

Statistical Opportunities for Comparing Stand Structural Heterogeneity in Managed and Primeval Forests: An Example from Boreal Spruce Forest in Southern Finland

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The horizontal and vertical stand structure of living trees was examined in a managed and in a primeval spruce-dominated forest in southern Finland. Tree size distributions (DBHs, tree heights) were compared using frequency histograms. The vertical distribution of tree heights was illustrated as tree height plots and quantified as the tree height diversity (THD) using the Shannon-Weaver formula. The horizontal spatial pattern of trees was described with stem maps and quantified with Ripley's K-function. The spatial autocorrelation of tree sizes was examined with semivariogram analysis. In the managed forest the DBH and height distributions of trees were bimodal, indicating a two-layered vertical structure with a single dominant tree layer and abundant regeneration in the understory. The primeval forest had a much higher total number of trees which were rather evenly distributed in different diameter and tree height classes. The K-function summaries for trees taller than 15 m indicated that the primeval stand was close to complete random pattern. The managed stand was regular at small distances (up to 4 m). The semivariograms of tree sizes (DBH, tree height) showed that the managed forest had a clear spatial dependence in tree sizes up to inter-tree distances of about 12 meters. In contrast, the primeval spruce forest had a variance peak at very short inter-tree distances (< 1 m) and only weak spatial autocorrelation at short inter-tree distances (1–5 m). Excluding the understory trees ($h < 15$ m) from the analysis drastically changed the spatial structure of the forest as revealed by semivariograms. In general, the structure of the primeval forest was both horizontally and vertically more variable and heterogeneous compared to the managed forest. The applicability of the used methods in describing fine-scale forest structure is discussed.

Keywords boreal forests, Norway spruce, spatial analysis, K-function, semivariance, structural variation, biodiversity

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1 Introduction

Heterogeneity of forest structure can be viewed at different hierarchical scales (Wiens 1989, Kotliar and Wiens 1990). From an eagle's perspective forest characteristics at the landscape scale are apparently most important, while for microlichens living on needle surfaces the structure and microclimate of individual branches or shoots are crucial. However, perhaps for most forest organisms an intermediate scale of perception, that defined by the structure of the forest at the patch or tree stand level (within meters to tens of meters), is most important. This is because the horizontal and vertical arrangement of foliage and woody biomass defines the spatial distribution of microclimatic conditions within the canopy space and in the forest understory (Pukkala et al. 1991, 1993, Canham et al. 1994). In addition, the spatial arrangement of trees defines the three dimensional geometry of habitat characteristics for birds, insects, tree epiphytes, understory plants and soil micro-organisms (Morse et al. 1985, Lesica et al. 1991, Barik et al. 1992, Gunnarsson 1992, Niemelä et al. 1992).

The structure of a tree stand is a reflection of both autogenic developmental processes, like regeneration pattern, competition and the consequent self-thinning, and past and present disturbance events. In managed forests, the most obvious disturbance factor affecting stand structure is silvicultural treatments like thinnings, which often aim at fully utilizing the site's capacity of quality wood production by homogenizing within-stand variation in tree characteristics. Accordingly, it has generally been concluded that natural tree stands are structurally more complex and diverse than managed stands (e.g. Hansen et al. 1991, Swanson and Franklin 1992).

Much of the recent ecological research of fine-scale forest structures is motivated by the idea that spatially heterogeneous forests may accommodate more species and particularly specific species requiring specialized microhabitats (e.g. Hansen et al. 1991, McComb et al. 1993). This is because structurally complex forests provide a greater variety of microclimates, hiding and nesting sites etc., compared to more homogeneous forests. For example, the complexity of vertical vegetation structure has been found to be related to the number of insect and bird species occupying a given forest area (e.g. McArthur and McArthur 1961, Murdoch et al. 1972, Cody 1975). Thus, the structural complexity of forest often seems to be a good predictor of overall species diversity (Begon et al. 1986). Accordingly, ecological inventories could use analyses of forest structure to assess the conservation or biodiversity value of forest stands (Hansen et al. 1991, Lindholm and Tuominen 1993, McComb et al. 1993).

Although forest ecosystems have a multitude of characteristics which can be used for descriptive purposes, the structure of the tree stratum obviously has a central role in determining the ecological processes and habitat characteristics in the forest. The structure of a tree stand can be defined in terms of tree size distribution and the spatial arrangement of trees. In this study we examine and discuss some statistical methods to quantify the structural heterogeneity of the forest in terms of size and spatial distribution of trees. These methods are of general nature, developed for georeferenced data in spatial statistics and geostatistics. We use these methods to compare the structure of a primeval and managed spruce dominated forest stand in southern Finland.

