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Forest structure in space: a case study of an old growth spruce-fir forest in Changbaishan Natural Reserve, PR China

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Abstract

Ecologists and foresters are becoming increasingly aware of the importance of spatial information in ecosystem analysis and resource management. An across-scale analysis of forest structure was conducted to characterize the spatial characteristics of a 2 ha spruce-fir forest located inside Changbaishan Natural Reserve (CNR), PR China. The study was designed to develop an approach for assessment of within-stand heterogeneity to increase understanding of the effects of heterogeneity on pattern–process relationships in forests. Univariate and bivariate Ripley's K functions were employed to capture stand heterogeneity in terms of intra- and inter-specific point patterns of tree distributions. Stem-mapped crowns were generated and analyzed as canopy patches within a geographic information system (GIS) to quantify patterns within the strata of the forest canopy. The dominant spruces were randomly distributed within each height class but aggregated when all height classes were analyzed. In addition, spruces had repulsive patterns to other species which exhibited clear aggregation. Canopy heterogeneity, both in terms of composition and spatial patterning, were complex – as expressed within canopy layers and among individual forest species. This across-scale complexity supports a multivariate spatial and across-scale approach to characterizing forest structure, and argues for linked pattern-process experiments. We suggest that joint field and simulation studies be conducted which relate changes in forest stand dynamics to changes in stand heterogeneity. These linked studies are needed to provide a measure of ecological significance relative to statistical significance of patterns. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Spatial analysis; Canopy gap; Stand dynamics; Ripley's K ; Scale; Spruce-fir; China

1. Introduction

Over the past decade, the scales at which forest studies are conducted have shifted to include multiple scales as a result of the convergence of new ecological theories (e.g., landscape ecology, hierarchy theory),

access to data-capture technologies (e.g., Geographical Information Systems (GIS), spatial statistics), and social impetus (e.g., conservation design, Bradshaw, 1998). The incorporation of spatial information into ecosystem analyses is a major challenge in the fields of forestry, ecology, and forest management for several reasons. First, while satellite imagery and GIS provide a large scale perspective of forested landscape patterns, the majority of ecological knowledge lies at

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much finer scales. It is therefore very important to understand how fine-scale patterns relate to larger scale dynamics. In the case of forestry practices, fine-scale patterns generally refer to the composition and spatial configuration of individual trees (e.g., diameter distribution) whereas larger-scale dynamics may refer to forest canopy and stand-level functions such as forest type and biomass).

A canopy and its environment may be viewed as the skin between the terrestrial and atmospheric systems responsible for several integral ecosystem functions: providing microhabitats for plants (e.g., mosses, herbs, lichens) and wildlife (e.g., arthropods, birds, mammals), and influencing the forest floor (e.g., understory species, seedling regeneration, microclimate) and below ground processes (e.g., soil respiration, heat transport, fungal diversity) (Lowman and Nadkarni, 1995). These processes are related to specific aspects of canopy structure, namely species composition and spatial configuration. For example, Nielsen and Ejleresen (1977) found four herbivorous species were directly related to the lower stratum of the forest canopy, while others were distributed in the dominant canopy stratum. Thus, while individual tree processes are reasonably well-understood, it is not clear how individual tree properties add to, interact with, and affect the larger, aggregate unit of the system.

A second reason for undertaking studies to characterize within-stand patterns involves data collection and analysis. Many forest ecology studies rely on more than one type of data. The use of mixed data having resolutions of varying dimensions helps to understand how fine-scale patterns translate with scaling-up (where 'scaling-up' is used here to mean decreased resolution and increased extent). Because the amount and type of information lost when scaling is performed varies with selected technology, it is first necessary to understand the types and significance of information associated with the object itself, namely within-stand spatial patterns and their relationship to forest function and dynamics. Since canopies are composed of multiple crowns related to unique spatial distributions of tree stems in a stand, a logical approach to examine the spatial interactions of canopies is to study the spatial distribution of stems (i.e., point patterns) and their interactions (Song et al., 1997). Substantive information on the relationships between within-stand patterns and canopy function

will have an influence on how forest managers can manipulate stands at the fine scale to optimize functions such as providing faunal habitat (e.g., snag retention).

To date, there has been considerable effort put forward toward the description of forest structure encompassing the description of such variables as age, height, and diameter class distribution, tree growth, stock density, and biomass (Oliver and Larson, 1990). Less, but recently much more, interest has been directed at the spatial characterization of these elements and their interactions and relationships (e.g., tree-tree interactions). As emphasized by several authors (e.g., Ford, 1975; Reed and Burkhart, 1985; Szwagrzyk, 1990; Mou and Fahey, 1993), spatial patterns imposed by tree distributions and their interactions significantly determine regeneration, growth, mortality, understory development, spread of disturbances (e.g., diseases), and other ecological characteristics manipulated by management (e.g., thinning, harvesting, planting, etc.).

We performed a spatial analysis on both the stems and canopy architecture by dividing the forest into three vertical layers. Generally, spatial studies of forest structure have focused on the descriptions of tree stems, ignoring the horizontal and vertical structure of the canopies. This previous dearth in canopy studies largely reflects sampling difficulties and a lack of appropriate techniques for both data collection and analysis, by which spatial characteristics of canopies can be quantified. Our central objective, therefore, is to examine the overall structure of an old-growth spruce-fir forest in Changbaishan Natural Reserve (CNR), People's Republic of China, with a special interest in its spatial characteristics, using spatial statistics (e.g., Ripley's K applied by Moer, 1993), GIS, and other quantitative measurements (i.e., diversity index). We were concerned with three main questions: (1) How are various tree species distributed across the stand (e.g., random, clustered) and at what scales; and (2) Are these patterns consistent with observed species' functions within the stand, life histories, and inter-species interactions? Specifically, we sought to quantify the spatial distributions of trees of different species and height classes (i.e., sub-populations) and examine inter-species and intra-species size-class interactions in terms of vertical and horizontal canopy structure.

