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Tree growth and competition in an old-growth *Picea abies* forest of boreal Sweden: influence of tree spatial patterning

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Keywords
Boreal forest; Competition index; Dendrochronology; Late-successional forests; Neighbourhood effects; Norway spruce; Tree mortality; Tree spatial pattern

Abbreviations
CI = competition index; CLI = clustering index

Nomenclature
Mossberg & Stenberg (2003)

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Abstract

Question: What factors best characterize tree competitive environments in this structurally diverse old-growth forest, and do these factors vary spatially within and among stands?

Location: Old-growth *Picea abies* forest of boreal Sweden.

Methods: Using long-term, mapped permanent plot data augmented with dendrochronological analyses, we evaluated the effect of neighbourhood competition on focal tree growth by means of standard competition indices, each modified to include various metrics of trees size, neighbour mortality weighting (for neighbours that died during the inventory period), and within-neighbourhood tree clustering. Candidate models were evaluated using mixed-model linear regression analyses, with mean basal area increment as the response variable. We then analysed stand-level spatial patterns of competition indices and growth rates (*via* kriging) to determine if the relationship between these patterns could further elucidate factors influencing tree growth.

Results: Inter-tree competition clearly affected growth rates, with crown volume being the size metric most strongly influencing the neighbourhood competitive environment. Including neighbour tree mortality weightings in models only slightly improved descriptions of competitive interactions. Although the within-neighbourhood clustering index did not improve model predictions, competition intensity was influenced by the underlying stand-level tree spatial arrangement: stand-level clustering locally intensified competition and reduced tree growth, whereas in the absence of such clustering, inter-tree competition played a lesser role in constraining tree growth.

Conclusions: Our findings demonstrate that competition continues to influence forest processes and structures in an old-growth system that has not experienced major disturbances for at least two centuries. The finding that the underlying tree spatial pattern influenced the competitive environment suggests caution in interpreting traditional tree competition studies, in which tree spatial patterning is typically not taken into account. Our findings highlight the importance of forest structure – particularly the spatial arrangement of trees – in regulating inter-tree competition and growth in structurally diverse forests, and they provide insight into the causes and consequences of heterogeneity in this old-growth system.

Introduction

In most forested settings, growth rates vary markedly from tree to tree (Coomes & Allen 2007). This variation strongly influences forest stand development and tree mortality, and it leads to diversity in tree sizes and tree spatial patterns (Franklin et al. 2002). Understanding the controls over growth variation is critical for forecasting stand devel-

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opment and assessing community organization, as well as evaluating community resistance and resilience to environmental change.

Competition for resources is one well-studied source of variation in individual tree growth. Studies of neighbourhood competitive interactions generally show that large, near neighbours exert higher competitive stress than small, distant neighbours (e.g. Wagner & Radosevich 1998; D'Amato & Puettmann 2004). A large number of neighbourhood competition indices are available for assessing the intensity or importance of inter-tree competition (e.g. Tomé & Burkhart 1989; Biging & Dobbertin 1992; Stadt et al. 2007). Advancements over the past decade have allowed the distinction between above- and below-ground competition (Canham et al. 2004; Coates et al. 2009), the recognition that species differ in the competitive stress they cause to target species (Canham et al. 2006), the separation of intra- and inter-specific competition (D'Amato & Puettmann 2004) and the identification of shifts in competitive interactions through time (Weber et al. 2008; Hartmann & Messier 2011), all contributing greatly to our understanding of tree–tree interactions and stand development.

Most studies assessing inter-tree competition have been conducted in actively managed or secondary forests. Factors governing competition, however, may differ markedly between these settings and those of old-growth forests. Active management, in particular, explicitly intends to reduce competition and increase tree growth and also to simplify tree spatial distributions to facilitate harvesting. Further, managed or secondary forests may not have reached a developmental stage in which growth variation is fully expressed. As stands approach maturity or old-growth, changes in species composition may occur (Bergeron 2000; Frelich 2002), spatial patterning of trees may progress from clustered to uniform (Kenkel 1988) and competitive stress may increase (Lorimer et al. 2001), all of which strongly influence tree growth. Also, because developmental dynamics have played out over an extended period, and resource-use hierarchies have fully developed, old-growth forests typically display a diversity of trees sizes, ages and growing conditions (Kuuluvainen et al. 1998; D'Amato et al. 2008; Fraver & Palik 2012), all of which could influence tree growth. Finally, in uneven-aged, old-growth conditions, older senescing trees may cause less competitive stress than would be predicted from their typically large sizes alone. For these reasons, expanding the assessment of inter-tree competition to the old-growth stage may place in perspective the previous work on managed or younger secondary forests.

In addition to potential changes in competitive interactions through stand development, the spatial patterning of trees may influence competitive interactions. This influence may be especially evident in structurally heterogeneous old-growth forests, where trees typically exhibit irregular spatial patterning (Aakala et al. 2012). It may be expressed within local neighbourhoods surrounding focal trees, or it may be expressed as stand-level variability in growth resulting from larger-scale spatial patterning. Regarding the local neighbourhood scale, we note that many existing neighbourhood competition indices account for focal-to-neighbour distances, but do not explicitly consider neighbour spatial patterning (but see Canham et al. 2004). We propose that the inclusion of tree spatial patterning in such assessments may better capture competitive effects, particularly in structurally heterogeneous forests.

