_2\mathrm{ELEVAT} + b_3N + b_4\mathrm{SDM}$

where ELEVAT is sample plot elevation (metres above sea level) and $N$ is initial stand density at the sample-plot level at the beginning of the growth period (number of trees·ha⁻¹); all other variables have been defined above.

We used log likelihood (logLik), the Akaike information criterion (AIC), and the Bayesian information criterion (BIC) to compare the performance of the various models. Using the "lrtest" function of the R package "lmtest" (Hothorn et al. 2015), we performed likelihood ratio tests of the nested models comparing each individual base model with the ones including a structural diversity measure. In addition, likelihood-ratio based pseudo-$R^2$ were calculated for the PAI and PAIs prediction models using the function "r.squaredLR" of the R package "MuMIn" (Bartoń 2014). To test the goodness of fit of the $\mathrm{COUNT_I}$ and $\mathrm{COUNT_M}$ models, we calculated Pearson's $\chi^2$ test statistic, which is the sum of a model's Pearson residuals. A general indication of a good model fit is if the ratio of a model's Pearson's $\chi^2$ test statistic to its degree of freedom is close to 1 (Affleck 2006; Li et al. 2011). Finally, we also calculated mean absolute bias (MAB) and root mean square error (RMSE) of prediction for all models.

## 3. Results

### 3.1. Treatment effects on forest structural heterogeneity

Significant treatment effects on forest structural diversity were only found for the mixed effects models of $N$, RD, DBHm, DBHclass, MDI, and SCI (Table 3). As a result, differences in the analyzed structural diversity measures were mainly nonsignificant. This was especially true for the three thinning treatments (Figs. 1 and 2). However, the following general trends in the data were evident.

(1) The spatially nonexplicit structural diversity measures $N$, DBHclass, and RD were higher, and DBHm in the majority of cases was lower, in CON plots when compared with the three thinning treatments throughout the entire 10-year study period (Table 2; Fig. 1). $N$ decreased in CON and HD, whereas DBHm increased in all treatments over the course of the study period. No differences among treatments were found in $H$. $N$, DBHsd, DBHclass, GC, and

**Table 3.** Fit statistics for linear mixed-effects models evaluating the influence of treatment (TRT), time since thinning (Time), and the interaction of TRT and time since thinning (TRT × Time) on structural diversity measures at the sample plot level ($n = 1941$).

| Measure[a] | Statistic[b] | Value | Parameter estimate | | | |
|---|---|---|---|---|---|---|
| | | | Intercept | TRT | Time | TRT × Time |
| | numDF | | 1 | 3 | 2 | 6 |
| | denDF | | 1099 | 18 | 1099 | 1099 |
| $N$ | $R^2_{\mathrm{fixed}}$ | 0.39 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.96 | | | | |
| | $F$ value | | 340.6*** | 27.2*** | 148.8*** | 18.3*** |
| RD | $R^2_{\mathrm{fixed}}$ | 0.45 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.61 | | | | |
| | $F$ value | | 415.6*** | 40.4*** | 159.4*** | 6.7*** |
| DBHm | $R^2_{\mathrm{fixed}}$ | 0.11 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.42 | | | | |
| | $F$ value | | 557.6*** | 3.6* | 474.5*** | 4.7*** |
| DBHsd | $R^2_{\mathrm{fixed}}$ | 0.02 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.19 | | | | |
| | $F$ value | | 451.1*** | 0.9 | 31.9*** | 2.1 |
| DBHclass | $R^2_{\mathrm{fixed}}$ | 0.20 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.91 | | | | |
| | $F$ value | | 659.7*** | 32.0*** | 49.7*** | 1 |
| GC | $R^2_{\mathrm{fixed}}$ | 0.04 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.17 | | | | |
| | $F$ value | | 686.9*** | 1.3 | 64.1*** | 3.8*** |
| $H$ | $R^2_{\mathrm{fixed}}$ | 0.01 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.43 | | | | |
| | $F$ value | | 30.1*** | 1.8 | 17.7*** | 4.2*** |
| TDM | $R^2_{\mathrm{fixed}}$ | 0.03 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.18 | | | | |
| | $F$ value | | 700.5*** | 0.2 | 69.3*** | 3.3** |
| MDI | $R^2_{\mathrm{fixed}}$ | 0.09 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.16 | | | | |
| | $F$ value | | 6478.2*** | 29.1*** | 4.9** | 0.8 |
| SCI | $R^2_{\mathrm{fixed}}$ | 0.10 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.26 | | | | |
| | $F$ value | | 584.4*** | 7.5** | 28.8*** | 5.0*** |
| $M$ | $R^2_{\mathrm{fixed}}$ | 0.02 | | | | |
| | $R^2_{\mathrm{fixed\&random}}$ | 0.50 | | | | |
| | $F$ value | | 24.6*** | 3.0 | 4.5* | 3.3** |

**Note:** Significance: *, $p \le 0.05$; **, $p \le 0.01$; ***, $p \le 0.001$.

[a]$N$, number of trees·ha⁻¹; RD, relative density; DBHm, mean stand diameter (cm); DBHsd, standard deviation of tree diameters (cm); DBHclass, number of 4 cm diameter classes; GC, Gini coefficient; $H$, Shannon–Weaver index; TDM, mean DBH differentiation index; MDI, mean directional index; SCI, structural complexity index; $M$, mingling index.

[b]numDF, numerator degrees of freedom for all models; denDF, denominator degrees of freedom for all models; $R^2_{\mathrm{fixed}}$, generalized coefficient of determination for fixed effects only; $R^2_{\mathrm{fixed\&random}}$, generalized coefficient of determination with the inclusion of random effects.

$H$ increased slightly from the first inventory to the second inventory (1–3 and 6 years after thinning, respectively) in most treatments, but a reverse trend was often observed towards the end of the study, with VD plots being the exception in DBHsd and $H$ (Fig. 1).