2. Methods

2.1. Study area

The study area was located within the Changbaishan Natural Reserve (CNR, 42°01'N and 120°05'E), PR China. In 1979, CNR was established as one of the three biosphere reserves in China as part of the International Biosphere Program (IBP). CNR is an active volcanic area located at the border of PR China and north Korea and was established in 1969 as China's first national park. Recently, CNR was selected as one of the 54 stations under the Chinese Ecological Research Network (CERN) – a parallel program to the Long-Term Ecological Research (LTER) program in the United States. The area encompasses ≈20 000 ha and is covered primarily by old-growth mixed broad-leaved Korean pine (*Pinus koraiensis*) forests, spruce-fir forests, Ermany birch (*Betula ermanii*) forests, and subalpine meadows (Shao et al., 1996). The spruce-fir forest is a common vegetation type, largely distributed in high elevations of the temperature zone and high altitude areas such as northern Asia and Canada (Barbour and Billings, 1988). Elevation ranges from 200 to 2700 m (Wang et al., 1980). The spruce-fir forest, commonly found in the high elevation of the west Pacific Crest, is found between the 1100 and 2100 m elevations in the CNR. This portion of the CNR landscape is the least disturbed by humans. Major tree species include spruce (*Picea jezoensis*), fir (*Abies nephrolepis*), Ermany birch, larch (*Larix olgensis*), mountain ash (*Sorbus pohuashanensis*), and maples (*Acer ukurunduense*, and *A. tegmentosum*) (Chen, 1986; Wang et al., 1980).

2.2. Sampling and analysis

A rectangular plot (100 m × 200 m) was established in the interior of the old-growth spruce-fir forest located at 1800 m elevations. The plot was subdivided into 10 m × 10 m grids to ensure an accurate and efficient sampling of stem coordinates (X , Y). Species names, diameter at breast height (DBH, diameter at 1.30 m), and crown cardinal radii were recorded for each stem larger than 6 cm DBH. Trees with stems rooted off the plot but with crowns intersecting plot boundaries were systematically included to alleviate bias introduced by edge effects.

In addition to sampling of trees larger than 6 cm DBH, we randomly selected and measured eight stems each of spruce, fir, and birch. These data were used to generate diameter height–DBH relationships from stem analysis of discs cut at 2 m intervals. All other species were lumped into one group and labeled as 'Others' in this paper. Diameter–height data for 'Others' were not collected and the empirical equation for birches was used instead. Linear and non-linear regression techniques were used to model relationships of crown diameter and tree height with DBH and to fit various exponential models stratified by species. Spruce, fir, and birch were treated separately during model development. Stems were divided into three sub-populations based on the height–diameter relationship from regression models: lower layer (<10 m), intermediate layer (10–15 m), and upper layer (<15 m). Throughout this paper, we use L, M, U for lower, intermediate, and upper layers and A for all stems combined. These layers are equivalent to the A, B, and C strata proposed by Oliver and Larson (1990). For example, '*Picea* (U)' is the upper spruce layer and '*Others* (A)' is the layer of '*Others*' species group. The following model comprises the best fit according to mean square error (MSE) values for both height and crown size variables:

$$Y = \beta_0 - \beta_1 e^{-\beta^2 \text{DBH}} \quad (1)$$

where Y is crown diameter or tree height (Table 1).

Statistical methods to quantify the point patterns have been developed and reviewed thoroughly by Greig-Smith (1964), Ripley (1981), Diggle (1983), Upton and Fingleton (1985), and Cressie (1993). These methods can be summarized as: (1) quadrat methods; and (2) distance methods. Quadrat methods test whether the density distribution of sampled plots follow a Poisson distribution (Cressie, 1993) or if spatial autocorrelation exists between plots. Distance methods quantify the nonrandomness of the distribution of distances between trees; commonly used techniques include nearest neighbor analysis (Greig-Smith, 1964), K -function (Ripley, 1981), and Moran's I autocorrelation (Reed and Burkhart, 1985). While several statistics have been developed for both quadrat and distance methods, Ripley's K function is frequently recommended primarily because it uses more information (i.e., distances between *all possible pair points*) and provides results relating to patterns at

Table 1

Species parameters estimated for predicting tree height (m) and crown diameters (m) from tree diameter (DBH, cm) using non-linear regression analysis ($Y = \beta_0 - \beta_1 e^{-\beta_2 \cdot \text{DBH}}$) in an old-growth spruce-fir forest. Standard errors of parameters estimates are given in parenthesis

	N	β_0	β_1	β_2	MSE	Pseudo- R^2
Crown diameter						
<i>Picea</i>	1392	7.458 (0.516)	5.555 (0.456)	0.0194 (0.003)	0.547	0.963
<i>Abies</i>	768	4.779 (0.277)	3.822 (0.159)	0.0645 (0.012)	0.399	0.963
<i>Betula</i>	232	123.14 (0.001)	121.02 (0.154)	0.0013 (0.001)	1.493	0.943
<i>Others</i>	243	6.617 (0.566)	4.849 (0.461)	0.0518 (0.015)	0.979	0.948
Tree height						
<i>Picea</i>	136	27.592 (0.662)	27.595 (0.599)	0.0298 (0.002)	1.181	0.993
<i>Abies</i>	204	19.249 (0.955)	19.635 (0.859)	0.0461 (0.015)	2.129	0.971
<i>Betula</i>	171	17.020 (0.785)	17.242 (0.673)	0.0714 (0.008)	3.801	0.961

multiple scales (Getis and Franklin, 1987; Moeur, 1993). Practical applications of these methods in forestry sciences, however, are still quite limited.

In our study, a total of 10 sub-populations (three height classes for spruce and birch and two height classes each for fir and 'Others'), were identified for analysis of stem patterns and canopies. Spatial patterns of trees were quantified using Ripley's K [$K(t)$] statistic (Ripley, 1977, 1981; Diggle, 1983; Szwagrzyk, 1990). The distance matrix d_{ij} between all pairs of the trees on the plot is tabulated and Ripley's K measures the degree to which pattern deviates from random. $K(d)$, is defined as:

$$K(d) = A \sum_{n=1}^n \sum_{j=1}^j \frac{\delta_{ij}(d)}{n^2} \quad \text{For } i \neq j \quad (2)$$

where

$$\delta_{ij}(d) = \begin{cases} 1 & \text{if } d_{ij} \leq d \\ 0 & \text{if } d_{ij} > d \end{cases}$$

where A is the area of the plot, d the distance interval, and n the number of trees in a plot (see Moeur, 1993). $K(d)$ is biased downward if no allowance is made for boundary effects (Moeur, 1993). We adopted an approach and program developed by Moeur (1993) who incorporated edge corrections suggested by Diggle (1983), and a square root transformation, $L(d)$:

