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Within-stand spatial structure and relation of boreal canopy and understorey vegetation

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Abstract

Question: How do spatial patterns and associations of canopy and understorey vegetation vary with spatial scale along a gradient of canopy composition in boreal mixed-wood forests, from younger Aspen stands dominated by *Populus tremuloides* and *P. balsamifera* to older Mixed and Conifer stands dominated by *Picea glauca?* Do canopy evergreen conifers and broad-leaved deciduous trees differ in their spatial relationships with understorey vegetation?

Location: EMEND experimental site, Alberta, Canada.

Methods: Canopy and understorey vegetation were sampled in 28 transects of 100 contiguous 0.5 m × 0.5 m quadrats in three forest stand types. Vegetation spatial patterns and relationships were analysed using wavelets.

Results: Boreal mixed-wood canopy and understorey vegetation are patchily distributed at a range of small spatial scales. The scale of canopy and understorey spatial patterns generally increased with increasing conifer presence in the canopy. Associations between canopy and understorey were highly variable among stand types, transects and spatial scales. Understorey vascular plant cover was generally positively associated with canopy deciduous tree cover and negatively associated with canopy conifer tree cover at spatial scales from 5-15 m. Understorey non-vascular plant cover and community composition were more variable in their relationships with canopy cover, showing both positive and negative associations at a range of spatial scales.

Conclusions: The spatial structure and relation of boreal mixed-wood canopy and understorey vegetation varied with spatial scale. Differences in understorey spatial structure among stand types were consistent with a nucleation model of patch dynamics during succession in boreal mixed-wood forests.

Keywords: Mixed-wood; *Picea glauca*; *Populus*; Spatial scale; Spatial pattern; Wavelet.

Abbreviations: DCA = Detrended Correspondence Analysis; EMEND = Ecosystem Management Emulating Natural Disturbance.

Nomenclature: Anderson et al. (1990); Moss (1994).

Introduction

In boreal forests, the majority of plant biodiversity is found in the understorey of vegetation which grows beneath a species-poor tree canopy. Understorey plant community diversity and composition at small spatial scales are controlled by numerous factors, including light availability, temperature, soil nutrient and moisture availability, dispersal limitation, competition, and herbivory (Collins et al. 1985; Dlott & Turkington 2000; Ehrlén & Eriksson 2000).

Stand- and landscape-scale relationships between canopy and understorey vegetation communities are well documented in boreal and near-boreal forests (Carleton & Maycock 1981; McCune & Antos 1981; Gagnon & Bradfield 1986). At the scale of forest stands and landscapes, understorey plant community cover, biomass, species richness and diversity may be related to stand canopy composition and tree density (Klinka et al. 1996; Pitkanen 1997; Brosofske et al. 1999; Naumberg & DeWald 1999; McKenzie et al. 2000), as well as stand-level edaphic variables such as soil type or moisture regime (Tonteri 1994).

Understorey non-vascular plant cover often increases, along with increasing canopy conifer cover, during successional change in boreal forests, while understorey vascular plants may respond differently to stand structure depending on their life-history strategy, with the abundance of shade intolerant early-successional shrubs, forbs, graminoids and herbs decreasing after canopy closure, while shade tolerant late-successional species and non-vascular vegetation show the opposite trend (Carleton & Maycock 1980; Morneau & Payette 1989; de Grandpré et al. 1993; Saetre et al. 1997). The abundance and diversity of shrubs and early-successional herbaceous species often show stronger relationships with canopy cover than do late-successional vascular plant species or mosses (McCune & Antos 1981; Klinka et al. 1996).

