At what scales and why does forest structure vary in naturally dynamic boreal forests? An analysis of forest landscapes on two continents

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TA designed the study. NK interpreted the aerial photographs, and TA, TK, and LD collected the field data. LP and LH developed the analysis methods, and LP and NK conducted the analyses. NK, LP, and TA wrote the first draft of the paper, and all authors contributed to writing the final version.

Abstract

Identifying the scales of variation in forest structures and the underlying processes are fundamental for understanding forest dynamics. Here, we studied these scale-dependencies in forest structure in naturally dynamic boreal forests on two continents. We identified the spatial scales at which forest structures varied, and analyzed how the scales of variation and the underlying drivers differed among the regions and at particular scales.

We studied three 2 km × 2 km landscapes in northeastern Finland and two in eastern Canada. We estimated canopy cover in contiguous 0.1-ha cells from aerial photographs and used scale-derivative analysis to identify characteristic scales of variation in the canopy cover data. We analyzed the patterns of variation at these scales using Bayesian scale space analysis.

We identified structural variation at three spatial scales in each landscape. Among landscapes, the largest scale of variation showed greatest variability (20.1 – 321.4 ha), related to topography, soil variability, and long-term disturbance history. Superimposed on this large-scale variation, forest structure varied at similar scales (1.3 – 2.8 ha) in all landscapes. This variation correlated with recent disturbances, soil variability, and topographic position. We also detected intense variation at the smallest scale analyzed (0.1 ha, grain of our data), partly driven by recent disturbances.

The distinct scales of variation indicated hierarchical structure in the landscapes studied. Except for the large-scale variation, these scales were remarkably similar among the landscapes. This suggests that boreal forests may display characteristic scales of variation that occur somewhat independent of the tree species characteristics or the disturbance regime.

Keywords

Forest dynamics, Canopy cover, Aerial photography, Bayesian inference, Eastern Canada, Northern Fennoscandia

Manuscript highlights

- We identified distinct scales of hierarchical variation in boreal forest structure
- The mid-scale variation occurred at remarkably similar scales among the landscapes
- Drivers of the structural variation depended on the observation scale

Introduction

The spatial variability of forest structure (e.g., tree sizes, distribution of stems and foliage, dead wood) is the result of multiple factors such as disturbances, succession, topography, and soil properties (Lavoie and others 2007; Gauthier and others 2010; Walker and Johnstone 2014). Knowledge of this structural variation is essential for understanding the processes that drive forest dynamics, habitat variability, and biodiversity (Niemelä and others 1996; Kuuluvainen and others 2017), along with nutrient and carbon dynamics (Wickland and Neff 2008; Bradshaw and others 2009) in forested landscapes.

Forest structure varies hierarchically at multiple spatial scales (Kotliar and Wiens 1990; Kuuluvainen and others 1998). However, the scales at which the variation occurs are often only described qualitatively (Angelstam and Kuuluvainen 2004; Bouchard and others 2008; Kuuluvainen and others 2014). The multiscale variation reflects the influence of drivers that shape forest structure at different scales, and their cumulative effects (Elkie and Rempel 2001; Wong and Daniels 2016). Some drivers create variation across multiple spatial scales. For example in the boreal forest, topography and soil properties may create variation at the landscape scale by changing the predisposition of stands to high winds (Ruel and others 1998) and by influencing the tree species composition (Sutinen and others 2002), and at the small, within-stand scales, by influencing the occurrence of suitable regeneration sites (Kuuluvainen and Kalmari 2003; Grenfell and others 2011). Similarly, disturbances such as forest fire may induce variation at the landscape scales (De Grandpré and others 2000; Gauthier and others 2010), while insect outbreaks and wind disturbances typically create variation at stand scales (Kuuluvainen and others 1998; Pham and others 2004). The influence of some other drivers, such as tree-tree competition (Aakala and others

2016), or the senescence-related deaths of individual trees (Aakala and others 2009) is limited to within-stand scales.

Studies on forest structures and dynamics often focus on *a priori*-selected scale, or on the effect of a specific driver. However, as structural variation occurs at multiple scales and results from multiple drivers, a single scale or focus on a specific driver is often insufficient for comprehensive landscape analysis (Habeeb and others 2005; Scholes 2017; Estes and others 2018). Furthermore, the patterns of structural variation and their linkages to the drivers of variation have a fundamental connection with the spatial scale of observation (Wu and Loucks 1995), highlighting that studies on forest structural variability would benefit from methods that do not rely on scales selected *a priori* (Hay and others 2002). Instead, the complex nature of forest ecosystems requires an analysis of patterns in forest structures and the underlying processes in which the scales of observation are reduced to those containing the most salient features (i.e. the characteristic scales of variation; Wu 1999). The identification of such scales is the first step towards understanding the multiscale linkages of ecological patterns and processes (Scholes 2017).

Here, we studied the scale-dependent variation in boreal forest structure and the factors influencing this variation. We hypothesized that in forest landscapes (1) structural variation occurs at specific, discernible spatial scales, but (2) these discernible scales of variation differ between regions and landscapes, and (3) we can identify different (scale-dependent) drivers of structural variation behind these patterns.

We tested these hypotheses in five naturally dynamic boreal forest landscapes in two regions, northern Finland and northeastern Quebec, Canada. Using visual interpretation of canopy cover variation on recent aerial photographs calibrated against field measurements, we applied scale-

derivative analysis (Pasanen and others 2013) and Bayesian scale space multiresolution analysis (Holmström and others 2011). These methods aim to recognize characteristic scales of forest structural variation, assess the spatial occurrence of structural variation, and identify structurally distinct areas in the study landscapes.

Material and Methods

Study area

We examined forests in two regions: northeastern Finland (67°44' N, 29°33' E) and the North Shore region in Quebec, Canada (49°38' N, 67°55' W; Fig. S1). In Finland, we examined two landscapes (2 km × 2 km) in Värriö Strict Nature Reserve (Hirvaskangas and Pommituskukkulat), and a third landscape in Maltio Strict Nature Reserve (Hongikkovaara). In Quebec, we studied two landscapes, Lac Dionne and Pistuacanis.

The studied landscapes are mosaics of forests on mineral soil, waterbodies, and forested and open peatlands. Soils in northeastern Finland consist mostly of undifferentiated glacial tills, with gentle slopes, and low mountain fells with treeless upper slopes. The elevation ranges between 200 and 500 meters above sea level (asl). In the North Shore region of Quebec, slopes vary from low to moderate. Undifferentiated glacial tills are common on the gentle slopes and depressions, as are glaciofluvial sand deposits in floors of larger valleys and rocky outcrops on moderate slopes and summits (Robitaille and Saucier 1988). Here, the elevation of the studied region ranges from 300 to 500 meters asl. Northern Finland has a subcontinental climate, with an annual mean temperature of +0.9 °C. The climate in the North Shore region is humid, with an annual mean temperature of +0.3 °C (see Supplementary material 1 for details).

Low tree species diversity is characteristic of both regions. The main tree species in Finnish landscapes are *Pinus sylvestris* (L.), *Picea abies* (L.) Karst, and *Betula pubescens* (Ehrh.). *Picea mariana* (Mill.) and *Abies balsamea* (L.) Mill. dominate in Quebecois landscapes. The tree species composition of both regions reflects site productivity and long-term disturbance history (Supplementary material 1).