$$L(d) = \sqrt{\frac{K(d)}{n}} - d \quad (3)$$

$L(d)$ linearizes $K(d)$, stabilizes its variance, and has an

expected value approximately zero under the Poisson assumption. An overall test of departures from a random distribution is evaluated by determining a 95% Monte Carlo envelope. For a clustering pattern, $L(d)$ is greater than this envelope, a random pattern within the envelope, and a regular pattern, $L(d)$ is below the envelope. Unlike nearest neighbor analyses (Greig-Smith, 1964) which consider only distances from any given tree to its nearest neighboring stems, Ripley's K considers distances between all pairs of stems, thereby providing information at multiple scales. For analysis of the relationship between two point patterns, $K(d)$ is calculated from the combined distributions of distance from each population (see Moeur (1993) for detailed descriptions). The null hypothesis is that there are no significant spatial interactions between the two point patterns or they are spatially independent. A computer program developed by Moeur (1993) was obtained through a public domain FTP site forest. (moscowfsl.wsu.edu) and used in this study to generate 95% confidence envelopes. A significant negative $L(d)$ indicates two patterns are repulsive and a significant positive $L(d)$ indicates two patterns are attractive; otherwise, two patterns are independent. Bivariate $L(d)$ was calculated for interactions between each combination of 10 sub-populations and interactions between four species. A total of 144 interactions were computed in this study.

To create two-dimensional canopy projections for individual canopy strata, we developed a crown-based simulation approach. Each crown projection was simulated by generating a rounded polygon that

consists of four truncated ellipses based on neighboring radii. The elliptical equation is:

$$\frac{(X - X_0)^2}{r_i^2} + \frac{(Y - Y_0)^2}{r_{i+1}^2} = 1 \quad i = 1, 2, 3, 4 \quad (4)$$

where (X,Y) are the node coordinates for generating crown polygons, (X₀, Y₀) the coordinates for stems, and r_i the maximum cardinal radius. The crown polygon generated using this equation is asymmetric and smoothly connected at junctions. A C++ program was written to generate the vertices (or arcs) for each crown polygon with 0.2 m increments in crown radius following the import format of ARC/INFO GIS (i.e., each crown is constructed as a polygon feature in ARC/INFO). Canopy cross-sections at various heights cannot be constructed as the vertical shape of the crowns are unknown. Instead, a GIS coverage of the maximum crown projections of all trees for each sub-population was generated to examine canopy structure and potential relationships among the sub-populations by the three height classes, i.e., U, M, and L (Song et al., 1997).

A coverage of canopy openings was also generated. All of the above GIS layers were then divided into grids of 12.5, 25, 50, and 100 m to explore the hierarchical structures of canopy patches at multiple scales. To quantify the structural heterogeneity (i.e., compositional heterogeneity) of canopies across scales, the Shannon–Wiener diversity index *D* (Pielou, 1969) was calculated for each grid cell:

$$D = \sum \{P_i^* \log(P_i)\} \quad (5)$$

where *P_i* is the proportion of non-gap area occupied by each sub-population (*i*). Higher *D* values indicate

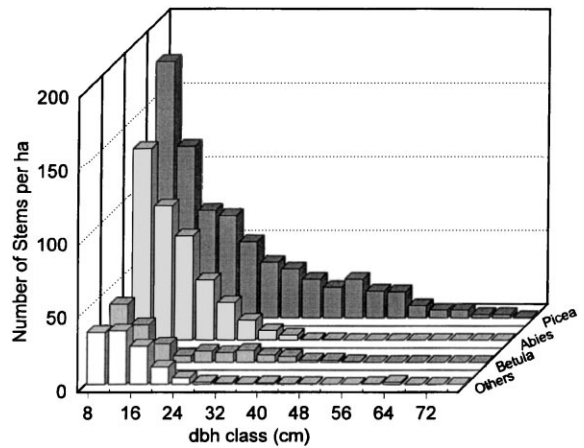


Fig. 1. Frequency distribution of tree size (DBH) by species in an old-growth Spruce-fir forest.

a more diverse canopy structure, i.e., a more heterogeneous canopy, caused by a relatively equal amount of coverage by each of 10 sub-populations.

3. Results

The forest as characterized by the study stand is dominated by spruce in terms of size, density, and basal area (72.8%) (Table 2). The size-class distribution of stems is *J*-shaped for all four species groups (Fig. 1). Larger stems were spruce trees and a few scattered *Larix* (Fig. 2). *Picea* (L) were also found to be abundant in the intermediate and the suppressed layers. Birches were typically found near canopy openings. Firs, maples, and mountain ashes were common in the lower canopies.

Table 2
Basic structural characteristics of an old-growth spruce-fir forest in Changbaishan Natural Reserve (CNR)

Species	<i>Picea</i>	<i>Abies</i>	<i>Betula</i>	Others	Total
Density (Trees ha ⁻¹)	693.5	384.0	116.5	121.5	1 315.5
Diameter (cm)					
total trees	1387	768	233	243	2631
mean	21.4	13.9	17.2	14.5	18.2
standard deviation	14.54	6.52	10.87	8.82	12.40
maximum	74.0	42.0	50.0	64.7	74.0
skewness	1.18	1.12	1.10	3.34	1.64
Basal area (m ² ha ⁻¹)	36.5	7.1	3.8	2.7	50.2
Composition (BA, %)	72.8	14.2	7.5	5.5	100

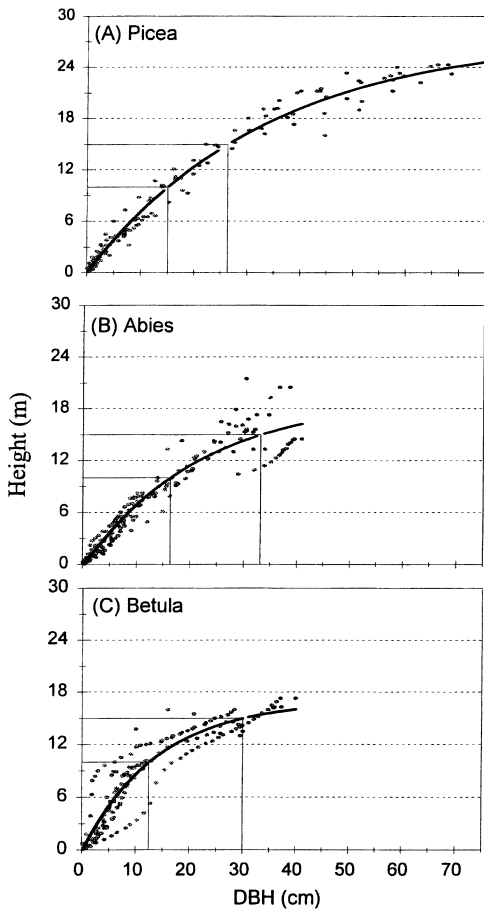


Fig. 2. Estimated tree height with diameter at breast height (DBH) for three major species: (a) *Picea*, (b) *Abies*, and (c) *Betula* in an old-growth spruce-fir-forest. Solid lines are produced based on a non-linear regression Eq. (1). See Table 1 for parameters associated with each species.

