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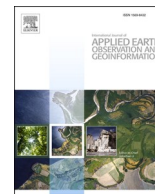
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Quantifying the effects of competition on the dimensions of Scots pine and Norway spruce crowns

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ABSTRACT

Inter-tree competition can be assessed using relatively simple indices derived from tree diameters, heights and locations, but they have often been found to be deficient for predicting tree growth. To better understand these linkages, we measure dimensions of Scots pine and Norway spruce crowns, which are assumed to be affected by competition pressure. We extract these features from terrestrial laser scanning point clouds and model their dependencies on competition. Our results indicate that while competition is a major determinant for crown morphology, the characteristics and most applicable indices of the two species are contrasting. We interpret our results primarily by light competition: pines are seeking for light and invest their resources on widening the crown only in suitable conditions, while spruce may grow large despite of shortage of light. We conclude that shade tolerance affects strongly on the identification of actual competitors, which should be addressed when modelling competition.

1. Introduction

Given certain site and stand conditions, growth of individual trees and consequent spatiotemporal dynamics of forest stands depend largely on competition for space and light as well as other potentially limiting resources such as water and nutrients (Caplat et al., 2008, Kolobov and Frisman, 2016). While competition is one of the fundamental factors for tree growth and survival, our understanding of its detailed consequences or potential mitigation strategies are however deficient. Challenges lie both in measuring the effects of competition and differentiating them from underlying site and stand level determinants. This is due to a highly complex system derived from inter-tree relationships, in which the distribution of resources depends on the species, sizes and spatial clustering of the competitors (Coomes and Allen, 2007, Das, 2012, Shi and Zhang, 2003). Better understanding of competition would benefit assessments related to the dynamics of natural stands as well as optimization of silvicultural management. In the latter case, management generally strives for minimizing excessive competition and increasing the available resources of the best trees by removing poor-quality or lower value trees.

To understand competition and its effects on tree growth, the occurrence and degree of competition need to be quantified. This

evaluation is often based on so called competition indices (CI), which can be regarded as describing resource sharing relationships between the subject tree and its competitors either using their dimensions, spatial arrangement, or both. CIs can be either spatially explicit, utilizing information on tree locations, or spatially implicit, relying only on general stand-wise features. Spatially explicit CIs are closely related to the concept of zone of influence which may be considered as the total area over which the tree may at present obtain or compete for site resources (Opie, 1968). The zone of influence will be maximized in case of unrestricted competition, but normally the zones of neighbouring trees will overlap which indicates competition. In practice, the zone of influence is often approximated as a circular area around the tree within a certain radius, which is potentially adjusted by a selected tree-related size parameter (e.g., García, 2014, Holmes and Reed, 1991, Opie, 1968). Alternatively, competition can be assessed using kernel functions which model the attenuation of competition with increasing distances (Häbel et al., 2019, Pommerening and Maleki, 2014).

Spatially explicit CIs with known locations of competitor trees could intuitively be regarded as a superior solution as compared to spatially implicit indices, derived from that they can capture certain deterministic biotic phenomena occurring at small spatial scales (DeAngelis and Yurek, 2017). During the years, several different approaches based on

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the number, locations and sizes of neighbouring trees have been developed for describing the competition and for modelling its effects on tree growth and survival (Burkhardt and Tomé, 2012, DeAngelis and Yurek, 2017, Miina and Pukkala, 2000). However, while the spatially explicit dependencies and related causalities can improve our understanding on forest structure, the use of actual tree locations had often seemed to add little additional value when predicting tree growth and mortality, even in structurally complex forests (Bianchi et al., 2020, Kuehne et al., 2019, Martin and Ek, 1984, Wimberly and Bare, 1996).

One phenomenon which diminishes the effects of knowing the explicit tree locations, is the plasticity of tree crowns. In other words, as a result of phototropism trees may aim at stretching upwards or leaning laterally towards less contested spaces, which also provides them abilities to reduce the negative effects of competition (García, 2014, García, 2022, Lee and García, 2016, Strigul et al., 2008). This behavior may significantly alter the crown size, structure and exposed crown area, which are important determinants for further tree growth (Cole and Lorimer, 1994, Hatch et al., 1975, Pretzsch, 2021, Wyckoff and Clark, 2005). If perfect plasticity is not expected – describing the state when equilibrium among neighbors is reached and tree locations become totally irrelevant (García, 2022) – weak performance of spatially explicit CIs can be interpreted to indicate that the expected competitors do not affect the subject trees' resources in similar proportions as assessed by the indices. Further, this reflects our knowledge gaps in estimating the nature and magnitude of competition relationships which do not always depend on the size and distance of the adjacent trees. As trees however react to competition pressure via the plasticity and altered morphology of their crowns, which leads to mitigating or even overriding the negative consequences of competition, the variation in sizes and shapes of their crowns can be regarded as applicable measures of competition pressure.

Simple crown-related structural parameters (mainly width or length) have been traditionally collected with time-consuming conventional field measurement tools. Modern technologies such as airborne and terrestrial laser scanning (ALS, TLS) nowadays enable capturing more complex information by direct measurements from standing trees in their natural environment (Jung et al., 2011, Seidel et al., 2011, Krůček et al., 2019). Given that these data are point clouds consisted of distinct observations in the x-y-z space, proxies for measuring crown dimensions have included, for example, convex hulls, alpha shape metrics, and voxel-based approaches (Zhu et al., 2021). Many of the studies have been based on ALS data (e.g., Vauhkonen et al., 2008, 2009) but, more recently, use of TLS-derived point clouds has increased. The fundamental difference between the two is the viewing angle; the top-down view of ALS is better for detecting features related to the canopy layer, whereas the bottom-up perspective of TLS allows capturing higher degree of details from lower parts of the crown (e.g., Barbeito et al., 2017, Bayer et al., 2013, Hess et al., 2018). As ALS and TLS capture different aspects of the trees, their combined use and fusion may also provide synergies which are not enabled by either of the two data sources alone (White et al., 2016, Zhu et al., 2021).

