Structural segregation and scales of spatial dependency in *Abies amabilis* forests

Larson, J. Andrew[1*] & Franklin, F. Jerry[1,2]

[1]*College of Forest Resources, University of Washington, P.O. Box 352100, Seattle, WA 98195-2100, USA;*
[2]*E-mail jff@u.washington.edu; *Corresponding author; Fax +1 2065437295; E-mail a975764@u.washington.edu*

Abstract

Question: Is a mosaic structure apparent in the spatial distribution of trees in old-growth *Abies amabilis* forests?

Location: Montane forests of the western Cascade Range, Washington, USA.

Methods: Maps of tree locations were created for study areas located in two, 300-year old stands and a single 600-year old stand. Stand structure parameters were calculated using several subsample quadrats sizes (56.25 - 306.25 m^2), which were drawn randomly with replacement at a density of 250 quadrats per ha from the stem maps in the computing environment. Spatial cross-covariance functions between different canopy strata were estimated using the spline cross-correlogram.

Results: Negative spatial correlation (segregation) between subcanopy tree density and areas of high overstorey occupancy was detected. Understorey and midstorey tree densities were positively spatially correlated. These general trends were apparent across the range of observational scales investigated. Significant spatial correlation between canopy strata was observed at spatial scales of 12 - 44 m and extended to the largest scales in the 600-year old stand.

Conclusion: The observed spatial segregation between canopy strata supports the hypothesis that old *A. amabilis* forests form fine-scale structural mosaics. Structural segregation at small scales may be due to competitive interactions as well as exogenous forcing of tree locations (e.g. by mortality due to pathogens or disturbance), however segregation at large scales in the 600-year old stand is likely due to exogenous factors alone. This study reinforces the idea that horizontal heterogeneity is an emergent property of old-growth forests.

Keywords: Canopy gap; Forest dynamics; Patch; Spatial correlation; Spatial covariance; Spatial pattern.

Nomenclature: Hitchcock & Cronquist (1973).

Introduction

Patch dynamics (Watt 1947) has been one of the most influential concepts in spatial vegetation ecology. The attractiveness of the patch concept in part stems from the intractability of describing and analysing communities at the individual plant scale. However, there is a trade-off associated with the expediency of patches as a bookkeeping method; arbitrary definitions must be adopted in order to classify different plant communities into a set finite of patch types (e.g. canopy gap or non-gap, Runkle 1982).

The patch dynamics concept is attractive for reasons other than methodical convenience. Many ecosystems, especially old-growth forests, display a complex yet visually apparent patch structure (Franklin & Van Pelt 2004, their Fig. 1; Van Pelt et al.2006, their Fig. 2). A more inclusive and holistic application of the patch dynamics concept in forest ecosystems is that of horizontal heterogeneity, defined as the presence of multiple structural units within a forest stand which together form a fine scale structural mosaic (Franklin & Van Pelt 2004). Horizontal heterogeneity is considered an emergent property of old-growth forests and is thought to originate primarily from spatially- aggregated tree mortality (Franklin et al. 2002).

Since the introduction of the patch concept advances in the description of vegetation spatial structure have been made with using spatial point pattern statistics and spatial point process models (Diggle 2003), spectral analysis (Franklin et al. 1985) and wavelets (Bradshaw & Spies 1992). These modern statistical methods have facilitated individual scale characterization of vegetation spatial patterns (e.g. Hou et al. 2004) and yielded insights into underlying mechanisms of pattern formation, particularly competition (Kenkel 1988). However, progress towards quantitatively characterizing the horizontal heterogeneity of old-growth forests has been slow. An important remaining advance is to test the hypothesis that old forests form structural mosaics in space without relying on arbitrarily defined structural units such as canopy gaps.

The highly shade-tolerant *Abies amabilis* is able to persist in the understorey with minimal height growth for decades or even centuries, creating a seedling bank in the understorey of old-growth *A. amabilis* stands (Schmidt 1957; Wilson 1991; Lertzman 1992; Antos et al. 2005). Following release from overstorey competition, a subset of the suppressed *A. amabilis* seedlings rapidly acclimate to more favourable conditions, and spatial patterns of understorey tree growth track gradients of light and competition (Van Pelt & Franklin 1999). Because subcanopy tree growth is positively correlated with light, which is in turn limited by overstorey conditions (Stewart 1986), it follows that in a particular location within a forest stand there should be an inverse relationship between overstorey occupancy and the density of subcanopy trees, i.e. those trees that have grown beyond the seedling stage but have not yet recruited into the overstorey. Seedlings are defined in this study as trees < 5 cm DBH (diameter at breast height, 1.37 m).