The spatial distribution of tree stems differed greatly by species and size class (Fig. 3). *Picea* stems were more or less randomly distributed when analyzed separately by height except at scales between 28 and 37 m in the lower canopy where marginal clustering was detected at the 95% confidence level. This species, however, was aggregated as a population. In contrast, *Other* species were clustered at scales between 0 and 50 m. Generally, larger *Abies* tended to aggregate more than smaller individuals, but both size classes are aggregated. Together they appeared as random patterns across all scales. *Betula* (L) also showed strong clustering patterns.

Betula (M&U) were randomly distributed at larger scales (>35 m). Only *Betula* (M) stems were found to be uniformly distributed at scales larger than 50 m (Fig. 4).

The spatial interactions among the 12 distributional patterns, or 144 interactions, were mostly independent at a 95% confidence level, as $L(d)$ falls within the Monte Carlo envelope (see Fig. 5(c) as an example). However, spatial patterns of *Picea*(U) showed significant repulsion to *Betula* (L) (Fig. 5(a), (b), and (d)), *Abies* (M) trees (Fig. 5(e)), and *Others* (L) (Fig. 5(f)–(h)). *Abies* (L) seemed to be attractive to *Others* and *Betula* (L) (Fig. 5(i)–(l)). The repulsive phenomenon of *Betula* to the *Picea* (U) layer existed at larger distances for smaller trees (<30 m, Fig. 5(a)) than for intermediate trees (<15 m, Fig. 5(b)). For the *Others* group, the repulsive responses were at scales of <20 m. Interestingly, a phenomenon of attraction between *Abies* and *Others* and *Betula* existed at relative larger scales (>20 m, Fig. 5(i)–(l)).

Individual crown sizes increased monotonically with DBH for all species (Fig. 5). Most crowns were less than 8 m in diameter; the outstanding exception was birches with crowns as wide as 15 m (Fig. 5(c)). In general, the means and variances of crown sizes were much lower for conifers than for broad-leaf species of the same DBH. Canopy structure, as represented by aggregates of crown projections, was diverse and complex (Fig. 6). Canopy coverage across the stand decreased from the west to the east side of the plot (Fig. 6(a)). Crowns tended to cluster by size across the stand. For example, larger and highly connected canopy openings predominated near the eastern limit of the stand. The northwest section of the stand was primarily composed of intermediate and larger crowns, with a small proportion of canopy openings (Fig. 6(a)). In contrast, smaller crowns dominated the canopies in the central-west section of the plot.

Canopy openings, as the inverse of canopy patches, were also clumped. These openings reached 791.6 m² in size and were characterized by an irregular morphology, being linear and highly connected. Smaller openings tended to be round. The nesting phenomenon (i.e., trees grow inside a gap) was common across the stand. Canopy heterogeneity, as represented by crown projections of suppressed, intermediate, and dominant crowns varied significantly among classes

