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ARTICLE

Local testing and calibration of species-specific competition indices in Sierran mixed-conifer forests: application transfer to evolving objectives

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Abstract: Forest growth processes are driven by site productivity and species functional traits, which are ultimately constrained by cumulative resource demand, resulting in competitive dynamics across successional forest communities. Historical efforts to quantify competition used density metrics or neighborhood crowding indices for yield modeling and reforestation surveys. These methods have expanded to include dendroclimatology and restoration applications that commonly assume similar competitive response across species of various functional types. We assessed the competitive indices of two focal species, *Pinus lambertiana* (Dougl.) and *Pinus ponderosa* (Dougl. ex P. Laws. & C. Laws.) in mixed-conifer forests of the Sierra Nevada to estimate stem radial growth under current stand structure. We ranked correlations of basal area increment of the last 10 years (BAI_{10}) separately across 20 competition indices (CIs). The best-ranked CIs were used to test the relative influence of competition, tree size, and site variables on BAI_{10} with linear mixed models. While crown overlap was a common variable in CIs among both species, BAI_{10} of *P. lambertiana* was less impacted by intraspecific competition, and *P. ponderosa* appeared sensitive to all competing stems. The results suggest that local calibration of CIs with crown parameters may aid in interpreting *Pinus* species growth patterns and that the relative impact of competition on growth is species specific.

Key words: tree competition, silviculture, stand dynamics, Sierra Nevada, mixed conifer.

Résumé : Les processus de croissance des forêts sont déterminés par la productivité de la station et les caractéristiques fonctionnelles des espèces tout en étant ultimement limités par la demande cumulative de ressources, ce qui entraîne une dynamique de concurrence entre les communautés forestières qui se succèdent. Les efforts antérieurs visant à quantifier la concurrence ont utilisé des mesures de densité ou des indices d'abondance locale des arbres pour modéliser la production et planifier les inventaires de reboisement. Ces méthodes se sont étendues aux applications en dendroclimatologie et en restauration qui supposent généralement une réaction concurrentielle similaire entre les espèces de différents types fonctionnels. Nous avons évalué les indices de concurrence de deux espèces d'intérêt, *Pinus lambertiana* (Douglas) et *Pinus ponderosa* (Douglas ex. P. Lawson et C. Lawson), dans des forêts mixtes de conifères de la Sierra Nevada pour estimer la croissance radiale des arbres avec la structure actuelle des peuplements. Nous avons ordonné les corrélations de l'accroissement en surface terrière des 10 dernières années (AST_{10}) séparément pour 20 indices de concurrence (IC). Les IC les mieux classés ont été utilisés pour tester l'influence relative de la concurrence, de la taille des arbres et des variables de la station sur AST_{10} à l'aide de modèles mixtes linéaires. Même si le chevauchement des cimes était une variable commune aux IC des deux espèces, AST_{10} de *P. lambertiana* était moins influencé par la concurrence intraspécifique et *P. ponderosa* semblait sensible à tous les arbres concurrents. Les résultats indiquent que l'étalonnage local des IC avec des paramètres de la cime peut aider à interpréter les patrons de croissance des espèces du genre *Pinus*, et que l'impact relatif de la concurrence sur la croissance est propre à chaque espèce. [Traduit par la Rédaction]

Mots-clés : concurrence entre les arbres, sylviculture, dynamique des peuplements, Sierra Nevada, forêts mixtes de conifères.

Introduction

Competition in forest vegetation communities reflect species-specific functional traits and collective demand for site-limiting resources, resulting in hierarchical structures and composition along successional gradients. Index-based estimates of tree and stand competition simplify complex biogeochemical processes and use areal mean density or tree-level neighborhood crowding metrics to predict survival and growth patterns (Burton 1993). Initial forest management applications of competition indices (CIs) were oriented to the prediction of tree growth and yield for timber commodity production (e.g., Krajicek et al. 1961; Bella 1971). These concepts were later adapted to assess the need for non-crop tree vegetation management in stand-regeneration stocking surveys (Brand 1986). More recently, CIs have been used to partition the variance of growth factors according to causal mechanisms and to isolate tree response to climatic conditions (Looney et al. 2016, 2018; Ford et al. 2017; Young et al. 2017), to build a framework that incorporates restoration objectives (Johnson et al. 2017; Slack et al. 2017), and to investigate experimental thinning simulations in mixed-species stands (Premer et al. 2017).

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However, the utility of traditional growth- and yield-oriented competition metrics may not capture the structural characteristics of the mixed-conifer cover type (sensu Dickinson et al. 2019) or align with contemporary restoration-oriented silvicultural practices. Therefore, a review of species-specific competitive frameworks is necessary to transfer the application of CIs to forest restoration and interpretation of growth response to dynamic causal factors.

Decades of wildfire suppression have shifted the composition and disturbance regimes of mixed-conifer forests of the North American Interior West (Fry et al. 2014). These changes are reflected in overly dense stands of shade-tolerant *Abies concolor* (Lindl. ex Hildebr.) and *Calocedrus decurrens* (Torr.) in California, coupled with increased susceptibility to crown fires (Cassell et al. 2019) and pest outbreaks (Ferrell 1996). In the Sierran mixed-conifer forests, both *Pinus lambertiana* (Dougl.) and *Pinus ponderosa* (Dougl. ex P. Laws. & C. Laws.) are focal species of thinning restoration treatments. Forest managers commonly use thinning to achieve fuel reduction, enhanced residual stem growth, and vigor of legacy *P. lambertiana* and *P. ponderosa* trees (Zhang et al. 2013, 2019), and promotion of heterogeneous structure (Churchill et al. 2013).

A common assumption in discerning the relative factors that influence mixed-conifer growth patterns is the uniform application of a single, static competition index (CI) across species with various functional traits (Battles et al. 2008; Das 2012). In some cases, applications may be beyond foundational settings of even-aged, single-species forest types. Species vary in their growth and mortality response to the defined metric of competition, and preliminary analyses aim to anneal model parameter estimates separately by species (Gómez-Aparicio et al. 2011). Yet, effort is seldom taken to review and calibrate localized, species-specific indices prior to testing the relative influence of tree size and climate on growth, as originally suggested by Alemdag (1978) and Noone and Bell (1980). Instead, a generalized, one-dimensional size-ratio weighted-distance approach is used (e.g., Hegyi 1974), assuming similar growth response across species, with adjustments for intraspecific and interspecific competition (Canham et al. 2004; Gómez-Aparicio et al. 2011). These approaches are useful in forming estimates of growth patterns at the landscape scale, yet broad generalizations based on regional means may fail to capture species patterns at the local, operational level.

While *P. lambertiana* and *P. ponderosa* belong to the same genus, they exhibit different mechanisms of regeneration and different responses to competition (Oliver 1996). Yet, in contemporary work in the Sierra Nevada, these species are regarded as proxies for one another when setting restoration objectives and interpreting climatic effects on vegetation (Johnson et al. 2017; Ma et al. 2018; Slack et al. 2017; Young et al. 2017). *Pinus lambertiana* is generally confined to the Mediterranean climate of the Sierra Nevada, Klamath, and Cascade ranges, where the species occurs in solitary or small groups of individual trees owing in part to irregularity in seed production, high seed predation, seedling drought stress, and infestation of blister rust caused by *Cronartium ribicola*. The species is noted for its moderate shade tolerance and ability to rapidly exploit and occupy canopy gaps through expansion of foliage and associated basal area, with stand growth contributions heavily disproportionate to growing stock (growth is approximately 500% of stock; Kinloch and Scheuner 1990) in gap recruitment events.

In contrast, *P. ponderosa* is an expansive generalist with noted regional plasticity, forming groups of cohorts scattered within mixed-conifer stands, and is dependent on frequent fires for seedbed preparation and control of competing species (Oliver and Ryker 1990). Height and radial growth are sensitive to density, and low shade tolerance inhibits regeneration and growth under moderate canopy coverage and low light availability (Zhang et al. 2013). Given the noted differences in species ecology, the application of a single, one-dimensional CI may fail to capture competitive effects in mixed-conifer forests. Other approaches to estimate tree response to competition in temperate mixed forests have demonstrated favorable performance for some species when using spatially explicit indices of crowding with modifications of traditional metrics of stem size-ratio (Ek and Monserud 1974; Lorimer 1983; Boeck et al. 2014; Kuehne et al. 2019). However, a relative comparison of competitive responses among focal tree species in mixed-conifer stands of the Sierra Nevada has been untested since the original work by Biging and Dobbertin (1992, 1995), which did not include *P. lambertiana*.