In a spatial framework, the simplest inference is that the locations of subcanopy trees are constrained by inhibitive interactions with overstorey trees: subcanopy tree locations depend on overstorey conditions. The natural extension of this reasoning is the hypothesis that *A. amabilis* forests are structured by gap processes (e.g. Watt 1925) – with seedlings recruiting into the subcanopy tree size class in canopy openings formed by overstorey tree mortality (subcanopy trees are defined here as trees greater than 5 cm DBH and less than 25 m tall) – leading to the development of a structural mosaic of different canopy strata. The gap dynamics model has been applied to *A. amabilis* forests (Lertzman & Krebs 1991; Lertzman 1992). However, these studies did not demonstrate that gap-phase regeneration occurred in the study stands. Rather, Lertzman & Krebs (1991) documented the occurrence of canopy gaps, and Lertzman (1992) assumed that gap replacement processes were the primary regeneration mechanism in old-growth *A. amabilis* forests and ignored subcanopy trees outside of canopy gaps in his study of community dynamics. More recently, Parish & Antos (2004) investigated tree population dynamics and growth in an old-growth *A. amabilis* dominated forest using dendrochronological methods, and concluded that dynamics in their study stand were driven by small-scale gap processes, providing some validation for the assumptions of Lertzman (1992). The authors also concluded that their study stand could be considered 'a shifting mosaic with a small grain size' (Parish & Antos 2004, p. 573), although they did not conduct a quantitative spatial analysis of forest structure. If dynamics in old *A. amabilis* forests are indeed driven by gap processes that create a structural mosaic, segregation of canopy strata should be apparent in the forest spatial structure. However, no spatial analysis of forest structure is currently available for old *A. amabilis* forests.

It is not entirely clear at what scale spatial segregation between canopy strata might occur in old *A. amabilis* forests. Parish & Antos (2004) concluded that forest dynamics operated at the scale of the individual tree or small groups of trees in their stand; spatial patterns in *A. amabilis* forests might then be expected to follow a similar scale. Analyses of competitive interactions between conifer trees have found that most competition occurs at local scales (3.5 - 15 m; Kenkel 1988; Canham et al. 2004). Therefore, we might expect segregation between tree height classes to be limited to local scales if subcanopy tree locations are determined primarily by inhibitive interactions with overstorey trees (Manabe et al. 2000). However, the extent to which segregation between overstorey and subcanopy trees is due to endogenous population processes – interactions between trees – compared to exogenous processes is unclear. Pathogens, disturbances such as wind or fire, and topographic variation are examples of exogenous factors that contribute to within-stand spatial patterns (Cooper 1961; Taylor 1990; Bradshaw & Spies 1992; Plotkin et al. 2002). While endogenous processes will be limited to creating patterns at relatively small spatial scales, i.e. the zone of influence of the crown or roots of an individual tree, there is no reason that exogenous processes would be limited to similar small scales. Therefore, while spatial patterns at local scales may be due to both interactions between trees and exogenous forcing of tree locations, larger scale patterns are most likely due to exogenous factors alone.

The subject of this paper is the spatial structure of old *A. amabilis* forests. The investigation was focused around two main questions: 1. Are different canopy strata spatially cross-correlated. 2. If present, what are the spatial scales of cross-correlation between canopy strata? Because spatial pattern in forest ecosystems can be strongly influenced by the scale of observation (Getis & Franklin 1987) we were also interested if the results of the above two questions vary with changes in the spatial scale of observation. We briefly describe the non-spatial size structure for each stand because the spatial pattern analysis was based on canopy strata (i.e. tree heights). The purpose of this study is to provide a quantitative description of spatial patterns in old *A. amabilis* forests, and to evaluate the hypothesis that trees in old *A. amabilis* forests form structural mosaics in space.

Methods

Study system

The *Abies amabilis* Zone, where *Abies amabilis* occurs as the principal climax species, occupies middle- and upper-slope sites in the western Washington Cascade Range (Franklin & Dyrness 1988). Environmental conditions within this zone are characterized by cool temperatures and heavy precipitation, with much precipitation falling as winter snow and accumulating to depths of 2 - 4 m (Packee et al. 1982; Franklin & Dyrness 1988).

The disturbance regime in *Abies amabilis* Zone forests is characterized by very infrequent, high severity fire. Mean fire return intervals in the western Washington Cascades range from 300-600 years (Agee 1993), and over 1000 years may pass between stand replacing fire events on some sites (Hemstrom & Franklin 1982). Further north, in the montane forests of coastal Canada, fires may be so infrequent that millennia may pass between stand replacement events (Lertzman 1992; Parish & Antos 2004). Given the long fire-free period in *A. amabilis* forests, the disturbance regime may be better characterized as one of small-scale canopy disturbances (Lertzman & Krebs 1991; Parish & Antos 2004) interrupted very infrequently by stand replacement events.

Three study sites, named Sutton Lake, Mosquito Lake and Sister Rocks, respectively, were established in the western Washington Cascades (Table 1). *A. amabilis* was numerically dominant at all three sites and associated with variable amounts of *Tsuga mertensiana* and *T. heterophylla*. Minor tree species were *Abies procera*, *Thuja plicata* and *Pseudotsuga menziesii* at Sutton Lake, *P. menziesii* at Mosquito Lake and absent at the Sister Rocks site.

