

Scales of variation in boreal forests

1 **At what scales and why does forest structure vary in naturally dynamic boreal**  
2 **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.

22 **Abstract**

23

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

29

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

34

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

41

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

46

47 **Keywords**

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

49 Fennoscandia

50

51 **Manuscript highlights**

52 · We identified distinct scales of hierarchical variation in boreal forest structure

53 · The mid-scale variation occurred at remarkably similar scales among the landscapes

54 · Drivers of the structural variation depended on the observation scale

55 **Introduction**

56

57 The spatial variability of forest structure (e.g., tree sizes, distribution of stems and foliage, dead  
58 wood) is the result of multiple factors such as disturbances, succession, topography, and soil  
59 properties (Lavoie and others 2007; Gauthier and others 2010; Walker and Johnstone 2014).

60 Knowledge of this structural variation is essential for understanding the processes that drive forest  
61 dynamics, habitat variability, and biodiversity (Niemelä and others 1996; Kuuluvainen and others  
62 2017), along with nutrient and carbon dynamics (Wickland and Neff 2008; Bradshaw and others  
63 2009) in forested landscapes.

64

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

79 2016), or the senescence-related deaths of individual trees (Aakala and others 2009) is limited to  
80 within-stand scales.

81

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

94

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

100

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

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

108

## 109 **Material and Methods**

### 110 **Study area**

111

112 We examined forests in two regions: northeastern Finland (67°44' N, 29°33' E) and the North Shore  
113 region in Quebec, Canada (49°38' N, 67°55' W; Fig. S1). In Finland, we examined two landscapes  
114 (2 km × 2 km) in Värriö Strict Nature Reserve (Hirvaskangas and Pommituskukkulat), and a third  
115 landscape in Maltio Strict Nature Reserve (Hongikkovaara). In Quebec, we studied two landscapes,  
116 Lac Dionne and Pistuacanis.

117

118 The studied landscapes are mosaics of forests on mineral soil, waterbodies, and forested and open  
119 peatlands. Soils in northeastern Finland consist mostly of undifferentiated glacial tills, with gentle  
120 slopes, and low mountain fells with treeless upper slopes. The elevation ranges between 200 and  
121 500 meters above sea level (asl). In the North Shore region of Quebec, slopes vary from low to  
122 moderate. Undifferentiated glacial tills are common on the gentle slopes and depressions, as are  
123 glaciofluvial sand deposits in floors of larger valleys and rocky outcrops on moderate slopes and  
124 summits (Robitaille and Saucier 1988). Here, the elevation of the studied region ranges from 300 to  
125 500 meters asl. Northern Finland has a subcontinental climate, with an annual mean temperature of  
126 +0.9 °C. The climate in the North Shore region is humid, with an annual mean temperature of  
127 +0.3 °C (see Supplementary material 1 for details).

128

## Scales of variation in boreal forests

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

134

### 135 **Visual interpretation of canopy cover**

136

137 To quantify forest structural variation at various spatial scales, we first visually interpreted canopy  
138 cover from recent aerial photographs in each of the five study landscapes. We used stereopairs of  
139 false-color aerial photographs with a pixel size of 0.5 m. Photographs for northern Finland were  
140 obtained from the National Land Survey of Finland, and were taken during summers 2011  
141 (Hirvaskangas and Pommituskukkulat) and 2010 (Hongikkovaara). Photos for Quebec were  
142 obtained from the Ministère des Forêts, de la Faune et des Parcs du Québec, and were taken in  
143 2011. We performed the stereointerpretation with EspaCity software (version 11.0.15306.1; Espa  
144 Systems Ltd., Espoo, Finland), using a passive 3D monitor.

145

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

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

156

### 157 **Calibration of and error in the visual interpretation**

158

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

175

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



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

186

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

194

195

## 196 **Identification of the scales and spatial patterns of canopy cover variation**

197

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

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

210

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

214

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

218

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

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

233

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

243

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

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

255

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

267

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

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

279

### 280 **Explanatory variables for canopy cover variation**

281

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

285

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

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

303

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

317

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

326 (each relative canopy cover map) and the topographic variables. If this correlation coefficient was >  
327 0.15, we assessed the uncertainty of the correlation by computing correlations between the  
328 particular topographic variable and all the 10 000 draws of the posterior predictive distribution, and  
329 assessed the mean and the 95% credibility intervals for these correlations.