In our study, we focus on crown characteristics of Scots pines (*Pinus sylvestris* L.) and Norway spruces (*Picea abies* (L.) Karst.). We aim at first, to measure and quantify various dimensions related to tree crowns; second, to model their dependencies on site-, stand- and competition-related variables; and third, to improve our understanding on how competition pressure alters tree crowns of the two studied species. Our hypothesis is that competition pressure can explain majority of the residual variance after inclusion of all the essential site- and stand-level variables.

We take advantage of TLS data collected from numerous locations in Finland, reflecting a range of site conditions in boreal forests. We extract various TLS-derived crown dimensions and use linear mixed modelling (LMM) to connect them to a range of field-observed determinants and competition measures. Competition pressure is included using both spatially implicit and explicit CIs which are based on the diameters,

basal areas, heights and locations of trees. These are expected to indicate the fundamental and practically quantifiable effects connected to inter-tree competition, which can potentially be linked to crown characteristics and reveal any differences between the two targeted species. This information can also further be used for developing better CIs and growth models for individual trees.

2. Materials and methods

2.1. Data collection

The study data was selected from a large pool of TLS data, scanned from plots ($n = 253$) belonging initially to the Finnish national forest inventory (NFI) and thereafter selected as a representative sample of boreal forest diversity in Finland based on a range of NFI-derived measurements. Of these plots, 105 were dominated by Scots pine (*Pinus sylvestris* L.), 60 by Norway spruce (*Picea abies* (L.) Karst.), 11 by silver birch (*Betula pendula* Roth), 9 by downy birch (*Betula pubescens* Ehrh.) and one by Siberian larch (*Larix sibirica* Ledeb.), as determined by the species having the largest proportion of the total basal area. Plot-wise mean diameters of the dominant storey varied between 10 and 440 mm and mean heights between 0.7 and 33.2 m, respectively.

New field data from these plots, including scanned TLS point clouds and field measurements from tally trees, were collected in 2017–18. Tally trees to be measured were first selected by angle count (Bitterlich) sampling by using the basal area factor of $q = 2$ (Tomppo et al., 2011), maximum distance of 9.00 m from the plot centre, and minimum diameter at breast height (DBH) of 50 mm. Each tally tree was recoded its location, species, DBH, tree height (h), canopy layer and base height of the living crown. Tally trees were also marked using duct tape, identifiable by TLS points' intensity values, to facilitate their later identification from the point cloud data. In addition, the previously measured NFI data provided plot- and stand-level variables to be applied in the study.

Each plot was scanned using Leica P40 time-of-flight TLS scanner by selecting 3.1 mm point spacing at 10 m distance and normally covering the plot with 4–6 stations, depending on the tree density and other potential obstacles. The aim was to maximise the visibility of the tally trees and their neighbours from several stations while simultaneously keeping the scanning workload limited. Individual scans were co-registered in Leica Cyclone software using spherical targets, which normally resulted in residual errors of 1–3 mm as recorded at target locations.

A subset among all the plots was selected with focus on the two commercially most important tree species, Scots pine and Norway spruce, which together dominate almost 90 % of the forested land in Finland. Plot selection was based on the following conditions, which were expected to indicate relatively normal boreal forest stands and enable successful extraction of individual trees from the TLS data:

1. Dominance by Scots pine or Norway spruce;
2. Compartment-wise average DBH between 100 and 250 mm;
3. Compartment-wise dominant height of 10 m or more;
4. No compartment edge within 5 m distance from the plot edge (to avoid edge effects); and
5. Visually evaluated to be applicable for individual tree extraction (i.e., excluding some of the densest plots with highly intermixed canopies).

Of all the potential plots satisfying these conditions, 12 spruce- and 12 pine-dominated plots were randomly selected for this study (Fig. 1), corresponding to the expected resources allocable for detailed tree segmentation and feature extraction. These 24 plots included altogether 255 field-measured tally trees (4–16 per plot), of which only Scots pines and Norway spruces without observed damages (e.g., having growth disturbances or obvious needle damages) were further processed for feature extraction and modelling. Other trees than pines and spruces

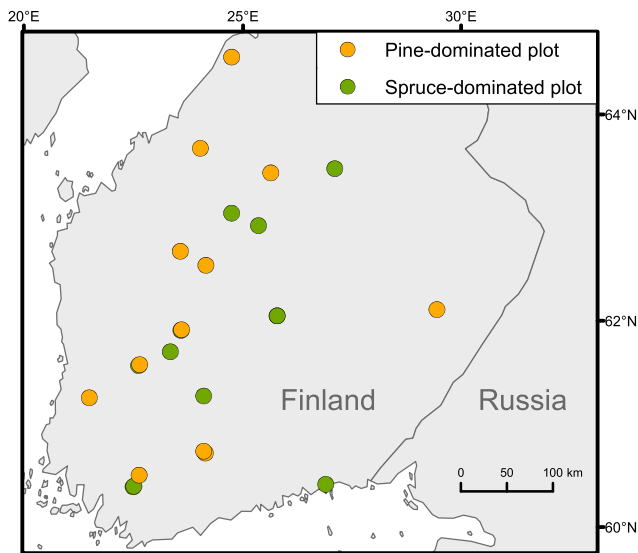


Fig. 1. Location of the study plots. Some of the plots are belonging to the same NFI clusters and therefore located relatively close to each other, resulting in partially overlapping symbols at the applied scale level.

were decided to be excluded, as they were mostly suppressed trees of several species, and were considered as not providing representative results. Therefore, the final set of tally trees consisted of 113 Scots pines and 96 Norway spruces, respectively.