Field methods

A large (1 or 2 ha), rectangular study plot was installed at each of the three study sites. Plots were subjectively located in study stands to minimize topographic variation within the plot and to avoid areas where forest structure was influenced by obvious edaphic factors (e.g. rock outcrops, streams). Within the plot boundaries the position of all live trees greater than 5 cm DBH was measured with a survey total station and staff mounted prism. Stems originating from a common base were mapped individually when the main stem forked entirely below 1.37 m. Species, DBH and total height were recorded for each stem. Trees were sorted into three canopy strata based on total height: understorey (< 10 m), midstorey (10 - 25 m) and overstorey (> 25 m). These data were used to create maps of tree locations at each study site.

Statistical analysis

Spatial cross-correlation functions were estimated between the different canopy strata with spline cross-correlograms calculated using the *R* library 'ncf' (*df* = 15; Bjørnstad, O. N. 2005. ncf: spatial nonparametric covariance functions. *R* package version 1.0-8. http://onb.ent.psu.edu/onb1/). The uncertainty of the estimate of the cross-correlation function was quantified with a bootstrapping algorithm (Bjørnstad & Falck 2001); 1000 bootstrap sample iterations were used to construct a 95% confidence envelope.

Two values of ecological interest can be extracted from the spline cross-correlogram (Seabloom et al. 2005). The value of the spatial correlation function at a lag of 0 m provides a measure of the degree of local segregation (negative values) or attraction (positive values) between the variables of interest. The location of the *x* intercept gives the correlation length, which is interpreted as the upper bound of the scale of spatial dependence. The spline cross-correlogram was also an attractive analytical tool because it allowed us to spatially cross-correlate common, ecologically meaningful stand structure variables (e.g. trees/ha) using our stem map data. Analysis of spatial dependencies between stand structure variables is not possible with other commonly used techniques such as the bivariate forms of distance-based spatial point pattern statistics.

In order to calculate spline cross-correlograms between different canopy strata a computer program was developed to locate subsample quadrats within the stem maps, building conceptually on the methods of Chen et al. (2004). Subsample quadrats were located randomly and with replacement at a density of 250 quadrats/ha. Subsample plot locations were constrained so that the centre point of each quadrat was contained within the stem map boundaries. Because of the large number of subsamples collected from each stem map, and the relatively high edge to interior ratio, an edge correction

Table 1. Study site locations and primary attributes.

Site name	Plot dimensions (m)	Location	Elevation (m)	Primary tree species	Stand age (a)
Sutton Lake	100 × 100	47.3º N, 121.5º W	1160	*A. amabilis, T. heterophylla, T. mertensiana*	ca. 300
Mosquito Lake	200 × 100	47.3º N, 121.4º W	1110	*A. amabilis, T. mertensiana*	ca. 300
Sister Rocks	100 × 100	45.9º N, 122.0º W	1200	*A. amabilis, T. heterophylla*	ca. 600
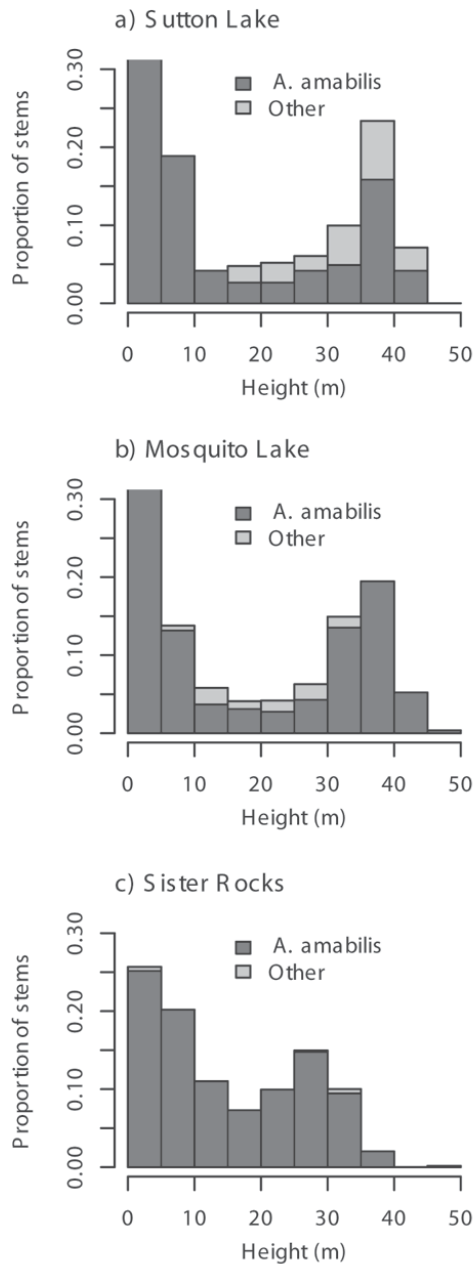
Fig. 1. Relative height frequency diagrams for three *Abies amabilis* Zone stands in the western Washington Cascade Range. All three stands showed a bimodal height distribution with the smallest height classes occupied nearly exclusively by *A. amabilis*. Trees were stratified based on height into three canopy strata, understorey (< 10 m), midstorey (10 - 25 m) and overstorey (≥ 25 m), for spatial analysis.