330

331

## 332 **Results**

333

### 334 **Canopy cover and scales of variation**

335

336 Canopy cover in the 0.1-ha cells ranged from 0 to 59% in the Finnish landscapes, with a posterior  
337 mean of average over all cells 25% (SD of posterior predictive sample  $\pm 8\%$ , 95% prediction  
338 interval 18 – 33%) (Fig. 2 a1 – c1). Canopy cover ranged from 3 to 70% in the Quebecois  
339 landscapes, with a posterior mean of average over all cells 35% (SD  $\pm 13\%$ , 95% prediction interval  
340 22 – 48%) (Fig. 2 d1 – e1).

341

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

350

## Scales of variation in boreal forests

351 Feature sizes at the largest scale identified varied among the landscapes. A typical large-scale  
352 feature diameter was 2023 m in Hirvaskangas, 696 m in Pommituskukkulat and Hongikkovaara,  
353 506 m in Lac Dionne and 1518 m in Pistuacanis. These diameters correspond to an area of 321.4 ha  
354 in Hirvaskangas, 38.1 ha in Pommituskukkulat and Hongikkovaara, 20.1 ha in Lac Dionne and  
355 181.0 ha in Pistuacanis.

356

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

361

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

370

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

374



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

383

#### 384 **Drivers of canopy cover variation**

385

##### 386 *Recent disturbances*

387

388 At mid-scale, average correlations between relative canopy cover and relative dead wood basal area  
389 varied from -0.02 to 0.09. However, we observed wide spatial variability in the correlations, from -  
390 0.78 to 0.83 (Fig. 4). In the Finnish landscapes, these correlations were credible in the eastern and  
391 northwestern parts of Hirvaskangas (Fig. 4f), in the middle, and southeastern part of  
392 Pommituskukkulat (Fig. 4g), and in two areas in the middle of Hongikkovaara (Fig. 4h). Several of  
393 the mid-scale features correlated credibly with relative dead wood basal area in the Quebecois  
394 landscapes (Fig. 4i – j).

395

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

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

405

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

412

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

415

#### 416 *Site productivity and disturbance history*

417

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

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

427

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

442

#### 443 *Topography*

444

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

449 0.21, 95% HDI 0.14 – 0.23) and Lac Dionne (posterior mean of  $r$  0.18, 95% HDI 0.08 – 0.20),  
450 elevation correlated positively with relative canopy cover.

451

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

456

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

460

## 461 **Discussion**

462

463 Forest structural variation occurred at discernible spatial scales, supporting our first hypothesis.

464 Using the scale-derivative analysis (Pasanen and others 2013), we identified three scales of  
465 structural variation in each landscape. These superimposed scales of variation demonstrated the  
466 distinctly hierarchical structure in the landscapes, i.e. that small-scale variation occurred within the  
467 larger-scale variation levels (Kotliar and Wiens 1990; Elkie and Rempel 2001; Hay and others  
468 2002), which is a characteristic feature of ecological systems (O'Neill and others 1986).

469

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

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

479

480 The results only partially supported our second hypothesis concerning the differences of the scales  
481 of structural variation. The largest identified variation occurred at scales ranging from 20.1 to 321.4  
482 ha, and differed most between the landscapes. In contrast, the second scale of variation (mid scale)  
483 was remarkably similar in all five landscapes, ranging from 1.3 to 2.8 ha. Qualitatively, the large-  
484 (Angelstam and Kuuluvainen 2004; Bouchard and others 2008) and mid-scales (D'Aoust and others  
485 2004; Kuuluvainen and others 2014) of variation have been recognized from boreal forests in both  
486 northern Europe and Quebec. Yet, objective quantification of these scales of variation has mostly  
487 been lacking.