In the present study we investigated the influence of neighbourhood competition on tree growth in an old-growth *Picea abies* (Norway spruce) forest of boreal Sweden. Our study is based on a re-inventory of permanent plots, with individually tagged and mapped trees, established in 1986. We augment these data with dendrochronological analyses of living and dead trees on these same plots. Our general objective was to explore the factors that influence tree growth in this structurally diverse old-growth forest. Our specific questions included: (1) what is the nature of competitive interactions affecting individual tree growth within these populations; (2) do poor vigour, declining neighbour trees have lower competitive effects (prior to their death) than would be predicted by their size alone; (3) does variation in tree spatial patterning influence competition intensity? This last question was addressed both within circular competitive neighbourhoods surrounding focal trees, as well as within larger populations encompassing our research plots. These results provide insight into interactions between forest structure and tree growth, which together contribute to the heterogeneity evident in this and many other old-growth systems.

Methods

Study area

We conducted this study in the Gardfjället Nature Reserve of Västerbotten County, boreal Sweden (centred at 65°26′ N, 15°53′E). Mean monthly temperatures range from −11.6 °C in January to 12.3 °C in July (annual mean 0.4 °C); mean annual precipitation is 667 mm (Swedish Meteorological and Hydrological Institute, records 1945–2005). The substrate consists of a 10– 15-cm thick humus layer underlain by fine-grained mineral soil derived from glacial till. Field observations and previous work (Esseen 1994) confirm the absence of logging within the reserve. No major natural disturbances have occurred in recent centuries; however, a moderate severity disturbance may have occurred ca. 1750 (Fraver et al. 2008). Forest dynamics are governed through gap-phase processes driven via parasitic fungi and wind (Edman et al. 2007); a finding that appears to be more common than had been previously thought for this forest type (Kuuluvainen & Aakala 2011). *P. abies* clearly dominates forests in the reserve, although *Betula pubescens* (downy birch), *Salix caprea* (goat willow) and *Sorbus aucuparia* (rowan) are present at low abundance (Fraver et al. 2008). The field layer is dominated by a relatively rich assemblage of vascular plants (given this latitude), which occur in patchy mosaics corresponding to microtopographic variation. *P. abies* trees rarely exceed 20 m in height, and tree density is rather sparse, such that trees may not form closed-canopy stands. Forest stands contain two or more age cohorts, with additional steady recruitment between cohorts, with oldest trees ca. 380 yrs old at the time of sampling. Estimates of site quality range between 3.0 and 3.6 $m^3 \cdot ha^{-1} \cdot yr^{-1}$.

Field and laboratory procedures

The three plots used in the current study were established in 1985–86 by the final author as controls to assess the effects of nearby clear-cutting (see Esseen 1994; Jönsson et al. 2007). Plots were 50 × 50 m, lying at ca. 550 m a.s.l. Distances between plots ranged from 0.5 to 3.2 km. All trees and snags were uniquely tagged during the initial inventory, and species, height and diameter at breast height (DBH, 1.3 m) were recorded. Plots were re-inventoried in 1987, 1988 and 1991. We inventoried plots again in 2004, recording DBH, tree height, height to base of live crown, as well as *x* and *y* coordinates for all previously inventoried trees. To determine the canopy projection area for each tree, we measured the horizontal distance from bole centre to the canopy drip line in four cardinal directions. Each of the resulting four quadrants was assumed to have the shape and area of a quarter ellipse (Lorimer & Frelich 1989); summing them provides an estimate of canopy projection area. We combined this area with tree height and base of live crown height to calculate crown volume, assuming the shape of a second-order paraboloid, which is typical of conifers (Pretzsch 2009). As reported by Fraver et al. (2008), the three plots varied somewhat with respect to living tree basal area (34.4, 28.9 and 27.7 $m^2 \cdot ha^{-1}$, plots A, B and C, respectively) and stem density (612, 664 and 552 $trees \cdot ha^{-1}$).

To determine growth rates over time, we extracted one increment core at breast height from each living and dead tree ≥10 cm DBH. Increment cores were mounted and sanded to a fine polish using standard methods. Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating was conducted following the marker-year method of Yamaguchi (1991), with statistical verification with COFECHA (Holmes 1983). We used the average annual basal area increment over the 18-yr sampling period (1986–2004) to characterize tree growth. The use of basal area increment reduces the diameter-dependent bias introduced by using radial increment as a measure of growth. It was calculated for each tree from tree ring measurements, correcting for off-centre piths using methods and rationale presented in Frelich (2002). For trees from which an intact core could not be obtained (8% of trees), basal area increment was estimated from field-measured diameters in 1986 and 2004.

Data analyses

The intensity of neighbourhood competition on individual tree growth was evaluated using two basic competition indices (CIs), each modified to allow for various metrics of tree size. Each CI assumes a circular neighbourhood centred on the focal tree, thereby defining the focal tree's competitive neighbourhood. The circular area provides a tally of all potential competitors, with higher crowding suggesting greater competitive effects. The first CI is based on Hegyi's (1974) index, which includes information on tree–tree distance, and the second on Lorimer's (1983) index, as follows:

$$\mathrm{CI}_f = \sum_{n=1}^{N} \left(\frac{S_n/S_f}{\mathrm{Distance}_{nf}} \right) \bullet \mathrm{w}_n \qquad \text{(Hegyi 1974)}$$