(2) Irrespective of the treatment, spatially explicit structural diversity measures changed only marginally over time (Fig. 2). TDM, SCI, and $M$ increased slightly in the first few years but often decreased to initial levels towards the end of the study period, with VD plots again being the exception in SCI and $M$. In compar-

**Fig. 1.** Change in spatially nonexplicit stand metrics of mean DBH (DBHm), standard deviation of DBH (DBHsd), Gini coefficient (GC), and Shannon–Weaver index (*H*) at the sample-plot level by treatment throughout the study period: control (CON: initial inventory 1–3 years after thinning, *n* = 68; second and final inventories (6 and 11 years after thinning, respectively), *n* = 158), high-density thinning (HD: initial inventory, *n* = 54; second and final inventories, *n* = 192), moderate-density thinning (MD: initial inventory, *n* = 63; second and final inventories, *n* = 191), and variable-density thinning (VD: initial inventory, *n* = 121; second and final inventories, *n* = 254). Depicted least-squares means and standard errors were derived from linear mixed-effects models.
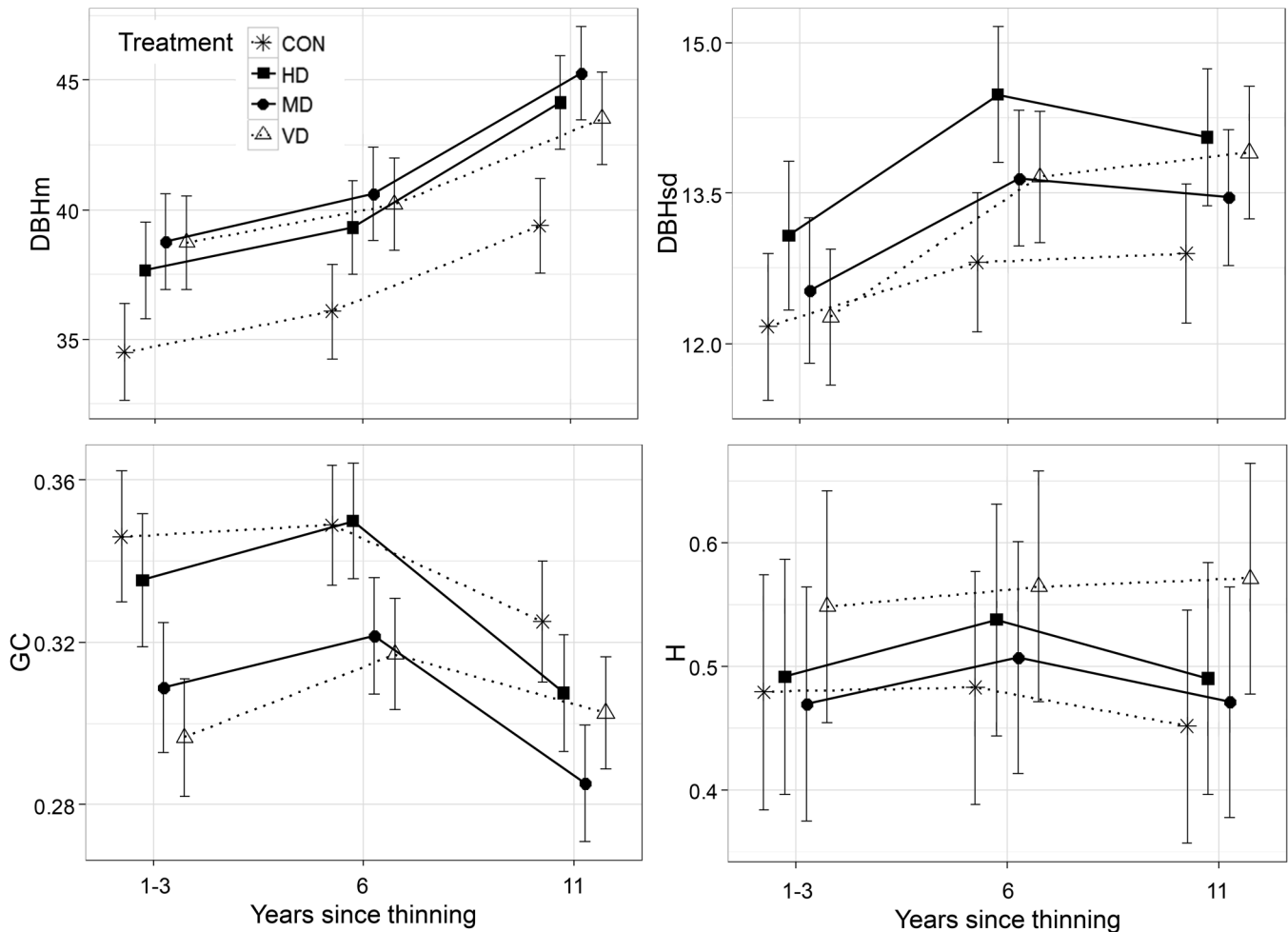


ison with the three thinning treatments, CON plots had higher SCI and lower MDI throughout the 10-year study period. Among the thinning treatments, SCI and MDI were initially highest in HD and VD, respectively. The differences, however, had diminished by the end of the study period.

### 3.2. Relationships between structural diversity measures

Strong to very strong positive correlations were found between the spatially nonexplicit stand metrics DBHsd, DBHclass, and GC and the spatially explicit measures TDM and SCI (*r* = 0.56–0.87; Table 4). TDM was also strongly correlated with DBHm (−0.54) and *H* (0.52). *M* was strongly correlated only with *H* (0.92), while MDI was best correlated with RD (−0.47).

Calibration models with satisfactory model statistics using spatially nonexplicit structural diversity measures were derived for the spatially explicit indices TDM, *M*, and SCI (Table 5). Mean prediction errors at the sample-plot level were reasonable for all three models, but there was considerable variation in these values. Despite a lower adjusted *R*² , the calibration model for MDI performed as well as the three other models, resulting in comparable mean relative residual errors.

### 3.3. Relationships between forest structure, growth, ingrowth, and mortality

Preliminary evaluation of forest growth and mortality revealed that $PAI_S$ and $COUNT_M$ decreased with greater thinning intensity, whereas $COUNT_I$ increased (Table 2).