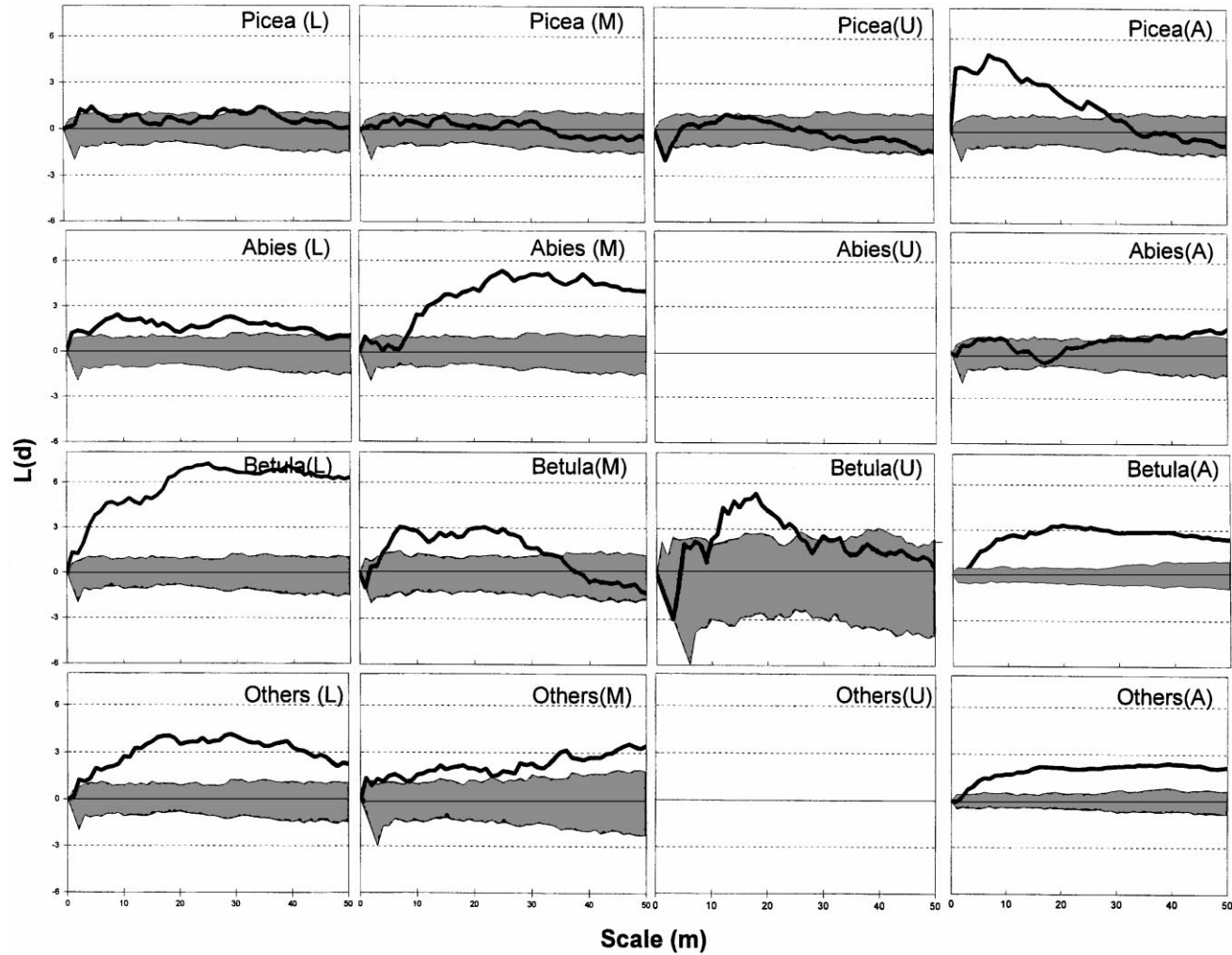


Fig. 3. Ripley's K for four tree species groups located in three canopy layers: L – lower layer (<10 m), M – middle or intermediate layer (10–15 m), and U – upper layer (>15 m). A indicates all stems of the species. The Monte Carlo envelope (shaded area) is constructed at the 95% confidence level. The square root transformation, $L(d)$, of Ripley's K were applied (see Section 2).

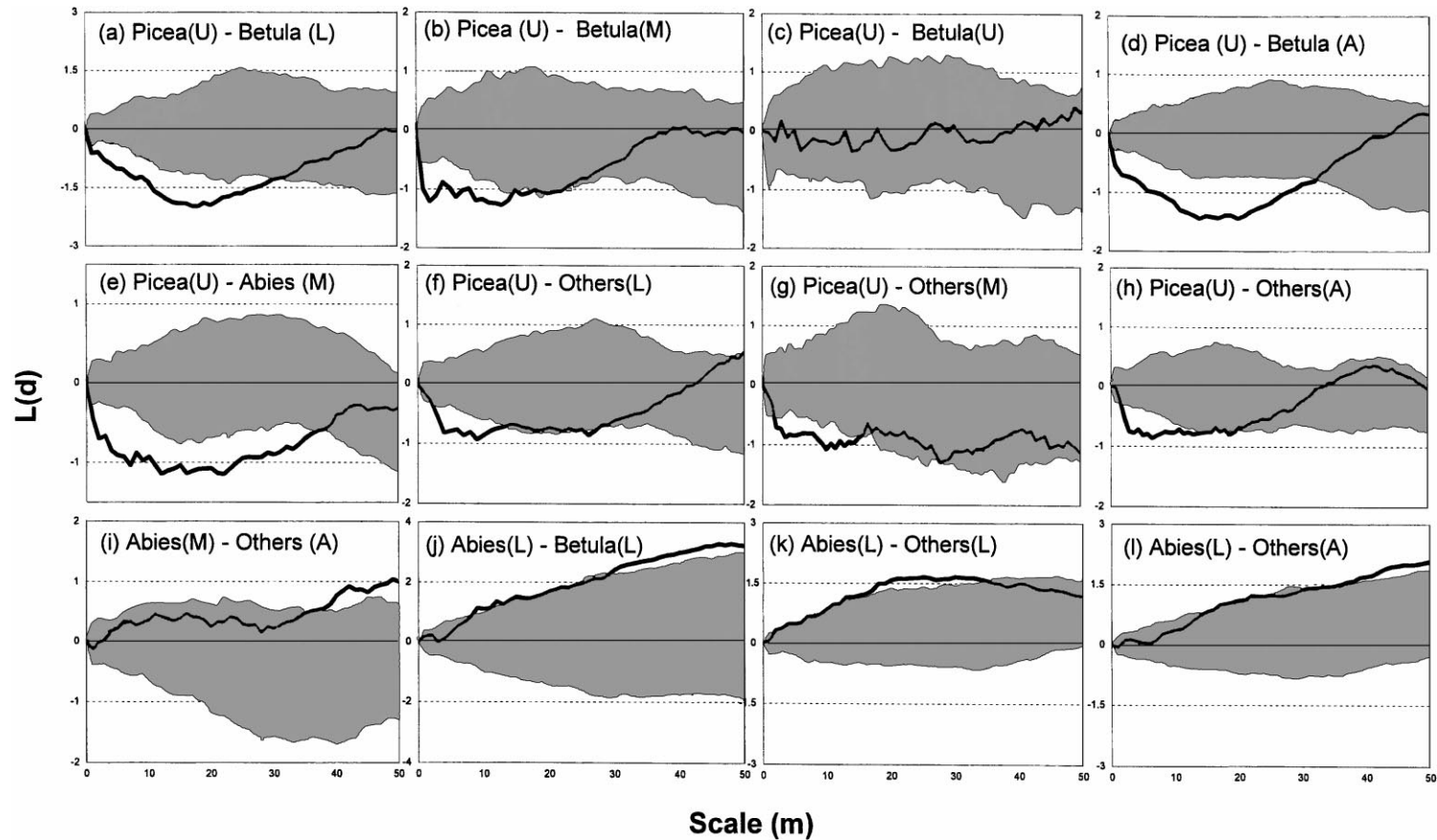


Fig. 4. Bivariate Ripley's K between two point patterns showing significant (95%) attractive or repulsive responses. L – lower layer (<10 m), M – middle or intermediate layer (10–15 m), and U – upper layer (>15 m). A indicates all stems of the species. The square root transformation, $L(d)$, of Ripley's K were applied (see Moer 1993).

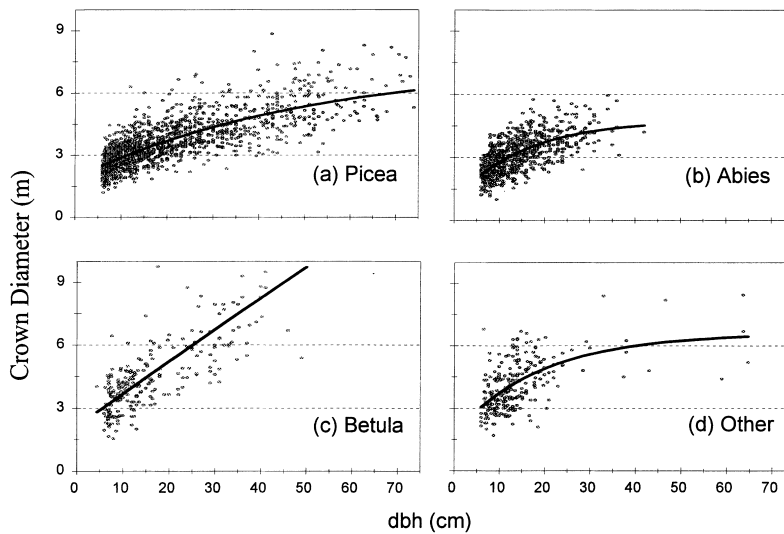


Fig. 5. Estimated crown width (m) with tree size (DBH) for three major species: (a) *Picea*, (b) *Abies*, (c) *Betula*, and (d) other species in an old-growth spruce-fir forest. Solid lines are produced based on a non-linear regression Eq. (1). See Table 2 for parameters associated with each species.