Given the noted differences in species ecology, changes in mixed-conifer forest structure and composition, and need for quantitative tools in restoration silvicultural support, our objectives were to assess the radial growth response of focal *P. lambertiana* and *P. ponderosa* to local competition indices. Our specific objectives were to (*i*) evaluate *P. lambertiana* and *P. ponderosa* tree growth with estimated competition across a range of indices; (*ii*) generate predictions of focal tree radial growth based on CI, tree, and site variables; (*iii*) assess patterns in intraspecific and interspecific competition; and (*iv*) test the relative contribution of competitor attributes on CI estimates. We anticipated that the growth response of *P. lambertiana* would be less impacted by competition than that of *P. ponderosa*, in parallel with differences in their shade tolerance. We expected *P. ponderosa* to exhibit correlations with symmetric competition of local density, and *P. lambertiana* growth to reflect the explicit spatial structure of neighboring stems. We further assumed that the radial growth of *P. lambertiana* would be comparatively less sensitive to intraspecific competition.

Materials and methods

Site description

We used a dataset of tree measurements collected in three contiguous stands (<5 km apart) located at 1500–1550 m elevation within a management subunit of the Lassen National Forest in Plumas County, California, USA. The climate in the study area is characterized as Mediterranean, featuring cool, wet winters and hot, dry summers, with mean temperatures ranging from 1.4 to 18.6 °C. The area receives ~1100 mm of mean annual precipitation, mainly in the form of snow during the dormant season (National Climate Data Center 2016). The soil types include Ultic and Vitrandic Haploxeralfs of volcanic origin that support a mixed-conifer forest common to the mid-elevation Sierra Nevada range. *Pinus lambertiana* and *P. ponderosa* are the dominant canopy species, both characteristically mid-early seral with moderate and low shade tolerance, respectively (Kinloch and Scheuner 1990; Oliver and Ryker 1990). High densities of shade-tolerant *A. concolor* and *C. decurrens* occupy the smaller size classes (Table 1). The natural disturbance regime is characterized by frequent low-intensity fires that have maintained pine-dominated stand density levels at 1–30 $m^2 cha^{-1}$; stands have since shifted to a greater proportion of *A. concolor* and *C. decurrens* relative to past levels in the absence of disturbance events (Fry et al. 2014). The current density of the study area is ~64.7 ± 9.13 $m^2 \cdot ha^{-1}$ across 318 ± 124 trees·ha^{-1} with diameter at breast height (DBH) > 20.3 cm (mean ± standard deviation) *Abies concolor* and *C. decurrens* maintain the highest densities of small to moderate size stems, while large-diameter *Pinus* sp. trees occupy the larger size classes and upper canopy strata. Further detailed descriptions of site conditions and historical stand structure can be found in Johnson et al. (2017).

Study design and field measurements

Preliminary sampling efforts used transects to survey the frequency and spatial distribution of large-diameter (DBH > 63.5 cm) stems of *P. lambertiana* and *P. ponderosa* to identify focal release trees in a planned restoration thinning project, where one of the objectives was to improve the vigor of these large pine trees using variable-radial release treatments. A total of 36 circular 260 m^2

Table 1. Number, mean, and range of all trees (focal and competitors) measured in the focal tree radial release treatment plots.

Species	*n*	DBH (cm)	Height (m)	Crown length (m)	Crown width (m)	BAI_{10} (cm)
Focal trees						
Pinus lambertiana	20	96.7 (63.5–128.0)	35.2 (21.9–47.5)	12.3 (4.65–28.4)	10.6 (5.8–16.6)	4.8 (0.6–8.6)
Pinus ponderosa	16	85.4 (64.0–112.0)	35.3 (21.3–45.1)	15.4 (4.8–31.4)	8.95 (6.74–12.1)	2.8 (0.7–6.2)
Competitor trees						
Abies concolor	277	35.5 (20.3–95.5)	15.2 (10–31.1)	10.7 (0.1–22.1)	5.5 (3.46–9.3)	2.9 (1.5–5.9)
Calocedrus decurrens	67	41.7 (21.1–86.4)	15.5 (5.6–29.7)	10.4 (1.5–18.2)	5.8 (4.7–9.7)	1.4 (0.1–7.8)
Pinus lambertiana	39	68.1 (29.5–110.0)	27.4 (11.6–37.5)	11.1 (3.9–21.3)	8.1 (3.7–14.4)	4.1 (1.3–8.3)
Pinus ponderosa	50	66.3 (36.8–100.0)	29.7 (14.5–41.8)	13.2 (3.1–26.2)	7.5 (5.0–11.2)	1.8 (0.7–3.6)

Note: DBH, diameter at breast height; BAI_{10}, basal area increment of the last 10 years.

sampling plots centered on the selected largest focal trees were established in 2014–2015, with greater sampling intensity of *P. lambertiana* (n = 20) than *P. ponderosa* (n = 16). All trees with DBH > 20.3 cm had their DBH and species recorded in parallel with minimum merchantable diameter limits in an upcoming harvest. The plot size corresponds with the standard gap-opening radial release treatments common to the ownership and silvicultural regime and aligns with the tree neighborhood scale recommendations by Lorimer (1983). Plot-level stem maps were generated by measuring the total distance and azimuth from the focal tree to each competitor. All trees within each focal release plot were measured for DBH (cm), total height (m), height to live crown (m), and crown width (m). Two perpendicular tree cores were extracted at a height of 0.5 m from all focal trees for dendrochronology analysis. Extracted tree cores were cross-dated using the list method (Yamaguchi 1991) and measured in CooRecorder, with statistical cross-dating conducted in COFECHA (Holmes 1983). For this study, we calculated basal area increment (BAI_{10}) across the 10-year period prior to field sampling (2005–2014) on each cored tree by taking the mean of the perpendicular cores. Across the sampled trees, *P. lambertiana* maintained the greatest BAI_{10} growth over the period of interest, followed by *A. concolor*, *P. ponderosa*, and *C. decurrens* (Table 1).

Calculation of competition indices

BAI_{10} response to competition was quantified across all measured plots using 20 CIs that are (*i*) the most commonly cited in the literature, (*ii*) included as the default setting in primary forest growth and yield simulation systems, and (*iii*) developed in similar regions or forest types as those reported here. We included 13 distance-dependent CIs (Table 2; index No. 1–13) and seven distance-independent indexes (Table 2; index No. 14–20) to calculate CI values at the plot level across all stands. The distance-independent CIs are attractive because implicit tree-crowding metrics do not require a detailed plot stem map and are common in growth predictions of forest simulation models. Krajicek et al. (1961) defines the CI as the sum of open-grown crown area as a proportion of plot size. For our purposes, we estimated open-grown crown metrics with the CA variant (Inland California and Southern Cascades) of the Forest Vegetation Simulator (Keyser 2019). Brand's (1986) approach uses competitor height to account for light availability in relation to the focal tree. Glover and Hool (1979) provide a simple ratio of the competitor-tree DBH to the plot-level DBH arithmetic mean, and Reineke's (1933) stand density index (SDI) relates the current stand density to an equivalent number of trees per unit area in a stand with a quadratic mean diameter (QMD) of 25.4 cm.

In parallel with the approaches by Kuehne et al. (2015), we included a spatially independent structural metric of tree size distribution through a mean DBH differentiation index (TDM; Füldner 1995) and assessed species diversity and interspersion with an intermingling index (Mingling; von Gadow 1993; Pastorella and Paletto 2013). Spatially explicit CIs require intensive measurements to create localized stem maps and have varied performance in predicting BAI trends across species and silvicultural activities. Early work by Bella (1971) quantified competition across even-aged forest types as the overlap of crown and basal diameter among stems; this work was later modified to adjust for competition by species (Canham et al. 2004) with a scaling approach to accommodate

Table 2. Distance-dependent and distance-independent competition index (CI) equations by source used in the analysis.