In comparison with typical stand and environmental predictor variables, spatially nonexplicit and spatially explicit structural diversity measures contributed similarly to the generalized boosted regression tree models for PAI, $PAI_S$, $COUNT_I$, and $COUNT_M$ (Table 6). To better compare the contributions of spatially explicit structural diversity measures and their potential spatially nonexplicit counterparts, we formed groups based on the preceding correlation analysis (Table 4). The total cumulative contributions of the four spatially explicit structural diversity measures TDM, MDI, SCI, and *M* varied considerably in comparison with the contribution of the spatially nonexplicit DBHsd, RD, GC, and *H*, mainly because of the importance of RD, and represented, on average, 21% and 13%, respectively, over all four generalized boosted regression tree models (Table 6).

The inclusion of a spatially nonexplicit structural diversity measure (DBHsd, RD, GC, or *H*) or the potential spatially explicit counterpart (TDM, MDI, SCI, and *M*, respectively) proved to be

**Fig. 2.** Change in spatially explicit measures of mean DBH differentiation index (TDM), mean directional index (MDI), structural complexity index (SCI), and mingling index (*M*) at the sample-plot level in control (CON), high-density thinning (HD), moderate-density thinning (MD), and variable-density thinning (VD) treatments throughout the study period. Depicted least-squares means and standard errors were derived from mixed-effects models. See Fig. 1 for number of sample plots per treatment and measurement period.
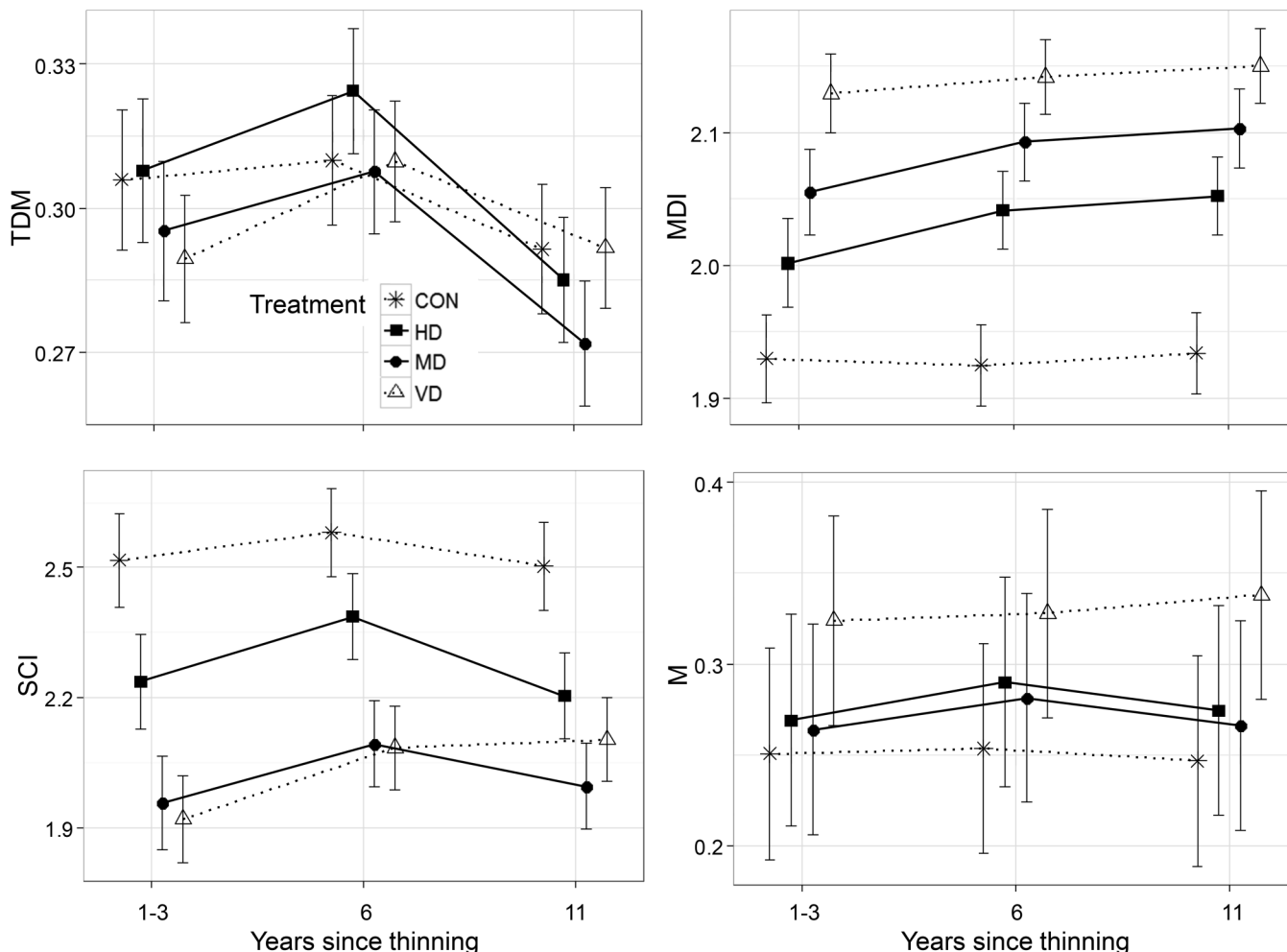


**Table 4.** Correlation matrix depicting relationships between spatially nonexplicit and spatially explicit structural diversity measures calculated at the sample-plot level.

| Measure | Spatially nonexplicit | | | | | | | Spatially explicit | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | *N* | RD | DBHm | DBHsd | DBHclass | GC | *H* | TDM | MDI | SCI | *M* |
| *N* | 1 | | | | | | | | | | |
| RD | 0.73 | 1 | | | | | | | | | |
| DBHm | −0.58 | −0.04 | 1 | | | | | | | | |
| DBHsd | −0.06 | 0.03 | −0.08 | 1 | | | | | | | |
| DBHclass | 0.50 | 0.62 | −0.26 | 0.56 | 1 | | | | | | |
| GC | 0.40 | 0.13 | −0.63 | 0.74 | 0.66 | 1 | | | | | |
| *H* | 0.20 | 0.04 | −0.35 | 0.41 | 0.32 | 0.50 | 1 | | | | |
| TDM | 0.21 | 0.01 | −0.54 | 0.78 | 0.56 | 0.87 | 0.52 | 1 | | | |
| MDI | −0.31 | −0.47 | 0.00 | 0.27 | −0.12 | 0.22 | 0.18 | 0.22 | 1 | | |
| SCI | 0.43 | 0.40 | −0.40 | 0.71 | 0.74 | 0.81 | 0.42 | 0.79 | 0.06 | 1 | |
| *M* | 0.08 | −0.02 | −0.24 | 0.40 | 0.24 | 0.39 | 0.92 | 0.50 | 0.14 | 0.37 | 1 |