Visual interpretation of canopy cover

To quantify forest structural variation at various spatial scales, we first visually interpreted canopy cover from recent aerial photographs in each of the five study landscapes. We used stereopairs of false-color aerial photographs with a pixel size of 0.5 m. Photographs for northern Finland were obtained from the National Land Survey of Finland, and were taken during summers 2011 (Hirvaskangas and Pommituskukkulat) and 2010 (Hongikkovaara). Photos for Quebec were obtained from the Ministère des Forêts, de la Faune et des Parcs du Québec, and were taken in 2011. We performed the stereointerpretation with EspaCity software (version 11.0.15306.1; Espa Systems Ltd., Espoo, Finland), using a passive 3D monitor.

During the interpretation, we visually estimated canopy cover in 0.1-ha cells. For this, we placed a square grid of 64 × 64 cells over each landscape. To reduce bias due to improving interpretation skill, we divided the grids into sixteen parts (256 cells each), and the first author interpreted these sub-grids in randomized order. For each cell, we recorded total canopy cover and the proportion of various tree species. We identified conifers to species level, but did not separate deciduous trees. We estimated canopy cover as the proportion of forest floor covered by the vertical projection of a tree crown. Further, we counted the number of standing and fallen dead trees, which we later used as a measure of recent disturbances (see below). If a cell was not completely within a forest (e.g.,

waterbody, open peatland), we excluded it from further analyses. In Pommituskukkulat, we also excluded cells overlapping or bordering a reindeer fence traversing the area.

Calibration of and error in the visual interpretation

To reduce bias in the visual interpretation and to quantify the interpretation error, we field-sampled randomly selected grid cells, and reconstructed canopy cover for these cells at the year corresponding to the aerial photographs. In Finland, we sampled 16 cells per landscape (as described in Aakala and others 2016). In Quebec, logistical constraints limited the sample size to nine cells per landscape. In each sampled cell, we mapped all living and dead trees with a minimum diameter of 10 cm at 1.3 m height whose crown reached within the cell. We extracted samples for tree-ring width measurements from each tree (see Supplementary material 2 for details). For live trees, we mapped crown projections by measuring 4 – 8 points along the crown dripline. We converted the crown measurements into irregular polygons and used the tree-ring width measurements to reconstruct the crown sizes corresponding to the year the aerial photograph for that landscape was taken. We used species-specific regression models between tree diameter and crown projection area to convert change in tree size to change in crown size (Figs. S2 – S3). We used tree-ring widths to cross-date the year of death for the sampled dead trees, and assumed circular crowns for trees that died between field sampling and the year the aerial photograph was taken. From the reconstructions, we calculated the canopy cover of the sampled cells as the non-overlapping sum of individual crown projections.

We calibrated the visual interpretation and quantified the interpretation error using regression models between the interpreted and reconstructed canopy covers for Finnish and Quebecois landscapes individually (Figure 1; see Supplementary material 3 for details). We tested the

influence of additional variables (tree species proportions, distance from cells to aerial photograph nadirs) for the calibration model in the Finnish landscapes. According to Akaike information criterion for small sample sizes (AICc), the model fit improved when we included the proportion of *P. abies* in the cell as a predictor (Table S1). Hence, we included it in the final calibration model for the Finnish landscapes (Fig. S4). We then compiled the calibrated canopy cover values into raster maps, and used the interpretation error (i.e. the residuals of the calibration model) in Bayesian inference (see below).

Similar to canopy cover, we calibrated the visual interpretation of the number of snags and logs (minimum diameter 10 cm at 1.3 m height) in each cell with the equivalent dead wood basal area measured in the field (Figs. S5 – S6). Zero snags and logs were interpreted in many grid cells. Hence, the dead wood posterior predictive samples could have had negative draws (negative dead wood basal area). We tested the influence of the negative samples to the results by replacing all the negative draws in the samples with zero. Truncation of the negative values did not affect the interpretation of the results (Supplementary material 3).

Identification of the scales and spatial patterns of canopy cover variation

Our aims were to identify spatial scales of variation for each landscape, and to assess the spatial patterns of this variation at the identified scales. For this, we used Bayesian scale space multiresolution analysis (Holmström and others 2011). The use of this approach on a canopy cover raster map relies on the idea that the raster consists of a sum of components of various spatial scales. Hence, smoothing the raster can reveal features that correspond to a signal at various scales. A low smoothing level maintains all but the smallest-scale variation in the signal, and a high level

of smoothing evens out the small-scale details and reveals only locally average behavior in the signal. To extract the relevant scales of variation and study the features at each particular scale separately (as suggested by e.g., O'Neill and others 1986), the scale space multiresolution analysis considers the differences of smooths, where a smooth with a higher smoothing level is subtracted from a smooth with a lower smoothing level. We henceforth call the product of this subtraction (signal at a particular scale) the 'scale-dependent component'.

The analysis consists of five steps (Fig. 1): 1) calibration of the visual interpretation, 2) scale identification, 3) multiresolution decomposition, 4) credibility assessment, 5) feature size estimation that are next described in more detail.

In step 1, based on the calibration models described above, we built a Bayesian model for the calibrated canopy covers using the interpreted and field-measured canopy cover (see Supplementary material 3 for details).

In step 2, the scales of variation are identified. The identification of the spatial scales at which the most salient features in the raster maps occur requires that the smoothing levels are determined carefully. For this, we used an objective approach based on a concept of 'scale-derivative', which refers to the derivative of a signal smooth with respect to the logarithm of the smoothing level (Pasanen and others 2013). The relevant scales are detected based on the locations of local minima of a scale-derivative vector norm. In brief (see Pasanen and others 2013 for full details), consider a signal that consists of a sum of two components of different scales. The location of a local minimum then represents a scale at which the smaller scale component is smoothed out, revealing the larger-scale component not yet affected by smoothing. Hence, the signal including the small-scale variation can be recovered as the difference between the original signal and the smooth

corresponding to the local minimum. In general, a smoothing level sequence is defined using such local minima of the scale-derivative norm, and the variations at different scales (i.e. scale-dependent components) are resolved as the differences between the smooths of two consecutive smoothing levels. Henceforth, we call these identified local minima as scale breaks (*sensu* Wu 1999).

In the context of forest structure, a scale break represents a transition between hierarchical levels of variation. Within a variation level, the first break represents the grain and the second the extent of the particular level. In our analysis, the scale-derivative did not always detect the scale breaks automatically. In such cases, we visually searched the norms for weaker signs of scale breaks such as saddle points or changes in slope. We verified the existence of the identified scales by comparing the scale-derivative norm of the canopy cover (sum of all scale-dependent components) to the scale-derivative norm of permuted canopy cover (Fig. S7). Only the small-scale component could be identified from the permuted data, confirming the existence of the identified characteristic scales of variation.