(Fig. 6(b)–(d)). The most complex structure occurred in the lower layer (Fig. 6(b)). In the upper layer, the canopy was dominated by spruces, birches, and a few remnant larches; occurrence of firs in this layer was occasional. Canopies in the middle and upper layers were patchier than the lower canopies. Dominance of canopy opening increased with height within the stand as indicated by the proportion of canopy opening to forest matrix which increased from 18.9% to 33.9%, 65.0%, and 89.0%, respectively, and by the numbers of openings, which decreased from 194 to 1 for the entire plot (Fig. 6(a)–(d)).

Heterogeneity of canopy composition, as measured by the Shannon–Wiener index (D), varied with spatial scale. D increased from 1.9 at an average scale of 12.5 m to ca. 2.5 at larger scales (50–100 m), and dropped to 2.3 for the entire plot (i.e., integrating across the plot; Fig. 7(a)). Variability in D (as measured by its standard deviation and maximum and minimum values) decreased as scale increased from 12.5 to 50 m (Fig. 7(a)). The mean percentage of canopy openings across grid size remained constant, but its variation was significantly higher at smaller scales, indicating high levels of heterogeneity at smaller scales and a strongly clustered pattern of canopy openings (Fig. 7(b)).

4. Discussion

Several hypotheses have been previously proposed to explain the spatial distributions of trees. In a study on the spatial interactions between sugar maple (*Acer saccharum*) and eastern hemlock (*Tsuga canadensis*) in Michigan's Upper Peninsula, Frelich et al. (1993) proposed three factors which influence forest patterns: (1) disturbance history; (2) competitive interactions; (3) invaders. These three sets of processes can predispose a stand independently or in concert to a non-random structure. The published results on tree distributions in unmanaged forests have shown a predominance of random patterns (Szwagrzyk, 1990; Tomppo, 1986). It has been suggested that clustering patterns are not common to most forests; smaller trees tend to exhibit more random features while larger trees show more uniform or regular patterns (Franklin et al., 1985; Moer, 1993; Kenkel, 1988). However, density of the stands and scale (i.e., distance used to quantify the pattern) are two major variables affecting the statistical conclusions on patterning (Cressie, 1993). The spatial distribution of trees can exhibit one pattern at smaller scales (or distances) but a different one at other scales. For example, Moer (1993) reported that trees in hemlock

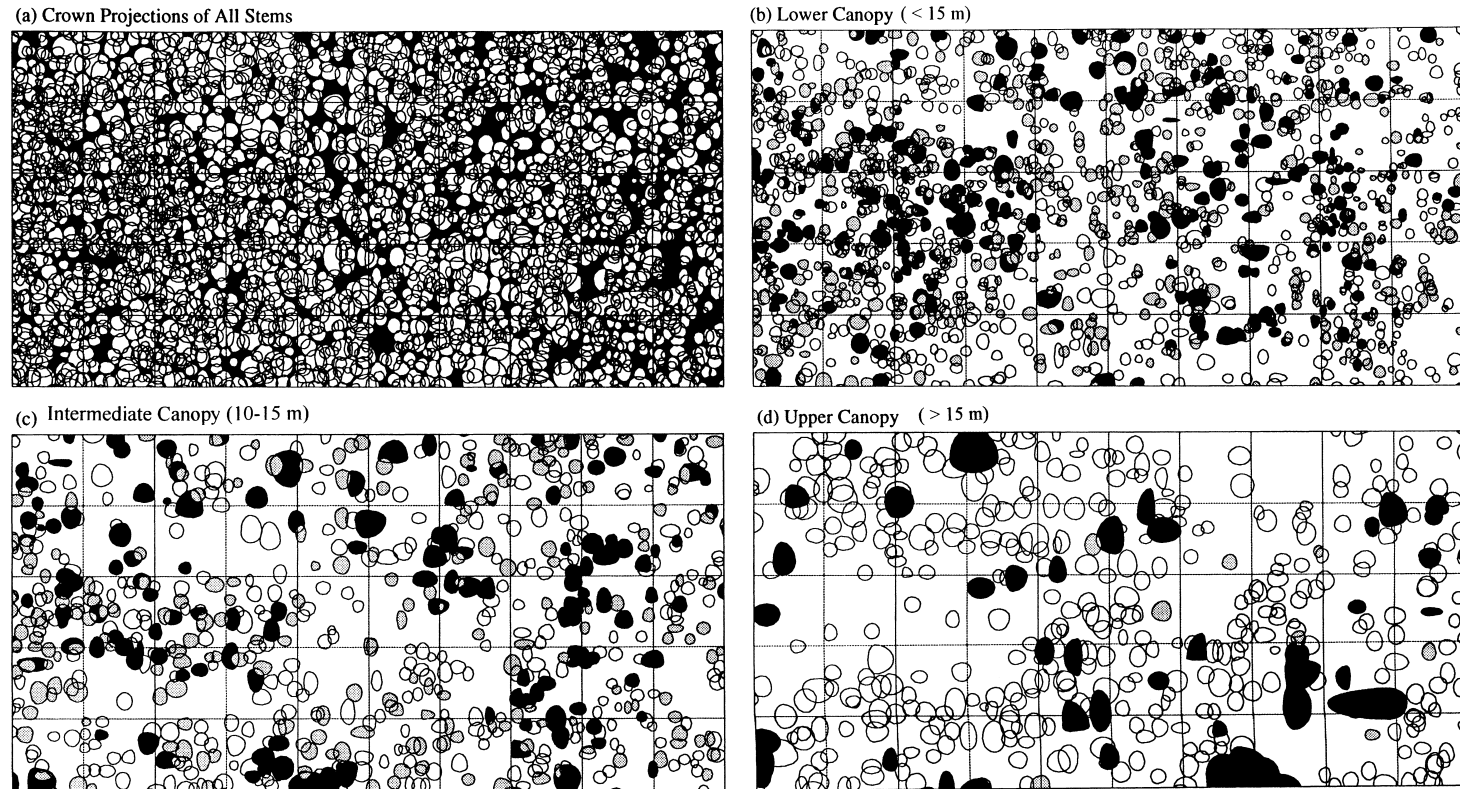


Fig. 6. Crown projections of trees in: (a) all three layers combined, (b) lower canopies, (c) intermediate canopies, and (d) upper canopies. Crowns of spruce, fir, birch, and other are shaded in (b), (c), and (d) as open, light-shaded, black, and heavy-shaded, respectively. Grid size is 20 m.