The structure of a community can vary depending on the spatial scale of observation (Jonsson & Moen 1998; Keitt & Urban 2005), and there have been relatively few studies of the small-scale spatial distributions of canopy and understorey vegetation within boreal forest stands. The spatial distribution of boreal understorey vegetation is known to be heterogeneous and patchy at small scales (Kuuluvainen et al. 1993; Saetre 1999). Individual trees can modify the environmental conditions under their canopy, often dramatically decreasing light availability, as well as modifying soil nutrient and moisture conditions (Økland et al. 1999; Pelletier et al. 1999; Saetre 1999). The nature and strength of tree influences on the understorey varies among canopy tree species growing within a stand (Pelletier et al. 1999). Evergreen conifers and deciduous broad-leaved tree species often differ in their effects on the understorey environment, with conifers generally transmitting less light to the understorey, and depositing more acidic leaf litter (Pelletier et al. 1999; Saetre 1999).

In addition to stand-level shifts in the abundance and distribution of understorey species, it has been hypothesized that within-stand spatial patterns of vegetation change predictably during succession. Yarranton & Morrison (1974) documented a pattern of patch dynamics during primary succession on sand dunes, where small patches of pioneer species grow via nucleation from isolated colonization points to cover a site, until invader species appear later in succession and expand via nucleation to cover the site, while the pioneers are again reduced to a patchy cover amongst a matrix of invader cover. It is not known whether similar patterns of nucleation and patch expansion take place during secondary succession, but we hypothesized that the spatial scale of vegetation patches would increase with increasing stand age and canopy conifer cover.

The objectives of this study were to quantify the small-scale spatial structure and relation of canopy and understorey vegetation within boreal mixed-wood forest stands in Alberta, Canada. We tested for changes in spatial patterns and associations between canopy and understorey vegetation along a gradient of stand composition, from younger Aspen stands dominated by *Populus tremuloides* and *P. balsamifera* to older Mixed and Conifer stands dominated by *Picea glauca*. We also tested for differences in the influence of canopy evergreen conifers and broad-leaved deciduous trees on understorey vegetation spatial distributions.

Methods

Study sites

During the summer of 1999, we established seven study plots at the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental site located northwest of Peace River, Alberta, Canada (56°46'13' N, 118°22'28' W). The forests at this site in the Upper Boreal Cordilleran ecoregion of the province are predominantly boreal mixed-wood forest stands dominated by deciduous broad-leaved (*Populus tremuloides*, *P. balsamifera*) and evergreen coniferous (*Picea glauca*) tree species. Each study plot was a square measuring 50 m on a side. All plots were located in 'control' compartments of the EMEND experiment, which had not been recently logged or burned. Each plot was situated randomly within a control compartment, with the restriction that it be at least 50 m from forest edges, contain no major topographical features, have a slope of 1% or less, and not contain signs of major human disturbance such as trails or experimental manipulations of vegetation. Plots were classified as belonging to one of three types: 'Conifer' (> 70% conifer canopy cover), 'Aspen' (> 70% deciduous canopy cover) or 'Mixed' (both conifer and deciduous canopy cover < 70%).

Four transects were established in each of the seven study plots, for a total of 28 transects, of which 12 were located in Conifer plots, 8 were located in Aspen plots and 8 were established in Mixed canopy composition plots. Each 50-m long transect consisted of 100 contiguous 0.5 m × 0.5 m square quadrats. In each plot, two transects were established running north-south and two running west-east. Start points of each transect were placed in a stratified random fashion, with one start point placed randomly in each half of the south and west edge of the core area of each plot. For recording purposes, the quadrats in each transect were numbered starting with the southernmost or westernmost quadrat in each transect.

For each quadrat, we visually estimated percent cover of all vascular and non-vascular plant species lying in or above the quadrat. We recorded cover estimates separately for canopy trees and understorey vegetation. Canopy cover was measured as a visual estimate of percent of sky obscured by canopy trees and foliage above the quadrat. Cover of understorey vegetation was estimated as vertically projected percent cover for each species present in the quadrat. Covers for both strata were estimated to the nearest 1%. Plants were identified to species in the field when possible, or collected and identified in a herbarium when their identity was uncertain. Mosses and lichens growing on tree stems, decaying wood or stumps were not identified or included in cover estimates.