In step 3, the canopy cover raster map is decomposed into scale-dependent components. Following the identification of the characteristic scales of variation, we assessed the spatial patterns of variation in canopy cover at the scales in question. We smoothed the canopy cover raster maps based on the identified scale breaks, and produced the scale-dependent components as subtractions of the smooths. The results were maps that depict canopy cover at a location relative to its surroundings, where sizes of the locations and surroundings depend on the smoothing level (i.e. with increased smoothing, larger areas are compared to their surroundings). When extracting the highest smoothing level component, we subtracted the mean of the original image from the highest smooth. We used a Nadaraya-Watson smoother with a Gaussian kernel for the smoothing (e.g.,

Wand and Jones 1994). We henceforth refer to these extractions as relative canopy cover maps, where each identified scale and landscape have their own map.

In step 4, the credibility of the canopy cover variation patterns is assessed. We used Bayesian inference to account for the uncertainty stemming from the calibration models and to distinguish credible variation from the visual interpretation error noise in the relative canopy cover maps. We developed posterior distributions for canopy cover, based on the error in the regression model between interpreted and field-measured canopy cover. We first drew a large sample from this posterior predictive distribution, and approximated the posterior distribution of each relative canopy cover map by applying the difference of smooths operator to each sampled image (see Supplementary material 3 for details). We then identified the credibly positive and negative cells from each relative canopy cover map, using simultaneous inference over all cells by applying the method of highest point-wise probabilities (HPW; Erästö and Holmström 2005; Holmström and others 2011), with a posterior probability threshold of 0.95.

In step 5, the sizes of the features in the relative canopy cover maps are assessed. To produce quantifiable and comparable information at the characteristic scales of variation, we assessed the sizes of the features detected in each of the relative canopy cover maps as the diameter of the representative circle, an approach similar to Pasanen and others (2018). In short (see Supplementary material 3 for details), for determining the diameter of a representative circular feature on each relative canopy cover map, we used the smoothing level indicated by the maximum in the component's scale-derivative norm and the concept of 'full width at half maximum', often used in medical imaging to represent the size of a feature without clear boundaries (Epstein 2007). We note that the size estimation depended on the locations of the scale breaks, a few of which were manually

placed. Hence, we assessed the sensitivity of the size estimation with respect to the scale break locations. The size estimates were fairly insensitive to small changes in the scale break locations.

Explanatory variables for canopy cover variation

To assess the role of various factors driving forest structural variation at multiple scales, we assessed the relationships between relative canopy cover and recent disturbances, edaphic and topographic factors, and long-term disturbance history.

For recent disturbances, we assumed that the dead wood quantity in a cell is indicative of recent disturbances in the cell. To analyze the relationship between relative canopy cover variation and recent disturbances, we extracted the scale-dependent features of the dead wood basal area, using the same smoothing levels as with canopy cover (henceforth relative dead wood basal area; Fig. S8). The exact way in which we analyzed the relationship between relative dead wood basal area and relative canopy cover depended on the scale analyzed. At the smallest scale, we examined whether the relative dead wood basal area in a cell differed for cells with negative and positive relative canopy cover. Due to the low number of credible canopy cover cells in Quebecois landscapes, we included an additional 50 cells with the lowest and highest relative canopy cover from both Quebecois landscapes in the comparison (total 158 positive, 64 negative cells in Finnish, and 129 positive, 113 negative cells in Quebecois landscapes). For larger scales, we tested the dependency using local correlation analysis, and assessed the credibility of the correlation in each landscape (cf. Pasanen and Holmström 2017). In this analysis, we calculated Pearson correlation coefficients between the relative dead wood basal area and the relative canopy cover on a moving window. We increased window size along with the increasing smoothing level. The credibilities of

the correlations were determined by drawing a large sample from the canopy cover and dead wood posterior probability distributions, using the HPW method with a credibility level of 0.95.

To assess the role of site productivity and long-term disturbance history as determinants of relative canopy cover, we relied on the predictability of tree species composition as a function of site productivity and/or disturbance history (Supplementary material 1). We compared tree species composition maps to the credible features of the relative canopy cover maps. We utilized independently compiled tree species composition maps for Quebec (Ministère des Forêts, de la Faune et des Parcs du Québec), based on the aerial photointerpretation of an experienced interpreter. We lacked such independent maps for Finland, and therefore used tree species compositions recorded during the visual interpretation of the aerial photographs, calibrated with field measurements (Figs S9−S11). To ensure that the correlation between tree species composition and canopy cover was not the result of including the proportion of *P. abies* in the calibration model for Finnish landscapes, we also performed the calibration without *P. abies* as a predictor, and tested the dependency with this model. The correlations between tree species composition and canopy cover were independent of the used calibration model.

To assess how topography affects relative canopy cover at various spatial scales, we computed topographic variables from digital elevation models with a spatial resolution of 20 m (National Land Survey Finland, Ministère des Forêts, de la Faune et des Parcs du Québec). Variables tested included elevation (mean elevation of each 0.1-ha cell), slope steepness (cell mean), slope aspect (cell midpoint aspect), and topographic position (cell mean; Jenness and others 2013). If an area is higher than its surroundings, its topographic position index is positive, and vice versa. We defined the index on three scales: between individual cells and between groups of 10 and 20 cells. We computed Spearman’s rank correlations between the means of the posterior predictive distributions

(each relative canopy cover map) and the topographic variables. If this correlation coefficient was > 0.15, we assessed the uncertainty of the correlation by computing correlations between the particular topographic variable and all the 10 000 draws of the posterior predictive distribution, and assessed the mean and the 95% credibility intervals for these correlations.

Results

Canopy cover and scales of variation

Canopy cover in the 0.1-ha cells ranged from 0 to 59% in the Finnish landscapes, with a posterior mean of average over all cells 25% (SD of posterior predictive sample ±8%, 95% prediction interval 18 – 33%) (Fig. 2 a1 – c1). Canopy cover ranged from 3 to 70% in the Quebecois landscapes, with a posterior mean of average over all cells 35% (SD ±13%, 95% prediction interval 22 – 48%) (Fig. 2 d1 – e1).

In the scale-derivative analysis, we identified three scales of forest structural variation in each landscape, which we henceforth call large-, mid-, and small-scale variation (Fig. 3). The analysis automatically identified the scale breaks between mid- and large-scale components. We manually placed the scale breaks between the small- and mid-scale components at the location in which the slope of the scale-derivative norm became less steep, indicating that the small-scale component appeared smoothed out. The permutation test, where we compared the scale-derivative norms for the canopy cover to the scale-derivative norm for permuted canopy cover confirmed the existence of the identified characteristic scales of variation (Fig. S7).

Feature sizes at the largest scale identified varied among the landscapes. A typical large-scale feature diameter was 2023 m in Hirvaskangas, 696 m in Pommituskukkulat and Hongikkovaara, 506 m in Lac Dionne and 1518 m in Pistuacanis. These diameters correspond to an area of 321.4 ha in Hirvaskangas, 38.1 ha in Pommituskukkulat and Hongikkovaara, 20.1 ha in Lac Dionne and 181.0 ha in Pistuacanis.

A typical mid-scale feature diameter was 190 m in each landscape except Hongikkovaara and Lac Dionne, corresponding to a circle area of 2.8 ha. In Hongikkovaara and Lac Dionne, a typical mid-scale feature diameter was 127 m (1.3 ha). The small-scale variation corresponded to the grain size in our data (0.1-ha grid cells, diameter 31.62 m) in each landscape.