scheme was necessary. We used the mirage edge correction method (Avery & Burkhart 1994), which entails double sampling a mirror image of the portion of the subsample quadrat that falls outside of the study area. For each quadrat, the density of understorey and midstorey stems (trees/ha) and overstorey basal area ($m^2.ha^{-1}$) were calculated. Quadrats with a side length of 7.5 m, 10 m, 12.5 m, 15 m and 17.5 m (56.25 - 306.25 m^2) were used in order to evaluate the influence of spatial scale of observation on the output of the spline cross-correlogram. At each of the five observational scales spline cross-correlograms for all of the possible combinations of canopy strata (overstorey-midstorey, overstorey-understorey, and midstorey-understorey) were calculated using the sets of subsample quadrats drawn from the respective mapped plots.

Results

Forest size structure

Forests at all three sites had bimodal height distributions (Fig. 1). Bimodality was most pronounced in the two 300-year-old stands (Sutton Lake and Mosquito Lake), which both had a distinctive two-tiered canopy structure and relatively few midstorey trees. The 600-year old Sister Rocks stand had a multistoried canopy structure, although the midstorey class was underrepresented relative to understorey and overstorey trees, and overstorey trees were overrepresented relative to a reverse-J shape size distribution commonly associated with old-growth forests (Oliver & Larson 1996). *A. amabilis* dominated forest composition, particularly the understorey stratum, at all three sites (Fig. 1). Additional details on the structural and compositional characteristics of the study stands are given in App. 1.

Influence of observational scale

General patterns of spatial correlation were similar across the range of observational scales (quadrat sizes) used (Fig. 2); the type of spatial relationship between canopy strata (i.e. segregation or attraction) at a given site was always the same regardless of observational scale. However, changing observational scale did result in different estimates of the strength of spatial correlation and maximum scales of spatial dependence. The magnitude of these changes was not constant across sites.

The strength of spatial correlation, particularly at spatial lags up to about 10 m, was strongly influenced by changing the scale of observation (Fig. 2).
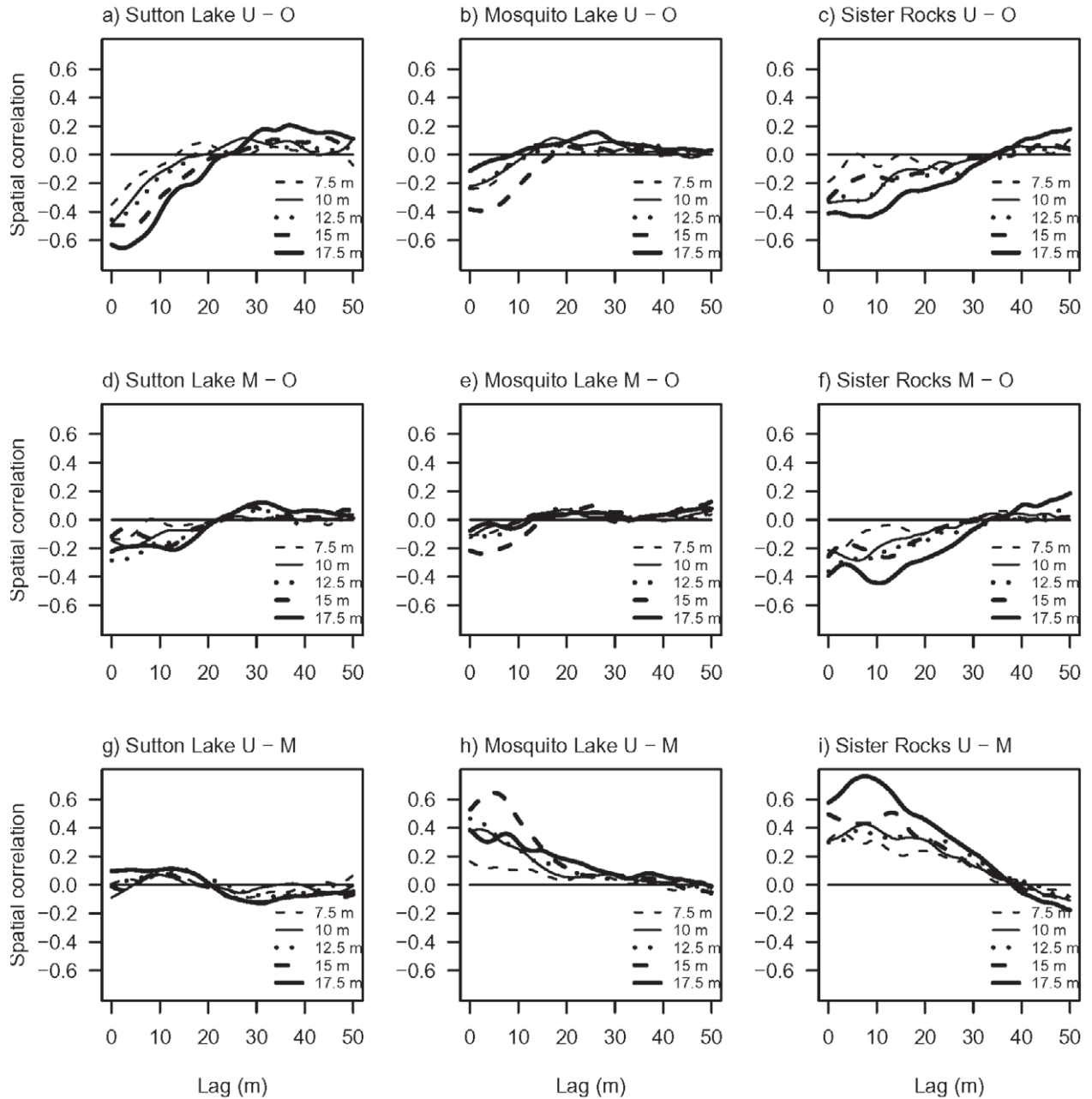
Fig. 2. Empirical cross-correlation functions calculated using quadrats with a side length of 7.5 m, 10 m, 12.5 m, 15 m and 17.5 m (56.25 - 306.25 m^2) in three *Abies amabilis* Zone stands. Bootstrap confidence envelopes are not shown for clarity. Cross-correlograms show both attraction (positive spatial correlation) and segregation (negative spatial correlation) between different canopy strata: U - understorey (< 10 m); M - midstorey (10 - 25 m); and O - overstorey (≥ 25 m). The type of spatial relationship between two given canopy strata (segregation/attraction) at a given site was always alike regardless of observational scale. Changing observational scale did result in different estimates of the strength of local segregation/attraction and maximum scales of spatial dependence (e.g. Fig. 2a).