2 Material and Methods

2.1 Sample Stands: Their History and Measurement

The material consisted of two forest sample plots, one representing a managed forest in Vuorijärvi and the other a primeval forest in Susimäki. The examined forests are located in southern Finland, close to the Hyytiälä Forestry Field Station of the University of Helsinki (61°50' N, 24°17' E, alt. 150 m a.s.l.). The area belongs to the south-boreal vegetation zone (Ahti et al. 1968) and the effective temperature sum (5° C threshold) of the location is approximately 1150 d.d. Both forest plots were growing on *Myrtillus* site type, which is a medium fertile type according to the Finnish site classification system.

The Susimäki forest preserve was officially established in 1955, because of its distinct old-growth forest characteristics. However, the Susimäki forest has developed largely without human influence for a long time, since there were no distinctive signs of human disturbance on the study

plot. For the Vuorijärvi stand there are no exact historical records on the management history of the forest. However, growth release analysis based on the widths of annual rings from tree borings (n = 5, data not shown), suggests that timber was extracted from the stand approximately 35 years ago. The area of the sample plots in both forests was 0.25 hectares (50 m × 50 m). On both plots trees taller than 1.3 m were measured for location, height, DBH and species (Table 1).

The forest of the Susimäki plot (Grid 27°E: 6864:354) was approximately 150 years old. There were 1756 trees per hectare of which 6.4 % were dead standing trees. Dead trees were most frequent in small diameter classes (Fig. 1). The total standing wood volume of the trees was 427 m³ ha⁻¹ of which dead standing trees comprised 5 m³ ha⁻¹ (1.2 % of volume). There were no recent treefalls or other natural disturbances on the plot (Table 1).

The age of the managed stand of Vuorijärvi (Grid 27°E: 6860:358) was approximately 105 years. There were 1360 standing trees per hectare, of which 0.6 % were dead. The total stand-

Table 1. Structural characteristics and tree species composition of the managed Vuorijärvi and the primeval Susimäki spruce-dominated forest sample plots.

Property	Vuorijärvi	Susimäki
Number of trees, ha ⁻¹		
Total	1360	1756
Living	1352	1644
H ≥ 15 m	400	664
H < 15 m	952	980
Tree species proportions, %		
H ≥ 15 m		
<i>Picea abies</i> L. Karst.	92.0	76.3
<i>Pinus sylvestris</i> L.	4.0	4.7
<i>Betula pendula</i> Roth., <i>Betula pubescens</i> Ehrh.	4.0	18.4
<i>Populus tremula</i> L.	-	0.6
H < 15 m		
<i>Picea abies</i> L. Karst.	52.7	94.8
<i>Pinus sylvestris</i> L.	0.8	1.1
<i>Betula pendula</i> Roth., <i>Betula pubescens</i> Ehrh.	32.7	4.1
<i>Sorbus aucuparia</i> L.	13.8	-
Stem volume of standing trees, m ³ ha ⁻¹		
Total	335	427
Living trees	329	422
Dead trees	6	5

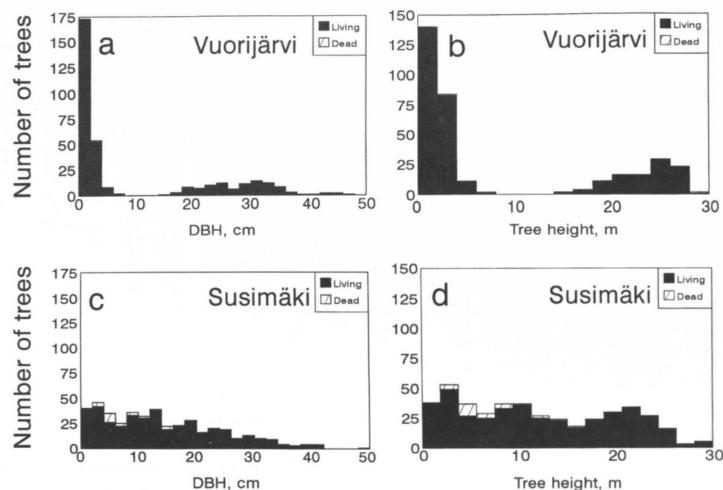


Fig. 1. Frequency distributions of DBH and tree height in the managed Vuorijärvi (a and b) and in the primeval Susimäki (c and d) forest plots.

ing wood volume was $335 \text{ m}^3 \text{ ha}^{-1}$, of which $6 \text{ m}^3 \text{ ha}^{-1}$ (1.8 % of volume) was dead trees. Thus, the Vuorijärvi stand had fewer but larger dead standing trees than the primeval Susimäki stand.