2.2. Feature extraction

Co-registered TLS point cloud from each plot was first cut to contain points within 12.5 m radius from the plot centre, intended at to include all the tally trees and their full or almost full crowns, as well as stems and partial crowns of other trees in their vicinity. Digital elevation model was created at 50 cm raster resolution, the point cloud was normalized to the ground level, and a vertical slice between the heights of 1.0 and 1.6 m was extracted from the normalized cloud for tree detection. The slice was first filtered by removing regions of low point densities and structures not having near-vertical orientation, as estimated using surface normals of adjacent points. Then, the locations and DBHs of all the potential trees were predicted using RANSAC method and arc-based tree detection similar to Pitkänen et al. (2021), approving features with at least 1/3 continuous circle arc with none or few points inside as candidate trees. Candidate trees were plotted as images and inspected manually to exclude any other structures erroneously detected as trees.

The approved tree detections were connected to the tally tree measurements based on their locations and the attached duct tapes (visible by TLS-derived reflection intensities). Tally trees were further processed to extract their crown dimensions whereas the remaining trees (*i.e.*, nontally trees) with no field measurements were included only in the calculation of competition indices. In addition to DBHs, heights of nontally trees were also estimated from point cloud data by fitting a cylinder near to the DBH level, calculating its direction, extending the cylinder upwards, and using the end of the point cloud or any substantial break in it to define the treetop. This strategy was considered as computationally light, relatively accurate for most trees, and capable of processing also suppressed trees.

For extraction of crown dimensions, individual point clouds of tally trees were semi-automatically extracted. This was done by dividing the point cloud first into 30 cm voxels, removing voxels with less than 100 points, and extracting TLS points within connected voxels in the vicinity of the tally tree. This initial tree-wise point cloud was thereafter carefully manually cleaned using Leica Cyclone software to include only parts belonging to the tally tree but excluding adjacent trees and ground

vegetation. Point cloud was further decimated to contain on average only one point per 5x5x5 mm voxel in order to reduce the effects of variable point densities in feature extraction. At this stage, and to be later used in modelling, trees were also defined a TLS quality class based on their visual outlook and potential occlusions. Three classes were distinguished: trees with no obvious deficiencies, trees with minor deficiencies (*e.g.*, some branches missing), and trees with moderate deficiencies (larger parts with missing points, but still acceptable for extracting major structural characteristics). Four spruces were excluded from the analysis due to heavily mixed canopies (preventing successful individual-tree extraction) or major deficiencies (likely to provide unrepresentative data of crown dimensions).

Finally, features according to Table 1 were extracted using the individual point clouds of each tally tree to be used as response variables in the modelling phase. All the crown-related measures consider only the living crown part, *i.e.*, above the field-measured base height of the living crown. Regarding to the stem leaning angle and direction, which were included to indicate whether contemporarily measured competition affects also on the stem, the upper measurement point was fixed at mid-stem level for practical reasons. First, completeness of the stem will gradually degrade when going upwards in the point cloud (*e.g.*, Liang et al., 2018, Saarinen et al., 2017) and second, with respect to co-registered multi-scan TLS data, wind may easily cause overlapping or diverging stem halves in the upper parts of stem thus complicating accurate stem detection (*e.g.*, Pitkänen et al., 2019, Vaaja et al., 2016). Therefore, mid-stem height was regarded as a compromise of enabling unambiguous stem detection yet providing relevant information with respect to the whole stem. The mid-stem coordinates were defined manually by visual interpretation, which was preferred instead of automatic methods to confirm the quality and consistency of the results.

2.3. Competition measures

The calculated CIs are presented in Table 2. Four distance-independent and four distance-dependent indices were applied, including both two- and one-sided measures, *i.e.*, distinguishing whether all or only larger competitors were included. Subject trees were the tally trees selected for the study with TLS-extracted features. Competitor trees included both tally and nontally trees, all of which had either field-measured or TLS-predicted DBH and height. Calculation of distance-independent indices was based on all the trees on the plot. Competitors for distance-dependent indices were selected within a radius of 6 m

Table 1

Response features and their extraction methods related to tally trees.

Feature and abbreviation	Description
Crown diameter (Diam)	Mean value of the longest horizontal diameter and its perpendicular diameter, calculated similarly to Fernández-Sarría et al. (2019)
Crown projection area (ProjA)	Calculated using two-dimensional top view perspective and the R package "alphahull" (Pateiro-Lopez and Rodriguez-Casal, 2019) with an α -value of 1, resembling the traditional crown projection measurement (Jacobs et al., 2021)
Crown volume (Vol)	Calculated using the R package "alphashape3d" (Lafarge and Rodriguez-Casal, 2020) with an α -value of 0.3, similarly to Hildebrand et al. (2021) and Owen et al. (2021)
Crown symmetry (Sym)	Ratio between the two horizontal diameters used to calculate the crown diameter (the longest vs perpendicular)
Crown displacement (Disp)	Horizontal distance between the stem centre at DBH level and the coordinate centroid of living crown TLS points (note: TLS-based crown centre is not connected to the stem location)
Stem leaning angle (SLAng) and direction	Angle from vertical direction and leaning direction (bearing) of the stem, detected between the stem centres at DBH and $0.5 \times h$ levels

Table 2
Competition indices used in this study, including calculation formulae, evenness and selected references.