a) Understorey – Overstorey

b) Midstorey – Overstorey

b) Understorey – Midstorey
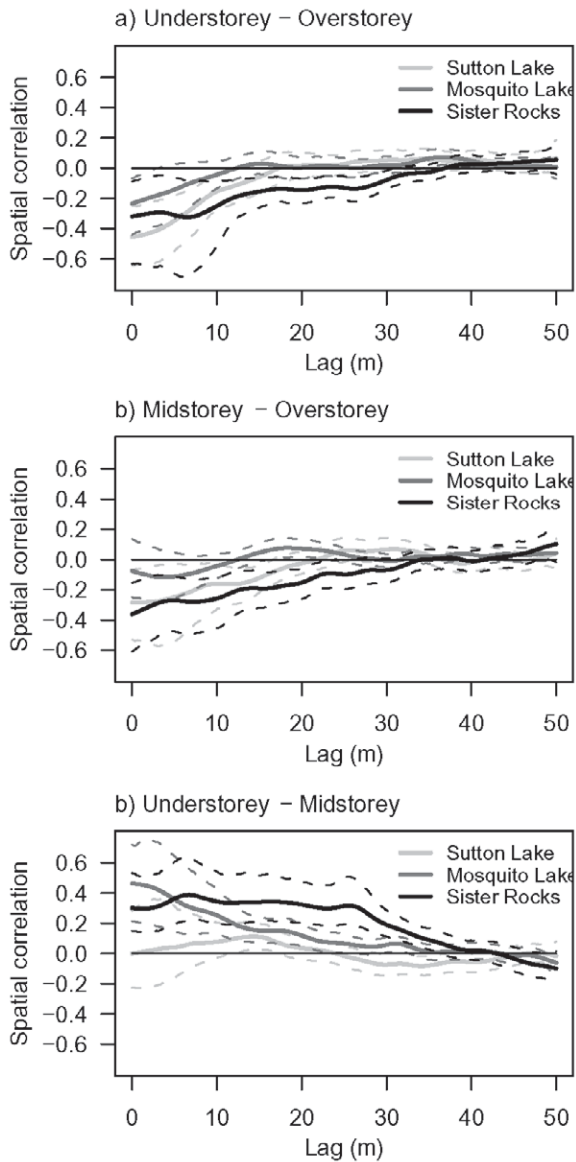
Fig. 3. Empirical cross-correlation functions calculated using 12.5 m quadrats (156.25 m^2) characterizing spatial dependence between understorey (< 10 m), midstorey (10 - 25 m), and overstorey (> 25 m) canopy strata in three *Abies amabilis* Zone stands. Understorey trees are segregated from overstorey trees in all stands at scales up to 12 - 37 m. Midstorey trees show segregation from overstorey trees at scales of up to 22 - 34 m in two stands, but are not correlated in the third. Aggregation between understorey and midstorey trees can be detected at up to 43 m in two stands, but is not apparent in the third.