Both plots had Norway spruce (*Picea abies* L. Karst.) as the dominant tree species and Scots pine (*Pinus sylvestris* L.) and birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.) as co-occurring species. In addition, the Vuorijärvi stand had rowan (*Sorbus aucuparia* L.) in the understorey and the Susimäki plot had one aspen (*Populus tremula* L.) in the upper story (see Table 1).

In the upper story ($h \geq 15 \text{ m}$) the primeval Susimäki stand had a more even species distribution, due to the more abundant occurrence of birch (18.4 %), when compared to the managed Vuorijärvi stand. In the lower story ($h < 15 \text{ m}$) the reverse was true, the managed Vuorijärvi stand had more species (due to the occurrence of rowan) with greater evenness than the primeval Susimäki stand (Table 1).

2.2 Methods

An intuitive method for comparing stand struc-

tures is to compare frequency histograms of tree sizes and to draw horizontal stem or crown maps and vertical profile diagrams (e.g. Hallé et al. 1978, Koop 1991). These methods were also used in this study. Graphical illustration was complemented with quantitative techniques to assess tree stand structure in order to facilitate rigorous comparisons between the different aspects of forest structure.

Vertical Distribution

The complexity of the vertical distribution of foliage weight or surface area is probably most important in creating the vertical modulation of microclimatic conditions and available feeding, mating and nesting sites for canopy-dwelling organisms. Since vertical foliage amounts are tedious to measure, we confined ourselves with the tree height distribution to characterize the vertical structure of the forest. First, we examined the downward cumulative percentage of the number of trees by 2 meter deep horizontal layers. This approach resembles the Kaplan-Meier curve used in survival analysis (Kaplan and Meier 1958).

Second, the tree height diversity (THD) was quantified with the Shannon-Weaver formula (e.g. MacArthur and MacArthur 1961, Murdoch et al. 1972) using 2 meter deep horizontal layers (0–2 m, 2–4 m ...). This measure of diversity is defined as

$$\text{THD} = H' = -\sum_{i=1}^n p_i \log_e p_i \quad (1)$$

where p_i is the proportion of trees in the i th height layer. The difference in THD between the two stands was tested using t-statistic as described by Hutcheson (1970), see also Magurran (1988).

Horizontal Distribution

The horizontal pattern of tree locations in a forest can be viewed as a two-dimensional point process. Three traditional distribution types are, *regular* pattern, *completely random* or Poisson pattern and *clustered* pattern. Three broad categories of methods to characterize spatial distributions of trees can be considered: quadrat methods, distance methods and second-order methods, which require stem-mapped data. Early studies of spatial point patterns were mainly concerned in comparing area (or quadrat) counts to Poisson distribution. In addition, among the most commonly used approaches are the so-called nearest-neighbor methods. Distances may be measured between trees and nearest neighboring trees or between sample points and nearest trees. The advantage of nearest-neighbor methods in applied purposes is that they were intended to be used in the field (Cressie 1991), but they are hampered by the restriction to small-scale pattern separation only and by the difficulty to obtain a random sample of trees in the field. Nearest neighbor methods have been further developed to account for scale effects and spatial location of quadrats (e.g. Moerur 1993).

For stem-mapped data the Ripley's K-function analysis is more powerful than nearest neighbor methods (e.g. Moerur 1993). Unlike nearest neighbor analysis, which considers only distances from a given point to its nearest neighbor, Ripley's K-function considers the distances between all pairs of points in the study area (Ripley

1981). For applications related to trees see e.g. Sterner et al. (1986), Tomppo (1986), Getis and Franklin (1987), Kenkel (1988), Penttinen et al. (1992) and Moerur (1993).

Ripley's K can be defined as follows. If λ is the density of trees (mean number per unit area), then $\lambda K(d)$ is the expected number of further trees within the distance d from a randomly chosen tree. The boundary-corrected estimator $\hat{K}(d)$ can be computed for n trees on an area A , as follows:

$$\hat{K}(d) = A \sum_{\substack{i,j=1 \\ i \neq j}}^n [\sigma_{ij}(d) / n^2] \quad (2)$$

where $1 / \sigma_{ij}$ is defined as the proportion within A of the circumference of a circle centered at tree i with boundary passing through tree j (Ripley 1981, p. 159). For a completely random pattern $E\hat{K}(d) = \pi r^2$. Therefore, instead of $\hat{K}(d)$ a transformed version $\hat{L}(t)$ is used:

$$\hat{L}(t) = \sqrt{[\hat{K}(d) / \pi]} \quad (3)$$

For determining the statistical significance of departures from random patterns, the 95 % confidence envelope has been done using simulations of the Poisson process. Another method is based on the approximation leading to the confidence bounds $\pm 1.45\sqrt{(A/N)}$, where A is the area of the plot and N is the number of trees on the plot (Ripley 1988). Crossing of the upper or lower limit of the confidence envelope can thus be considered as a significant departure from randomness.