488

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

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

500

501 The smallest scale of variation that we identified equaled the grain of our data, and had high  
502 variation intensity. This suggests that intense structural variability in these naturally dynamic boreal  
503 forests typically occurs at within-stand scales ( $< 0.1$  ha). Our choice for the grain of the data (i.e.,  
504 the interpretation grid) was based on practical reasons for combining fieldwork and the  
505 photointerpretation, but also limited our analysis to scales larger than 0.1-ha. However, this scale is  
506 similar to the plot size in many (if not most) field-based studies on forest dynamics (Kuuluvainen  
507 and Aakala 2011). Hence, the significance of the small-scale variation in the boreal (e.g., Hamel  
508 and others 2004; Grenfell and others 2011), as well as the temperate zone (e.g., Runkle and Yetter  
509 1987) has clearly been demonstrated. This applies also to both of our study regions (Pham and  
510 others 2004; Aakala and others 2016). The low number of credible small-scale relative canopy  
511 cover cells in the Quebecois landscapes is the result of their relatively high interpretation error,  
512 which is probably related to abundant regeneration following the previous spruce budworm  
513 outbreak, which occurred from the 1970s to the mid-1980s (Bouchard and Pothier 2010). In the  
514 field measurements, only trees over 10 cm at 1.3 m height were recorded. This distinction was  
515 difficult to make in the aerial photointerpretation, leading to high interpretation error.

516

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

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523 Hirvaskangas, Hongikkovaara, and Pistuacanis landscapes, the relative canopy cover correlated  
524 negatively with elevation. This suggests a productivity limitation with increasing elevation, as  
525 described earlier in the North Shore region (Boucher and others 2006) and in northeastern Finland  
526 (Roiko-Jokela 1980). In both regions, the differences in elevation were modest (100-150 m). Hence,  
527 temperature differences are unlikely to explain these findings. Instead, we consider changes in soil  
528 nutrient and moisture regimes with topography a more plausible explanation (Seibert and others  
529 2007).

530

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

537

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

546

## Scales of variation in boreal forests

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

552

553 The negative relationship between relative canopy cover and relative dead wood basal area  
554 demonstrated the role of recent disturbances in shaping forest structure, as tree mortality at these  
555 scales caused reduced canopy cover relative to its surroundings. The areas we suspect were related  
556 to the previous spruce budworm outbreak and windthrow areas (high numbers of similarly oriented  
557 logs) in the Hirvaskangas and Lac Dionne landscapes were visible as negative correlations, and  
558 showed that disturbances were responsible for creating variability at these mid scales. The larger  
559 number of openings likely caused by the spruce budworm outbreak in *A. balsamea*-dominated  
560 *P. marianus*-dominated Lac Dionne is explained by the high susceptibility of *A.*  
561 *balsamea* to spruce budworm (Hennigar and others 2008). Spatial variation in boreal forest  
562 structures at these patch-scales has previously been linked with disturbances (D'Aoust and others  
563 2004; Kuuluvainen and others 2014).

564

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



## Scales of variation in boreal forests

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

574

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

585

586 At the small scale (0.1 ha, the grain of our data), we discovered a relationship between forest  
587 structural variation and recent disturbances. Earlier studies have attributed this type of 'stand-scale'  
588 variation to tree mortality (Kuuluvainen and others 1998; Aakala and others 2007), which creates  
589 structural variation especially in patches smaller than 100 m<sup>2</sup> (Pham and others 2004). However,  
590 this small-scale variability also results from a number of other processes, including the occurrence  
591 of regeneration microsites (Grenfell and others 2011), edaphic differences (Hamel and others 2004),  
592 and tree interactions (Aakala and others 2016).