We used the scales identified in the scale-derivative analysis to produce relative canopy cover maps (Fig. 2). In these maps, negative relative canopy cover means low canopy cover in relation to the surroundings, while the opposite is true for positive canopy cover. At the large scale, relative canopy cover ranged from -10 to 10 percentage points in Finnish landscapes and from -13 to 10 in Quebec (Fig. 2 a2 – e2). At the mid scale, relative canopy cover ranged from -13 to 15 percentage points in Finnish landscapes and between -24 and 21 in Quebec (Fig. 2 a4 – e4). At the small scale, relative canopy cover ranged from -15 to 18 in Finnish landscapes and between -26 and 24 in Quebec (Fig. 2 a6 – e6).

The range of canopy cover values was greatest in Pistuacanis (Fig. 2 e1), which is reflected in the relative canopy cover map intensities (Fig. 2). This intensity difference, visible in the mid- and small-scale components, is also visible as differences in the scale-derivative norms (Fig. 3).

At the large scale, Hirvaskangas (Fig. 2 a2) and Pistuacanis (Fig. 2 e2) showed two contrasting credible canopy cover areas. We observed several smaller areas of credibly high (low) relative canopy cover in Pommituskukkulat (Fig. 2 b2), Hongikkovaara (Fig. 2 c2), and Lac Dionne (Fig. 2 d2). All five landscapes showed a higher number of credibly negative or positive relative canopy cover features at the mid scale than at the small scale, and more credible features were observed in Finnish than in Quebecois landscapes (Fig. 2 a2 – e7). Pommituskukkulat had the most credible patches of all the Finnish landscapes at the mid- and small-scales (Fig. 2 b5, b7). In Quebec, Pistuacanis landscape had the most small- and mid-scale scale credible patches (Fig. 2 e5, e7).

Drivers of canopy cover variation

Recent disturbances

At mid-scale, average correlations between relative canopy cover and relative dead wood basal area varied from -0.02 to 0.09. However, we observed wide spatial variability in the correlations, from -0.78 to 0.83 (Fig. 4). In the Finnish landscapes, these correlations were credible in the eastern and northwestern parts of Hirvaskangas (Fig. 4f), in the middle, and southeastern part of Pommituskukkulat (Fig. 4g), and in two areas in the middle of Hongikkovaara (Fig. 4h). Several of the mid-scale features correlated credibly with relative dead wood basal area in the Quebecois landscapes (Fig. 4i – j).

We visually judged which of the credible mid-scale canopy cover patches in Quebec likely resulted from a previous spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak, based on field observations. In *P. mariana*-dominated Lac Dionne, 10% of the credible negative mid-scale patches occurred at openings that were likely caused by the spruce budworm outbreak. In *A. balsamea*-

dominated Pistuacanis, 35% of the negative mid-scale patches were located at these openings. As the variable examined was the canopy cover relative to its surroundings, it is also possible that the loss of canopy cover due to the outbreak results in credibly positive relative canopy cover in the adjacent area. Accordingly, 15% and 30% of the positively deviating patches were next to these openings in Lac Dionne and Pistuacanis, respectively.

Small-scale relative canopy cover had a connection with relative dead wood basal area (Fig. 5). In both regions, the cells with credibly positive relative canopy cover had a lower posterior median relative dead wood basal area (our surrogate measure for recent disturbances) than the cells with credibly negative relative canopy cover (Fig. 5). Thus, cells with high canopy cover tended to have less dead wood than cells with low canopy cover. However, the relative dead wood amounts did not deviate credibly from zero.

We did not detect large-scale correlations that would link the relative dead wood basal area (recent disturbances) to relative canopy cover.

Site productivity and disturbance history

At the large scale, most areas with positive relative canopy cover in the Pommituskukkulat landscape were in areas with a high proportion of deciduous trees (productive sites with shorter time since fire than sites with higher proportion of spruce; Fig. S10-11), whereas the negative relative canopy cover areas were mostly located in *P. abies*-dominated sites (old-growth productive sites). The credible large-scale features in Hirvaskangas and Hongikkovaara occurred independent of tree species composition. Roughly 70% of the areas with positive relative canopy cover in Lac Dionne were dominated by *A. balsamea* and roughly 60% of the areas with negative relative canopy

cover by *P. mariana*. The credible large-scale features in Pistuacanis landscape occurred independent of tree species composition.

The comparison of credible mid-scale canopy cover patches against tree species composition (our surrogate for site productivity and long-term disturbance history, see Supplementary material 1 for details) showed that sites with credible canopy cover features tended to be located in areas where tree species composition changed (Figs. S10-11). This was especially apparent in Pommituskukkulat (roughly 70% of credible mid-scale patches), Hongikkovaara (80%), and Lac Dionne (70%). Particularly the large mid-scale patches with credibly positive relative canopy cover in Pommituskukkulat were located in areas with a high proportion of deciduous trees (productive sites with shorter time since fire). Here, roughly 60% of the negative relative canopy cover areas were on *P. abies*-dominated productive old-growth sites. In Hongikkovaara approximately 60% of the negative patches were on *P. abies*-dominated productive old-growth sites. In Lac Dionne, roughly 80% of the areas with positive relative canopy cover were on *A. balsamea*-dominated sites (productive sites), whereas approximately 60% of the negative relative canopy covers were on *P. mariana*-dominated areas (poor sites; Figs. S10-11). In Pistuacanis, the mid-scale relative canopy cover was independent of tree species composition.

Topography

At the large scale, elevation correlated negatively with relative canopy cover in Hirvaskangas (posterior mean of Spearman's rho (r) -0.89, 95% highest density interval (HDI) -0.90 – -0.87; Table 1), Hongikkovaara (posterior mean of r = -0.34, 95% HDI -0.38 – -0.30), and Pistuacanis (posterior mean of r = -0.54, 95% HDI -0.56 – -0.51). In Pommituskukkulat (posterior mean of r

0.21, 95% HDI 0.14 – 0.23) and Lac Dionne (posterior mean of r 0.18, 95% HDI 0.08 – 0.20), elevation correlated positively with relative canopy cover.

Slope steepness in Hirvaskangas (posterior mean of r -0.29, 95% HDI -0.31 – -0.26) and Pommituskukkulat (posterior mean of r = 0.20, 95% HDI 0.17 – 0.21) and topographic position in Lac Dionne (posterior mean of r = 0.20, 95% HDI 0.16 – 0.23) correlated with large-scale relative canopy cover. Other large-scale correlations with topographic variables were negligible (Table 1).

The topographic position index at the mid-scale correlated with relative canopy cover only in Lac Dionne (posterior mean of r = 0.19, 95% HDI 0.16 – 0.25). Otherwise, mid-and small-scale relative canopy cover varied independent of topographic variables (Table 1).

Discussion

Forest structural variation occurred at discernible spatial scales, supporting our first hypothesis. Using the scale-derivative analysis (Pasanen and others 2013), we identified three scales of structural variation in each landscape. These superimposed scales of variation demonstrated the distinctly hierarchical structure in the landscapes, i.e. that small-scale variation occurred within the larger-scale variation levels (Kotliar and Wiens 1990; Elkie and Rempel 2001; Hay and others 2002), which is a characteristic feature of ecological systems (O'Neill and others 1986).