In the Sutton Lakes and Sister Rocks stands the strength of spatial correlation increased with increasing quadrat size, with the strongest spatial correlations obtained using 17.5-m quadrats (Fig. 2a, c, d, f, i). This relationship did not hold for the Mosquito Lake stand however, where 15-m quadrats showed the

strongest spatial correlations and spatial correlations were quite weak when calculated using 17.5-m quadrats (Fig. 2b, e, h).

Changing observational scale caused estimates of the maximum scale of spatial dependency to vary in some cases. The most dramatic variation in the maximum scale of spatial dependency as a function of observational scale was between understorey and overstorey trees of the Sutton Lake and Mosquito Lake stands (Fig. 2a, b). Changing the scale of observation had virtually no influence on the scale of spatial dependence relationships between different tree size classes at the Sister Rocks site (Fig. 2c, f, i).

Spatial cross-correlation between tree height classes

In this section we report the specific nature of the spatial relationships between different canopy strata at the three study sites. For simplicity, we illustrate our results using the midpoint of the range of observational scale (12.5 m quadrats). Cross-correlograms calculated from subsample data at this observational scale tended to plot in the middle of the range observed for the various quadrat sizes (Fig. 2).

Overstorey and understorey trees were spatially segregated at all three sites (Fig. 3a). Estimates of the upper limit of spatial dependency between overstorey and understorey trees range from 12 - 37 m. Segregation between overstorey and understorey trees in the two 300-year-old stands was only apparent at local scales (< 20 m). Local segregation between understorey and overstorey size classes was most pronounced at the Sutton Lake site, indicating a relatively stronger spatial dependency of understorey trees locations on local overstorey conditions in this stand.

Overstorey and midstorey trees were segregated at two of the sites, but no relationship was apparent at Mosquito Lake (Fig. 3b). The maximum observed range of spatial dependency between overstorey and midstorey trees was 22 m at Sutton Lake and 34 m at Sister Rocks. The strength of local segregation was similar at Sutton Lake and Sister Rocks.

Midstorey and understorey trees were spatially attracted in the Mosquito Lake and Sister Rocks stands, but no clear pattern emerged at Sutton Lake (Fig. 3c). Spatial correlation at long distances (43 - 44 m) was observed at both sites where attraction was detected, although the relationship declined rapidly and is weak beyond about 25 m at Mosquito Lake. In contrast, the spatial dependency between understorey and midstorey trees at Sister Rocks stayed relatively constant up to scales of 25 m. This pattern of strong spatial correlation up to moderate distances was not observed in the two 300-year-old stands (Fig. 3).

Plate 1. An upward view into a region of low overstorey occupancy in the 300-year-old *Abies amabilis* stand at Mosquito Lake. Virtually all of the trees in the photo, including the two clearly visible in the centre, are *A. amabilis*. (Photo by Seth G. Cowdery.)

Discussion

The spatial segregation detected between subcanopy and overstorey canopy strata is supporting evidence for the hypothesis that trees in old *A. amabilis* forests form structural mosaics in space. The general trend of segregation was observed at various observational scales (Fig. 2), reinforcing this conclusion. Segregation between subcanopy and overstorey trees is also consistent with the idea that the recruitment of understorey and midstorey trees from the seedling bank is limited by inhibitive interactions with overstorey trees, and therefore mediated by processes that act to remove portions of the overstorey canopy (see Introduction for development of this idea and relevant citations). However, while a structural mosaic is apparent, we do not describe any of the study stands as having a strong patch structure. If the spatial structure of the study stands was organized into distinct patches composed of trees belonging to the same canopy stratum we would expect very strong local spatial cross-correlation (i.e. the value of the spline cross-correlogram at a lag of 0 m). While the local spatial cross-correlations reported here are relatively high, they are not so high as to suggest a strong patch structure. Moreover, this type of sharply delineated patch structure is clearly not present based on visual inspection of the study stands (Plate 1). Rather, the forest stands studied here might be better described as having a 'fuzzy' patch structure, with regions with low overstorey occupancy and abundant subcanopy trees transitioning gradually to regions with high overstorey occupancy and relatively few subcanopy trees.

Repulsion between canopy trees and subordinate strata has been observed in other coniferous (Moeur 1993; Van Pelt & Franklin 2000; Dovčiak et al. 2001; Miyadokoro et al. 2003), mixed (Chen & Bradshaw 1999) and broad-leaved (Manabe et al. 2000) forests,

suggesting a degree of generality for a pattern of structural segregation across forest ecosystems. However, not all studies have found segregation between overstorey and subcanopy trees (Szwagrzyk 1990), or evidence of a marked patch or gap structure (Antos & Parish 2002). It is important to note that these studies employed an assortment of statistical techniques, all different from that used here, and thus direct comparison of results across studies must be made cautiously.