Spatial Autocorrelation of Tree Sizes

The shortcoming of spatial point pattern analysis is that they only account for the locations of trees but not for their size variation in space, which is an essential characteristic of forest structure (Matérn 1960) and important from the ecological point of view (Rossi et al. 1992). Here we use the semivariogram to examine the spatial autocorrelation in tree sizes. In particular, the semivariogram can suggest the scales of patchiness of the forest structural mosaic (Palmer 1988, Biondi et al. 1994).

Semivariogram is a measure of the degree of spatial dependence between samples, which summarizes the variance as a function of scale. More specifically, the semivariance is the sum of squared differences between all possible pairs of points separated by a given distance (often given as a distance class). The semivariance is defined as:

$$\gamma(h) = \frac{1}{2} E[z(i) - z(i+1)]^2 \quad (4)$$

and its estimator is:

$$\hat{\gamma}(h) = 1/2N(h) \sum_{i=1}^n [(z(i) - z(i+1))]^2 \quad (5)$$

where $z(i)$ and $z(i+1)$ respectively are the values of a variable measured at locations separated by distance h , and $N(h)$ is the number of pairs of points separated by distance h . Other estimators can be found in Cressie (1991).

The summary is a plot of $\hat{\gamma}(h)$ as a function of h . As the distance between points increases the values of the measured variables usually become increasingly dissimilar, and the semivariance increases. The increase continues until the points are so far apart that they are not related to each other and their squared difference becomes equal to the average variance of the samples. This flat region of the graph is called the sill. The maximum distance within which the samples are still autocorrelated is called the range. If the semivariogram is a straight horizontal line (“pure sill”), the variable is not spatially correlated.

The advantage of the semivariogram approach is that different data forms, i.e. transect, quadrat and point data, can be readily utilized (Burroughs 1987, Turner et al. 1991). In this study the semivariogram is applied to individual mapped trees (their sizes and locations, assuming the locations of the trees to be fixed). Although trees are discrete objects their sizes can be thought to be realizations of the effects of spatially continuous variables, like radiation and soil nutrients, thus motivating their autocorrelation analysis. However, for inventory purposes it would probably be more convenient to use transect or quadrat methods instead of mapping individual trees.

3 Results

3.1 Size Distribution of Trees

Frequency Histograms of DBH and Height

In the managed Vuorijärvi forest the DBH distribution of trees exhibit a distinct bimodal pattern, so that most of the trees are smaller or equal than 5 cm at DBH and a second broad peak in the distribution is in the 18–36 cm DBH-classes (Fig. 1). When compared to the managed forest, the primeval Susimäki forest has a much higher total number of trees which are more evenly distributed in different diameter classes. Also in this case small trees are most abundant but the frequency of trees decline more or less continuously with increasing diameter.

The tree height distributions of the two forest plots naturally resemble those of BHD (Fig. 1). The managed Vuorijärvi forest has a two-peaked height distribution of trees, while the primeval Susimäki forest has trees in all of the defined 2-m-wide height classes up to 32 m. The difference in tree height distributions is further illustrated in Fig. 2, showing the downward cumulative percentage of the number of trees in 2 meter deep layers. The greater frequency of smaller trees in the managed Vuorijärvi forest is clearly seen when compared to the Susimäki plot.

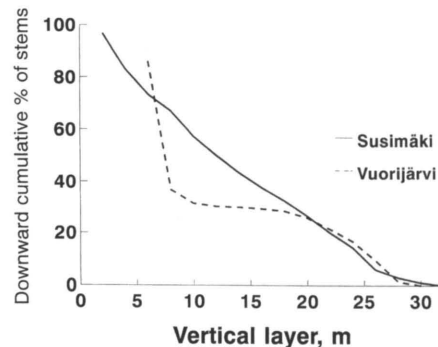


Fig. 2. The downward cumulative percentage of tree numbers in 2 meter deep layers in the managed Vuorijärvi and in the primeval Susimäki forest plots.