In identifying the scales of variation, we manually placed the scale breaks between the small- and mid-scale, based on the changes in the slope of the scale-derivative norm. In the implemented permutation test, only the small-scale component was identified, confirming the existence of the discerned characteristic scales of variation (Fig. S7). This indicates that the identified scales of

variation did not result from a random process. Hence, despite the potential subjectivity involved in placing the scale breaks between the small- and mid-scales, the existence of all the multiresolution components was objectively verified. Further, the identification of scale breaks and multiple scales of variation is consistent with the idea of characteristic scales of variation in naturally dynamic boreal forest landscapes (natural scale steps; Scholes 2017).

The results only partially supported our second hypothesis concerning the differences of the scales of structural variation. The largest identified variation occurred at scales ranging from 20.1 to 321.4 ha, and differed most between the landscapes. In contrast, the second scale of variation (mid scale) was remarkably similar in all five landscapes, ranging from 1.3 to 2.8 ha. Qualitatively, the large- (Angelstam and Kuuluvainen 2004; Bouchard and others 2008) and mid-scales (D'Aoust and others 2004; Kuuluvainen and others 2014) of variation have been recognized from boreal forests in both northern Europe and Quebec. Yet, objective quantification of these scales of variation has mostly been lacking.

Traditionally in landscape ecology, landscape variability is assumed to occur as clearly delineating patches (Kotliar and Wiens 1990). Our results imply that in addition to abrupt changes, gradual structural variability is also typical in naturally dynamic boreal forests. In the Bayesian scale space multiresolution analysis, the variation components are extracted by subtracting successive smoothing levels (Holmström and others 2011). As smoothing suppresses patch edges, features with clear edges also appear as smooth in the mid-scale component. However, if the contrast in the patch edge is strong, the mid-scale patch edges are expected to show as positive and negative bands at the patch edges, visible in the small-scale component. In our results, such banded features were not present. Furthermore, the smoothness of the corresponding patch was visible in the canopy

cover maps (Fig. 2 a1 – e1). Hence, our results indicate that structural variability occurs as gradual (but detectable) variability within the forest matrix.

The smallest scale of variation that we identified equaled the grain of our data, and had high variation intensity. This suggests that intense structural variability in these naturally dynamic boreal forests typically occurs at within-stand scales (< 0.1 ha). Our choice for the grain of the data (i.e., the interpretation gird) was based on practical reasons for combining fieldwork and the photointerpretation, but also limited our analysis to scales larger than 0.1-ha. However, this scale is similar to the plot size in many (if not most) field-based studies on forest dynamics (Kuuluvainen and Aakala 2011). Hence, the significance of the small-scale variation in the boreal (e.g., Hamel and others 2004; Grenfell and others 2011), as well as the temperate zone (e.g., Runkle and Yetter 1987) has clearly been demonstrated. This applies also to both of our study regions (Pham and others 2004; Aakala and others 2016). The low number of credible small-scale relative canopy cover cells in the Quebecois landscapes is the result of their relatively high interpretation error, which is probably related to abundant regeneration following the previous spruce budworm outbreak, which occurred from the 1970s to the mid-1980s (Bouchard and Pothier 2010). In the field measurements, only trees over 10 cm at 1.3 m height were recorded. This distinction was difficult to make in the aerial photointerpretation, leading to high interpretation error.

Supporting our third hypothesis, we were able to identify the scale-dependent processes creating structural variation in the studied landscapes. The identification of different processes at particular scales also meant that these processes are underlying the patterns at that particular scale (Elkie and Rempel 2001), but also that some of the processes we examined produced patterns at multiple scales. At the largest scale identified, of the topographic variables, elevation had the strongest relationship with structural variation, although the mechanisms differed among the landscapes. In

Hirvaskangas, Hongikkovaara, and Pistuacanis landscapes, the relative canopy cover correlated negatively with elevation. This suggests a productivity limitation with increasing elevation, as described earlier in the North Shore region (Boucher and others 2006) and in northeastern Finland (Roiko-Jokela 1980). In both regions, the differences in elevation were modest (100-150 m). Hence, temperature differences are unlikely to explain these findings. Instead, we consider changes in soil nutrient and moisture regimes with topography a more plausible explanation (Seibert and others 2007).

In contrast, elevation and relative canopy cover correlated positively in the Lac Dionne landscape, suggesting increased productivity with increasing elevation. In boreal forests such a relationship has been related to high soil water table levels at low-lying sites (Simard and others 2007), which can cause structural variation even at landscape scales (Kljun and others 2006). In the Lac Dionne landscape, hydric conditions likely locally limit the productivity in low-lying areas, where sparse low productivity *P. mariana*-stands typically dominate (De Grandpré and others 2000).

Elevation and relative canopy cover also correlated positively in Pommituskukkulat. Here, higher elevation areas were dominated by deciduous trees and had high canopy cover, whereas *P. abies* stands at low elevations had low canopy cover. The areas with a higher deciduous component experienced a fire in 1831 (Aakala 2018), and are separated from the areas with higher dominance of *P. abies* by an open peatland running through the landscape. The peatland probably acted as a fire break, creating variability within the landscape. Hence, the positive correlation between elevation and relative canopy cover in Pommituskukkulat probably reflects the landscape disturbance history more than an elevational effect *per se* (Niklasson and Granström 2000).

At the mid scale, we detected both negative and positive correlations between relative canopy cover and relative dead wood basal area. The counter-intuitive positive relationship can be explained by variation in soil properties. In the more productive sites, more trees equates to more dead trees, while in less productive sites less trees equates to less dead trees (De Grandpré and others 2000; Kuuluvainen and others 2017).

The negative relationship between relative canopy cover and relative dead wood basal area demonstrated the role of recent disturbances in shaping forest structure, as tree mortality at these scales caused reduced canopy cover relative to its surroundings. The areas we suspect were related to the previous spruce budworm outbreak and windthrow areas (high numbers of similarly oriented logs) in the Hirvaskangas and Lac Dionne landscapes were visible as negative correlations, and showed that disturbances were responsible for creating variability at these mid scales. The larger number of openings likely caused by the spruce budworm outbreak in *A. balsamea*-dominated Pistuacanis than in *P. mariana*-dominated Lac Dionne is explained by the high susceptibility of *A. balsamea* to spruce budworm (Hennigar and others 2008). Spatial variation in boreal forest structures at these patch-scales has previously been linked with disturbances (D'Aoust and others 2004; Kuuluvainen and others 2014).

In addition to disturbances, the credible variation at the mid-scale was related to changes in tree species composition, and to topography in the Lac Dionne landscape. Many of these patches were located in areas where tree species composition changed. This probably reflects changes in edaphic conditions or in time since the last stand-replacing disturbance, as these both affect the tree species composition and tree density (De Grandpré and others 2000; Kuuluvainen and others 2017). The relationship between the topographic position and the mid-scale relative canopy cover in Lac Dionne is likely a result of the same process as observed at the large-scale, i.e. low topographic

positions associated with paludification and consequent low relative canopy cover (Lavoie and others 2007; Simard and others 2007).