Index	Formula	Evenness	Reference
<i>Distance-independent indices</i>			
CI ₁	N	Two-sided	Biging and Dobbertin (1995)
CI ₂	$\frac{\sum a_{vox}}{A}; h_{vox} > 1.3 \text{ m}$	Two-sided	Rivas et al. (2005); Contreras et al. (2011)
CI ₃	$\frac{\sum_{j=1}^n BA}{BA_i}$	Two-sided	Daniels (1976); Dimov et al. (2008)
CI ₄	$\frac{\sum_{j=1}^n BA}{BA_i}; d_j > d_i$	One-sided	Wykoff (1990)
<i>Distance-dependent indices</i>			
CI ₅	$\sum_{j=1}^n d_j / (d_i \times dist_{ij})$	Two-sided	Hegyi (1974)
CI ₆	$\sum_{j=1}^n h_j / (h_i \times dist_{ij})$	Two-sided	Braathe (1980), cited in Pukkala and Kolström (1987)
CI ₇	$\sum_{j=1}^n \alpha_j; d_j \geq (0.8 \times d_i)$	One-sided	Pukkala and Kolström (1987)
CI ₈	$360^\circ - \max_{j,k \in n} \beta_{jk}; d_{j,k} \geq (0.8 \times d_i)$	One-sided	Rouvinen and Kuuluvainen (1997)

N total number of trees (stems) detected on the plot; a_{vox} horizontal projection area of a point-filled voxel, A total plot area; h_{vox} relative height of the respective voxel from the ground; BA basal area of a single tree; i subject tree; j, k, \dots, n competitor trees; d diameter (DBH) of a single tree; $dist_{ij}$ distance between the subject tree i and the competitor tree j ; h height of a single tree; α_j horizontal angle covered by the stem of the competitor tree j ; β_{jk} horizontal angle between the stems of competitor trees j and k without any other competitors.

around the subject tree, corresponding to the value indicated for Scots pines by Miina and Pukkala (2000). They suggested a longer distance for Norway spruce, but a flat range of 6 m was applied to all the trees in our study. This was due to that non-tally trees had been detected within a maximum radius of 12.5 m whereas tally trees could be located up to a 9 m radius from the plot centre, therefore providing only a 3.5 m edge zone at shortest. As tally tree selection however had been performed using angle count sampling, *i.e.*, favouring the inclusion of trees close to the plot centre, approximately 80 % of all the tally trees were located within the radius of 6.5 m from the plot centre. Further, as only a small fraction of the remaining 20 % of trees were likely influenced by trees missing from the data, the 6 m radius was concluded to be a suitable compromise for competitor selection.

Distance-independent indices included total number of trees (CI₁), canopy closure fraction (CI₂, *i.e.*, the area of tree crowns as projected on a horizontal plane, proportioned to the total plot area) and two indices based on basal areas (CI₃ and CI₄). Calculation of the canopy closure was based on the TLS data by dividing the point cloud into 25 cm voxels, selecting only point-filled voxels above the DBH level, and proportioning their x,y projection area to the total plot area. Basal areas were expected to provide a robust and straightforward way to evaluate competition at the stand level, and they were applied as indices proportioned to the subject tree. For index CI₄, only basal areas of larger trees (in terms of the DBH) were included.

The distance-dependent indices included the widely used Hegyi's (1974) index, based on difference between competitors weighted by their distance, considering either diameter or tree height as a size parameter (respectively CI₅ and CI₆). We assumed that an index based on height would better describe the competition for light with further consequences on crown plasticity, while the index based on diameter would rather indicate competition for water and nutrients. CI₇ was related to the sum of angles (α) covered by the stems of competitor trees, and CI₈ was based on the largest free angle between the competitor trees (β) without any other competitors, thus quantifying potential responses to directional competition. Subtracting the angle from 360° intends to

transpose the index CI₈ similar to other indices, *i.e.*, larger values denoting expected higher competition pressure. This also changes its interpretation to indicate the smallest continuous horizontal angle which includes all the competitors. For indices CI₇ and CI₈, size-related threshold for competitors was set to 80 % with respect to the subject diameter. This aimed at selecting all the potential nearby competitor trees which belonged most likely to the same canopy layer while providing some flexibility for prediction inaccuracies of the diameters.

While the applied indices can measure the current competition situation of the given stand, there will remain a certain degree of unexplained variance which arises from past competition and cannot be depicted by the present conditions. In particular, if focusing on managed forests, occasional management activities by thinning or selective logging will alter both stand-level conditions as well as spacing of the individual trees. Time is required before the increased growth of the remaining trees will compensate their removed competitors (Mehtätalo et al., 2014). As the NFI observations from the plots included the time of the last thinning within certain estimated spans, it was included as one model parameter to indicate these effects.