Index No.	CI name	Equation
Distance-dependent competition index		
1	Bella	$\sum_{i=1}^{n}(O_{ij} \times d_i)/(Z \times d_j)$
2	Biging and Dobbertin	$\sum_{i=1}^{n}(CC_i/CC_j) \times (Dist_{ij}+1)$
3	Canham et al.	$\sum_{i=1}^{n}\lambda_i(d_i)^{\alpha}/(Dist_{ij})^{\beta}$
4	Ek and Monserud	$\sum_{i=1}^{n}(Z_i/O_{ij}) \times [(h_i \times CW_i)/(h_j \times CW_j)]$
5	Hegyi	$\sum_{i=1}^{n} d_i/(d_j \times Dist_{ij})$
6	Lorimer	$\sum_{i=1}^{n}(d_i/d_j)/Dist_{ij}$
7	MDI	$\left[\left(\sum_{i=1}^{n}\cos a_{ij}^2\right)+\left(\sum_{i=1}^{n}\sin a_{ij}^2\right)\right]^{0.5}$
8	Rouvinen 1	$\sum_{i=1}^{n}\arctan(d_i/Dist_i)$
9	Rouvinen 2	$\sum_{i=1}^{n}(d_i/d_j) \times \arctan(d_i/Dist_i)$
10	Rouvinen 3	$\sum_{i=1}^{n}\arctan(h_i/Dist_i)$
11	Rouvinen 4	$\sum_{i=1}^{n}(h_i/h_j) \times \arctan(h_i/Dist_i)$
12	SCI	$\frac{SCI}{A_t}$; $SCI = \sum_{k=1}^{N}\frac{1}{2}\lvert a_k \times b_k\rvert$
13	Tome and Burkhart	$\sum_{i=1}^{n}(d_j/d_i) \times (1/Dist_{ij})$
Distance-independent competition index		
14	Basal area	$\sum_{i=1}^{n} d_i^2(\pi/4)$
15	Brand	$\sum_{i=1}^{n}(h_i \times c_i/n)/h_j$
16	Glover and Hool	$d_j^2/\left[\left(\sum_{i=1}^{n} d_i\right)/n\right]$
17	Krajicek	$\sum_{i=1}^{n}[(\pi \times CW_i^2)/4]/S$
18	Mingling	$1/n\sum_{i=1}^{n} m_{ij}$; $m = [1, sp_i \neq sp_j, 0]$
19	Reineke	$10^{(\log N+1.605\log QMD-1.605)}$
20	TDM	$1-1/n\sum_{i=1}^{n}\min(d_i,d_j)/\max(d_i,d_j)$

Note: DBH is a general reference to tree diameter at breast height, d_i and d_j is the DBH of the competitor and subject trees, respectively. O_{ij} is the crown overlap area between the subject and competitor tree, Z_i is the zone of influence, CC represents the crown area at 66% of the tree's height, and α_{ij} is the angle reference between a reference bearing and the competitor tree. $Dist_{ij}$ corresponds to the distance (m) between stems, and h_j and h_i represent the total height of the subject and competitor trees. α, β, and λ estimate the crowding scale, distance adjustments, and interspecies modifiers, respectively, and $a_k \times b_k$ are the absolute value of the vector ***ab*** product forming the kth triangle, where A_t is the sum of the triangular projection.

Table 3. Scaling parameter estimates of the Canham et al. (2004) index (CI 3), where α, β, and λ estimate the crowding scale, distance adjustments, and intraspecies–interspecies modifiers, respectively.

Parameter	*Pinus lambertiana*	*Pinus ponderosa*
α	2.01 (1.83–2.18)	2.83 (2.59–3.07)
β	0.72 (0.65–0.78)	0.73 (0.67–0.79)
λ		
Abies concolor	0.40 (0.01–0.21)	0.43 (0.19–0.68)
Calocedrus decurrens	0.29 (0.09–0.49)	0.22 (0.11–0.77)
Pinus ponderosa	0.48 (0.13–0.76)	0.33 (0.18–0.84)
Pinus lambertiana	0.27 (0.0–0.47)	0.26 (0.43–0.96)

intraspecies–interspecies competition and anneal the generalized size-ratio approach to localized conditions. Scaling parameters for the Canham index (CI 3) were fit to the dataset and estimated using maximum likelihood (Table 3). Perhaps a less reported approach that is similar to Bella's (1971) work used the crown overlap approach and modified by relative tree crown height in northern hardwoods of the Great Lakes region (Ek and Monserud 1974). Further work in jack pine (*Pinus banksiana* Lamb.) stands by Hegyi (1974) found a strong correlation between growth and differences in stem diameter and proximity of individuals; this work was later modified to reflect crown dynamics in mixed-conifer stands (Biging and Dobbertin 1992). Spatially dependent models originally developed in loblolly pine (*Pinus taeda* L.) (Daniels 1976) were extended to northern hardwood applications by Lorimer (1983) through a straightforward size ratio by the inter-tree distance method. Rouvinen and Kuuluvainen (1997) extended this approach to include combinations of horizontal and vertical angle summation modifiers in Scots pine (*Pinus sylvestris* L.) stands, and has been investigated in *P. ponderosa* growth dynamics in the intermountain west (Contreras et al. 2011), similar to our work reported here.

We omitted the traditional basal area larger index (Wykoff et al. 1982), as our focal trees were the largest in the study plots, and thus the competitive values default to zero. Plot-level stem spatial uniformity and clustering was assessed with a mean directionality index (MDI; Corral-Rivas 2006) originally established in mixed *Pinus* sp. forests of central Mexico and outlined in Kuehne et al. (2015). Finally, we used a Delaunay triangulation routine to estimate a diameter-based spatially explicit structural diversity index along horizontal gradients (SCI) following Zenner and Hibbs (2000).

Statistical analyses

Initial analyses examined the correlations of focal tree BAI_{10} across all calculated plot competition values using Spearman's correlation statistics for ranking using base functions in the R software programming environment (v 3.5.1; R Core Team 2018). The best-ranked species-specific CIs were subsequently identified for modeling and further analysis. CI and BAI_{10} values were square-root and log transformed, respectively, to stabilize variance, and then assessed with Shapiro–Wilk's test and qqplots. The base BAI_{10} model was estimated as a function of stem size (DBH), cumulative competition (CI), and their interaction, with stand treated as a random effect because of the hierarchical nature of the data, using the nlme package (Pinheiro et al. 2017) and the following model form:

$$(1)\quad \mathrm{BAI}_{10_i} = \beta_{10_i} + \beta_{11_i}\log\mathrm{DBH} + \beta_{12_i}\mathrm{CI}^{0.5} + \beta_{13_i}\log\mathrm{DBH}\times\mathrm{CI}^{0.5} + \varepsilon_i$$
$$i = 1,2,3 \quad \beta_i \sim N(0,\sigma_i^2) \quad \varepsilon_i \sim N(0,\sigma^2)$$

where DBH is diameter at breast height (1.37 m) of the focal tree, CI is the corresponding best-ranked species-specific CI value from results of the Spearman's rank test, β_{10}–β_{13} are the fixed effects associated with the focal tree, i is the additive random effect at the stand level, and ε_{ij} is the model residual, following the procedures of Smith (1977) and Noone and Bell (1980).

Models were fit separately for each focal tree species (*P. lambertiana*, *P. ponderosa*). To test the effects of intraspecific and interspecific competition on focal tree growth, we partitioned the best-performing CI by competitor species with additional terms as follows:

$$(2)\quad \mathrm{BAI}_{10_i} = \beta_{10_i} + \beta_{11_i}\log\mathrm{DBH} + \beta_{12_i}\mathrm{CI}^{0.5} + \beta_{13_i}\log\mathrm{DBH}\times\mathrm{CI}^{0.5} + \beta_{14_i}\mathrm{CI}_{\mathrm{ABCO}}^{0.5} + \beta_{15_i}\mathrm{CI}_{\mathrm{CADE}}^{0.5} + \beta_{16_i}\mathrm{CI}_{\mathrm{PILA}}^{0.5} + \beta_{17_i}\mathrm{CI}_{\mathrm{PIPO}}^{0.5} + \varepsilon_i$$

where β_{10}–β_{17} are fixed effects, as defined in eq. 1, and the subscripts ABCO, CADE, PILA, and PIPO correspond to the partitioned CI values calculated for *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa*, respectively.