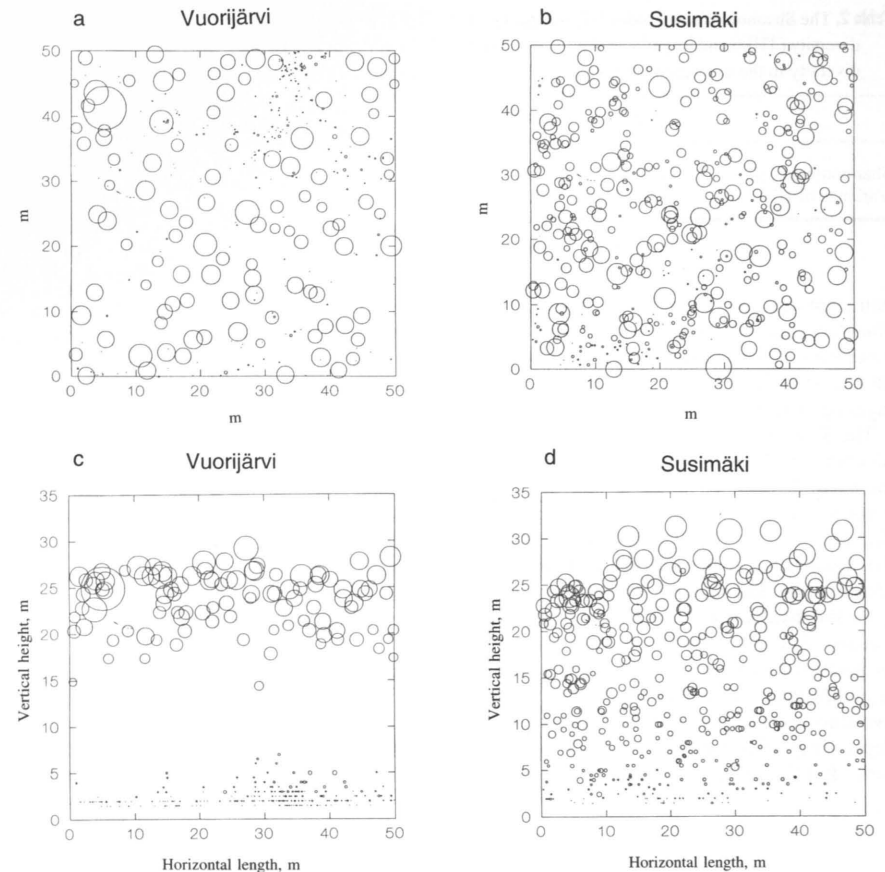


Fig. 3. Stem maps of (a) the managed Vuorijärvi and (b) the primeval Susimäki forest plots, and tree height distribution diagrams of (c) the managed Vuorijärvi and (d) the primeval Susimäki spruce forests. The size of the circle is proportional to the DBH in all figures; in the tree height diagrams tree heights are indicated by circle midpoints.

3.2 Spatial Description

Horizontal and Vertical Patterns

The horizontal stem maps of the two forest plots reveal the greater density and size variation of trees in the primeval Susimäki plot as compared to the managed Vuorijärvi forest plot (Fig. 3). In Vuorijärvi there is more understory regeneration

and a distinct dense regeneration group in a gap in the north-eastern corner of the area. This regeneration may have been enhanced by the last logging operation, allowing more light to penetrate the stand and providing favourable regeneration microhabitats due to soil disturbance.

The illustration of the vertical distribution of tree heights shows the distinctive two-layered structure of the managed forest, consisting of a

Table 2. The Shannon-Weaver index (H') for tree height diversity (THD) and its variance for the tree height diversity in the two sample plots.

	Vuorijärvi	Susimäki
Shannon index (H')	1.656	2.707
Variance of H'	0.00422	0.00225

dominant tree layer of trees taller than 15 m and abundant regeneration in the understory. On the other hand, the primeval Susimäki forest has an all-size structure, without any distinct vertical layering (Fig. 3).

The Shannon-Weaver index (H') for tree height diversity (THD) was considerably higher in the unmanaged Susimäki forest (2.71), when compared to the managed forest of Vuorijärvi (1.66) (Table 2). An attempt was also made to assess the significance of this difference in tree height distributions. The method of Hutcheson (1970) gave the t -value of 15.71 on 380 degrees of freedom, indicating that the tree height diversity, as quantified with the Shannon-Weaver formula, is significantly different ($p < 0.001$) between the two forest plots. However, the test assumes independency of tree heights which is not necessarily fulfilled. Hence the p -value obtained can

only be regarded as a crude approximation.