We identified tree species composition, long-term disturbance history and recent disturbances as the most important drivers of mid-scale forest structural variation in both regions. However, these factors are related to soil characteristics, which influence the tree species composition (Rowe 1972; Sutinen and others 2002), and the occurrence of fires (Wallenius and others 2004; Mansuy and others 2010) in both regions. Tree mortality from the spruce budworm outbreaks that we identified as a cause for some of the mid-scale patches in the Quebecois landscapes is to a large extent influenced by the tree species composition, and concentrates especially on the *A. balsamea*-dominated stands (D'Aoust and others 2004; Hennigar and others 2008). Hence, although not directly measured here, it seems likely that the variability in soil characteristics creates patch-scale forest structural variation, corresponding to what we observed in this study.

At the small scale (0.1 ha, the grain of our data), we discovered a relationship between forest structural variation and recent disturbances. Earlier studies have attributed this type of 'stand-scale' variation to tree mortality (Kuuluvainen and others 1998; Aakala and others 2007), which creates structural variation especially in patches smaller than 100 m² (Pham and others 2004). However, this small-scale variability also results from a number of other processes, including the occurrence of regeneration microsites (Grenfell and others 2011), edaphic differences (Hamel and others 2004), and tree interactions (Aakala and others 2016).

Similar to the grain of our data that excluded the within-stand variability from our analyses, it is evident that some relevant large-scale variability occurred at scales beyond the extent of the study. Most obviously, stand-replacing fires in Quebec cause variability at larger scales than we assessed

(De Grandpré and others 2000), and for example, the Lac Dionne landscape is completely within a forest fire area dated to 1810 (Bouchard and others 2008). From a methodological perspective, although we argue that avoiding the selection of study scales *a priori* is a useful approach, the spatial extent and grain still obviously impose limitations on the scales that can be identified and analyzed (Estes and others 2018). Here, the practical limitations related to the calibration data limited the extent, but future work could benefit from the increasing availability of data that is less dependent on well-distributed field plots, such as light detection and ranging (LiDAR) data. However, especially in Finnish landscapes the extent is at the same time limited by the generally small size of the reserves in which natural forest dynamics can be studied.

Earlier studies have attempted to describe landscape variability over multiple scales using, for instance, scale space theory with blob-feature detection in the hierarchy theory context (Hay and others 2002; Hay 2014), or scalograms that visualize how landscape metrics respond to changing grain and extent (Zhang and Li 2013). The advantage of our approach is that the scale-derivative analysis identifies the characteristic scales of variation uniformly over the entire landscape and extracts the hierarchical components in a mathematically well-defined manner (Pasanen and others 2013), using a custom-built metric (cf. Zhang and Li 2013). Thus, it can be widely applied to explore multiscale variability in any raster-form data. The scale space analysis with Bayesian inference (Holmström and others 2011) allows identifying structures at the characteristic scales of variation so that the error associated with the production of the raster data is incorporated in the feature detection. Hence, the credibility of the variability can be assessed whenever the associated error can be quantified.

That the scale-derivative analysis did not automatically identify all the scale breaks suggests difficulties in the feature extraction due to which information close to a scale break may have been

displaced to wrong hierarchical level. It is obvious that the scale breaks may not always produce a local minimum in the norm, and instead weaker signs, such as saddle points or slope changes, should also be inspected as possible scale breaks. The ability of the scale-derivative analysis to separate scale-dependent components automatically depends on the size difference of the features within the components. The smaller the difference, the more difficult the extraction. Large feature size variation within a component and a large intensity difference between successive scale-dependent components can also hamper feature extraction (Pasanen and others 2013). The difficulties in scale break identification represent a typical situation where vague scale level boundaries prove hard to detect (Scholes 2017). We also note that while placing the scale break points manually we introduced subjectivity in the scale identification process. However, small changes in the scale break locations did not cause notable changes in the size estimates and hence our analyses appear robust to this subjectivity.

The presence of the scale-dependent components, and the occurrence of credible canopy cover features in each extracted scale-dependent component supported the notion of hierarchically structured landscapes, i.e. that there were characteristic scales of variation that contain the most salient structural features (the near-decomposability in the hierarchy theory; O'Neill and others 1986). Further, we identified different factors underlying the structural variation at particular scales that is similarly expected from hierarchically structured landscapes (Wu and Loucks 1995; Wu 1999). Related to these processes, the hierarchy theory suggests that at large scales variability would be driven by processes changing slowly in time (e.g., topography), whereas at small scales the driving processes occur abruptly (e.g., disturbances) (O'Neill and others 1986; Wu 1999). The occurrence of small-scale disturbances and stand-replacing fires indicates that abrupt processes influence forest structure at local scales, as well as at scales beyond the extent of our study. In contrast, the influence of slowly changing processes was limited to large scales.

Conclusions

Our analyses showed that hierarchical structural variation can be discerned from naturally dynamic boreal forest landscapes without relying on the delineation of distinct patches or on *a priori* selected scales. Further, these scale-dependent variations are linked to a number of different processes that partly crossed spatial scales (i.e. same processes created structural variation at multiple scales). Except for the largest scale variation that was related to landscape-specific topography and the large-scale fires typical in the North American boreal forests, the detected similarity in spatial scales of variation among landscapes suggests that boreal forests may display characteristic scales of variation that are somewhat independent of the dominant tree species or disturbance regime of a landscape.

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Data availability statement

Calibration data, and the calibrated raster maps of canopy cover produced in this study will be made available in Figshare at DOI:xxx/xxx upon acceptance.

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Table

Table 1. Spearman's rank correlation coefficients between the relative canopy covers at the detected scales (SS = small-scale, MS = mid-scale, LS = large-scale) and the topographic variables for the 0.1-ha cells.

	Hirvaskangas			Pommitus-kukkulat			Hongikkovaara			Lac Dionne			Pistuacanis		
	SS	MS	LS	SS	MS	LS	SS	MS	LS	SS	MS	LS	SS	MS	LS
Elevation	0.00	-0.10	-0.89	0.01	0.06	0.21	0.01	-0.01	-0.34	0.00	-0.01	0.18	0.00	-0.06	-0.54
Slope steepness	-0.01	-0.07	-0.29	0.01	0.09	0.20	0.02	0.04	-0.07	0.01	-0.02	-0.09	0.01	-0.02	0.12
Slope aspect	0.01	0.12	-0.07	0.00	0.02	-0.11	-0.01	-0.03	0.03	0.00	-0.02	-0.04	0.01	0.02	-0.04
TPI	0.01	0.01	-0.05	0.01	0.07	0.09	0.03	0.09	-0.08	-0.01	0.19	0.20	0.01	-0.01	0.11