$$\mathrm{CI}_f = \sum_{n=1}^{N} (S_n/S_f) \bullet \mathrm{w}_n \qquad \text{(Lorimer 1983)}$$

where CI_f is the competition index for the focal tree; *N* is the number of neighbour trees; S_n and S_f are sizes of neighbour and focal trees; $Distance_{nf}$ is the distance (m) between the neighbour and focal tree; and w_n is a weighting factor to account for neighbour mortality (below). Three expressions of size were analysed in separate models: diameter at breast height (m), canopy projection area (m^2) and crown volume (m^3). We selected these two CIs based on their previously demonstrated success in characterizing tree growth in managed forested settings (Biging & Dobbertin 1992; D'Amato & Puettmann 2004; Stadt et al. 2007; Weber et al. 2008), as well as in old-growth pine forests (our unpublished data). When Hegyi's CI includes crown volume as the size metric, it is equivalent to that proposed by Biging & Dobbertin (1992).

For all CIs, only *P. abies* trees ≥10 m from plot borders could serve as focal trees to avoid analytical complications from edge effects; however, all trees (of any species) could potentially serve as neighbours. Only focal and neighbour

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trees ≥10 cm DBH at the beginning of the sampling period (1986) were used in analyses.

We further modified these basic CIs to include a down-weighting factor (w_n) to account for neighbours that died during the sampling period (1986–2004), expressed as the proportion of years the neighbour remained alive during the sampling period. For trees that died prior to 1991 (during a time of regular inventories, above), mortality years were assigned to the midpoint of an inventory interval. For trees that died after 1991, we used the outermost ring as an estimate of the year of death.

To account for the possibility that the spatial dispersion of trees within the circular neighbourhoods may influence focal tree growth, we included in our analyses an index of within-neighbourhood clustering. Our index averages two metrics: (1) a measure of angular dispersion of neighbours, which emphasizes neighbour azimuths relative to the focal tree, with common directionality suggesting clustering (Canham et al. 2004) and (2) the mean neighbour-to-neighbour distances within the neighbourhood radii, with lower means indicative of clustering. The index of angular dispersion has a theoretical range of 0–1 (higher indices suggest common directionality; Zar 1999); mean neighbour-to-neighbour distances were inverse-scaled to a range of 0–1 (such that higher indices indicate clustering), based on possible maxima given the selected neighbourhood radii (below). Although these two metrics are correlated (Pearson $r = 0.53$), they capture different aspects of neighbour spatial patterning; together they form a clustering index that provides a means of testing the importance of small-scale neighbour spatial patterning on focal tree growth. Our competition indices were thus modified to include a clustering index (CLI) as follows.

$$\mathrm{CI}_f = \left[\sum_{n=1}^{N}\left(\frac{S_n/S_f}{\mathrm{Distance}_{nf}}\right)\right](1-\mathrm{CLI})$$

$$\mathrm{CI}_f = \left[\sum_{n=1}^{N}(S_n/S_f)\right](1-\mathrm{CLI})$$

To avoid an inordinately large number of candidate models (considering various combinations of radii [see below], CIs, size metrics, mortality weighting, clustering index, initial size, interactions), we conducted our analyses in two steps, each explained in detail below. In the first step, we selected an appropriate neighbourhood radius for the pooled data set, as well as for each plot. In the second step, we evaluated the influence of the remaining factors on focal tree growth (given the selected radius) for the pooled data, as well as for each plot.

Selecting an appropriate neighbourhood size (i.e. radii when using circular neighbourhoods) within which to evaluate competition has long posed a challenge for researchers. Approaches range from the *a priori* selection of a radius of biologically meaningful size (He & Duncan 2000; Roberts & Harrington 2008; Thorpe et al. 2010) to computationally complex approaches that determine the shape (and ultimately the optimal length) of the competitive influence depletion curve using maximum likelihood estimation and simulated annealing (Canham et al. 2004). We selected neighbourhood size (step 1, above) by evaluating the relative performance of numerous candidate models (see below for model details), each at a specified radius, assuming that top performing models included appropriate radii for assessing competition. Using the various forms of the CI and size metric combinations, we thus tested models with neighbourhood radii ranging from 5 to 10 m, at 0.5-m increments. This lower limit was selected to ensure that a sufficient number of neighbours were included in the clustering index, and because preliminary analyses suggested that neighbourhoods smaller than 5 m exhibited poor model performance. The upper limit of 10 m was selected to allow adequate sample sizes of focal trees for each plot, given that only those trees ≥10 m from plot borders could serve as focal trees. This upper limit is within the range of previous studies of temperate or boreal conifer forests (He & Duncan 2000; Roberts & Harrington 2008; Thorpe et al. 2010), and it sufficiently covers the 'search radius' of 3.5 × the mean canopy radius (1.8 m) recommended by Lorimer (1983). Finally, the radii from the confidence model sets (models with Δ AICc < 2, see below) were averaged to provide an appropriate (but perhaps not 'optimal', *sensu* Canham et al. 2004) radius for each of the three plots, as well as the pooled data set.

Once appropriate neighbourhood radii were selected, we evaluated a series of candidate models based on *a priori* hypotheses regarding the nature of inter-tree competition within these populations, expressed by the various CIs, size metrics, mortality weights and within-neighbourhood clustering indices (step 2, above), using mean basal area increment as the response variable. Thus, our model equation was: basal area growth = $f(\mathrm{CI} + \text{initial size} + \mathrm{CI} \times \text{initial size})$, testing various CI forms and modifications to account for neighbour mortality and within-neighbourhood clustering, as above.