**Note:** *N*, number of trees·ha$^{-1}$; RD, relative density; DBHm, mean stand diameter (cm); DBHsd, standard deviation of tree diameters (cm); DBHclass, number of 4 cm diameter classes; GC, Gini coefficient; *H*, Shannon–Weaver index; TDM, mean DBH differentiation index; MDI, mean directional index; SCI, structural complexity index; M, mingling index.

significant in 17 of the 32 mixed-effects models that evaluated the relationships between hectare-based net volume growth, ingrowth, or mortality and structural diversity measures (Tables 7 and 8). COUNT$_I$ and COUNT$_M$ prediction models almost always improved when adding a structural diversity measure, whereas only three of the total 16 PAI and PAIs models with a structural diversity measure performed better than the respective base model. However, we found no or only marginal improvement in prediction accuracy as a result of a significant structural diversity measure despite lower AICs and BICs. Low overall prediction ac-

**Table 5.** Fit and prediction statistics of best multiple linear regression models using spatially non-explicit stand metrics to predict the spatially explicit structural diversity measures mean DBH differentiation index (TDM), mean directional index (MDI), structural complexity index (SCI), and mingling index ($M$) at the sample-plot level.

| Response | Parameter[a] | Estimate | Adj. $R^2$ | Calibration % residual error (min to max) RMSE | Prediction % residual error (min to max) RMSE |
|---|---|---|---|---|---|
| TDM | Intercept | 0.31108 | 0.85 | −2 (−128 to +40) | −1 (−182 to +83) |
| | RD | −0.02418*** | | 0.0400 | 0.0433 |
| | DBHm | −0.00564*** | | | |
| | DBHsd | 0.01632*** | | | |
| | $H$ | 0.01827*** | | | |
| MDI | Intercept | 2.13167 | 0.31 | −1 (−38 to +43) | ±0 (−30 to +36) |
| | RD | −0.67788*** | | 0.2060 | 0.2017 |
| | DBHsd | 0.01374*** | | | |
| | $H$ | 0.06587*** | | | |
| SCI | Intercept | 1.27432 | 0.76 | −2 (−66 to +72) | ±0 (−57 to +83) |
| | RD | 0.00219*** | | 0.3414 | 0.3865 |
| | DBHm | −0.02717*** | | | |
| | DBHsd | 0.10311*** | | | |
| $M$ | Intercept | −0.05012 | 0.85 | −1 (−492 to +627) | −1 (−392 to +613) |
| | DBHm | 0.00215*** | | 0.1861 | 0.1890 |
| | DBHclass | −0.00321*** | | | |
| | $H$ | 0.56093*** | | | |

**Note:** Calibration models were derived from inventories conducted 1–3 and 6 years after thinning, whereas data collected 11 years after thinning was used to evaluate prediction accuracy. Asterisks denote significant effects of the explanatory variables: *, $p \le 0.05$; **, $p \le 0.01$; ***, $p \le 0.001$.

[a]RD, relative density; DBHm, mean stand diameter (cm); DBHsd, standard deviation of tree diameters (cm); $H$, Shannon–Weaver index; DBHclass, number of 4 cm diameter classes.

**Table 6.** Summary of the relative contributions (%) of explanatory variables for generalized boosted regression tree models for hectare-based annual net volume growth (PAI), annual volume growth of survivor trees (PAI$_S$), annual number of ingrowth trees (COUNT$_I$), and annual number of dead trees (mortality, COUNT$_M$) at the sample-plot level.

| Explanatory variable | PAI | PAI$_S$ | COUNT$_I$ | COUNT$_M$ | Mean[b] |
|---|---|---|---|---|---|
| Stand volume | 12.3 | 25.3 | 5.7 | 1.8 | 11.3 |
| Elevation | 4.9 | 2.8 | 8.6 | 5.1 | 5.4 |
| Stand age | 6.5 | 9.3 | 2.6 | 2.7 | 5.3 |
| Topographic index | 6.6 | 3.9 | 6.6 | 2.6 | 4.9 |
| % Non-Douglas-fir volume | 6.7 | 7.7 | 3.4 | 1.1 | 4.7 |
| Mean annual precipitation | 1.5 | 1.3 | 7.8 | 1.4 | 3.0 |
| Mean annual temperature | 2.3 | 1.7 | 4.9 | 0.1 | 2.3 |
| Growing season precipitation | 3.3 | 2.3 | 1.1 | 1.3 | 2.0 |
| Time since thinning | 2.3 | 2.8 | 1.5 | 0.6 | 1.8 |
| Available water capacity | 1.3 | 0.8 | 3.4 | 0.4 | 1.5 |
| Site index | 0.1 | 0.1 | 0.7 | 0.5 | 0.4 |
| Precommercial thinning | 0.1 | 0.7 | 0.0 | 0.0 | 0.2 |
| Structural diversity measures[a] | | | | | |
| DBHm | 5.1 | 3.2 | 5.5 | 32.5 | 11.6 |
| $N$ | 4.5 | 3.3 | 1.3 | 34.9 | 11.0 |
| RD | 10.4 | 15.8 | 14.5 | 2.3 | 10.8 |
| MDI | 6.6 | 3.7 | 6.8 | 0.9 | 4.5 |
| GC | 4.0 | 2.0 | 4.0 | 5.9 | 4.0 |
| DBHsd | 5.6 | 2.2 | 4.1 | 0.8 | 3.2 |
| TDM | 3.6 | 2.0 | 5.9 | 1.1 | 3.1 |
| SCI | 4.3 | 3.9 | 1.8 | 1.9 | 3.0 |
| $M$ | 2.7 | 1.5 | 5.7 | 0.9 | 2.7 |
| $H$ | 2.8 | 1.6 | 2.8 | 0.8 | 2.0 |
| DBHclass | 2.3 | 1.8 | 1.2 | 0.4 | 1.4 |

[a]DBHm, mean stand diameter (cm); $N$, number of trees·ha$^{-1}$; RD, relative density; MDI, mean directional index; GC, Gini coefficient; DBHsd, standard deviation of tree diameters (cm); TDM, mean DBH differentiation index; SCI, structural complexity index; $M$, mingling index; $H$, Shannon–Weaver index; DBHclass, number of 4 cm diameter classes.