Figures

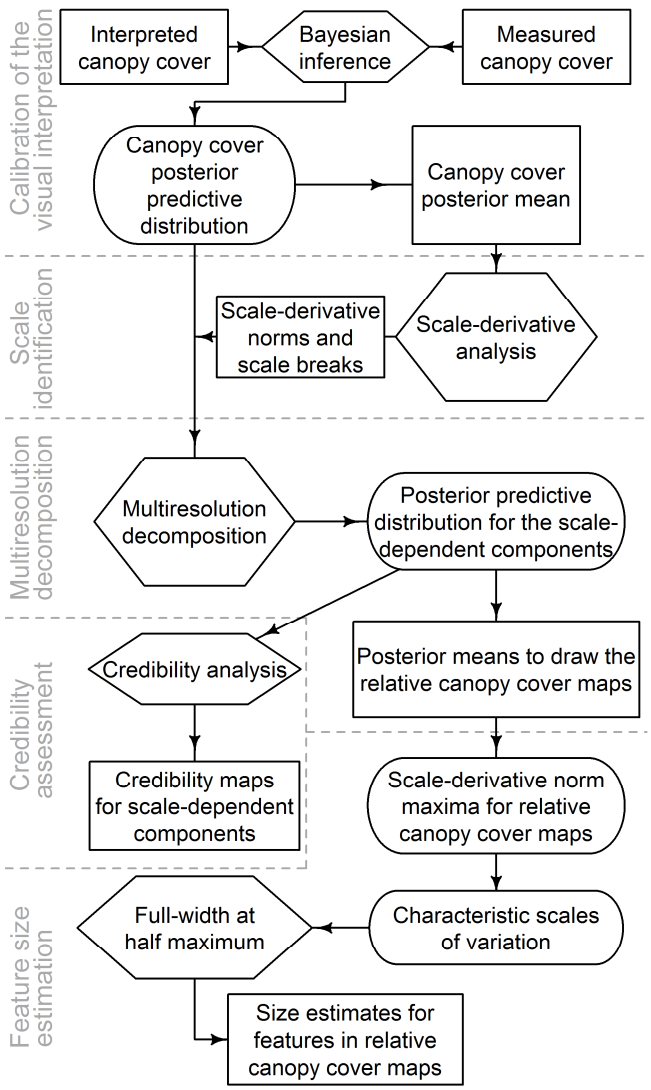

Figure 1. The analysis workflow. The rectangles represent input and output data, the hexagons are analyses, and the rounded rectangles transitional stage data.

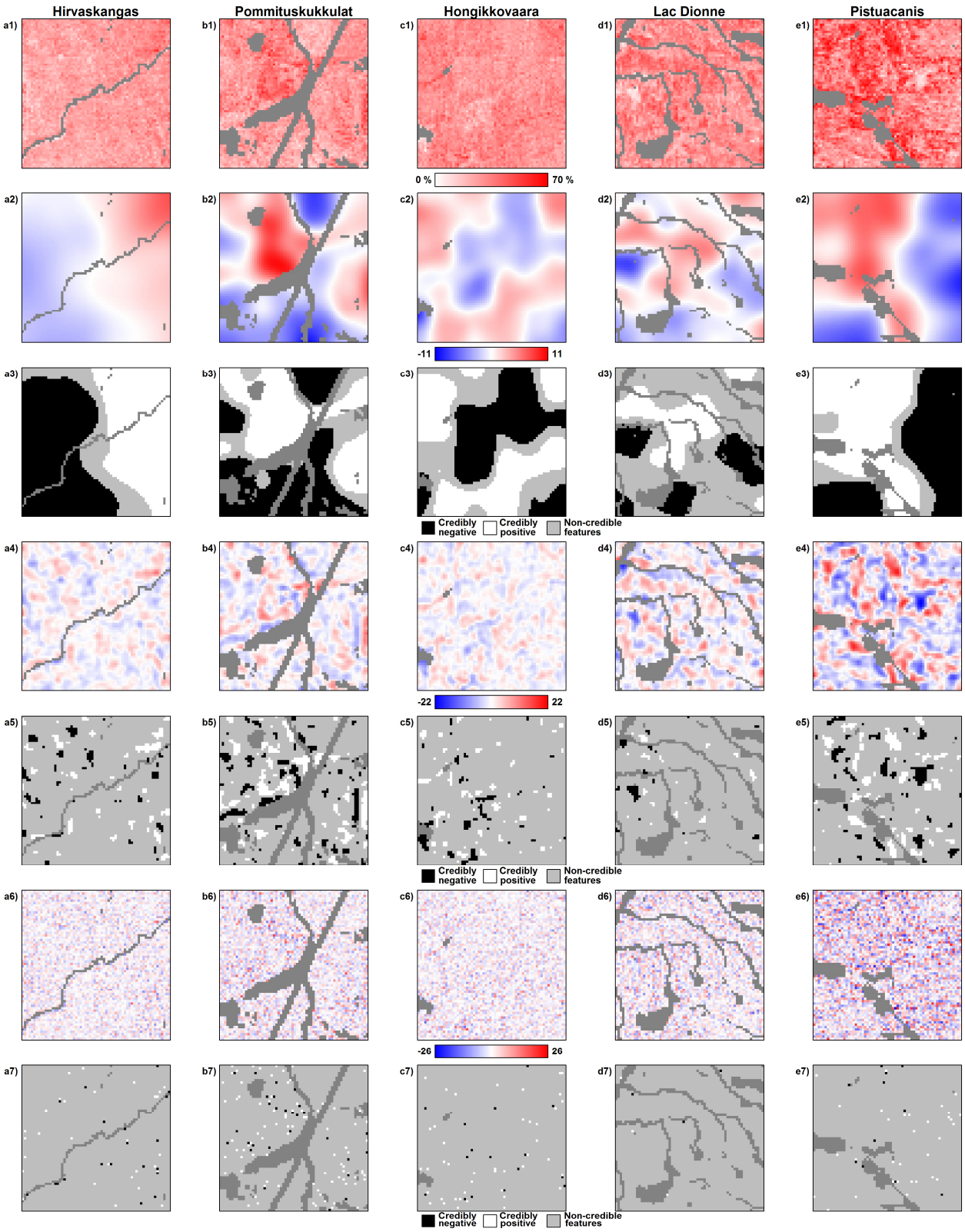

Figure 2. Canopy cover maps of the study landscapes, canopy cover in the 0.1-ha cells (a1 – e1). The large-scale relative canopy cover maps (a2 – e2) and their credibilities (a3 – e3), the mid-scale relative canopy cover maps (a4 – e4) and their credibilities (a5 – e5), and the small-scale relative

canopy cover maps (a6 – e6) and their credibilities (a7 – e7). Dark gray areas are nonforest cells, i.e. lakes, streams, open peatlands, and a reindeer fence and its surroundings in the Pommituskukkulat landscape.