For both analytical steps, we evaluated model performance using mixed-model linear regression analyses. Each candidate model (for both steps) included site as a random effect and contained a power spatial correlation structure to account for differences in growing conditions across sites, as well as spatial autocorrelation. Each model also included initial basal area (1986) as a predictor, so that variance attributable to initial size would not confound our interpretation of growth–competition relationships (MacFarlane & Kobe 2006). A model including initial basal area

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alone was considered the null model for comparisons. For all models, natural-log transformations were applied to the response and explanatory variables to meet linearity assumptions and to stabilize variance. Candidate models were evaluated using corrected Akaike's information criterion (AICc), allowing us to determine which models, and hence predictors, were best supported by the data (Burnham & Anderson 2002). We also calculated Akaike model weights to gauge the probability of a given model being the best in the model set (Burnham & Anderson 2002). The model with the lowest AICc score was selected as the best model in the set (i.e. strongest level of support for predicting focal tree growth) and used for describing competitive dynamics; however, all models within 2 ΔAICc units of the best model were also considered when selecting appropriate radii (step 1) and interpreting the nature of competition (step 2). In addition we relied on summed AICc weights (Johnson & Omland 2004), to evaluate the relative importance of individual predictors using the full set of candidate models. For example, because half of our candidate models included mortality as a modifier to the competition index, the sum of AICc weights for these models, over the sum of weights for models without mortality, yields a modified *evidence ratio* (Burnham & Anderson 2002). In this example, an evidence ratio of $X > 1$ would suggest that models including mortality are X times more likely to best characterize competitive effects, given this set of candidate models and these data.

Residual plots were examined for all models to evaluate lack of fit and homogeneity of variance. After this set of candidate models was evaluated using data pooled from all three sites, we repeated the model-fitting process described above (excluding site as a random effect) for each individual site to determine if the appropriate radii and factors affecting individual tree growth differed across these three populations. Goodness-of-fit for each model was determined based on the correlation between observed and predicted basal area growth (cf. Canham et al. 2004). All candidate model analyses were performed in SAS (SAS Institute Inc., Cary, NC, US).

We analysed plot-level spatial patterns of trees, competition indices and tree growth rates to determine if the relationship between these patterns could elucidate factors influencing tree growth within and among plots. Specifically, our intent was to visually determine if neighbourhoods with high competitive effects had correspondingly low basal area growth (and *vice versa*), as one would expect if competition were influencing growth. Thus, two kriged surfaces were created for each plot, the first using individual basal area increments and the second using competition indices. Because we intended to visually compare the kriged surfaces among plots, we applied the best-fitting competition model and neighbourhood radius based on pooled data to each plot. We used ordinary kriging, based on a spherical model, set to include at least four neighbours, and with lag distances of at least 2 m. Because basal area growth on Plots B and C exhibited a first-order directional trend (higher growth to the north in Plot B, higher to the south in Plot C), we removed the trend *via* linear regression prior to kriging analyses. Finally, we analysed tree spatial patterns, testing for each plot if trees displayed random, uniform or clustered distributions, using the function *L(t)*, a transformation of Ripley's *K(t)* function (Fortin & Dale 2006). This approach allowed us to assess the influence of tree spatial patterns on within-stand variability on competition intensity, and hence growth rates. Kriging was conducted in ArcGIS (v. 10.1, Esri, Redlands, CA, USA) and the *L(t)* functions were calculated in the *spatstat* package in R (R Foundation for Statistical Computing, Vienna, AT).

Results

The appropriate radii with which to evaluate competition varied somewhat among plots: 8.5 ± 1.0 m (±SD, Plot A), 6.7 ± 0.6 m (Plot B) and 8.0 ± 1.5 m (Plot C), with a pooled data mean of 7.3 ± 0.6 m. Model results based on these radii demonstrate that neighbourhood competition explained much variation in basal area growth; that is, focal tree growth decreased with increasing competition indices (Fig. 1). R^2 values for best-fit models (lowest AICc scores) were 0.81, 0.68, 0.59 and 0.73 (plots A, B, C, pooled data, respectively). For the pooled data, as well as Plots B and C, neighbourhood competition was best characterized by distance-dependent models that included tree crown volume as the size metric, with neighbour trees weighted by distance to the focal trees (Hegyi's index modified) (Table 1). Evidence ratios supporting the Hegyi index were quite high: 4.1 and 38.5, Plots B and C, respectively (Table 2). In contrast, on Plot A, neighbourhood competition was somewhat equally characterized using the distance-weighted (Hegyi's index modified) and non-distance-weighted (Lorimer's index modified) models, as the confidence model set (defined as models with Δ AICc < 2) included both forms (Table 1). The evidence ratio (1.3) provided weak support in favour of Lorimer's index. On all three plots, crown volume was consistently a stronger predictor compared to the alternate size metrics (diameter, canopy projection area): it was present in all of the 24 confidence models (Table 1), and its evidence ratios were 72.0, 392.7 and 84.1 (Plots A–C, respectively; Table 2). Only on Plot C did the confidence model set include interaction terms, suggesting that tree growth was influenced by the interaction between a tree's neighbourhood competitive environment and its initial size (Table 1). In all cases, models including neighbourhood