593

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

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

606

607 Earlier studies have attempted to describe landscape variability over multiple scales using, for  
608 instance, scale space theory with blob-feature detection in the hierarchy theory context (Hay and  
609 others 2002; Hay 2014), or scalograms that visualize how landscape metrics respond to changing  
610 grain and extent (Zhang and Li 2013). The advantage of our approach is that the scale-derivative  
611 analysis identifies the characteristic scales of variation uniformly over the entire landscape and  
612 extracts the hierarchical components in a mathematically well-defined manner (Pasanen and others  
613 2013), using a custom-built metric (cf. Zhang and Li 2013). Thus, it can be widely applied to  
614 explore multiscale variability in any raster-form data. The scale space analysis with Bayesian  
615 inference (Holmström and others 2011) allows identifying structures at the characteristic scales of  
616 variation so that the error associated with the production of the raster data is incorporated in the  
617 feature detection. Hence, the credibility of the variability can be assessed whenever the associated  
618 error can be quantified.

619

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

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

634

635 The presence of the scale-dependent components, and the occurrence of credible canopy cover  
636 features in each extracted scale-dependent component supported the notion of hierarchically  
637 structured landscapes, i.e. that there were characteristic scales of variation that contain the most  
638 salient structural features (the near-decomposability in the hierarchy theory; O'Neill and others  
639 1986). Further, we identified different factors underlying the structural variation at particular scales  
640 that is similarly expected from hierarchically structured landscapes (Wu and Loucks 1995; Wu  
641 1999). Related to these processes, the hierarchy theory suggests that at large scales variability  
642 would be driven by processes changing slowly in time (e.g., topography), whereas at small scales  
643 the driving processes occur abruptly (e.g., disturbances) (O'Neill and others 1986; Wu 1999). The  
644 occurrence of small-scale disturbances and stand-replacing fires indicates that abrupt processes  
645 influence forest structure at local scales, as well as at scales beyond the extent of our study. In  
646 contrast, the influence of slowly changing processes was limited to large scales.

647

## 648 **Conclusions**

649

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

659

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661

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669

## 670 **Data availability statement**

671

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

674

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807 **Table**

808

809 **Table 1.** Spearman's rank correlation coefficients between the relative canopy covers at the

810 detected scales (SS = small-scale, MS = mid-scale, LS = large-scale) and the topographic variables

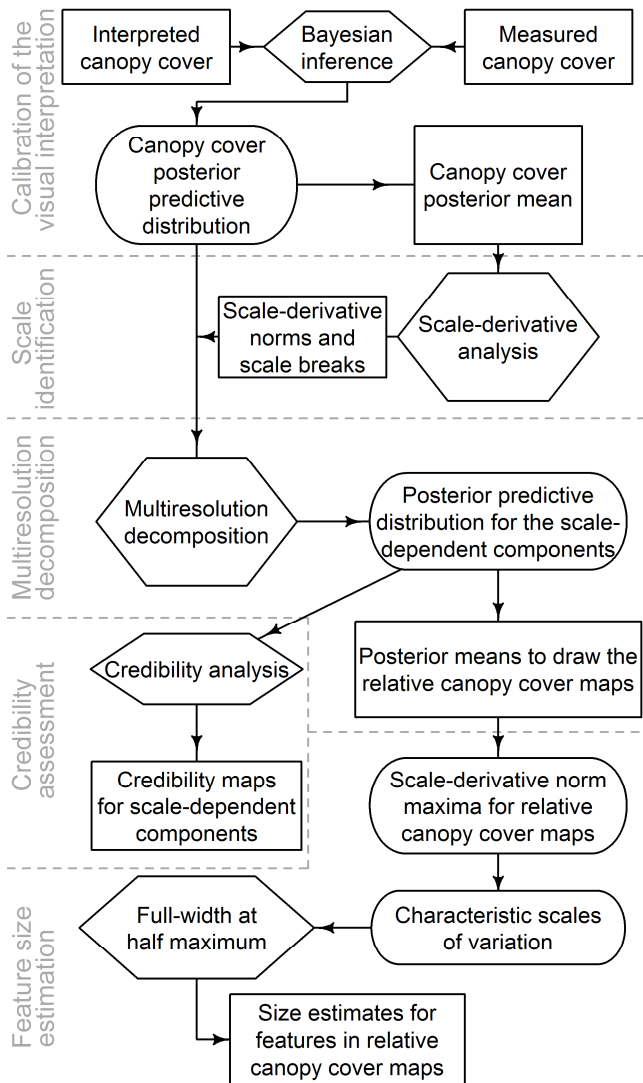
811 for the 0.1-ha cells.