Next, we evaluated several additional stem attributes (total height, crown ratio, height/diameter ratio) and site variables, including elevation, slope, aspect, and topographic index (Stage 1976), to identify covariates of focal tree growth response not explicitly captured in the framework of the base model. We evaluated key covariates and candidate model performance through all possible subsets using the regsubsets function in the leaps package (Lumley 2020) and assessed multi-collinearity with a variance inflation factor threshold of 2. Final candidate models of growth response for each focal species were compared using Akaike information criterion (AIC) values and Akaike weights, implemented with the MuMIn package (Bartoń 2020). Finally, we assessed the relative influence of competition variables (i.e., stem size, species, distance) and contribution to plot-level CI using the following form:

$$(3)\quad \mathrm{CI}^{0.5} = \beta_{20_i} + \beta_{21_i}X_{1_i} + \ldots + \beta_{n_i}X_{n_i} + \varepsilon_i$$

where $X_1, \ldots, X_n$ are parameters specific to the best-ranked CI with focal tree growth (e.g., crown width, total height, height to live crown), $B_{20_i}, \ldots, B_{n_i}$ are the coefficients of the competitive parameters, and ε_i is the residual. CIs with multiple predictor variables were compared with all subsets and models assessed with performance metrics as previously described. Figures were created using the visreg package (Breheny and Burchett 2020) and base R functions. A significance level of $\alpha = 0.05$ was used for all tests. We calculated mean absolute bias (MAB) and residual mean standard error (RMSE) of the final BAI_{10} and CI predictive models to assess goodness of fit.

Results

Correlation of BAI_{10} and competition index

Results from the Spearman's rank correlation tests revealed species-specific patterns of BAI correlation, with distance-dependent CIs generally exhibiting stronger correlations with growth than with the spatially implicit approaches (Table 4) as well as with the locally annealed one-dimensional estimators (CI 3). The plot-level estimates of focal species across all tested CIs are presented in Table 5. The BAI_{10} for sugar pine exhibited a significant correlation with the Bella index (CI 1; $r = -0.430$, $p = 0.027$; Table 4) and includes a zone of crown overlap, focal tree crown area, and relative differences in subject and competitor tree stem diameter. *Pinus lambertiana* sample plots for Bella's CI ranged from 0.01 to 1.83 (Table 5). Similarly, *P. ponderosa* showed strong correlations with Bella's index ($r = -0.596$, $p = 0.011$; Table 4) across a similar range. Yet, results suggest that the highest-ranked CI for *P. ponderosa* was Ek and Monserud (CI 4; $r = -0.618$ and $p = 0.008$), which uses total height of competing neighbors in addition to crown overlap and crown width.

Table 4. Results of Spearman's rank correlation test of BAI_{10} and included competition indices (CI).

		Pinus lambertiana		*Pinus ponderosa*	
Index No.	CI	*r*	*p*	*r*	*p*
1	Bella	−0.430	0.027	−0.596	0.011
2	Biging	0.066	0.614	0.211	0.779
3	Canham	0.040	0.571	−0.239	0.195
4	Ek and Monserud	−0.294	0.098	−0.618	0.008
5	Hegyi	−0.082	0.362	−0.357	0.096
6	Lorimer	−0.072	0.354	−0.293	0.144
7	MDI	0.192	0.801	0.130	0.676
8	Rouvinen 1	0.086	0.760	0.086	0.623
9	Rouvinen 2	0.043	0.421	0.043	0.564
10	Rouvinen 3	0.043	0.715	0.043	0.564
11	Rouvinen 4	−0.121	0.445	−0.121	0.333
12	SCI	−0.279	0.110	−0.341	0.117
13	Tome and Burkhart	0.184	0.112	0.004	0.508
14	Basal area ($m^2 \cdot ha^{-1}$)	−0.021	0.465	−0.300	0.138
15	Brand	−0.032	0.445	−0.286	0.151
16	Glover and Hool	0.099	0.667	0.096	0.638
17	Krajicek	−0.368	0.506	−0.368	0.089
18	Mingle	0.068	0.615	−0.023	0.470
19	Reieneke	0.106	0.680	−0.096	0.367
20	TDM	−0.111	0.317	−0.359	0.104

Note: See Table 2 for definition of competition indices. BAI_{10}, basal area increment of the last 10 years.

Table 5. Mean and range in plot-level competition index (CI) values by focal tree species.

Index No.	CI	*Pinus lambertiana*	*Pinus ponderosa*
1	Bella	0.61 (0.01–1.83)	0.52 (0.01–1.62)
2	Biging and Dobbertin	2.66 (0.50–11.97)	2.09 (0.29–7.82)
3	Canham et al.	0.60 (0.12–1.00)	0.39 (0.01–1.00)
4	Ek and Monserud	0.28 (0.01–0.89)	0.33 (0.01–0.89)
5	Hegyi	0.84 (0.32–3.11)	0.65 (0.18–1.75)
6	Lorimer	4.20 (1.57–15.1)	3.31 (0.91–8.75)
7	MDI	2.72 (1.35–4.0)	2.22 (1.07–3.94)
8	Rouvinen 1	13.12 (6.79–30.50)	10.55 (5.08–19.17)
9	Rouvinen 2	5.85 (2.64–15.59)	4.75 (1.90–8.53)
10	Rouvinen 3	10.44 (5.13–25.00)	8.41 (3.41–15.71)
11	Rouvinen 4	5.44 (2.27–14.07)	4.22 (1.19–8.66)
12	SCI	2.42 (1.81–3.24)	2.67 (1.94–3.37)
13	Tome and Burkhart	−5.40 (−17.21 to −1.10)	−4.03 (−16.25 to −1.01)
14	Basal area	16.71 (4.47–19.91)	13.33 (4.42–19.06)
15	Brand	0.58 (0.15–1.34)	0.52 (0.16–1.34)
16	Glover and Hool	7.39 (2.63–20.45)	5.53 (1.83–9.41)
17	Krajicek	0.75 (0.30–1.42)	0.63 (0.21–1.11)
18	Mingle	0.82 (0.60–1.00)	0.76 (0.08–1.00)
19	Reineke	3608.53 (862.82–9624.06)	2546.84 (479.30–6478.31)
20	TDM	0.97 (0.87–1.00)	0.95 (0.81–1.00)

Note: See Table 2 for definition of competition indices.

Species BAI predictive models and intraspecific–interspecific competition

The best-ranked CI of each focal species (*P. lambertiana*: Bella; *P. ponderosa*: Ek and Monserud) and their intraspecific–interspecific partitioned values were used as explanatory variables in BAI_{10} predictive models. Model covariate subset comparisons revealed species-specific growth trends for focal trees. The CI metric was the best predictor of BAI_{10} for both focal tree species, yet each displayed unique patterns with intraspecific–interspecific species competition (Tables 6 and 7; Fig. 1*a*). The partitioned Bella CI was the best-performing model for *P. lambertiana* according to the ranking criteria (Table 6). Trends suggest that the growth of *P. lambertiana* sharply declines with increasing CI levels ($\beta_{11} = -0.871$), yet appears less affected by the competition posed by *P. ponderosa* ($\beta_{16} = -0.504$). Intraspecies CI effects on *P. lambertiana* growth appear comparatively minimal ($\beta_{17} = -0.224$). In contrast, growth of *P. ponderosa* exhibited a consistent decline ($\beta_{11} = -0.376$) with increasing CI levels, yet did not reveal differences by competing species (Table 7; Fig. 1*b*). Furthermore, results suggest that the growth of *P. ponderosa* may be less sensitive to cumulative and non-*Pinus* sp. competition when compared with trends observed in *P. lambertiana*. Models explained a higher proportion of variance in *P. lambertiana* ($r^2_{(marg/cond)} = 0.65/0.90$) compared with that in *P. ponderosa* ($r^2_{(marg/cond)} = 0.43/0.93$), in parallel with lower RMSE and MAB values (Table 7).

Table 6. BAI_{10} model ranking by focal tree species.