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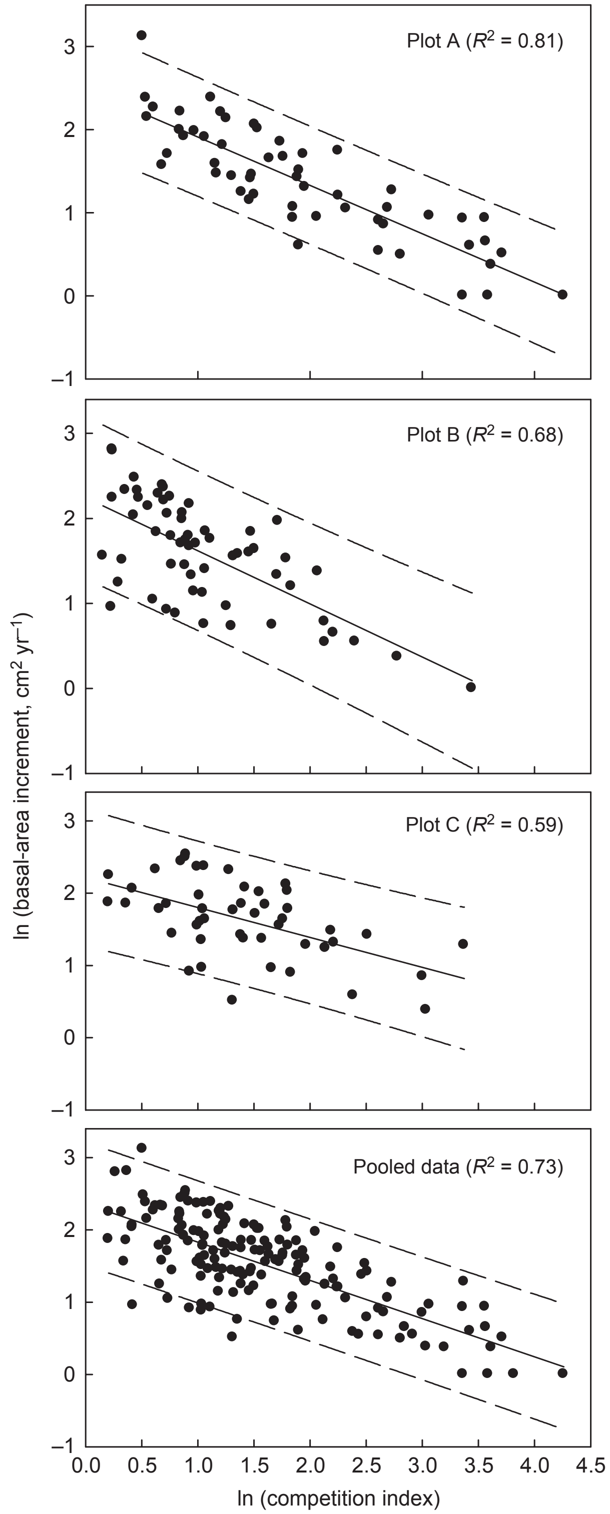

Fig. 1. The negative relationship between growth rate and competition intensity, for the three old-growth *Picea abies* populations, and for all populations combined. Dashed lines indicate 95% prediction intervals. R^2 values correspond to fit of the best-fit model for a given population.

competition ranked well above the null model, which included initial size only, further pointing to the role of competition in regulating tree growth. Additional metrics related to these analyses are summarized in Table 2, and parameter estimates and their confidence limits for the best-fit models are presented in Table 3.

Model rankings provide modest support for down-weighting the competitive effect of neighbour trees that died during the 18-yr sampling period, as best-fit models for two of the three plots, as well as the pooled data, included mortality down-weighting, and such models represented 14 of the 24 confidence model sets (Table 1). However, evidence ratios provided only weak support for mortality down-weighting (Table 2). Model rankings provide weak support for the influence of within-neighbourhood clustering on focal tree growth, as models including clustering represented seven of the 24 confidence models (Table 1); however evidence ratios provide little or no support for the inclusion of clustering (Table 2).

In contrast to the findings regarding within-neighbourhood spatial patterning, results from the stand-level spatial pattern analysis revealed that underlying arrangement of trees had a pronounced effect on competition intensity, and that this effect varied among plots. Plot A showed significant tree clustering to a distance of ca. 15 m (aside from a tendency toward randomness at very short distances); Plot B showed random patterning (aside from clustering at very short distances); Plot C showed random patterning at short distances, with a tendency toward uniformity beyond ca. 5 m. Similarly, the evidence of local spatial variation in growth and competition intensities, as revealed by kriging, differed markedly between plots (Fig. 2). For example, Plot A showed distinct local 'hot spots' of high competition intensity, which roughly correspond to local regions of low tree growth. In contrast, Plots B and C show more homogenous kriged surfaces for both competition intensity and tree growth.

Discussion

Inter-tree competition clearly affected growth rates, as evidenced by superior performance of models that included competition indices, when compared to null models (i.e. initial size alone). Tree crown volume was consistently the size metric that best described the neighbourhood competitive environment. Specifically, neighbours with large crowns had a higher competitive effect than neighbours with small crowns, suggesting the influence of above-ground competition on individual tree growth (Biging & Dobbertin 1992). The few studies that have included crown volume as a size metric for describing competitive interactions have also reported favourable, albeit more modest, results (Biging

Table 1. Ranking of the confidence model sets (those within 2 ΔAICc units) for the three old-growth *Picea abies* populations, as well as all populations pooled (lower AICc scores indicate stronger support). Also included is the highest-ranked model based on a size metric (used in the competition index) other than crown volume, as well as the null model based on initial size alone. Mortality weighting accounts for neighbours that died during the sampling period; the clustering index accounts for within-neighbourhood tree clustering. Interaction refers to the competition index × initial size interaction present in models.