[b]Mean contribution over all generalized boosted regression tree models.

curacy in all PAI models mainly stemmed from large retention tree mortality. The resulting strongly negative sample plot level growth rates caused high variability in the data and thus inhibited a better fit. To evaluate a potential interaction between measures of tree size and species diversity, a final model including both terms and their interaction was developed (GC × $H$). The model indicated that the interaction was not significant ($p = 0.0893$), while only GC remained statistically significant ($p = 0.0385$) when the interaction was removed.

No clear trend was found with regard to whether the inclusion of spatially nonexplicit or spatially explicit structural diversity measures resulted in better prediction model performance. Higher tree species diversity and species interspersion ($H$, $M$), as well as higher tree size variation and interspersion (DBHsd, SCI, TDM), significantly increased mortality and ingrowth. Higher levels of crowding (MDI) lowered ingrowth but increased mortality and hence decreased net volume growth PAI. PAI was also negatively related to tree size inequality (GC), which also significantly increased ingrowth and mortality. With the exception of a significantly positive effect of RD, prediction of PAIs was not improved by any of the tested structural diversity measures.

## 4. Discussion

### 4.1. Treatment effects on forest structure

Eleven years after thinning, stand metrics and structural diversity measures of the control plots differed only marginally from plots of the three thinning treatments. Aside from obvious variation in stocking ($N$ and RD) in the control plots, we found significant differences only in average tree size (larger DBHm in MD), tree aggregation (a more clustered spatial distribution of trees as reflected in higher MDI in all thinning treatments), and lower canopy ruggedness (SCI) in MD and VD. Although RD, GC, TDM, and SCI suggested slightly higher structural heterogeneity in the control plots when compared with HD, MD, and VD throughout the entire study period, DBHsd, $H$, MDI, and $M$ suggested the opposite. A more pronounced difference in structural heterogeneity between the control and thinned plots was likely inhibited

**Table 7.** Fit statistics of linear mixed-effects models for hectare-based annual net volume growth (PAI) and annual volume growth of survivor trees (PAI$_S$).

| Model[a] | $b_0$ | $b_1$ | $b_2$ | $b_3$ | $b_4$ | $b_5$ | $b_6$ | logLik | AIC | BIC | MAB | RMSE | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **PAI** | | | | | | | | | | | | | |
| Base | 23.253 | −0.458 | −0.015 | 0.0007 | 0.039 | −0.00003 | | −3621 | 7266 | 7326 | 4.577 | 6.723 | 0.27 |
| +DBHsd | 23.254 | −0.458 | −0.015 | 0.0007 | 0.039 | −0.00003 | −0.001 | −3621 | 7268 | 7333 | 4.577 | 6.723 | 0.27 |
| +TDM | 23.315 | −0.456 | −0.015 | 0.0002 | 0.039 | −0.00003 | −0.585 | −3621 | 7268 | 7333 | 4.575 | 6.721 | 0.27 |
| +RD | 23.611 | −0.463 | −0.016 | 0.0001 | 0.043 | −0.00003 | −3.742 | −3621 | 7268 | 7333 | 4.574 | 6.730 | 0.27 |
| +MDI | 27.740 | −0.444 | −0.018 | −0.0056 | 0.036 | −0.00003 | −2.072** | −3617** | 7261 | 7326 | 4.563 | 6.713 | 0.28 |
| +GC | 23.366 | −0.440 | −0.018 | 0.0004 | 0.039 | −0.00003 | −3.325* | −3619* | 7264 | 7329 | 4.556 | 6.699 | 0.28 |
| +SCI | 23.274 | −0.443 | −0.016 | −0.0003 | 0.039 | −0.00003 | −0.420 | −3620 | 7267 | 7332 | 4.388 | 6.488 | 0.28 |
| +$H$ | 23.421 | −0.457 | −0.017 | 0.0012 | 0.039 | −0.00003 | −0.693 | −3620 | 7267 | 7332 | 4.571 | 6.717 | 0.28 |
| +$M$ | 23.431 | −0.459 | −0.016 | 0.0002 | 0.039 | −0.00003 | −0.532 | −3621 | 7268 | 7333 | 4.574 | 6.721 | 0.27 |
| **PAI$_S$** | | | | | | | | | | | | | |
| Base | −1.047 | −0.032 | −0.0009 | 0.0010 | −0.0009 | 0.933 | | −44 | 111 | 171 | 0.182 | 0.254 | 0.66 |
| +DBHsd | −1.042 | −0.032 | −0.0009 | 0.0010 | −0.0009 | 0.932 | −0.001 | −43 | 113 | 178 | 0.182 | 0.254 | 0.66 |
| +TDM | −1.076 | −0.032 | −0.0009 | 0.0011 | −0.0009 | 0.936 | 0.087 | −43 | 112 | 177 | 0.182 | 0.254 | 0.66 |
| +RD | −0.940 | −0.031 | −0.0008 | 0.0013 | −0.0011 | 0.897 | 0.344* | −41* | 109 | 174 | 0.182 | 0.253 | 0.66 |
| +MDI | −0.769 | −0.032 | −0.0009 | 0.0012 | −0.0009 | 0.905 | −0.078 | −42 | 109 | 174 | 0.182 | 0.252 | 0.66 |
| +GC | −1.057 | −0.032 | −0.0009 | 0.0010 | −0.0009 | 0.934 | 0.043 | −43 | 113 | 178 | 0.182 | 0.254 | 0.66 |
| +SCI | −1.035 | −0.032 | −0.0009 | 0.0010 | −0.0009 | 0.932 | −0.008 | −43 | 113 | 178 | 0.182 | 0.254 | 0.66 |
| +$H$ | −1.044 | −0.032 | −0.0009 | 0.0009 | −0.0009 | 0.931 | 0.039 | −43 | 112 | 177 | 0.182 | 0.254 | 0.66 |
| +$M$ | −1.063 | −0.032 | −0.0009 | 0.0009 | −0.0009 | 0.934 | 0.062 | −43 | 112 | 177 | 0.182 | 0.254 | 0.66 |

**Note:** Asterisks denote significant effects ($b_6$) or significant differences to the base model (logLik) associated with the inclusion of a spatially nonexplicit (DBHsd, RD, GC, $H$) or spatially explicit structural diversity measure (TDM, MDI, SCI, $M$): *, $p \leq 0.05$; **, $p \leq 0.01$.