Model form	AIC	LL	ΔAIC	w_i
Pinus lambertiana				
$CI^{0.5} + CI^{0.5}_{PILA} + CI^{0.5}_{PIPO}$	−196.2	107.312	0.00	0.844
$CI^{0.5} + CI^{0.5}_{PILA} + CI^{0.5}_{PIPO} + ELEV$	−191.7	107.533	4.43	0.092
$CI^{0.5} + \ln(DBH) \times CI^{0.5}$	−190.1	102.187	6.07	0.041
$CI^{0.5} + \ln(DBH)$	−188.9	101.612	7.22	0.023
$CI^{0.5} + Ht + CR + ELEV + TPI$	−158.1	106.554	38.05	0.000
Pinus ponderosa				
$CI^{0.5}$	−113.5	63.631	0.00	0.620
$CI^{0.5} + \ln(DBH)$	−112.5	66.263	1.02	0.372
$CI^{0.5} + ELEV + HD$	−104.6	66.718	8.91	0.007
$CI^{0.5} + CR + ELEV + HD$	−92.2	67.095	21.36	0.000
$CI^{0.5} + \ln(DBH) + CI^{0.5}_{ABCO} + CI^{0.5}_{CADE}$	−91.8	66.916	21.72	0.000

Note: BAI_{10}, basal area increment of the last 10 years; DBH, tree diameter at breast height; Ht, tree total height; CR, crown ratio; ELEV, elevation; HD, height/diameter ratio; TPI, topographic position index; AIC, Akaike information criterion; LL, log likelihood. ABCO, CADE, PILA, and PIPO correspond to the partitioned CI values calculated for *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa*, respectively. ΔAIC and w_i correspond to the relative difference and conditional probabilities of the compared models, respectively.

Table 7. Growth model parameter estimates for focal tree species by specific competition index (CI).

Model term	*Pinus lambertiana*	*Pinus ponderosa*
β_{10}	0.811	0.570
$\beta_{11}\ CI^{0.5}$	−0.871	−0.376
$\beta_{12}\ \log(DBH)$		
$\beta_{13}\ CI^{0.5} \times \log(DBH)$		
$\beta_{14}\ CI^{0.5}_{ABCO}$		
$\beta_{15}\ CI^{0.5}_{CADE}$		
$\beta_{16}\ CI^{0.5}_{PILA}$	−0.224	
$\beta_{17}\ CI^{0.5}_{PIPO}$	−0.504	
$r^2_{(marg,\ cond)}$	0.65, 0.90	0.43, 0.93
MAB	0.105	0.118
RMSE	0.139	0.149

Note: DBH, tree diameter at breast height; $r^2_{(marg,\ cond)}$, marginal and conditional coefficient of determination. Mean absolute bias (MAB) and residual mean standard error (RMSE) of the final CI predictive models assess goodness of fit. ABCO, CADE, PILA, and PIPO correspond to the partitioned CI values calculated for *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa*, respectively.

Competitor tree attributes and relative contribution to CI

For both focal species, the best-performing CIs included crown overlap area, yet *P. lambertiana* and *P. ponderosa* appeared to be

Fig. 1. BAI_{10} model estimates of focal tree *Pinus lambertiana* according intraspecific–interspecific competitive values of *Pinus lambertiana* (pila), *P. ponderosa* (pipo), and cumulative competition (CI) along the Bella index (left panel). BAI_{10} trends in *P. ponderosa* according to cumulative competition indices (CI) along the Ek and Monserud index (right panel). CIs have been modified to common scale for comparison. Solid lines and shaded areas correspond to the model fit trajectory and 95% confidence intervals, respectively.

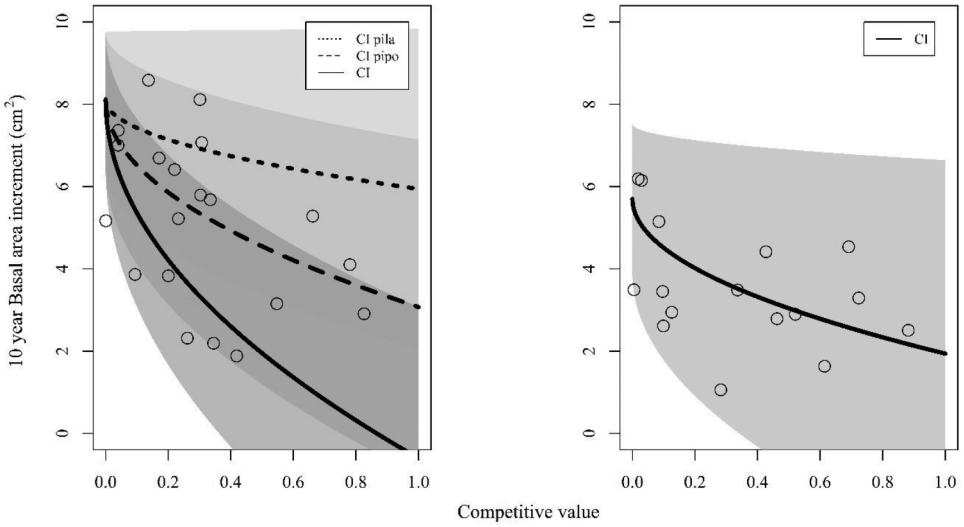


Table 8. Model ranking of the relative contribution of competitor attributes to plot-level competition index (CI) value.

Model form	AIC	LL	ΔAIC	w_i
Pinus lambertiana				
$O_{ij} \times d_i$	−300.7	156.619	0.00	1.000
O_{ij}	−285.4	146.808	15.35	0.000
O_{ij} + Spec	−268.2	141.458	32.50	0.000
Pinus ponderosa				
O_{ij}	−61.0	34.877	0.00	1.000
$O_{ij} + CW_i + O_{ij} \times CW_i$	−47.7	30.713	13.24	0.001
$O_{ij} + h_i + (h_i \times O_{ij})$	−41.4	27.560	19.54	0.000

Note: CI variables defined in Table 2. Spec, species; CW, crown width; AIC, Akaike information criterion; LL, log likelihood. ΔAIC and w_i correspond to the relative difference and conditional probabilities of the compared models, respectively.

Table 9. Model estimates of the effect of competitor attributes on plot competition levels.

Model term	*Pinus lambertiana*	*Pinus ponderosa*
β_{20}	0.0112	0.1021
$\beta_{21}O_{ij}$	0.0257	0.0129
$\beta_{22}d_i$	0.0029	
$\beta_{23}O_{ij} \times d_i$	0.0002	
$r^2_{(marg, cond)}$	0.75, 0.84	0.56, 0.83
MAB	<0.001	<0.001
RMSE	0.071	0.078

Note: CI variables defined in Table 2. $r^2_{(marg, cond)}$, marginal and conditional coefficient of determination. Mean absolute bias (MAB) and residual mean standard error (RMSE) of the final CI predictive models assess goodness of fit.

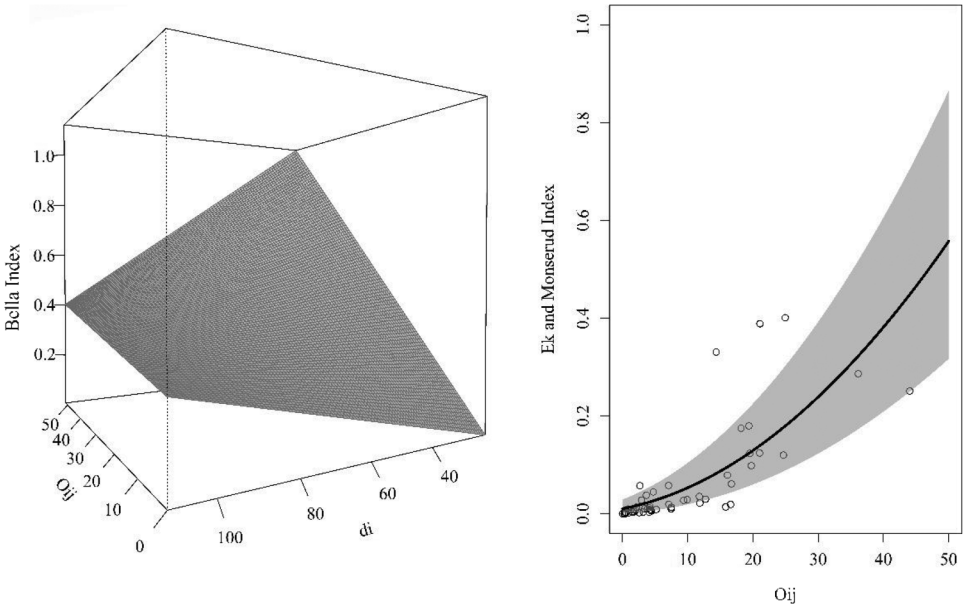
uniquely affected by competitor attributes, in parallel with variables included in the Bella and Ek and Monserud indices (Table 2). Tests of the relative influence of competitor attributes on plot CI values further suggest differences in focal tree response to local conditions. Competitor stem diameter and crown overlap accounted for the best representation of competition in the *P. lambertiana* plots (Table 8). Model parameters reveal a stronger effect of crown overlap (β_{21} = 0.0257) than that of neighbor diameter (β_{22} = 0.0029) on CI, yet the interaction term suggests an enhanced competitive effect in smaller stems (d_i) with high overlap area (O_{ij}; Table 9; Fig. 2*a*) past 20 m^2. In comparison, Ek and Monserud CI values in the *P. ponderosa* plots were primarily related to crown overlap according to model comparisons (Tables 8 and 9), without the additional terms of crown width and height. The plot-level values of Ek and Monserud appear to increase past the O_{ij} levels of ~10–12 m^2 (Fig. 2*b*).