Source	CI form	Size metric	Interaction	Mortality weight	Clumping index	k	AICc	ΔAICc	AIC wt
Plot A	Hegyi	crown volume	no	yes	no	4	47.6	0.000	0.123
	Lorimer	crown volume	no	yes	no	4	47.7	0.128	0.115
	Hegyi	crown volume	no	no	no	4	47.8	0.237	0.109
	Lorimer	crown volume	no	no	no	4	47.9	0.302	0.106
	Lorimer	crown volume	no	yes	yes	4	48.5	0.906	0.078
	Lorimer	crown volume	no	no	yes	4	48.5	0.947	0.076
	Hegyi	crown volume	no	yes	no	5	49.4	1.842	0.049
	Lorimer	crown volume	no	yes	no	5	49.6	1.972	0.046
	Hegyi	canopy area	no	yes	no	4	54.3	6.677	0.004
	Null	–	–	–	–	4	112.1	64.513	0.000
Plot B	Hegyi	crown volume	no	no	yes	4	85	0.000	0.179
	Hegyi	crown volume	no	yes	yes	4	85.1	0.178	0.164
	Hegyi	crown volume	no	no	no	4	85.9	0.959	0.111
	Hegyi	crown volume	no	yes	no	4	86.1	1.126	0.102
	Hegyi	diameter	no	no	yes	4	99.2	14.264	0.000
	Null	–	–	–	–	4	116.3	31.314	0.000
Plot C	Hegyi	crown volume	no	yes	no	5	66.1	0.000	0.137
	Hegyi	crown volume	yes	yes	no	6	66.3	0.241	0.122
	Hegyi	crown volume	no	yes	no	4	66.3	0.247	0.121
	Hegyi	crown volume	no	no	no	4	66.7	0.583	0.103
	Hegyi	crown volume	no	no	no	5	66.7	0.594	0.102
	Hegyi	crown volume	yes	yes	yes	6	67	0.918	0.087
	Hegyi	crown volume	no	yes	yes	4	67.5	1.395	0.068
	Hegyi	crown volume	yes	no	no	6	67.6	1.546	0.063
	Hegyi	crown volume	no	no	yes	4	67.9	1.855	0.054
	Hegyi	canopy area	no	yes	no	4	74.2	8.138	0.002
	Null	–	–	–	–	4	82.2	16.140	0.000
Pooled	Hegyi	crown volume	no	yes	no	4	190.6	0.000	0.319
	Hegyi	crown volume	no	no	no	4	191.7	1.064	0.187
	Hegyi	crown volume	no	yes	no	5	192.3	1.728	0.134
	Hegyi	canopy area	no	no	no	4	223.9	33.242	0.000
	Null	–	–	–	–	5	304.3	113.699	0.000

CI, competition index; AIC wt, AIC weight; k, number of model parameters.

Table 2. Plot-level values describing growth and competition for three old-growth *Picea abies* plots. Values in columns two through four are means (±SD). Evidence ratios (see text) provide a level of support (higher = more support) for the various predictors and weights.

			Basal area	Evidence ratios			
Plot	No. neighbours Per focal	CLI	Growth ($cm^2 \cdot yr^{-1}$)	CI	Mort. wt.	CLI	Crn. vol.
A	17.3 (5.8)	0.43 (0.08)	3.19 (3.46)	1.3 (Lorimer)	1.1	0.4	72.0
B	8.5 (2.6)	0.42 (0.11)	3.54 (3.18)	4.1 (Hegyi)	1.0	1.4	392.7
C	10.1 (2.6)	0.39 (0.09)	4.46 (3.14)	38.5 (Hegyi)	1.5	0.5	84.1

CLI, clustering index; CI, competition index; Mort. wt., mortality weight; Crn. vol., crown volume, one of the size metrics used in the CI.

& Dobbertin 1992; Filipescu & Comeau 2007). Similar conclusions may be inferred from studies reporting superior performance of models that include both crown projection area and tree height (Castagneri et al. 2008). Although numerous previous studies disagree on the merits of weighting the competitive effects of a given neighbour by tree distance (e.g. Lorimer 1983; Tomé & Burkhart 1989; D'Amato & Puettmann 2004), our results from two of the three plots, as well as the pooled data, provide strong support for distance weighting, given that all models in these confidence sets (those <2 ΔAIC units) included focal-to-neighbour tree distance, *via* Hegyi's index. This importance may reflect the increased range of

Table 3. Parameter estimates and confidence limits (parentheses) for the best-fit models for each plot, as well as the pooled data. *N* = number of focal trees used in analyses.