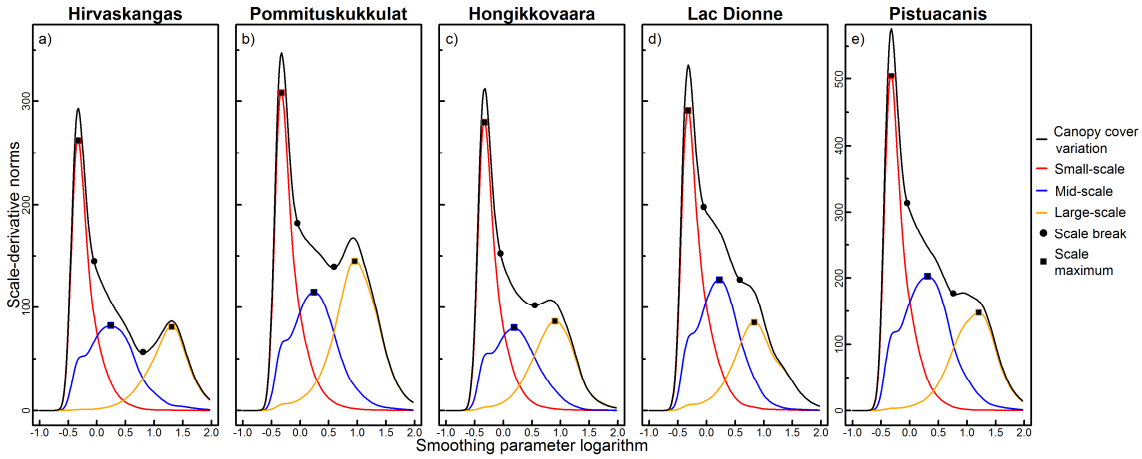

Figure 3. The scale-derivative norms as a function of the smoothing parameter logarithm. The colored lines show individual components. The points represent the component scale breaks and the squares depict the components' local maxima. *N.B.* the ten-raised smoothing parameter values and the different y-axis scale in the Pistuacanis landscape.

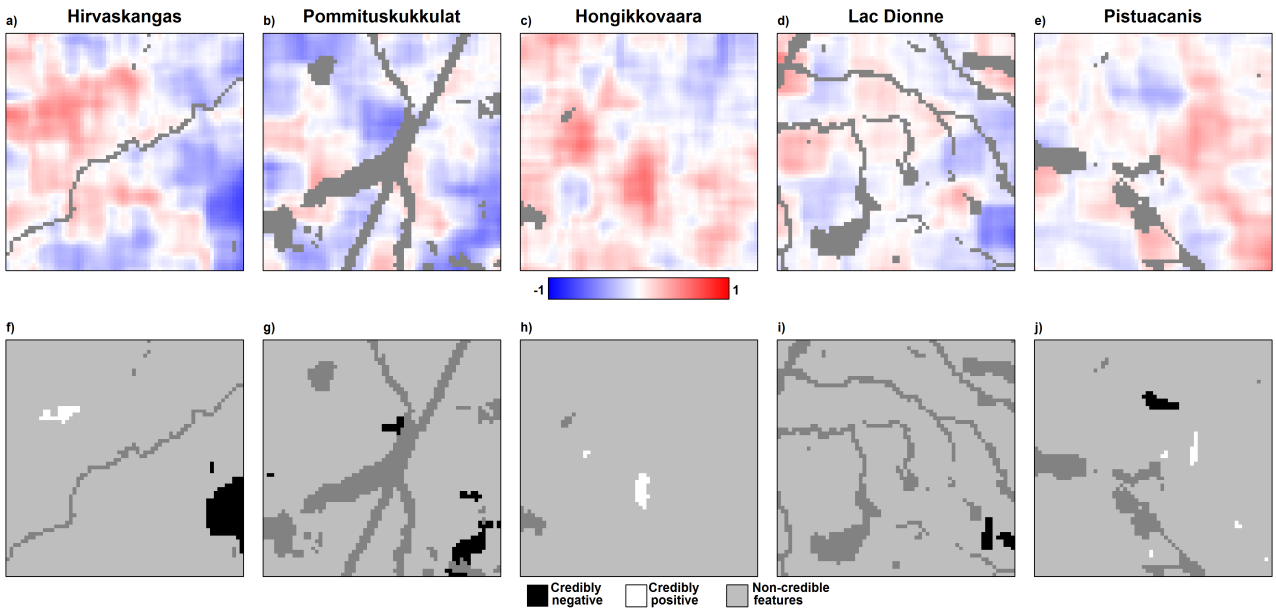

Figure 4. Local Pearson correlations at the mid scale between relative canopy cover and relative dead wood basal area (posterior mean values, a – e), and their credibilities (f – j). Dark gray cells are non-forested.

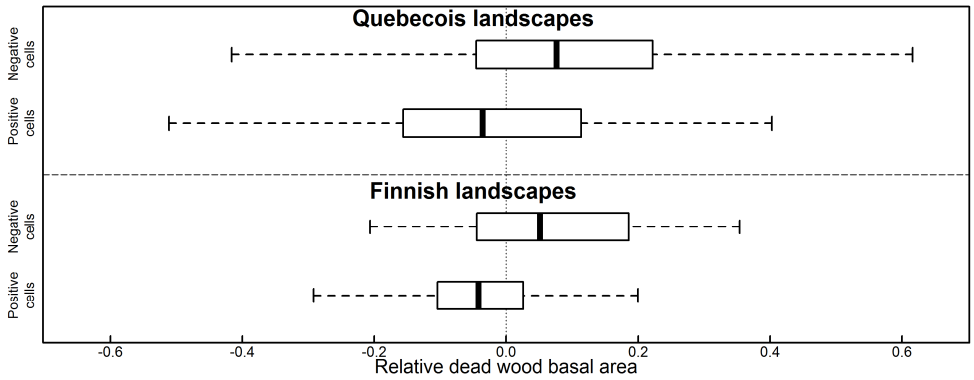

Figure 5. The posterior distributions of the relative dead wood basal area medians in the small-scale cells with credible relative canopy cover. The distributions consist of 158 positive and 64 negative cells in the Finnish landscapes and 129 negative and 113 positive cells in the Quebecois landscapes.

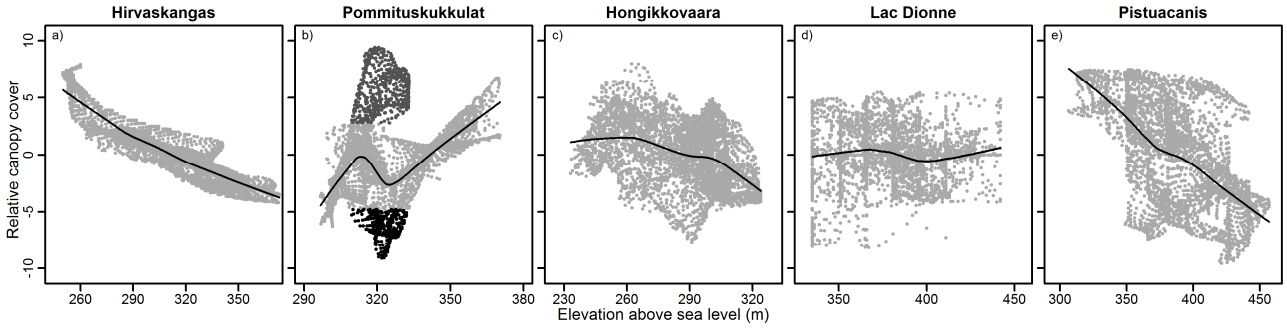

Figure 6. Large-scale relative canopy cover in relation to elevation in the studied landscapes, illustrated with a lowess regression. Pommituskukkulat (b) landscape has areas that clearly deviate from the main pattern. Here, the dark gray dots represent a birch-dominated area, and the black dots represent a hilltop spruce-dominated area. The light gray dots form the main pattern.