2.4. Modelling

Competition-related LMM modelling was performed using R statistical software version 4.1.1 (R Core Team, 2021) with packages *lme4* (Bates et al., 2015) and *AICcmodavg* (Mazerolle, 2020). Scots pine and Norway spruce were divided into individual data sets, and each species and extracted feature (Table 1) were modelled separately with the following method with exception of stem leaning direction that is explained later. In addition, the response features were divided into two larger groups which were evaluated separately. These groups were features related to size (crown diameter, projection area and volume), indicating direct responses to site conditions and competition, and features related to shape (crown symmetry, displacement and stem leaning angle), reflecting the lateral plasticity of trees. The general approach for modelling is presented in Fig. 2 and explained in further detail below.

We started preparing base models by including plot ID and Qclass as random variables and DBH as a fixed variable (Table 3). This targeted at providing a parameter describing the tree size (DBH) while accounting for variation between the plots (plot ID) regarding to, for example, growing conditions or previous management, and mitigating problems related to the deficiencies of TLS data (Qclass). Then, additional field-measured variables were tested one at a time by adding them to the base model and selecting the best performing one with respect to the targeted response feature. This procedure was repeated for the remaining variables until no further improvement was gained. Distance of the subject tree from the plot centre was also included into this set of variables, intended to capture any visually negligible quality differences of the TLS data between the core areas and edges of the scanned plots, or influence of missing neighbours outside of the plot edge. Potential interactions between the variables were not tested to keep the base model simple. Comparison of the candidate models was based on Akaike information criteria, designed to select a model with minimized prediction error from a set of candidate models, using the version corrected for small sample sizes (AIC_c; Hurvich and Tsai, 1989). Improvement was determined based on AIC_c difference (ΔAIC_c , *i.e.*, subtraction between the AIC_c of the base model and the model to be compared) of more than 2 k units per the number of added extra parameters k , considering that a factorized variable increased k potentially by more than one (Arnold, 2010). As stated by Arnold (2010), using a threshold of 2 k units with ΔAIC_c may not be exactly precise for comparison, but it was regarded as a sufficient approximation to be applied in this context.

After determining the base model, the performance of each competition index was evaluated one at a time by using ΔAIC_c as before. If competition indices were found to improve the base model, the best and the second best of them were recorded. This aimed at balancing the

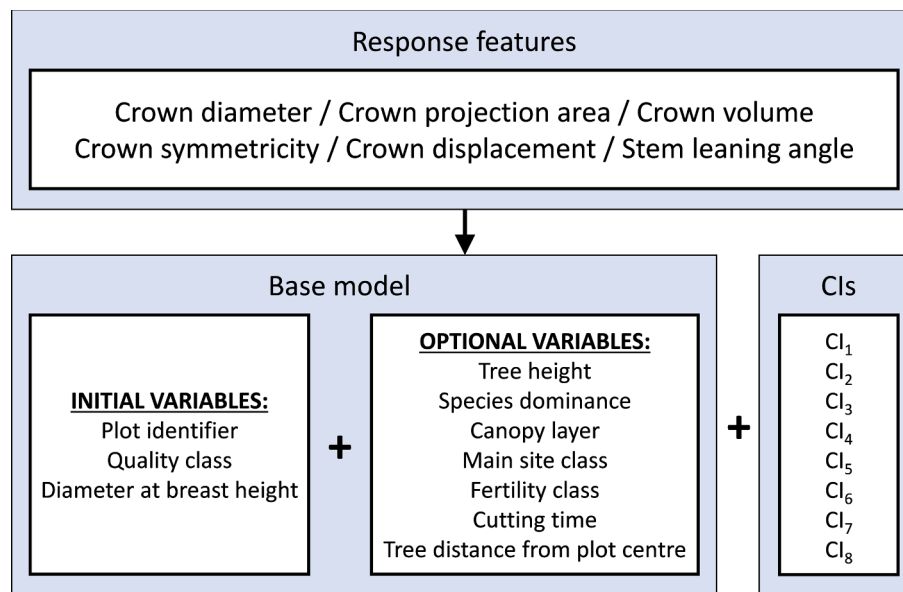


Fig. 2. Modelling approach used in this study, including the construction of the base model and inclusion of competition indices.

evaluation of competition indices, given that ΔAIC_c of several indices were potentially close to each other. The evaluation targeted only on single indices, *i.e.*, inclusion of more than one competition index or their interactions were not tested.

Finally, stem leaning direction was analysed to observe whether it correlates with the direction of competition pressure, potentially so that stems facilitate horizontal growth towards less contested space. The target was to analyse long-term effects of past competition on the growth of tree stems and, therefore, only upper canopy trees of the dominant storey were included. Directions (bearing) of the least competition pressure were defined for each subject tree with assistance of the competition index CI_8 as the mid-direction of the largest free angle between the competitor trees. Stem leaning directions were then transferred to relative to the directions of least competition, that is, calculated into continuous variables between 0..1 with value 0 standing for leaning towards the least competition, 1 indicating totally opposite direction, and other values expressing intermediate directions without differentiating between the two sides. Finally, the mean values of these relative measures were compared to the value of 0.5 by using two-tailed *t*-test, indicating whether the leaning direction of the stem is random (*i.*

e., no statistically significant difference to 0.5), or it leans either away (mean value significantly less than 0.5) or towards (mean value significantly more than 0.5) competition pressure.

3. Results

3.1. Tree detection

Of all the tally trees, 99.0 % were detected automatically from the plot-wise point clouds. The two non-detected trees, which were then manually included in the individual-tree extraction, appeared to result from point cloud deficiencies around the DBH level. The high detection rate also implied that most of the non-tally competitor trees had been detected as well. Diameter and height distributions of tally trees are presented in Fig. 3. Of these trees, 109 of 113 Scots pines and 73 of 92 Norway spruces were upper canopy trees of the dominant storey, whereas most of the remaining trees were mid-canopy trees of the dominant storey with a few individuals belonging to lower canopy layers.