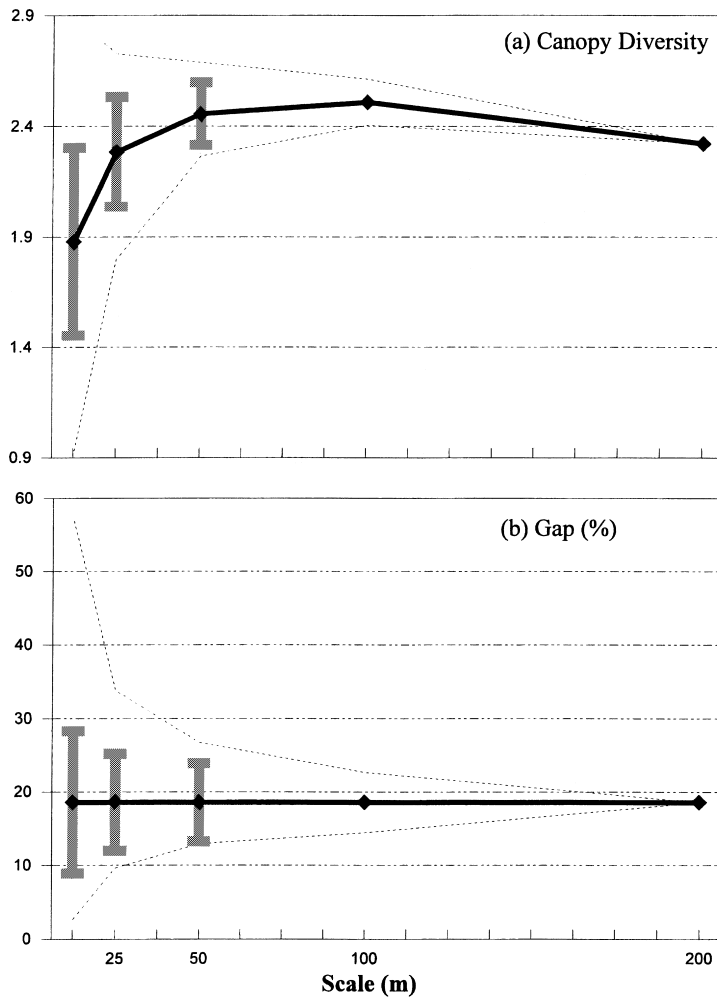


Fig. 7. Changes in mean (◆), standard deviation (vertical bars), maximum, and minimum values (dashed lines) of (a) canopy diversity measured by Shannon–Wiener index, and (b) canopy gaps across spatial scales in an old-growth spruce-fir forest.

forests tend toward regular patterns at smaller scales but clustered patterns at larger scales. Combined with Kenkel's (1988) results on nonrandom mortality distributions and Moer's (1993) arguments on the complexity of microsites, we believe that competition and self-thinning are the two major processes causing random patterns of spruces, although competition and self-thinning were believed to produce regular patterns (Ford, 1975). In contrast, we suggest that the non-random formation of canopy openings and downed log distribution are the primary reasons for aggregated patterns of other species found at the CNR.

Initially, it was believed that, as downed logs are usually clumped across the stand (Kenkel, 1988), the distribution of the dominant, late successional species spruce would reflect this early establishment structuring. However, spruce was randomly distributed for all size classes even though 82% of its seedlings and saplings were found on downed logs (Chen, 1986). Random patterns for all height classes of spruce were unexpected as spruce needs fallen trees to regenerate (Chen, 1986). One possible explanation for the observed random spruce patterns is that disturbance and competition processes act in concert to effectively

counteract and remove aggregation patterns derived from stand initiation (Holmgren et al., 1997). For example, the stand may begin with a highly aggregated distribution of spruce seedlings on downed logs but through mortality by resource competition and windthrow, only a small portion of these seedlings will survive (<0.05%, Chen, 1986) and emerge as the overstory canopy. Such a repulsive relationship between live and dead trees has been found for jack pine (*Pinus banksiana*) in Ontario, Canada (Kenkel, 1988).

Although previous studies have found that tree species were distributed randomly (Moeur, 1993; Szwagrzyk, 1990), our field data did not fully agree with other research. For example, like spruce, Ermany birch is another species which relies on uprooting and downed logs. However, unlike spruce, adults exhibit strong aggregation in the forest (Fig. 3). As an early successional species, birch requires disturbed microsites (e.g., uprooting) and, as a sun-loving species (or a gap species, Wang et al., 1980), canopy openings for regeneration in the forest. These patterns appeared to persist in the distribution of adult trees and were consistent with highly aggregated patterns of canopy openings caused by natural disturbances or senescence across the stand (Fig. 6). As shade-tolerant species (i.e., canopy species), fir seedlings and saplings were observed in canopy openings (Chen, 1986) but it appeared that adult firs had very high survival within larger canopy openings (see Fig. 6).

The spatial distribution of larger spruces, although random, seemed to be crucial in determining the distribution of other species (Fig. 4(a)–(h)), especially smaller stems of birches, intermediate firs, and 'Others' species which showed repulsive patterns to larger spruces. Chen (1986) reported that most birches regenerate on spruce down logs or uprooting sites, suggesting lack of preferred habitat for birches where larger spruces exist. For firs and other species, we hypothesize that larger spruces eliminate birches, firs, and other species by shading and nutrient and water competition. As larger spruces fall or become snags, they create nurse logs for birches and release nutrients and water for firs and other understory species. The spatial distributions of all species observed, excluding spruce, are probably controlled by canopy openings, down logs, and seedling establishment before competition takes over to promote a random pattern. Such

mechanisms could explain why birches and other smaller stems are repulsive to larger firs (Fig. 4(a)–(h)), while firs and 'Others' stems are attractive to each other (Fig. 4(i)–(l)).