Segregation between overstorey and subcanopy stems is evidence for underlying ecological processes that cause different tree size classes to partition the growing space within forest stands. Dovčiak et al. (2001) inferred that recruitment of *Pinus strobus* seedlings into successive size classes was limited by interactions with competing vegetation, with spatial patterns of different *P. strobus* size classes structured by the spatial patterns of refugia from competition. Differences in suitable micro-environmental conditions between species and between developmental stages of a single species are an alternative explanation for a pattern of spatial segregation (Manabe et al. 2000). Substrate, particularly decayed wood, may also cause segregation between conspecific tree size classes (Chen & Bradshaw 1999) and differences in spatial distribution between species (Duncan 1991). Clearly, many different mechanisms can potentially give rise to a pattern of structural segregation, which could explain the apparent generality of segregation between canopy strata across a wide range of forest ecosystems. Based on the current understanding of *Abies amabilis* Zone forest dynamics (see Introduction), it appears that competitive interactions between overstorey and subcanopy trees coupled with overstorey mortality are the main determinants of forest spatial structure in the old *A. amabilis* stands studied here.

The local attraction between understorey and midstorey trees (Fig. 2) is evidence that these two classes of subcanopy trees occupy similar regions within *A. amabilis* stands – locations with low levels of overstorey occupancy. A possible explanation for this pattern might be that within regions of low overstorey occupancy, understorey trees have differential growth rates (e.g. Parish & Antos 2004, their Fig. 2). Differential height growth rates would allow some understorey trees to grow into the midstorey stratum while other nearby slow growing individuals would remain in the understorey stratum longer. Such a pattern might arise due to small scale variation in growing conditions (Van Pelt & Franklin 1999), one-sided competition for light between understorey trees (Kenkel 1988), or simply variable rates of growth acclimation in old, suppressed seedlings.

Obvious differences were apparent in the scales of

spatial cross-correlation between the two 300-year-old stands and the 600-year old stand. Spatial dependency between canopy strata extended to relatively large scales in the older stand, but was generally restricted to less than about 20 m in the younger stands. The characteristic horizontal heterogeneity of old-growth forests is largely due to chronic disturbances such as wind, insects and pathogens – exogenous factors – that cause mortality of overstorey trees (Franklin et al. 2002; Franklin & Van Pelt 2004). These factors are known to create spatial heterogeneity of overstorey trees at larger spatial scales than competition processes, and spatial patterns at large scales tend to be more apparent in the structure of old forests compared to young forests (Bradshaw & Spies 1992). Based on these observations, and also because sites were selected to minimize topographic variation and obvious edaphic features, we suggest that the large correlation lengths detected in the Sister Rocks stand are primarily the result of exogenous factors that have influenced current forest spatial structure through overstorey tree mortality earlier in stand development.

We detected significant local segregation between overstorey and subcanopy trees, in spite of the potential for other processes to limit the development of structural segregation. Areas of sparse overstorey might be unoccupied by subcanopy trees because they were formed from recent overstorey mortality and seedlings have had insufficient time to grow into the subcanopy tree size class. Alternatively, seedling establishment and growth could be limited by factors other than inhibition by the overstorey, such as competition with shrubs or herbivory. At high latitudes, the low angle of incoming light may further complicate spatial relationships between overstorey and subcanopy trees due to the displacement of irradiance away from canopy openings, as has been argued for *A. amabilis* forests (Parish & Antos 2004). Therefore, while an inverse relationship between overstorey occupancy and the density of trees in subordinate canopy positions is expected, the relationship may not be strong due to potential for spatio-temporal decoupling of favorable growing conditions and seedling growth into the subcanopy tree size class. Our results are rather striking when viewed in this context. Competitive interactions between overstorey and subcanopy trees and overstorey tree mortality appear to emerge from a host of ecological processes as the dominant mechanisms of spatial pattern formation in old *A. amabilis* forests.

References

Agee, J.K. 1993. *Fire ecology of Pacific Northwest forests*. Island Press, Washington, DC, US.

Antos, J.A. & Parish, R. 2002. Structure and dynamics of a nearly steady-state subalpine forest in south-central British Columbia, Canada. *Oecologia* 130: 126-135.

Antos, J.A., Guest, H.J. & Parish, R. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. *J. Ecol.* 93: 536-543.

Avery, T.E. & Burkhart, H.E. 1994. *Forest measurements*. McGraw-Hill, Inc., New York, NY, US.

Bjørnstad, O.N. & Falck, W. 2001. Nonparametric spatial covariance functions: Estimation and testing. *Environ. Ecol. Stat.* 8: 53-70.

Bradshaw, G.A. & Spies, T.A. 1992. Characterizing canopy gap structure in forests using wavelet analysis. *J. Ecol.* 80: 205-215.

Canham, C.D., LePage, P.T. & Coates, K.D. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Can. J. For. Res.* 34: 778-787.

Chen, J. & Bradshaw, G.A. 1999. Forest structure in space: a case study of an old growth spruce-fir forest in Changbaishan Natural Reserve, PR China. *For. Ecol. Manage.* 120: 219-233.

Chen, J., Song, B., Rudnicki, M., Moeur, M., Bible, K., North, M., Shaw, D.C., Franklin, J.F. & Braun, D. 2004. Spatial relationship of biomass and species distribution in an old-growth *Pseudotsuga-Tsuga* forest. *For. Sci.* 50: 364-375.