[a]See Material and methods for details on model forms and equations. DBHsd, standard deviation of tree diameters; TDM, mean DBH differentiation index; RD, relative density; MDI, mean directional index; GC, Gini coefficient; SCI, structural complexity index; $H$, Shannon–Weaver index; $M$, mingling index.

**Table 8.** Fit statistics of zero-inflated generalized linear mixed-effects models for hectare-based number of ingrowth trees (COUNT$_I$) and hectare-based number of dead trees (mortality, COUNT$_M$).

| Model[a] | $b_0$ | $b_1$ | $b_2$ | $b_3$ | $b_4$ | logLik | AIC | BIC | MAB | RMSE | Pearson's $\chi^2$/df |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **COUNT$_I$** | | | | | | | | | | | |
| Base | 4.409 | −0.064 | −0.003 | | | −902 | 1820 | 1860 | 0.940 | 1.230 | 1.515 |
| +DBHsd | 5.076 | −0.098 | −0.003 | 0.080*** | | −895*** | 1809 | 1854 | 0.976 | 1.408 | 1.984 |
| +TDM | 4.836 | −0.095 | −0.003 | 3.234*** | | −895*** | 1808 | 1853 | 0.968 | 1.425 | 2.032 |
| +RD | 4.136 | −0.062 | −0.006 | 2.813 | | −901 | 1820 | 1865 | 0.936 | 1.257 | 1.581 |
| +MDI | 4.769 | −0.061 | −0.003 | −0.218 | | −902 | 1822 | 1867 | 0.936 | 1.222 | 1.495 |
| +GC | 5.183 | −0.097 | −0.003 | 2.676** | | −896*** | 1810 | 1855 | 0.990 | 1.478 | 2.186 |
| +SCI | 4.962 | −0.093 | −0.004 | 0.525*** | | −896*** | 1810 | 1855 | 0.951 | 1.360 | 1.851 |
| +$H$ | 4.648 | −0.084 | −0.003 | 1.143*** | | −896*** | 1811 | 1856 | 0.994 | 1.565 | 2.452 |
| +$M$ | 3.777 | −0.076 | −0.003 | 2.642*** | | −892*** | 1801 | 1846 | 0.998 | 1.684 | 2.838 |
| **COUNT$_M$** | | | | | | | | | | | |
| Base | −5.177 | 0.089 | 0.001 | 0.003 | | −2876 | 5770 | 5815 | 0.816 | 0.981 | 0.964 |
| +DBHsd | −5.104 | 0.076 | 0.001 | 0.003 | 0.048*** | −2857*** | 5733 | 5784 | 0.811 | 0.988 | 0.978 |
| +TDM | −5.365 | 0.075 | 0.001 | 0.003 | 2.772*** | −2846*** | 5711 | 5761 | 0.817 | 0.999 | 1.001 |
| +RD | −5.232 | 0.097 | 0.001 | 0.004 | −1.515*** | −2866*** | 5751 | 5801 | 0.831 | 0.994 | 0.999 |
| +MDI | −6.352 | 0.086 | 0.001 | 0.003 | 0.621*** | −2866*** | 5751 | 5801 | 0.824 | 1.024 | 0.988 |
| +GC | −4.902 | 0.069 | 0.001 | 0.002 | 3.218*** | −2818*** | 5657 | 5707 | 0.834 | 0.997 | 1.050 |
| +SCI | −5.096 | 0.075 | 0.001 | 0.002 | 0.394*** | −2850*** | 5720 | 5770 | 0.818 | 0.991 | 0.994 |
| +$H$ | −5.214 | 0.083 | 0.001 | 0.003 | 0.702*** | −2858*** | 5735 | 5785 | 0.825 | 0.983 | 0.983 |
| +$M$ | −5.335 | 0.087 | 0.001 | 0.003 | 0.867*** | −2869*** | 5757 | 5807 | 0.817 | 0.981 | 0.967 |

**Note:** Asterisks denote significant effects ($b_3$ or $b_4$) or significant differences to the base model (logLik) associated with the inclusion of a spatially nonexplicit (DBHsd, RD, GC, $H$) or spatially explicit structural diversity measure (TDM, MDI, SCI, $M$), respectively: *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

[a]See Material and methods for details on model forms and equations. DBHsd, standard deviation of tree diameters; TDM, mean DBH differentiation index; RD, relative density; MDI, mean directional index; GC, Gini coefficient; SCI, structural complexity index; $H$, Shannon–Weaver index; $M$, mingling index.

by the comparatively short time period since the thinning, the initial comparatively low structural forest heterogeneity of the studied stands prior to treatment implementation, and the thinning-from-below prescriptions (cf. Bose et al. 2015). The relatively homogeneous and predominantly even-aged secondary Douglas-fir forests of the Density Management Study did not offer much structural heterogeneity to be enhanced or promoted at the onset of the study (Cissel et al. 2006). Although, for example, individuals of uncommon tree species were deliberately retained in the course of the thinning operations, the relative enrichment did not enhance tree species diversity ($H$ and $M$) because of the initial low number of such trees (Dodson et al. 2012). In addition and as seen in SCI and GC, the thinning-from-below prescription created a more homogenous and more simplified structure in the

matrix of the thinning treatments by removing under- and mid-story trees and by creating a more uniform spatial tree distribution (Zenner et al. 2011; Dodson et al. 2012).