Ripley's K -function was used to compare the spatial pattern of the locations of the trees in the two plots. Because large trees comprise most of the forest biomass and thus contribute significantly to the overall structure and microclimatic conditions of the forest, we first chose trees taller than 15 m for the analysis. Ripley's K -function indicated that the managed Vuorijärvi forest is regular up about 4 m distances (Fig. 4). However, in the primeval Susimäki forest the deviation from random pattern is not significant. The more regular spatial pattern in the managed Vuorijärvi forest is possibly caused by thinnings that have homogenized the spatial pattern of trees.

The K -function analysis was also done for trees smaller than 15 m. The results (not shown) indicated that in Vuorijärvi the spatial pattern of understory trees show strong heterogeneity. The same was true for Susimäki, but to a lesser extent.

Semivariograms of Tree Size

The omnidirectional semivariograms of DBH and tree height, computed for all trees taller than 1.3 m, indicate that in the managed Vuorijärvi forest plot there exists clear spatial autocorrelation in both the DBHs and heights of trees up to tree

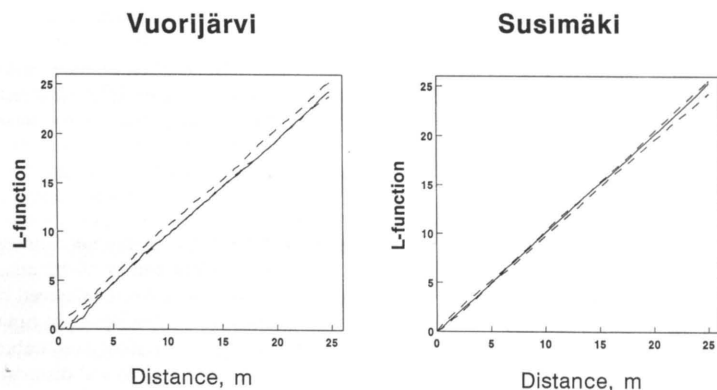


Fig. 4. Ripley's K -function analyses of the spatial pattern of tree locations for trees taller than 15 m in the managed Vuorijärvi forest and in the primeval Susimäki forest.

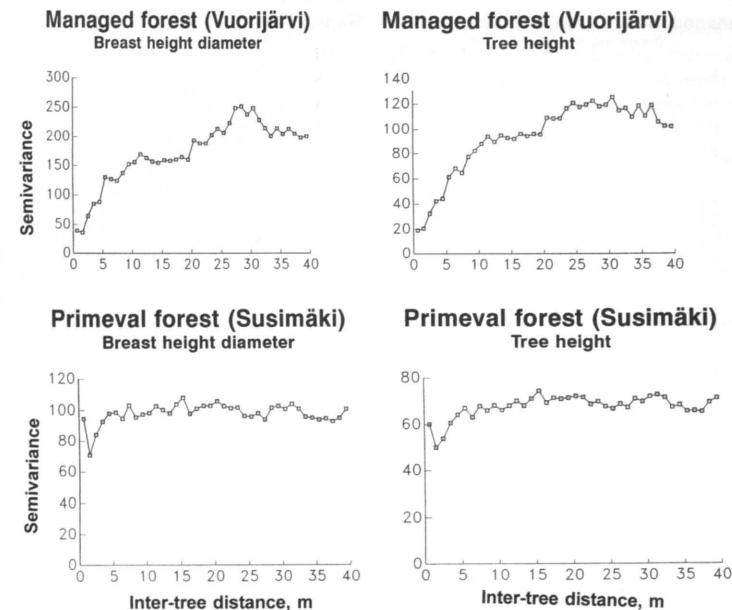


Fig. 5. Omnidirectional semivariograms (showing the semivariance $\gamma(h)$ (= gamma) as a function of lag distance h) for DBH and height of trees in the managed Vuorijärvi and in the primeval Susimäki forest plots. The first lag distance class shown includes 130 and 240 pairs of trees in Vuorijärvi and Susimäki, respectively; further points represent over 400 pairs of trees.

distances of about 12 m (Fig. 5). This means that especially trees closer than 12 meter apart are in general more of the same size while trees farther apart are not. The Vuorijärvi semivariograms also show a nested-like pattern, since there is strong autocorrelation up to inter-tree distances of about 10 m, then a levelling off up to approximately 20 m and then again a rise in semivariance up to 25–30 m.

In contrast to the managed forest, the semivariograms of the primeval Susimäki forest come close to a horizontal pattern ("pure sill"), indicating only weak spatial autocorrelation in tree size. However, an interesting feature is the local high semivariance value within very small inter-tree distances (< 1 m), and positive autocorrelation at inter-tree distances 1–5 m.