Plot	Intercept	Competition index	Initial size	*N*	R^2
A	2.493	−0.582 (−0.678, −0.486)	–	55	0.81
B	2.243	−0.625 (−0.801, −0.448)	–	60	0.68
C	2.533	−0.526 (−0.748, −0.304)	−0.356 (−0.782, 0.071)	48	0.59
Pooled	2.362	−0.529 (−0.606, −0.453)	–	163	0.73

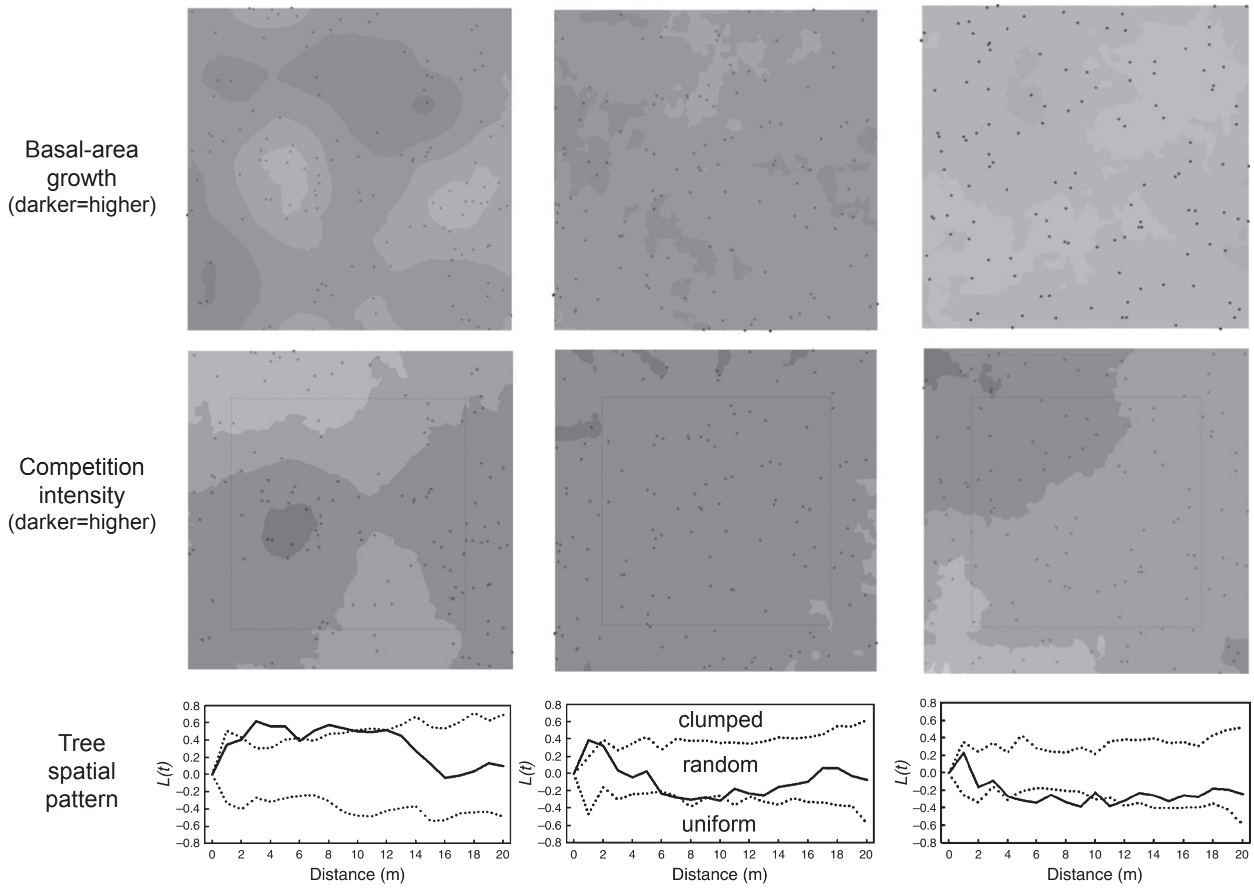

Fig. 2. Kriged images (two top rows) showing within- and among-plot variation in tree growth (basal area increment) and competition intensity (assessed by modifications to Hegyi's distance-dependent index) in three old-growth *Picea abies* populations. Populations form a gradient in tree spatial dispersion (*L(t)* function, solid line in bottom row of figures), from generally clustered (Plot A) to random (Plot B) to random–uniform (Plot C). Due to the search radius used in calculating the competition index, only the delineated inner core of the competition intensity images should be strictly evaluated. Small dots indicate tree locations. Plot size is 50 × 50 m.

competitive environments found within the old-growth populations examined here relative to the younger natural and managed populations typically used for describing relationships between tree growth and neighbourhood competition. Finally, the inclusion of the interactive effects of initial size and competition within the confidence model set for Plot C (Table 1) lends support to the notion that the relative influence of neighbourhood competition on tree growth may vary across size classes within a population (D'Amato & Puettmann 2004).

Neighbourhood indices of competition have been criticized for their inability to account for stochastic and developmental processes that may alter neighbourhood conditions over the growth interval examined (Burton 1993; Metsaranta & Lieffers 2010; Hartmann & Messier 2011). We partially addressed this concern by down-weighting the competitive influence from neighbour trees that died during the sampling period. Although models including this down-weighting appeared in the confidence model sets for all plots, evidence ratios provided only weak support for including mortality. Logically, competitive stress on the focal tree would be reduced by the death of a vigorous neighbour (arguing for down-weighting). However, the weights are applied only to dead neighbours' contributions to the competition index; for neighbourhoods with many living trees, relative to dead, this contribution may be negligible. We note that the plot with the highest evidence ratio in favour of mortality weighting (Table 2) also had the highest mean percentage of dead neighbours per neighbourhood (22%, Plot C) compared to 9% and 8% (Plots A and B). Further, trees experiencing mortality in this system very typically have poor vigour, as evidenced by their declining or persistently slow growth prior to death (Fraver et al. 2008). As a consequence, a declining neighbour tree, with relatively low rates of resource capture, may have exerted limited competitive stress on the focal tree in the years prior to its death. Further, if the neighbour remained standing as a snag, its crown could continue to shade the focal tree, as this species may retain fine twigs for ten or more years following death (Storaunet & Rolstad 2002). Taken together, these conditions provide insight into the confounding factors that may explain why down-weighting according to mortality during the sampling period did not receive stronger support in our model evaluation.