	Hirvaskangas			Pommitus- kukkulat			Hongikkovaara			Lac Dionne			Pistuaicanis		
	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

812

813

814 **Figures**

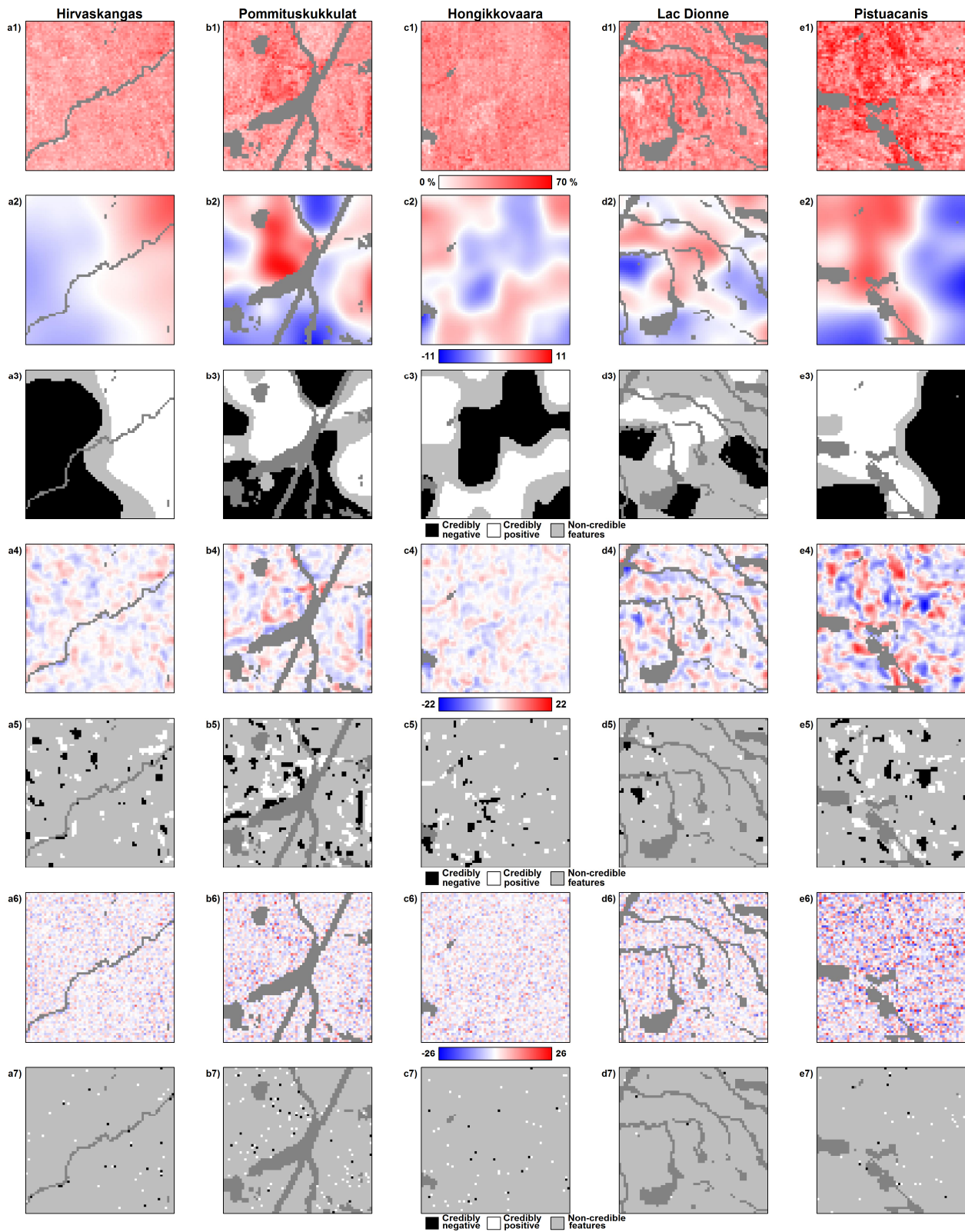


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816 **Figure 1.** The analysis workflow. The rectangles represent input and output data, the hexagons are

817 analyses, and the rounded rectangles transitional stage data.