Cooper, C.F. 1961. Pattern in ponderosa pine forests. *Ecology* 42: 493-499.

Diggle, P.J. 2003. *Statistical analysis of spatial point patterns*. Arnold, London, UK.

Dovčiak, M., Frelich, L.E. & Reich, P.B. 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. *J. Ecol.* 89: 280-291.

Duncan, R.P. 1991. Competition and the coexistence of species in a mixed Podocarp stand. *J. Ecol.* 79: 1073-1084.

Franklin, J.F. & Dyrness, C.T. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, OR, US.

Franklin, J.F. & Van Pelt, R. 2004. Spatial aspects of structural complexity in old-growth forests. *J. For.* 102: 22-27.

Franklin, J., Michaelsen, J. & Strahler, A.H. 1985. Spatial analysis of density dependent pattern in coniferous forest stands. *Vegetatio* 64: 29-36.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B.,

Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155: 399-423.

Getis, A. & Franklin, J. 1987. Second-order neighborhood analysis of mapped point patterns. *Ecology* 68: 473-477.

Hemstrom, M.A. & Franklin, J.F. 1982. Fire and other disturbances of the forests of Mount Rainer National Park. *Quater. Res.* 18: 32-51.

Hitchcock, C.L. & Cronquist, A. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, WA, US.

Hou, J.H., Mi, X.C., Liu, C.R. & Ma, K.P. 2004. Spatial patterns and associations in a *Quercus-Betula* forest in northern China. *J. Veg. Sci.* 15: 407-414.

Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69: 1017-1024.

Lertzman, K.P. 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. *Ecology* 73: 657-669.

Lertzman, K.P. & Krebs, C.J. 1991. Gap-phase structure of a subalpine old-growth forest. *Can. J. For. Res.* 21: 1730-1741.

Manabe, T., Nishimura, N. Miura, M. & Yamamoto, S. 2000. Population structure and spatial patterns in an old-growth evergreen broad-leaved forest in Japan. *Plant Ecol.* 151: 181-197.

Miyadokoro, T., Nishimura, N. & Yamamoto, S. 2003. Population structure and spatial patterns of major trees in a subalpine old-growth coniferous forest, central Japan. *For. Ecol. Manage.* 182: 259-272.

Moeur, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. *For. Sci.* 39: 756-775.

Oliver, C.D. & Larson, B.C. 1996. *Forest stand dynamics*. John Wiley and Sons, Inc. New York, NY, US.

Packee, E.C., Oliver, C.D. & Crawford, P.D. 1982. Ecology of Pacific silver fir. In: C. D. Oliver & Kenady, R.M. (eds.) *Proceedings of the biology and management of true fir in the Pacific Northwest* symposium, pp. 19-34. University of Washington, Seattle, WA, US.

Parish, R. & Antos, J.A. 2004. Structure and dynamics of an ancient montane forest in coastal British Columbia. *Oecologia* 141: 562-576.

Plotkin, J.B., Chave, J. & Ashton, P.S. 2002. Cluster analysis of spatial patterns in Malaysian tree species. *Am. Nat.* 160: 629-644.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533-1546.

Schmidt, R.L. 1957. *The Silvics and plant geography of the genus* Abies *in the coastal forests of British Columbia*. B. C. Forest Service Technical Publication T-46.

Seabloom, E.W., Bjørnstad, O.N., Bolker, B.M. & Reichman, O.J. 2005. Spatial signature of environmental heterogeneity, dispersal, and competition in successional grasslands. *Ecol. Monogr.* 75: 199-214.

Stewart, G.H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade

Range, Oregon. *Can. J. For. Res.* 16: 558-568.

Szwagrzyk, J. 1990. Natural regeneration of forest related to the spatial structure of trees: A study of two forest communities in Western Carpathians, southern Poland. *Vegetatio* 89: 11-22.

Taylor, A.H. 1990. Disturbance and persistence of Sitka spruce (*Picea sitchensis* (Bong-Carr.) in coastal forests of the Pacific Northwest, North America. *J. Biogeogr.* 17: 47-58.

Van Pelt, R. & Franklin, J.F. 1999. Response of understory trees to experimental gaps in old-growth Douglas-fir forests. *Ecol. Appl.* 9: 504-512.

Van Pelt, R. & Franklin, J.F. 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. *Can. J. For. Res.* 30: 1231-1245.

Van Pelt, R., O'Keefe, T.C., Latterell, J.J., & Naiman, R.J. 2006. Riparian forest stand development along the Queets river in Olympic National Park, Washington. *Ecol. Monogr.* 76: 277-298.

Watt, A.S. 1925. On the ecology of British beechwoods with special reference to their regeneration: part II, sections II and III. The development and structure of beech communities on the Sussex Downs. *J. Ecol.* 13: 27-73.

Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.

Wilson, M.V. 1991. Age structure patterns in *Abies amabilis* stands of the Cascade Mountains. *Am. Midl. Nat.* 125: 331-339.