Accounting for the potential influence on competition intensity resulting from the spatial arrangement of local competitors has long been suggested as a way to improve predictions of focal plant growth (Mack & Harper 1977; Burton 1993). However, our results suggest that the within-neighbourhood clustering of trees, assessed by our clustering index, had little or no influence on competition intensity. Similarly, Canham et al. (2004) found that including an index of clumping did not improve model predictions of tree growth. This negative result may be explained in part by the lack of strong within-neighbourhood clustering evident in these populations (mean indices were relatively low; Table 2), despite strong spatial clustering at stand scales for Plot A, as well as the lack of variation in clustering indices (SD low; Table 2).

The relationship between tree spatial dispersion, competition intensity and growth rate varied from plot to plot. The three plots conveniently formed a gradient of tree spatial dispersion, from generally clustered (Plot A) to random (Plot B) to random–uniform (Plot C). Tree clustering on Plot A locally intensified inter-tree competition, creating areas of low growth rates (Fig. 2). Conversely, areas with sparse tree density on this plot tended to have higher growth rates. However, the two kriged images (competition intensity and growth rate) are not mirror images of one another, in part because competition on this plot accounted for only 81% of the variance in growth (Fig. 2). Nevertheless, results from this plot show the striking influence of underlying tree spatial patterning on the processes of competition and tree growth, which in turn may regulate tree vigour and mortality risk (Das et al. 2008). A visual interpretation of the kriged surfaces for this plot also suggests that the ideal radius of influence for focal trees likely varies from location to location within the plot; however, our models do not account for this within-plot variation. Biondi et al. (1994) and Nanos et al. (2004) show within-plot variability in tree growth, with patchiness at a scale similar to that seen in Plot A, which these authors attribute in part to competitive interactions. In contrast, the random tree dispersion on Plot B and the random–uniform dispersion on Plot C resulted in weak spatial dependence in competition intensity, which appears to be spatially unrelated to the similarly weak spatial dependence in tree growth on these two plots (Fig. 2). The poor spatial relationships between competition intensity and tree growth may be reflected in the relatively low explanatory power of the top competition models for these plots: 68% and 59% of growth variance explained, Plots B and C, respectively.

In locations where competition is relatively unimportant, the influence of underlying site conditions on tree growth becomes more clearly expressed (Fox et al. 2007). Thus, variation in tree growth not attributable to inter-tree competition, as evaluated here, could be explained in part by within-plot variability in soil fertility, water availability and microtopography, as boreal forests typically exhibit spatial heterogeneity in these attributes (Järvinen et al. 1993; Kuuluvainen 1994; Økland et al. 2008). In addition to their potential influence on tree growth rates, these intrinsic site conditions may influence the strength and outcome of competitive interactions (Woods 2000; Coomes & Allen 2007). Further, although not mapped or quantified, patches of dense herbs and shrubs on these plots likely exert competitive stress on trees, an effect that has been demonstrated in mature *Picea* trees in similar settings (Cortini & Comeau 2008).

Tree growth rates, as well as competition intensity, varied not only within plots, but also among plots within this small landscape. Although the importance and/or intensity of competition has been shown to vary along large-scale environmental gradients (Filipescu & Comeau 2007; Canham et al. 2006), these three plots do not span such pronounced gradients. Instead, the differences likely reflect tree spatial patterning (as above), as well as site heterogeneity within this small landscape. Thus, the relative importance of inter-tree competition vs intrinsic site conditions may vary according to location within stands or within a small landscape (see also Baribault & Kobe 2011).

Conclusion

Inter-tree competition has only rarely been addressed in old-growth forests, particularly those at high latitudes. Our findings point to competition as an important structuring mechanism in this system, demonstrating that competition continues to influence forest processes and structures in an old-growth system that has not experienced major disturbance for at least two centuries. Our results suggest that the spatial arrangement of potential competitors within a focal tree's immediate neighbourhood, assessed by our within-neighbourhood clustering index, has little or no influence on competition intensity. In contrast, competition intensity is influenced by the underlying stand-level tree spatial arrangement: tree clustering locally intensified competition and reduced tree growth, whereas in the absence of such clustering, inter-tree competition played a lesser role in constraining tree growth. This finding may have profound influence on the interpretation of typical tree competition studies, in which within-stand spatial patterning is rarely taken into account. This consideration is especially relevant to late-successional forests, which often exhibit clustered tree distributions (Lingua et al. 2008; Aakala et al. 2012). Our results also demonstrate that competition intensity can vary markedly across spatial scales; that is, its influence varied within stands as well as among stands within a small landscape. Although this study addresses just one forest type in boreal Sweden, our findings nicely illustrate a more general principle, namely the importance of forest structure – particularly the within-stand spatial arrangement of trees – in regulating inter-tree competition and growth in structurally diverse forests.

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