To examine the importance of different cano-

py layers for the autocorrelation patterns detected, the semivariograms were also calculated only for trees taller than 15 m, which form the dominant tree layer (Fig. 6). In the Vuorijärvi plot the clear autocorrelation structure seen in Fig. 5 for all trees disappears, and, although there is much variation in semivariance, the overall variogram is "pure sill", i.e. no autocorrelation. In the Susimäki stand the most notably change in the variograms compared to Fig. 5 is the disappearance of the variance peak at small distances. This is a logical result of the exclusion of small suppressed trees from the analysis. The positive autocorrelation at distances 1–5 m, shown in Fig. 5, remains for DBH, but disappears for tree height.

In conclusion, the semivariograms show that the spatial size-structure pattern of the primeval Susimäki forest is clearly different from the man-

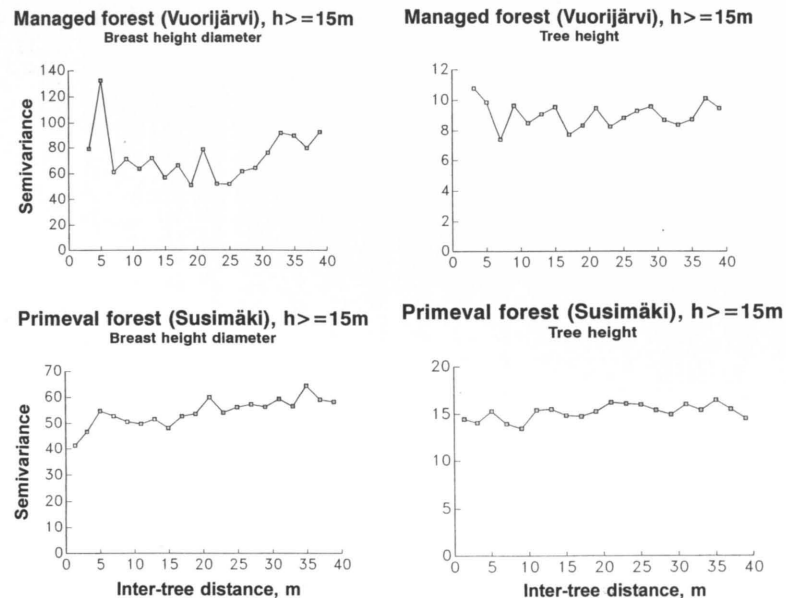


Fig. 6. Omnidirectional semivariograms of trees taller than 15 m for DBH and tree height in the managed Vuorijärvi and in the primeval Susimäki stands. The first lag distance class represents 65 and 70 pairs of trees in Vuorijärvi and Susimäki, respectively.

aged Vuorijärvi forest, and that this difference is largely due to the structure of the understory. The primeval Susimäki forest is spatially more “unpredictable”, i.e. more heterogeneous and complex when compared to the managed Vuorijärvi forest.

4 Discussion

To evaluate the potential contribution of different forest stand structures to species conservation or ecological diversity, we should ideally know the habitat requirements of all the different forest-dwelling organisms. To approach this goal in boreal forests, significant research has been carried out recently (e.g. Kouki 1994). At the moment, however, our understanding of the habitat preferences of many forest organisms or groups of organisms is very limited. On the oth-

er hand, it is often impossible to inventory taxonomic groups like arthropods and soil invertebrates, because of practical problems related to sampling and availability of taxonomic expertise. In this situation a conservative strategy would be to use forest structure as a surrogate for other organisms and to try to maintain and enhance such structural properties of the forest that seem to accommodate diversity in general (Hansen et al. 1991, Pielou 1992, McComb et al. 1993, Kuuluvainen 1994, Mladenoff and Pastor 1994). When considering the ecological significance of forest structure at the within-patch or within-stand scale, the leading principle appears to be that structural complexity of vegetation enhances species diversity. Accordingly, analyses of forest stand structures and dynamics show promise in predicting and evaluating the conservation or diversity values of forests. Forest structural analyses are also needed for developing alternative silvicultural practices (e.g. Hansen et al.

1991, McComb et al. 1993, Haila et al. 1994).

Quantitative assessments of conservation and biodiversity values in forests are needed to include these assessments in forest management planning procedures and to develop practices of sustainable ecosystem management (Hansen et al. 1991, Pielou 1992, Swanson and Franklin 1992, Kangas and Kuusipalo 1993, Mladenoff and Pastor 1994). However, tree stands are highly complex in their three-dimensional structure and one problem is to find quantitative measures of forest structure, which are ecologically relevant and facilitate rigorous structural comparisons among stands.