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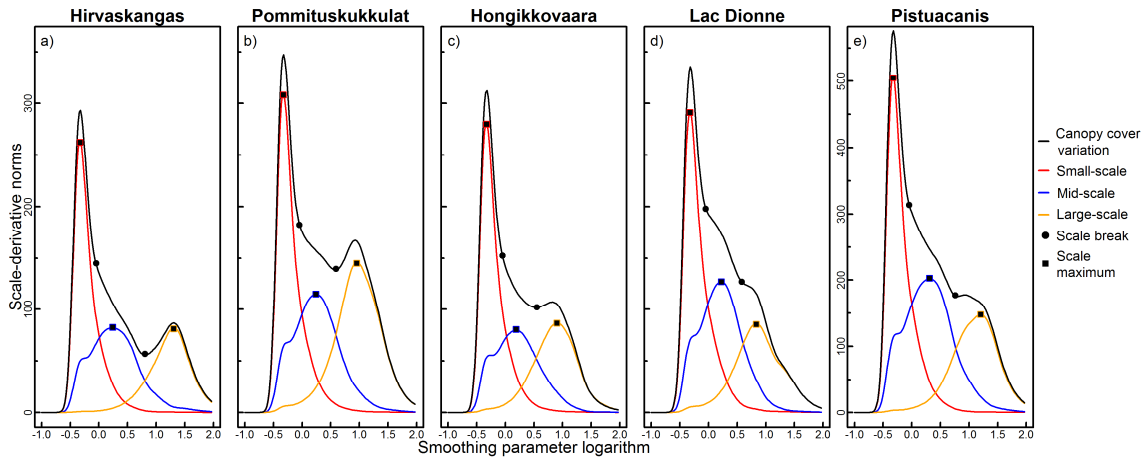
819 **Figure 2.** Canopy cover maps of the study landscapes, canopy cover in the 0.1-ha cells (a1 – e1).

820 The large-scale relative canopy cover maps (a2 – e2) and their credibilities (a3 – e3), the mid-scale

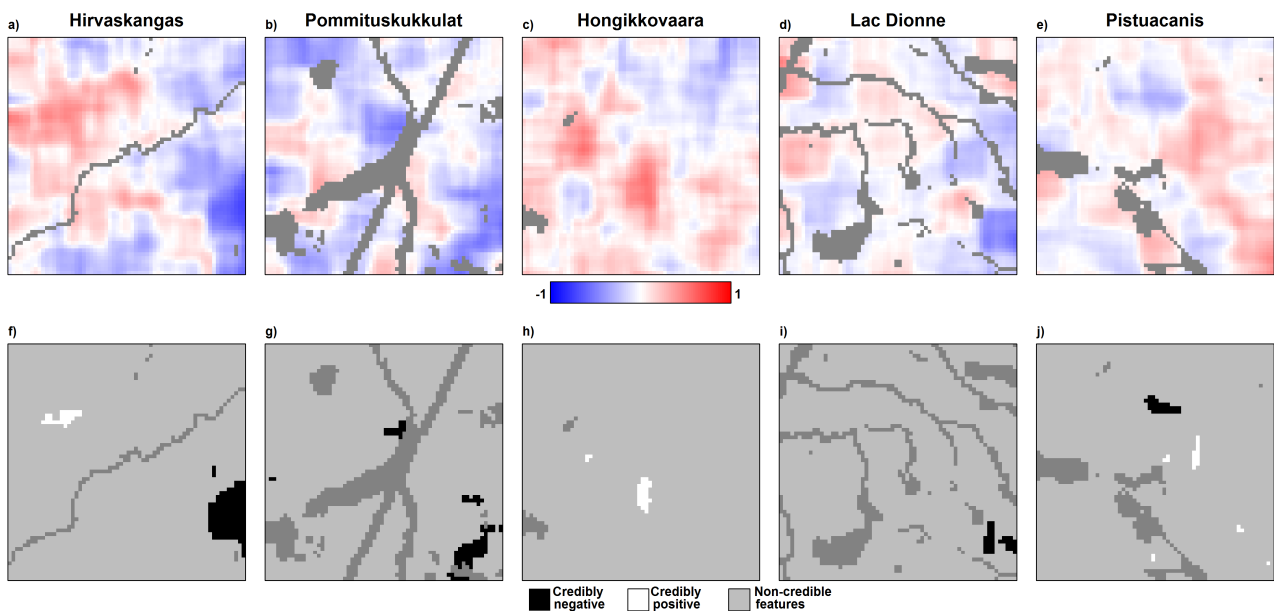
821 relative canopy cover maps (a4 – e4) and their credibilities (a5 – e5), and the small-scale relative