Table 3
Field-measured variables used in the construction of the base models.

Variable and abbreviation	Variable description	Variable type	Model parameter type
<i>Initial variables</i>			
Plot identifier (plot ID)	Unique identifier for each individual plot	Factor	Random
Quality class (Qclass)	Quality class of the TLS data, based on visual assessment (see chapter 2.2)	Factor	Random
Diameter at breast height (DBH)	Averaged diameter (cm) of the subject tree based on two perpendicular measurements at $h = 1.3$ m, transformed by square root to reduce the influence of extreme values	Continuous	Fixed
<i>Optional variables</i>			
Tree height (h)	Height of the subject tree (m) between the base (ground) and the treetop, measured using Haglöf Vertex hypsometer	Continuous	Fixed
Species dominance (dom)	Boolean variable defining whether the subject tree is of dominant or non-dominant species of the plot	Factor	Fixed
Canopy layer (can)	Canopy layer of the subject tree: upper-, mid- or low-canopy tree of the dominant storey, or tree not belonging to the dominant storey	Factor	Fixed
Main site class (msite)	Mineral soil or peatland sites	Factor	Fixed
Fertility class (fert)	Classification used to group forests into uniform classes based on their site fertility and wood production capacity	Factor	Fixed
Cutting time (ctime)	Assessed time of last thinning, divided into three classes (within 10 years; 11–30 years ago; over 30 years ago)	Factor	Fixed
Tree distance from plot centre (dist)	Distance of the tree from plot centre (m), <i>i.e.</i> proxy of TLS data quality with intention to capture differences related to the completeness of the point cloud data	Continuous	Fixed

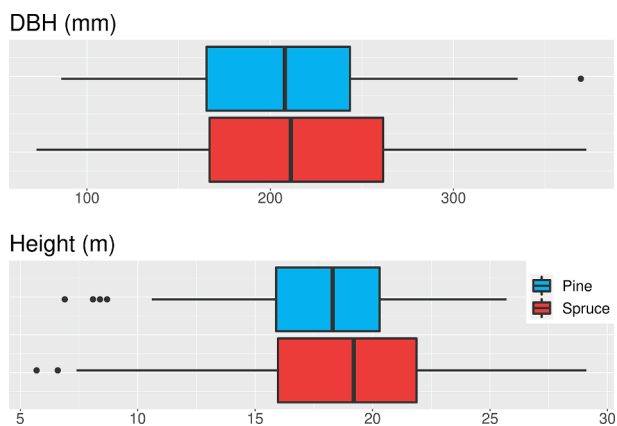


Fig. 3. DBH and height distributions of the individual subject (tally) trees, hinges indicating the first and third quartiles and whiskers extending up to the highest/lowest value within $1.5 \times$ interquartile range of the hinge.

3.2. Modelling results

The LMM results indicate that in most cases additional field-measured variables will improve the initial base model (Table 4). Regarding to size-related response features of Scots pines, the most determining factor in addition to the initial base model seems to be whether pine is the dominant species or not. As a dominant species, crown diameter, projection area and volume are larger as compared to pines growing on spruce-dominated stands. Additionally, pines located further away from the plot centre have generally smaller crown volumes. Regarding to shape-related features, pines growing on mineral soil have larger crown displacement as compared to peatland sites, and pines as dominant species have straighter stems than for those as non-dominant species. For crown symmetry, no improvement is gained by any field-measured variables in addition to the initial base model.

For both Scots pine and Norway spruce, competition indices have potential to improve the prediction of most size-related features as well as crown symmetry. Regarding to Scots pine, size-related features are enhanced most by the distance-dependent indices CI_7 and CI_8 , which consider only trees of similar size or larger as competitors. Their behaviour is also intuitively logical from the perspective of competition pressure: crown diameters and projection areas of pines are smaller when the sum of competitor stem angles is larger (CI_7), and when competitors are occupying a larger horizontal angle (CI_8). CI_7 is also the only index capable of improving the crown symmetry prediction,

indicating that increased competition pressure (i.e., larger sum of competitor stem angles) will make the crowns less symmetric. The two remaining shape features of Scots pines – crown displacement and stem leaning angle – as well as crown volume do not seem to be gaining additional improvement from competition indices in addition to the base model and field-measured variables added to it.

For Norway spruce, species dominance plays much smaller role; it will only improve the prediction of crown volume so that spruces growing as non-dominant species will have larger crown volumes. For the two other size-related response features, tree height and main site class are the most influential field-derived parameters in addition to the initial base model. Both crown diameter and projection area of spruce are larger when the tree is growing on mineral soil as compared to peatland sites, and when it is shorter (with a given DBH, as provided in the base model). Regarding to shape features, only displacement of the crown is improved by field-measured variables. These are fertility class and distance of the tree from the plot centre; crown shift is larger if the site is less fertile, and when the tree locates further away from the plot centre.

In terms of competition indices and their effects on Norway spruce, improvement can be gained for all the size features as well as crown symmetry. All of their effects, however, are not intuitively as predictable as for Scots pines. Crown diameter is smaller when competition increases, measured using the same distance-dependent indices CI_7 and CI_8 as Scots pine. But the other size-related features of Norway spruce behave differently: both crown projection area and crown volume are larger when competition pressure increases, measured by basal areas either considering all trees (CI_3) or only larger trees (CI_4) as competitors. Adding these competition indices will however also mean that projection areas and volumes are predicted larger on plots which, on average, are having smaller number of larger trees. Of the shape-related features, only crown symmetry can be improved by CI_7 and its effect is similar to Scots pine: higher competition pressure (i.e., larger sum of competitor stem angles) will make spruces less symmetric. It is also worth of noticing that while Scots pine was improved solely by distance-dependent CIs, Norway spruce gains much stronger assistance from distance-independent indices.