The variation in tree sizes is a fundamental characteristic of forest structure, that reflects both previous disturbance events and autogenic developmental processes of the forest. The coefficient of variation and the gini coefficient have been used for the quantification of the variation in tree sizes (e.g. Weiner 1990). In fact these two indices, when applied to tree size distributions, have been shown to correlate closely (Knox et al. 1989). However, the problem with these two common indices is, when applied to heterogeneous forests, that it is statistically senseless to compare forests of bimodal (or multimodal) and unimodal size distributions. Therefore, we used the Shannon-Weaver formula, which is derived from information theory, to calculate tree height diversity index (THD). The computed THD's indicated that the vertical complexity of the primeval forest was considerably greater compared to the managed forest. This is also in accordance with the visual impression obtained from the histograms of tree height distributions (Fig. 1) and from the graphs showing the vertical distribution of tree heights on the plots (Fig. 3). Ideally the THD index should be computed based on the vertical stratification of foliage area or mass (FHD, foliage height diversity) (MacArthur and MacArthur 1961). Although this may be possible for research purposes, it may be too laborious for inventory purposes, for which the measurement of tree height distributions may suffice. The THD (or FHD) index has been used successfully in a number of ecological studies (e.g. MacArthur and MacArthur 1961, Murdoch et al. 1972), and it seems to provide a robust measure of the vertical complexity of the forest. In gener-

al, in the description and comparison of tree size distributions, distribution-free methods are preferable, because tree size distributions, being frequently bi- or multimodal, often fail to conform any conventional distribution model.

The horizontal pattern of locations of trees taller than 15 m was examined with Ripley's K-function analysis. In the primeval Susimäki stand the deviation from random pattern was not statistically significant. In the managed Vuorijärvi stand the analysis indicated a regular pattern of tree distribution within distances up to about 4 m. This difference compared to the primeval stand may be caused by thinnings (from below) in the managed forest, which usually aim at making the spatial distribution of trees more even. The spatial pattern of understory trees showed strong heterogeneity in both plots.

The computed semivariograms of tree sizes (DBH, tree height) for all measured trees ($h \geq 1.3$ m) revealed clear differences in stand structures between the managed Vuorijärvi forest and the primeval Susimäki forest. In the managed Vuorijärvi plot there was a clear spatial dependence in tree sizes up to distances of about 12 meters, while in the primeval spruce forest of Susimäki only weak spatial autocorrelation was detected (Fig. 5). The semivariograms of the Vuorijärvi plot also showed a nested pattern with two steep rises in semivariance as a function of distance (0–10 m and 18–25 m). This pattern suggests that the forest structure is regulated by two factors operating at different spatial scales. The first factor could be small scale regeneration and/or competition interactions, while the larger scale structural variation could be caused e.g. by variation in soil properties.

In the primeval Susimäki forest the semivariograms suggested only weak spatial dependence in tree sizes at inter-tree distances of 1–5 m. An interesting feature of the semivariogram was the variance peak in tree sizes in trees very close (< 1 m) to each other. This is apparently mostly because in natural stands even severely suppressed spruce trees (which there were many) are able to survive for prolonged periods of time beneath taller trees (asymmetric competition). In general, the semivariograms indicated that trees of different sizes occur throughout the forest largely independent of each other. Thus, a high

fine-scale variation in tree sizes characterized the studied primeval spruce stand.

To examine the importance of the understory for the detected autocorrelation patterns of tree size, the semivariograms were also calculated solely for trees taller than 15 m, which form the dominant tree layer (see Figs. 3 and 6). The analysis indicates that the detected differences in the variograms in the spatial structure between the two stands were mainly due to the lower story ($h < 15$ m). This result suggests that the structure of the lower storey (dominated trees) may be of fundamental importance to the habitat characteristics of the forest.

This paper has explored some quantitative methods to characterize the structural properties of tree stands that could be used in evaluating the biodiversity-related non-timber values of the forest. These methods were used to characterize forest structure of two contrasting stands, a managed and a primeval spruce-dominated stand. Because these two forests are similar in site type and age, and grow close to each other, their comparison has potential to illustrate the effects of human intervention on stand structure in this forest type. The analysis suggests that from the point of view of an organism living in the environmental space defined by a tree stand, the examined managed and primeval spruce-dominated forest plots differ considerably from each other as spatial environments.

We emphasize that, in addition to commonly applied measures of forest structure like tree species composition and size variation, especially small-scale spatial analyses, utilizing methods from spatial statistics and geostatistics, are useful for detecting and quantifying differences in the structure of the forest.

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