## Scales of variation in boreal forests

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

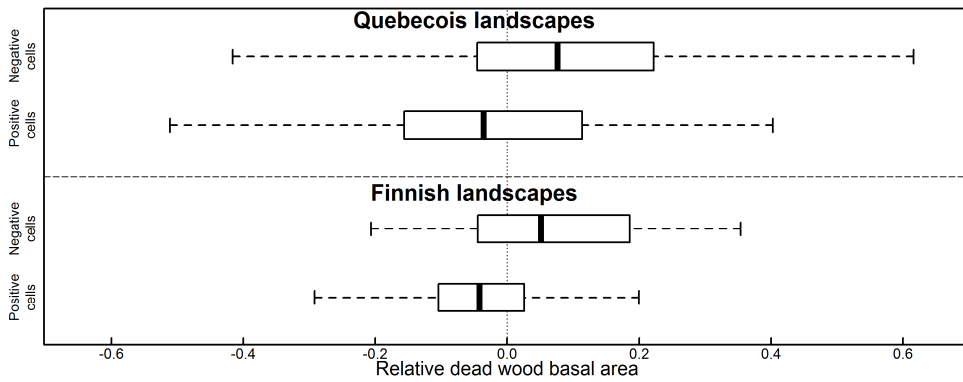


825  
826 **Figure 3.** The scale-derivative norms as a function of the smoothing parameter logarithm. The  
827 colored lines show individual components. The points represent the component scale breaks and the  
828 squares depict the components' local maxima. *N.B.* the ten-raised smoothing parameter values and  
829 the different y-axis scale in the Pistuacanis landscape.



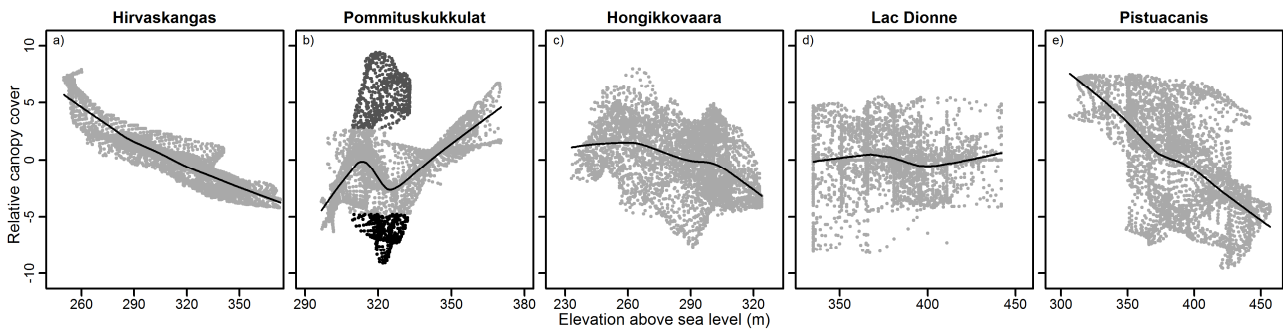
830  
831 **Figure 4.** Local Pearson correlations at the mid scale between relative canopy cover and relative  
832 dead wood basal area (posterior mean values, a – e), and their credibilities (f – j). Dark gray cells  
833 are non-forested.

## Scales of variation in boreal forests



834

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



838

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