When stem leaning directions were analysed in relation to the direction of competition pressure, no statistically significant evidence of their correlations was found. For Scots pine, mean value of the stem leaning in relation to competition was 0.46, gaining a two-tailed p value of 0.161 for differing from the value of 0.5 (i.e., random leaning direction with respect to competition pressure). Norway spruce had a similar mean value of 0.46, and a two-tailed p value of 0.228. While for both

Table 4

LMM modelling results for different species and response variables. The operator (+/-) after the ΔAIC_c value with colour codes denotes the direction of larger CI values (i.e., expected higher competition) on the predicted feature values (positive/red = crown has larger diameter, projection area and volume, it is less symmetric and more displaced, and stem leaning angle is larger; negative/blue indicates the opposite).

Species	Feature group	Response feature	Field-measured variables added to the base model	Best CI (ΔAIC_c)	Second best CI (ΔAIC_c)
Scots pine	Size	Diam	dom	CI_7 (22.01) ⁻	CI_8 (13.58) ⁻
		ProjA	dom	CI_8 (16.06) ⁻	CI_7 (15.48) ⁻
		Vol	dom + dist	-	-
	Shape	Sym	-	CI_7 (5.97) ⁺	-
		Disp	msite	-	-
		SLAng	dom	-	-
Norway spruce	Size	Diam	h + msite	CI_8 (5.48) ⁻	CI_7 (4.24) ⁻
		ProjA	h + msite	CI_4 (2.53) ⁺	-
		Vol	dom	CI_4 (7.36) ⁺	CI_3 (6.51) ⁺
	Shape	Sym	-	CI_7 (2.85) ⁺	-
		Disp	fert + dist	-	-
		SLAng	-	-	-

species the mean directions are slightly towards the less contested space, no statistically justified conclusions on leaning directions can be made.

4. Discussion

The results indicate that in addition to site conditions, the crown sizes and shapes of both Scots pines and Norway spruces were influenced by competition pressure. The two targeted species, however, had important differences in terms of their morphological determinants as well as sensitivity and adaptation to competition.

Scots pine is generally capable of growing on drier and less fertile sites than Norway spruce, but pine on such sites is also highly sensitive to the availability of light which affects its growth (Øyen et al., 2006, Hynynen et al., 2011). The tendency to stretch towards light was apparently an important determinant for the explanatory power of species dominance for size-related features in our data. As a dominant species, pines are the tallest trees and on managed stands generally of similar height, which makes them to invest their growth on widening the crown. Non-dominant Scots pines however are often shaded, which makes them to allocate more growth on their stems, grow taller, and lift the height of crown base upwards (Harja et al., 2012, Mäkelä and Vanninen, 1998, Vanninen and Mäkelä, 2000).

In terms of competition indices, predictions of pine crown diameter and projection area were strongly improved by distance-dependent competition indices CI_7 and CI_8 , which can be primarily interpreted through current competition between the adjacent trees. But contrary to them, crown volume appeared to gain little advantage of competition measures. A potential explanation for this is that when a crown gets wider, its base height will simultaneously shift upwards due to self-shading (Oker-Blom and Kellomäki, 1982), which further makes the volumetric changes smaller. The observed tendency of increased competition to make crowns less symmetric is not corresponding to some earlier findings, which are suggesting more regular canopy structure in case of higher competition pressure (e.g., Kellomäki and Oker-Blom, 1983, Longuetaud et al., 2013). This deviation may however derive from excluding the densest plots from the data due to difficulties in TLS data processing.

Lack of connections between competition indices and the observed crown displacement, stem leaning angle and leaning direction of Scots pines may reflect the complicated nature of these features. For example, responses may depend on the size of the target tree: for a mature, dominant pine, a strong pressure posed by nearby peers may be expected to increase crown displacement as a response to horizontal competition. For a suppressed tree, however, strong local competition will rather make it grow taller without affecting substantially to its crown displacement. Another issue, as pointed out by Rouvinen and Kuuluvainen (1997), is the tendency of boreal trees in the northern hemisphere to grow their canopies towards south, *i.e.*, towards the direction of the Sun. This characteristic was also observable in our data, increasing potentially noise in the models and diminishing the quantification of purely competition-related effects.

While Scots pine was apparently favored by dominance and ample availability of light, for Norway spruce the reality was principally the opposite: they appeared to have grown large regardless of light shortage. This good shade-tolerance is exemplified by the only model improved by dominance – crown volume – for which non-dominance had positive effects. This could be explained so that on pine-dominated plots, spruces are generally growing under the taller pines, where they have sufficient horizontal space around them among the branchless or short-branched parts of pines. Unfortunately, we could not investigate species-specific competition effects as the species of non-tally trees were not known. Tendency of including height in the crown diameter and projection area models is expectedly due to slenderness of taller spruces, therefore increasing crown dimensions for a given DBH when the tree is shorter. In terms of soil properties, mineral soil is likely to provide more favorable conditions for spruce to grow, thus increasing its crown diameter and

projection area. Lower fertility as a predictor of higher crown shift is potentially indicating competition on scarce resources but may also derive from various underlying reasons not measured in this study.