Overall canopy patterns appeared to be composed of a mosaic of patches. These patches were often determined by vertical structuring. For example, there were irregular and sparse (Fig. 6(d)) upper canopies with relatively denser intermediate and lower canopies (Fig. 6(c) and (b)) in the middle-east side of the plot. The canopies of this patch were shorter and lacked dominant spruces that we showed repulsive to other species. Outside of this patch, canopies were characterized by denser and taller spruces and birches, sparse intermediate canopies, and dense lower canopies. (Although the focus of this study is not to attempt to delineate canopy patches, quantitative methods (e.g., Fortin and Drapeau, 1995) are available to examine the significance of point patterns in canopy patch formation.)

Results from Ripley's K statistic and Shannon–Wiener diversity index strongly suggest that the spatial characteristics of the forest structure are a function of spatial scale; for example, birch stems may have aggregated patterns at one scale but random patterns at other scales. Generally, while smaller patches could be identified based on individual trees at finer scales or larger patches at >50 m scales (Fig. 6), canopy heterogeneity stabilized at scales >50 m (Fig. 7). To determine the significance of the >50 m pattern, a coarser-scale study should be undertaken to acquire a greater number of samples. A joint field and remotely-sensed sampling effort is currently underway which will examine these scales (Franklin et al., 1985).

From a technical viewpoint, the study demonstrated the ability of GIS to provide a three-dimensional perspective of forest structure across multiple scales. An increase in dimensionality is a significant contribution to elucidating forest patterns and processes which are intrinsically three-dimensional but for reasons of tractability have been limited to one- and two-dimensions (e.g., Bradshaw and Spies, 1992). Canopy gaps in the old-growth spruce-fir forest, as a special type of canopy patch, appeared distinctly different from traditional views. Typically, canopy gaps are viewed as independent units of a forest stand and described by their size, shape, and age distribution (Runkle, 1991). Although canopy gaps are defined as

the land surface directly under a canopy opening (Runkle, 1982), a minimum size is generally used in the literature (e.g., White et al., 1984; Runkle, 1991; Spies et al., 1990). In addition, gaps are usually treated as relatively round or elliptically shaped, created mainly by natural disturbances, and isolated across the stand. Our results suggest that canopy openings in the spruce-fir forest form a spectrum of sizes as reported by Runkle (1991). Some openings were formed because of specific aggregations of trees, stochastic establishment of seedlings, or responses to environmental mosaics. The spatial arrangement of, and relationships among canopy patches (e.g., adjacency) are other characteristics of canopy openings in a forest and are as heterogeneous and important as size and shape of gaps (Lieberman et al., 1989). This method allows a continuum of gap and canopy attribute dimensions to be examined without an initial classification which may introduce an artificial bias.

The crowns and canopies developed in this study also provide us with many further opportunities for field and theoretical studies, especially when spatial information is used. For example, leaf area index and leaf mass have been widely used in forest ecology to predict the volume growth of individual trees (i.e., the growth efficiency) or, cumulatively, of a stand based on pipe model theory (Waring and Running, 1998). A major challenge involved in this approach is quantifying the leaf distribution (e.g., Gilmore et al., 1996; Gilmore and Seymour, 1996; Van Pelt, 1995). Through development of leaf distributions within a crown (see Seymour and Smith, 1987), our results can be readily applied across the entire stand for exploring the spatial distribution of leaves and its relationship to other ecological functions such as growth (Rudnicki, 1997) and habitat suitability for plants and animals (e.g., Mathiasen, 1996). Additionally, our modeling results can provide direct linkages to many remote sensing data to predict associated ecological structure and function at stand and landscape levels.

A detailed spatial analysis is imperative in quantifying overstory–understory relationships, including their spatial autocorrelations (Reed and Burkhart, 1985). Specifically, knowledge of tree distributions and canopy patchiness has direct implications for forest practices (e.g., thinning) and understanding of natural disturbances (e.g., windthrow). For example, spatial patterns resulting from individual tree deaths

by various disturbance agents can be simulated by removing trees from lower layers to develop a process of thinning-from-below or green tree retention practices in ecosystem management (Seymour and Hunter, 1992; Swanson and Franklin, 1992). Similarly, thinning-from-above, windthrows, and tree mortality processes can be simulated by removing designated overstory trees. Retention silviculture in ecosystem management, for example, stresses the importance of biological materials left behind after harvest. Our models presented in this paper can assist foresters to individually select retention trees toward a desired patterns or canopy cohort. Changes in spatial characteristics caused by these events can be further summarized and evaluated using spatial statistics such as Ripley's K , Shannon–Wiener index, and other quantitative methods. The results based on these exercises will be very useful in studying other ecological processes. In old-growth forest studies, it has been found (Van Pelt, 1995) that a very patchy understory exists particularly because of a heterogeneous overstory (i.e., canopy structure in Fig. 7). As another example, mistletoe is a major parasite causing tree mortality of western hemlocks (*Tsuga heterophylla*) and true firs in the Pacific Northwest. However, the mistletoes are exclusive to Douglas-fir (*Pseudotsuga menziesii*). In the old-growth Douglas-fir forests, the repulsive relationship between western hemlock and Douglas-fir is believed to be a major structural feature limiting the spread of the mistletoes.

Although the importance of tree distribution and canopy patches at multiple scales has been recognized in the scientific community (Watt, 1947), challenges remain. Such challenges include developing an understanding of the spatial mosaics and relationships between two or more populations (e.g., Fig. 4), their dynamics (Mou and Fahey, 1993; Pacala et al., 1993), and the irregularity of mosaics at multiple scales. Theories of stand dynamics describe the forest as a replacement of patches induced by various disturbance, growth, and mortality processes, but treat forest patches as independent and regularly-shaped units (e.g., in gap models). Spatial information, and in particular, canopy mosaics, has only recently been considered explicitly in studies of stand dynamics and in growth and yield models which have been designed to predict species and volume changes. While results

from this study should not be generalized to other forest ecosystems, they support the view that special attention needs to be paid to quantifying the structure of mosaics and incorporating this information into dynamic modeling and future studies on structure and function of forest ecosystems.

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