Discussion

Our collective results reflect species-specific radial growth patterns of large, focal *P. lambertiana* and *P. ponderosa* stems that vary with unique competitive neighborhoods. Furthermore, these trends can be locally captured with CI metrics at a relatively low sampling intensity (Alemdag 1978; Noone and Bell 1980). In the past, efforts to calibrate intraspecies–interspecies competition have been conducted at (sub)regional scales and across a range of sites and phases of stand development. These approaches commonly use annealed one-dimensional abstractions of plant competition (CI 3, CI 5) (Canham et al. 2004; Gómez-Aparicio et al. 2011) or a single predictive variable in reviewed CIs (e.g., DBH, Looney et al. 2016, 2018). While parsimonious, the pooled estimated means across regions may distort local competition-growth site patterns and potentially confound interpretations of species growth response when applied at the scale of local operational management blocks. Broad assumptions of similarities in species and regional response to competition may not adequately represent site conditions and potentially overestimate climatic influences on growth (e.g., Johnson et al. 2017) or defense compound production (e.g., Slack et al. 2017). The CIs used in our analysis include common tree attributes (DBH, height, crown width) and crown overlap area to generate composite variables representing spatially explicit two- and three-dimensional structures of tree neighborhoods. CIs with higher dimensional structure (Bella: CI 1; Ek and Monserud: CI 4) performed favorably, and may accommodate a localized calibration approach for mixed-conifer stands when management objectives favor retention of large *P. lambertiana* and *P. ponderosa*.

Standard symmetrical competitive metrics of basal area — CCF, SCI, or SDI — failed to account for any significant correlations

Fig. 2. Relative contribution of competitor attributes on measured plot-level competition index (CI) values of *Pinus lambertiana* (left panel) and *Pinus ponderosa* (right panel). O_{ij} refers to the focal tree and competitor crown overlap area (m^2) and d_i is the diameter of the *i*th competitor. The solid line and shaded areas in the right panel correspond to the model fit and the 95% confidence intervals, respectively.



with BAI_{10} for either focal tree species. This finding reflects our sampling design, which focused on locally large, dominant trees, in parallel with operational thinning release specifications. For *P. lambertiana*, only the Bella (1971) index displayed significant trends with BAI_{10}. Our results highlight the sensitivity of *P. lambertiana* to crown overlap and neighbor stem diameter, and competition seems to be pronounced in small neighbors with >20 m^2 overlap area (Fig. 2) and high stocking densities. Assuming consistent relationships between sapwood area, crown width, site water availability (Shinozaki et al. 1964; Waring et al. 1982; Long and Smith 1984), and noted shade tolerance of *P. lambertiana*, we hypothesize that Bella's CI of weighted crown overlap may reflect water rather than light limitations (Watkinson et al. 1983). Our results reveal that competitive effects on growth are exacerbated when the overlapping space is occupied by non-pine competitors, possibly owing to species differences in rooting structure and water use efficiency. Collectively, these findings support competitive influence zone concepts originally posited by Aaltonen (1926). It is noteworthy that the datasets used by Bella (1971) span multiple single-species plantation forest types across the globe and performed well here in the mixed-conifer forests of the Sierra Nevada.

In comparison, while the BAI_{10} for *P. ponderosa* similarly exhibited correlation with competing variables proposed by Bella, the Ek and Monserud approach, which incorporates competitor height, was the best-performing CI. While the approaches of Bella (1971) and Ek and Monserud (1974) are conceptually similar, the latter is specifically constructed for mixed-species stands and adjusts crown overlap by the tree height of competing trees, and performed best in our dataset. In our analysis, crown overlap (O_{ij}) was the primary competitive effect of the Ek and Monserud CI in *P. ponderosa* plots, suggesting a spatially explicit influence of crowding. These trends correspond to the species' noted shade intolerance, as increased shading from competitors could result in self-pruning and declining BAI_{10} or reallocation of carbohydrates to apical growth (Assmann 1970). Owing to its expansive range, *P. ponderosa* has been subject to multiple efforts to quantify competitive limitations to potential tree growth. The relative size–distance approach taken by Rouvinen and Kuuluvainen (1997) (CI 8; Table 2) has been noted as a robust CI estimator in western Montana (Contreras et al. 2011), yet it did not perform well here. Our results align with earlier work in the Sierra Nevada by Biging and Dobbertin (1992, 1995), who noted increased performance of BAI predictive models with CIs that included crown parameters. We anticipate that additional and continued measurements of height and crown growth may further reveal growth–competition interactions. While radiation-oriented CIs offer an attractive solution to capturing competition in heterogeneous stands, these tools have shown low to moderate performance in mixed forests (Stadt et al. 2007; Kuehne et al. 2019), likely reflecting species differences in shade tolerance. Indeed, the locally dominant *P. lambertiana* and *P. ponderosa* included in our study may be more limited by water than sunlight in arid, Mediterranean climates, as noted by Contreras et al. (2011) and Cattaneo et al. (2018).

We acknowledge that our sampling regime and associated data frame of a relatively limited sample size of locally large trees limits extrapolation to operational growth and yield programs. Rather than attempting to form broad, generalized predictive equations that could mask within-stand development patterns, we were interested in investigating species-specific differences in the growth of focal trees according to size and competition. Our results highlight the growth and competitive trends of favored *Pinus* species in the context of the multi-decadal absence of fire and intraspecies–interspecies patterns that may be of practical utility to silviculturists in restoration thinning regimes. In the absence of wildfire and active management, the current conditions of the study area parallel the regional trend of increased *C. decurrens* and *A. concolor* regeneration and subsequent decline in *P. ponderosa* pine tree growth. By comparison, *P. lambertiana* maintains greater radial growth and appears less impacted by the increased density of neighboring *Pinus* sp. If the area is left unmanaged, we anticipate that mortality of *P. ponderosa* will favor recruitment and expansion of mid-upper canopy *P. lambertiana*. However, continued *P. lambertiana* dominance may be limited by susceptibility to *Cronartium ribicola* outbreak and recruitment of shade-tolerant *A. concolor* and *C. decurrens* (Waring and O'Hara 2009). Dominance by late-successional species with characteristically

low light transmittance may limit *Pinus* sp. regeneration in the absence of disturbance. Therefore, density management is a practical tool to emulate natural processes.

Restoration thinning in mixed-conifer forests use radial release gaps of focal *Pinus* sp. to remove overstocked *A. concolor* and *C. decurrens* to mitigate wildfire risk (Stephens 1998) and promote structural heterogeneity through residual tree clumping across size classes (Churchill et al. 2013).Our findings suggest that *P. lambertiana* may be better suited to group retention when competition is intraspecific, and that radial release gaps prioritize *P. ponderosa* stems, highlighting the complexity of mixed-stand dynamics. We further acknowledge that our minimum stem threshold (DBH $\geq$ 20.3 cm) could be underestimating the cumulative competitive effect on focal trees. Yet, we also recognize that the operational costs of restoration thinning programs require an offset by minimum piece size and merchantable diameter limits. Thus, our dataset and findings may be of greatest utility in applied settings.