Understanding the competition-related effects of Norway spruce requires a bit different interpretation as compared to Scots pine. For crown diameter, the results were intuitively logical: more competitor trees surrounding a Norway spruce resulted in a smaller crown diameter. This can also be connected to earlier observations of spruce crowns to be slenderer when growing in high-density stands (Niemistö and Valkonen, 2021, Mäkinen and Hein, 2006). From this perspective, enlarged crown projection area and volume at higher competition pressure sound somewhat unexpected or even contradictory, although CI-based improvement for projection area model was relatively minor as interpreted based on the AIC values.

The determinants for three size features, however, are somewhat different: large crown diameter may derive from existence of single large branches, whereas projection area and volume will principally require denser and larger overall crown structure. Particularly crown volume of Norway spruce was positively affected by increased competition as measured using distance-independent basal area -based indices CI_3 and CI_4 , which suggests that the applied distance-dependent indices related to neighboring trees did not capture the actual competition pressure as experienced by a Norway spruce. This can be explained by various issues: competitors may potentially be pines whereas spruces are growing below them, horizontally more regular crown shape of spruces will make it easier for them to grow among peers, spruces may need to compete less on nutrients and water compared to pines on the sites they normally grow, and most importantly, light is not the main limiting factor for their growth. Crown symmetry of spruce seemed to have similar tendency as for pine: when there were more competitors, spruce crowns were less symmetric.

While TLS-derived crown dimensions have obvious correlations to both site characteristics and competition, a lot of residual variation will remain unexplained. This can derive from various reasons. First, our measurements could measure only structural conditions on top of the ground related to the availability of light and space, whereas resource allocation will also depend markedly on soil properties, particularly on the availability of nutrients and water. Roots of both Scots pines and Norway spruces can extend up to 10 m distance for mature trees (Kallikoski et al., 2008), and competition pressure for pines can be detected at least until 5–7 m distance (Björkman and Lundberg, 1971). Second, both size and shape of crowns will depend on a combination of various ecological processes and gradients which are complicated to measure (Uria-Diez and Pommerening, 2017), but which will have important implications for the survival and growth of the trees. Third, particularly on managed stands, part of the past competitors has potentially been cut away, but their earlier effects may still be detectable in morphology of the remaining trees. We assumed similarly to Kaitaniemi and Lintunen (2010) that as most of the studied stands had not been undergoing recent thinning operations, the present CI-derived competition values should reasonably well correlate also with past competition. And fourth, genetic differences will also affect tree morphology, although variability in crown dimensions may be high even at low level of genetic variation (Albaugh et al., 2020, Caré et al., 2018, Kroon et al., 2008). Additionally, quantification strategies of competition derive from our current – and potentially deficient – understanding on resource sharing relationships between the nearby trees. Distance-dependent competition indices, for example, may fail to perform well if competitors, their impacts or effective distances from the subject tree are not properly selected (Cole and Lorimer, 1994, Miina and Pukkala, 2000).

With respect to tree growth and vigor, foliage (needle) mass alone is known to be already a good predictor (O'Hara et al., 1999, Vanninen and Mäkelä, 2000). Given the additional explanatory power of competition indices for size-related response features found in our study, competition should be regarded as an essential determinant for tree growth, and it is reflected in the current dimensions of the tree crowns. However, the effects of competition are highly complex, variable and

often cumulative in nature, and inclusion of competition measurements may sometimes rather complicate than assist growth modelling (Pedersen et al., 2012). Based on our results, modelling strategies related to competition should also be carefully selected to fit to the targeted species. Scots pine seeks advantage from being the tallest tree on the stand, at least on poorer sites where it is normally grown, and competes heavily on light with its peers. As pines are often also surrounded by other pines, distance-dependent competition indices are working efficiently by describing the surrounding light conditions. Norway spruce, instead, will not allocate a high proportion of resources on emphasizing its height, but rather reacts on lateral space around it. In addition, pines surrounding a spruce may not pose any truly negative consequences on the growth of spruce, regardless of potentially high measures of competition pressure. These may lead to similar or better performance of distance-independent competition indices for modelling the crown dimensions of Norway spruce as compared to distance-dependent ones, similarly as found by Biging and Dobbertin (1995). In this case, distance-independent indices will assumedly have correlations to larger site- and stand-level characteristics which may be missing from the other measured variables, and have capabilities of providing more robust evaluation of the overall competition state.

5. Conclusions

Ability to understand both sizes and shapes of tree crowns are highly important: size can be considered as the main determinant for current tree growth while differences in shape may reflect trees' mitigation strategies towards competition pressure and, therefore, have significance for planning of optimized stand management. Our study indicates that quantifying competition between trees will improve the prediction of their crown dimensions with further effects on their growth, but the selection of the most applicable competition index is not a trivial task. Traditional distance-independent indices will be the most efficient when competition is largely on light and happens between the peers of the same species. For a shade-tolerant species, however, a substantial proportion of competition occurs in horizontal rather than vertical space which complicates the conventional measures on distance-dependent competition pressure. Further, the essential question for shade-tolerant species may not be the radius of the zone of influence, but rather determining which of the neighboring trees are the ones to be counted as actual competitors. In this matter, data on the tree species would provide important additional information.

CRedit authorship contribution statement

T.P. Pitkänen: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Visualization. **S. Bianchi:** Conceptualization, Methodology, Writing – original draft. **A. Kangas:** Methodology, Writing – original draft, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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