Although not analyzed here, retention tree islands and patch cuts potentially enhanced forest structural heterogeneity in the otherwise homogenous thinning treatments. However, this enhancement of structural heterogeneity at the treatment-unit level seems to have been counterbalanced by the structural loss of intermediate and suppressed trees still found in the control plots. We believe that tree recruitment (ingrowth) in the thinned matrix and in the patch cuts resulted in higher MDI and DBHsd, denoting a stronger clustering of trees and a larger variation in tree diameter (higher MDI and DBHsd), respectively (Kuehne and Puettmann 2008; Zenner and Peck 2009). Our finding of comparable forest structural heterogeneity in the control and thinned plots may also support a recent assertion that secondary young Douglas-fir stands are not as homogenous and limited in forest structure as they have often been portrayed (Spies and Franklin 1991; Dodson et al. 2012). In fact, six of the seven sites of the Density Management Study established naturally after clearcutting with or without residuals and without site preparation (Cissel et al. 2006). In comparison with the uniformly spaced large-scale plantations that are much more common today, considerable initial small-scale spatial variability in tree density and tree size (Tappeiner et al. 1997; Donato et al. 2012; Freund et al. 2014), as well as in tree species diversity and the spatial aggregation of trees (Lutz and Halpern 2006), is therefore very likely for these sites. This initial variability in stand structure might have contributed to the lack of more pronounced differences in structural heterogeneity between the control and thinned plots.

Forest structural heterogeneity did not differ significantly among the three thinning treatments of this study. This was most likely a result of the highly comparable silvicultural prescriptions of each of the thinning treatments, which all contained under-plantings, riparian buffers, leave islands, and canopy openings (only MD and VD) of varying sizes (Cissel et al. 2006). Because of the inclusion of these structurally enriching management elements, HD and MD very much resembled VD, which in turn prevented distinctly different development pathways towards higher structural heterogeneity. However, VD plots showed constant structural enrichment in this study as tree size, tree species diversity, tree clustering, and canopy ruggedness (DBHsd, $H$, $M$, MDI, and SCI) continuously increased over the course of the three inventories. In contrast, several measures increased initially (e.g., DBHsd, SCI, and $M$) but often returned to initial levels towards the end of the study period in the HD and MD units. The contrasting trends were likely the result, at least in part, of the varying stand dynamics in the matrix of the different thinning treatment units. Thinning in all treatments promoted establishment and growth of saplings that swiftly surpassed the DBH threshold and thus became recruited several years after thinning (Dodson et al. 2012, 2014). Likely as a result of this ingrowth, almost all structural diversity measures displayed increased heterogeneity in the course of the first measurement period 1–3 to 6 years after thinning, irrespective of the thinning treatment.

However, thinning also changed growth characteristics of the majority of residual trees, causing slower crown recession and enhanced crown expansion leading to increasing canopy closure (Davis et al. 2007). Reduced light levels consequently caused mortality among the ingrowth, especially for less shade-tolerant hardwood species in the second phase of the study period (6 to 11 years after thinning), as has been shown previously (Dodson et al. 2012). The loss of previously established trees was more pronounced in HD and MD where tree density in the matrix was targeted at 300 or 200 trees·ha$^{-1}$, respectively, whereas in VD, the retention level varied between 100 and 300 trees·ha$^{-1}$. Increased mortality rates and lower probabilities of ingrowth trees during the second measurement period 6 to 11 years following thinning in HD and MD as

compared with VD appear to further verify this assertion (see also Dodson et al. 2012).

The observed patterns and trends in the structural diversity measures can be linked to stand dynamics and successional pathways that have been intensively studied for Douglas-fir forest ecosystems in recent years, in part to draw insights on the formation and accrual of forest structural heterogeneity (e.g., Halpern and Lutz 2013; Tepley et al. 2013). Decreasing stand density ($N$) and a trend of decreasing tree species diversity ($H$ and $M$) suggest that the majority of control plots were still in the stem exclusion stage of forest stand development (Oliver and Larson 1996; see also Franklin et al. 2002). Stands in this stage experience high density-dependent mortality rates as they follow the self-thinning trajectory (Reineke 1933; Lutz and Halpern 2006), while differentiation into crown classes leads to canopy stratification as suggested in comparatively high SCI values in our study (Barnes et al. 1998). The eventual death of intermediate and suppressed trees through the stem exclusion stage also leads to a more regular tree spatial patterning, reflected in low MDI values of our control plots.

In contrast, thinning triggered a shift to an understory re-initiation stage that in turn fostered recruitment of new individuals (Oliver and Larson 1996). The understory re-initiation stage usually follows the stem exclusion stage when large canopy gaps resulting from the death of mature trees are no longer fully occupied and closed by gap edge tree crown expansion (Van Pelt and Nadkarni 2004). As a result of the improved light conditions, existing or newly established seedlings and saplings experience rapid diameter and height growth, eventually creating a new canopy layer and thus enhancing structural heterogeneity (Larson et al. 2008). Recruitment in patch cuts and the thinned matrix of this study consisted mainly of species other than Douglas-fir, resulting in increased tree species diversity ($H$ and $M$; Kuehne and Puettmann 2008). Because ingrowth often occurs in clusters, MDI values signaled a tendency towards a more aggregated tree spatial distribution (e.g., Buermeyer and Harrington 2002). Lower tree density ($N$, RD), larger tree size (DBHm), higher tree species diversity ($H$ and $M$), a pronounced tree size variation (DBHsd), and a more irregular tree distribution (MDI) were all characteristics described as being lacking in rather structurally poor Douglas-fir second growth but found in structurally complex Douglas-fir old-growth (Spies and Franklin 1991; Van Pelt and Nadkarni 2004; Freund et al. 2015). Recent studies have shown that secondary Douglas-fir forests can develop higher forest structural heterogeneity comparatively early, irrespective of deliberate management interventions (Gerzon et al. 2011; LePage and Banner 2014). The observed patterns and trends in the analyzed structural diversity measures of our study suggest that this natural dynamics towards higher structural heterogeneity was at least in part accelerated by the silvicultural manipulations evaluated here (Zenner 2005; Bauhus et al. 2009; Bose et al. 2015).