Approaches to discerning tree growth due to the confounding influences of age, size, resource competition, and climatic conditions inherently require assumptions of similarities in causal–response mechanisms of growth production. Simplifying these processes through generalized predictive yield models can obscure site- and species-specific patterns that may influence data interpretation and relevant conclusions in dendroclimatology and restoration objectives. These assumptions may be particularly invalid in mixed-species stands. Indeed, while the original intention of periodic BAI measurements was to estimate timber volume forecasts, the utility of this metric in climatic response studies may further overlook apical carbon allocation (i.e., height and root growth), production of secondary metabolites used in defense (Slack et al. 2017), or reproductive functions. Furthermore, these metrics assume simple, static competitive interactions (Burton 1993) that may obscure stand dynamic processes, especially in species mixtures with niche complementarity. Therefore, the broad utility of CIs may be best suited to short-rotation, single-species forests. Any potential misinterpretations are further exacerbated by differences in species functional traits and phase of forest successional development, and may ultimately provide misleading conclusions that form the basis of silvicultural practices. In practice, the chosen metric of tree competition should not only be tested and ranked by correlation prior to interpreting the relative impacts of confounding factors, but the framework of the index should be logical within the context of the question at hand. The historical objective of quantifying stand- and tree-level competition was intended to develop robust prediction models of timber commodity-oriented growth and yield. This is perhaps subtly reflected through the commonly assessed mean growth period (5–10 years) of BAI that corresponds to the temporal lag between research and operational inventory measurement cycles along the stand rotation. We anticipate extending our approaches described here to assess long-term changes in species competitive trends within refined temporal periods. We expect that analyzing continuous measurements of tree and neighborhood attributes at an annual time step may further reveal competitive thresholds on species growth patterns.

Conclusions

Stand competition and density metrics have traditionally been used to develop timber yield prediction models, yet are increasingly used in contemporary restoration silviculture to prioritize thinning and interpret confounding influences on tree growth and stand development. These new applications make broad assumptions regarding tree growth rates according to stem size, competitive neighborhoods, and genus' response to physiological stressors. We assessed radial growth patterns according to stem size and competition of *P. lambertiana* and *P. ponderosa* focal trees in Sierran mixed-conifer forests across a variety of competition indices to test for similarity in species response and to assess potential differences in competitive neighborhood influence. Our results reveal constraints to BAI_{10} by competition that varied uniquely by species and appeared to correspond with crown overlap area. Collectively, our results highlight the importance of a priori review and local calibration of CIs to facilitate identification of species differences in competitive responses when interpreting the causal influences on stem radial growth. Furthermore, our observations suggest that restoration thinning treatments aimed at reducing competition should consider crown dynamics in addition to traditional diameter limit guidelines, and that residual *P. lambertiana* may be better suited to intraspecific group retention than density-sensitive *P. ponderosa*.

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References

Aaltonen, V.T. 1926. On the space arrangement of trees and root competition. J. For. **26**: 627–644. doi:10.1093/jof/24.6.627.

Alemdag, I.S. 1978. Evaluation of some competition indices for the prediction of diameter increment in planted white spruce. Forest Management Institute, Ottawa, Ont. Information Rep. FMR-X-108.

Assmann, E. 1970. The principles of forest yield study. 1st ed. Pergamon Press Ltd., Oxford, 506 pp.

Bartoń, K. 2020. MuMIn: Multi-model inference. R package version 1.43.17. Available from https://CRAN.R-project.org/package=MuMIn.

Battles, J.J., Robards, T., Das, A., Waring, K., Gilless, J.K., Biging, G., and Schurr, F. 2008. Climate change impacts on forest growth and tree mortality: a data-driven modeling study in the mixed-conifer forest of the Sierra Nevada. Clim. Change, **87**(S1): S193–S213. doi:10.1007/s10584-007-9358-9.

Bella, I.E. 1971. A new competition model for individual trees. For. Sci. **17**: 364–372. doi:10.1093/forestscience/17.3.364.

Biging, G.S., and Dobbertin, M. 1992. A comparison of distance-dependent competition measures for height and basal growth of individual conifer trees. For. Sci. **42**: 695–720. doi:10.1093/forestscience/38.3.695.

Biging, G.S., and Dobbertin, M. 1995. Evaluation of competition indices in individual tree growth models. For. Sci. **38**: 360–377. doi:10.1093/forestscience/41.2.360.

Boeck, A., Dieler, J., Biber, P., Pretzsch, H., and Ankerst, D.P. 2014. Predicting tree mortality for European beech in southern Germany using spatially explicit competition indices. For. Sci. **60**(4): 613–622. doi:10.5849/forsci.12-133.

Brand, D.G. 1986. A competition index for predicting the vigour of planted Douglas-fir in southwestern British Columbia. Can. J. For. Res. **16**(1): 23–29. doi:10.1139/x86-005.

Breheny, P., and Burchett, W. 2020. Visreg: visualization of regression models. R package version 2.7.0. Available from http://pbreheny.github.io/visreg.

Burton, P.J. 1993. Some Limitations inherent to static indices of plant competition. Can. J. For. Res. **23**(10): 2141–2152. doi:10.1139/x93-267.

Canham, C.D., LePage, P.T., and Coates, K.D. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Can. J. For. Res. **34**(4): 778–787. doi:10.1139/x03-232.

Cassell, B.A., Scheller, R.M., Lucash, M.S., Hurteau, M.D., and Loudermilk, E.L. 2019. Widespread severe wildfires under climate change lead to increased forest heterogeneity in dry mixed-conifer forests. Ecosphere, **10**(11): e02934. doi:10.1002/ecs2.2934.

Cattaneo, N., Bravo-Oviedo, A., and Bravo, F. 2018. Analysis of tree interactions in a mixed Mediterranean pine stand using competition indices. Eur. J. For. Res. **137** (1): 109–120. doi:10.1007/s10342-017-1094-8.

Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, J.F., Hessburg, P.F., and Lutz, J.A. 2013. Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. For. Ecol. Manage. **291**: 442–457. doi:10.1016/j.foreco.2012.11.007.

Contreras, M.A., Affleck, D., and Chung, W. 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. For. Ecol. Manage. **262**: 1939–1949. doi:10.1016/j.foreco.2011.08.031.

Corral-Rivas, J.J. 2006. Models of tree growth and spatial structure for multispecies, uneven-aged forests in Durango (Mexico). Ph.D. dissertation, Göttingen University, Cuvillier Verlag, Göttingen.

Daniels, R.F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. For. Sci. **22**(4): 454–456. doi:10.1093/forestscience/22.4.454.

Das, A. 2012. The effect of size and competition on tree growth rate in old-growth coniferous forests. Can. J. For. Res. **42**(11): 1983–1995. doi:10.1139/x2012-142.

Dickinson, Y.L., Battaglia, M.A., and Asherin, L.A. 2019. Evaluation of the FVS-CR diameter growth model in structurally-heterogenous ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) stands in the southern Rockies, and potential modifications. For. Ecol. Manage. **448**: 1–10. doi:10.1016/j.foreco.2019.05.031.

Ek, A.R., and Monserud, R.A. 1974. FOREST: A model for the growth and reproduction of forest stands. Department of Forestry – The University of Wisconsin, Madison. Res. Rep. R26535.

Ferrell, G.T. 1996. The influence of insect pests and pathogens on Sierra forests. In Sierra Nevada Ecosystem Project: Final report to Congress. Vol. II. The University of California – Cent. Wat. Wild. Res. Davis, Calif., pp. 1177–1192.

Ford, K.R., Breckheimer, I.K., Franklin, J.F., Freund, J.A., Kroiss, S.J., Larson, A.J., et al. 2017. Competition alters tree growth response to climate at individual and stand scales. Can. J. For. Res. **47**(1): 53–62. doi:10.1139/cjfr-2016-0188.

Fry, D.L., Stephens, S.L., Collins, B.M., North, M.P., Franco-Vizcaíno, E., and Gill, S.J. 2014. Contrasting spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth mixed conifer forests. PloS ONE, **9**(2): e88985. doi:10.1371/journal.pone.0088985.

Füldner, K. 1995. Zur Strukturbeschreibung in Mischbeständen. Forstarchiv, **66**: 235–240.

Glover, G.R., and Hool, J.N. 1979. A basal area predictor of loblolly pine plantation mortality. For. Sci. **25**(2): 275–282. doi:10.1093/forestscience/25.2.275.

Gómez-Aparicio, L., Garcia-Valdés, R., Ruiz-Benito, P., and Zavala, M.A. 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: Implications for forest management under global change. Global Change Biol. **17**(7): 2400–2414. doi:10.1111/j.1365-2486.2011.02421.x.

Hegyi, F. 1974. A simulation model for managing jackpine stands. *In* Proceedings of IUFRO meeting S4.01.04 on growth models for tree and stand simulation. *Edited by* J. Fries. Royal College of Forestry, Stockholm, Sweden, pp. 74–90.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. **43**: 69–78.

Johnson, C., Chhin, S., and Zhang, J.W. 2017. Effects of climate on competitive dynamics in mixed conifer forests of the Sierra Nevada. For. Ecol. Manage. **394**: 1–12. doi:10.1016/j.foreco.2017.03.017.

Keyser, C.E. 2019. Inland California and Southern Cascades (CA) Variant overview – Forest Vegetation Simulator. USDA For. Serv. Int. Rep.

Kinloch, B.B., Jr., and Scheuner, W.H. 1990. *Pinus lambertiana* Dougl. *In* Silvics of North America, Volume 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. USDA agriculture handbook 654. pp. 370–380.

Krajicek, J., Brinkman, K., and Gingrich, S. 1961. Crown competition-a measure of density. For. Sci. **7**: 35–42. doi:10.1093/forestscience/7.1.35.

Kuehne, C., Weiskittel, A.R., Fraver, S., and Puettmann, K.J. 2015. Effects of thinning-induced changes in structural heterogeneity on growth, ingrowth, and mortality in secondary coastal Douglas-fir forests. Can. J. For. Res. **45**(11): 1448–1461. doi:10.1139/cjfr-2015-0113.

Kuehne, C., Weiskittel, A.R., and Waskiewicz, J. 2019. Comparing performance of contrasting distance-independent and distance-dependent competition metrics in predicting individual tree diameter increment and survival within structurally-heterogenous, mixed-species forests of the Northeastern United States. For. Ecol. Manage. **433**: 205–216. doi:10.1016/j.foreco.2018.11.002.

Long, J.N., and Smith, F.W. 1984. Relation between size and density in developing stands: A description and possible mechanism. For. Ecol. Manage. **7**: 191–206. doi:10.1016/0378-1127(84)90067-7.

Looney, C.E., D'Amato, A.W., Fraver, S., Palik, B.J., and Reinikainen, M.R. 2016. Examining the influences of tree-to-tree competition and climate on size-growth relationships in hydric, multi-aged *Fraxinus nigra* stands. For. Ecol. Manage. **375**: 238–248. doi:10.1016/j.foreco.2016.05.050.

Looney, C.E., D'Amato, A.W., Palik, B.J., Fraver, S., and Kastendick, D.N. 2018. Size-growth relationship, tree spatial patterns, and tree-tree competition influence tree growth and stand complexity in a 160-year red pine chronosequence. For. Ecol. Manage. **424**: 85–94. doi:10.1016/j.foreco.2018.04.044.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. **6**: 343–360. doi:10.1016/0378-1127(83)90042-7.

Lumley, T. 2020. Leaps: regression subset selection, including exhaustive search. R package version 3.1.0. Available from https://CRAN.R-project.org/package=leaps.

Ma, Q., Su, Y., Tao, S., and Guo, Q. 2018. Quantifying individual tree growth and competition using bi-temporal airborne laser scanning data: a case study in the Sierra Nevada Mountains, California. Int. J. Digit. Earth, **11**(5): 485–503. doi:10.1080/17538947.2017.1336578.

National Climate Data Center. 2016. National oceanic and atmospheric administration [online]. Available from http://www.ncdc.noaa.gov/climate-information [accessed on 22 Nov 2016].

Noone, C.S., and Bell, J.F. 1980. An evaluation of eight inter tree competition indices. Forest Research Laboratory - Oregon State University, Corvallis. Res. Bull. 66.

Oliver, W.W. 1996. Silvics of sugar pine: clues to distribution and management. In Proceedings of a Symposium presented by the California Sugar Pine Management Committee: Sugar Pine: Status, Values, and Roles in Ecosystems. *Edited by* B. Kinloch, Jr., M. Marosy, and M.E. Huddleson. University of California – Div. Ag. Nat. Res. Davis, California. Publication 3362. pp. 28–33.

Oliver, W.W., and Ryker, R.A. 1990. *Pinus ponderosa* Dougl. Ex Laws. *In* Silvics of North America. Vol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. USDA Agriculture Handbook 654. pp. 413–424.

Pastorella, F., and Paletto, A. 2013. Stand structure indices as tools to support forest management: an application to Trentino forests (Italy). J. For. Sci. **59**(4): 159–168. doi:10.17221/75/2012-JFS.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Development Team, 2017. nlme: linear and nonlinear mixed effects models. R Package version 3.1.

Premer, M.I., Chhin, S., and Zhang, J.W. 2017. Alternative approaches to mixed conifer forest restoration: partitioning the competitive neighborhood. New For. **48**(2): 1–16. doi:10.1007/s11056-017-9598-0.

R Core Team. 2018. R: A language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/.

Reineke, L.H. 1933. Perfecting a stand-density index for even aged forests. J. Agric. Res. **46**: 627–638.

Rouvinen, S., and Kuuluvainen, T. 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scot pine forest. Can. J. For. Res. **27**(6): 890–902. doi:10.1139/x97-012.

Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. 1964. A quantitative analysis of plant-form- the pipe model theory. I. Basic analyses. Jpn. J. Ecol. **14**(3): 97–104. doi:10.18960/seitai.14.4_133.

Slack, A.W., Kane, J.M., Knapp, E.E., and Sherriff, R.L. 2017. Contrasting impacts of climate and competition on large sugar pine growth and defense in a fire-excluded forest of the Central Sierra Nevada. Forests, **8**(7): 244. doi:10.3390/f8070244.

Smith, S.H. 1977. The evaluation of competitive stress index as a measure of stand density for young growth Douglas-fir. M.Sc. thesis, School of Forestry, Oregon State University, Corvallis, Ore., 188 pp.

Stadt, K.J., Huston, C., Coates, K.D., Feng, Z., Dale, M.R.T., and Lieffers, V.J. 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. Ann. For. Sci. **64**: 477–490. doi:10.1051/forest:2007025.

Stage, A.R. 1976. An expression for the slope, aspect, and habitat type on tree growth. For. Sci. **22**: 457–460.

Stephens, S.L. 1998. Evaluation of the effects of silvicultural and fuels treatments on potential fire behavior in Sierra Nevada mixed-conifer forests. For. Ecol. Manage. **105**: 21–35. doi:10.1016/S0378-1127(97)00293-4.

Von Gadow, K. 1993. Zur Bestandesbeschreibung in der Forsteinrichtung. Forst und Holz. **48**: 601—606.

Waring, K.M., and O'Hara, K.L. 2009. Stand development and tree growth response to sugar pine mortality in Sierran mixed-conifer forests. Northwest Sci. **83**(2): 89–100. doi:10.3955/046.083.0201.

Waring, R.H., Schroeder, P.E., and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. Can. J. For. Res. **12**(3): 556–560. doi:10.1139/x82-086.

Watkinson, A.R., Lonsdale, W.M., and Firbank, L.G. 1983. A neighborhood approach to self-thinning. Oecologia, **61**: 381–384. doi:10.1007/BF00379716.

Wykoff, W.R., Crookston, N.L., and Stage, A.R. 1982. User's guide to the stand prognosis model. USDA For. Serv. Gen-Rep INT-133. General Technical Report INT-133. USDA Forest Service.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. **21**(3): 414–416. doi:10.1139/x91-053.

Young, D.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., and Latimer, A.M. 2017. Long term climate and competition explain forest mortality patterns under extreme drought. Ecol. Lett. **20**: 78–86. doi:10.1111/ele.12711.

Zenner, E.K., and Hibbs, D.E. 2000. A new method for modeling the heterogeneity of forest structure. For. Ecol. Manage. **129**: 75–87. doi:10.1016/S0378-1127(99)00140-1.

Zhang, J.W., Ritchie, M.W., Maguire, D.A., and Oliver, W.W. 2013. Thinning ponderosa pine (*Pinus ponderosa*) stands reduces mortality while maintaining stand productivity. Can. J. For. Res. **43**(4): 311–320. doi:10.1139/cjfr-2012-0411.

Zhang, J.W., Finley, K., Nels, J., and Ritchie, M.W. 2019. Lowering stand density enhances climate resiliency of ponderosa pine forests to disturbances and climate change. For. Sci. **65**(4): 496–507. doi:10.1093/forsci/fxz006.