## 4.2. Relationships between structural diversity measures

The spatially nonexplicit DBHsd and GC measures proved to be strongly correlated with the spatially explicit TDM and SCI measures, while as expected, the spatially nonexplicit metric $H$ was highly correlated with spatially explicit $M$. Our findings therefore corroborate results of previous studies that reported similar strong relationships and found prediction models with comparable precision (Zenner 2000; Sterba and Zingg 2006; Peck et al. 2014). Because GC was strongly correlated to DBHm and DBHsd, predictors that together apparently explained more variation in the TDM and SCI data than did GC alone, GC was not selected as an independent variable in the respective linear prediction models. Nonetheless, the strong associations of GC with several spatially nonexplicit stand metrics and spatially explicit diversity measures suggested its superiority for differentiating between varying stand structures (Sterba and Zingg 2006; Peck et al. 2014). Because all of our prediction models showed wide ranges in prediction

error, this study confirmed a recent finding that spatially explicit structural diversity measures cannot be reliably modeled using only spatially nonexplicit stand metrics (Peck et al. 2014). This proved to be especially true for MDI, a spatially explicit aggregation index that is comparable to the Clark and Evans' (1954) *R* index.

The lack of a better MDI prediction model may be attributable to the stands having a rather simple forest structure that did not differ strongly among each other (Peck et al. 2014). However, the predictor variables tree density (RD in this study) and DBHsd selected for our MDI prediction model are also strongly associated with the Clark and Evans' (1954) index, as has been shown in previous works that explored associations across structurally more heterogeneous forests (Zenner 2000; Neumann and Starlinger 2001). Additional work on this issue in forests with a wider range of species and stand structures is needed to fully confirm these findings.

### 4.3. Relationships between forest structure, stand growth, ingrowth, and mortality

Although often only marginal in their effect, the inclusion of a spatially nonexplicit stand metric or a spatially explicit structural diversity measure proved to be statistically significant in a few stand volume growth models, as well as most of the ingrowth and mortality prediction models. Tree species diversity (*H*, *M*) tended to be associated with both increased mortality (thereby reducing net stand volume growth) and ingrowth (increasing net stand volume growth), likely resulting in no effect on total volume growth, whereas tree aggregation (MDI) was associated with increased mortality and thus lower net volume growth. The observed similar positive effects of tree species diversity and tree size variation on the number of ingrowth trees likely reflects the presence of subcanopy seed source trees of shade-tolerant species (e.g., western hemlock), as well as resprouting and fast-growing species (e.g., bigleaf maple, red alder). As above, such stand structures eventually may result in higher tree mortality once the overstory canopy closes towards the end of the study period.

Our findings corroborate previous studies showing that structural diversity measures can contribute to models aimed at predicting stand growth and mortality (Sterba and Monserud 1995; Liang et al. 2005, 2007; Young et al. 2011). Outcomes of these previous studies, however, were not always in agreement with each other, and our results likewise fit this pattern (Edgar and Burk 2001; Lei et al. 2009). For example, tree species diversity metrics were likely not influential in our analysis because of the limited number of species present. Consequently, different age or cohort structures of the studied forest ecosystems, as well as different modeling approaches, might explain the varying findings (O'Hara 1996; Woodall et al. 2009). In addition, when both tree species and tree size diversity, as well as their potential interaction, were included in the same model, the tree size diversity metric was the only influential factor. Given the small number of species present and the limited change in species diversity with time, this suggests that the observed changes in structural heterogeneity were caused more by size differentiation within a species rather than by size differentiation between species.

We suspect that spatially nonexplicit structural diversity metrics performed as well as or even better than spatially explicit measures because (*i*) volume growth and mortality were analyzed at the sample-plot level, (*ii*) the small-scale spatial diversity indices were averaged to derive sample plot values (except for SCI), and (*iii*) the measures used depend on sample plot size. In general, spatially explicit approaches are thought to require sample plot sizes larger than those of spatially nonexplicit approaches, although there is no consensus on the optimal sample plot size. In this analysis, a 0.1 ha sample plot size was used, which we deemed sufficient for capturing the variation in forest structure and tree spatial patterns given the initial stand conditions and species

composition. In fact, the 0.1 ha sample plot size used in this analysis was consistent with the size used in several other studies that have used spatially explicit metrics (e.g., Saunders and Wagner 2008), whereas it was much larger than sample plot sizes used in some studies (e.g., Zenner et al. 2011; Zenner and Hibbs 2000).

We assume that the spatially explicit measures TDM, MDI, and *M* that characterize forest structure for tree neighborhoods would outperform spatially nonexplicit metrics if growth or mortality were modelled and predicted at the individual-tree level (D'Amato and Puettmann 2004; Puettmann et al. 2009; Fraver et al. 2014). Thus, although spatial information was not especially beneficial in predicting growth or mortality at the sample-plot level, as demonstrated in this study, it may be quite beneficial for predictions at the individual-tree level, suggesting that tree-level (neighborhood) information may not scale up to sample plot level predictions. In a subsequent analysis, we will test this hypothesis by analyzing the effect of the structural diversity measures used here on individual-tree volume growth and mortality.

## 5. Conclusions

This study found only marginal differences in stand structural heterogeneity among the various treatments, most likely because of the short developmental time assessed (<12 years). Given the observed continuous structural enrichment, however, our results tend to confirm previous findings suggesting that variable-density thinning appears to be a suitable management tool to increase structural heterogeneity in young even-aged stands (Harrington et al. 2005; Zenner et al. 2011; O'Hara et al. 2012). However, thinning operations may have to go beyond traditional thinning-from-below prescriptions to accomplish this goal as the changes in structure observed in this study were relatively small. For example, high thinning operations (i.e., thinning from above) that not only release overstory trees, but also retain mid- and under-story trees, might further accelerate the development of structural heterogeneity (Peck et al. 2014; Bose et al. 2015). Of course, long-term observations of forest structure and tree spatial distribution following thinning will be needed to verify this, highlighting the importance of studies like the Density Management Study used in this analysis. Given the changes in structure and tree spatial arrangement following thinning observed in this analysis, these attributes likely need to be reflected in growth and mortality models despite the marginal gain in predictive performance. However, the specific relationship between stand structure, as reflected by various structural measures, and stand growth needs further research.

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