Data analysis

To examine relationships between canopy and understorey vegetation at several spatial scales, we used wavelet analysis of the cover data for each transect. Wavelets are a family of mathematical functions which are widely used for pattern analysis in remote sensing, geophysics and computer vision (Chui 1992; Daubechies 1992; Schowengerdt 1997), and which have been applied in several studies of ecological patterns at a range of temporal and spatial scales (Bradshaw & Spies 1992; Dale & Mah 1998; Brosofske et al. 1999; Keitt & Urban 2005). The type of wavelet analysis most commonly used in ecological studies is the continuous wavelet transform, which involves moving a windowing function (the 'wavelet') along a data set and assessing the match between wavelet and data at each point along the data train. A range of wavelet sizes is used, giving a transformation of the data by wavelet at several scales.

The continuous wavelet transform value W at point x_i for scale of analysis b_k is described by the equation:

$$W\left(b_k, x_i\right) = \frac{1}{b_k} \sum_{j=1}^{n} y\left(x_j\right) g\left(\left(x_j - x_i\right)/b_k\right) \quad (1)$$

The function $y(x)$ is the data value at point x, and g(x) is the analysing wavelet function. This equation states that a wavelet function is moved along the data series and the match between data and analysing wavelet is calculated at each position. This process is repeated for a range of wavelet sizes, from very small to relatively large. Positive wavelet transform values indicate a good match between wavelet and data, and negative scores represent a poor match between wavelet and data. For certain wavelet functions such as the Sombrero wavelet, extreme values of the wavelet transform correspond to structures in the data such as patches or gaps. Positive wavelet transform values indicate patches in the data, and negative wavelet transform values indicate gaps.

Wavelet analysis was used to determine scales of spatial pattern for several canopy and understorey variables, including deciduous canopy cover, coniferous canopy cover, total cover of understorey vascular and non-vascular plants, and ordination scores of each quadrat on the first axis of a detrended correspondence analysis (DCA) performed on the cover of understorey species in all quadrats using PC-ORD version 4.14 (McCune & Mefford 1999). The ordination was performed using percent cover estimates for all understorey species that occurred in at least 20 of the 3647 quadrats sampled.

All analyses were performed using the Sombrero (or 'Mexican Hat') wavelet function, which has been widely used in ecology due to its ability to smooth noisy data and to detect patches and gaps at a range of spatial scales (Bradshaw & Spies 1992; Dale & Mah 1998; Saunders et al. 1998; Brosofske et al. 1999), and is described by the equation:

$$g\left(x\right) = \frac{2}{3^{0.5}} \pi^{-0.25} \left(1 - 4x^2\right) e^{-2x^2} \quad (2)$$

where x is the relative distance from the centre of the analysing wavelet, scaled by the spatial scale of analysis (see Eq. 1). For all variables in each transect, the wavelet variance was calculated for spatial scales from 1 to 15 m using the equation:

$$V_W\left(b_k\right) = \sum_{i=1}^{n} W^2\left(b_k, x_i\right)/n \quad (3)$$

The resulting plot of wavelet variance versus scale (the 'scalogram') is analogous to the variance plots used in techniques such as two- or three-term local quadrat variance, with peaks or shoulders in the wavelet variance at a particular scale indicating the dominant scales of pattern in the data (Dale & Mah 1998, Dale 1999). An example of wavelet transform scores and associated wavelet variances is provided in Fig. 1.

In addition, we calculated the covariance between canopy variables and all understorey variables at all scales in each transect using the formula (Greig-Smith 1983):

$$C_{CU}\left(b_k\right) = \left(V_{C+U}\left(b_k\right) - V_C\left(b_k\right) - V_U\left(b_k\right)\right)/2 \quad (4)$$

where C_{CU} is the canopy-understorey wavelet covariance at scale b_k, and V_C, V_U and V_{C+U} are the wavelet variances of the canopy, understorey, and canopy and understorey combined respectively. Peaks or shoulders in the covariance scalograms indicate the spatial scales at which there are relationships between the spatial patterns of canopy and understorey variables. We calculated wavelet covariances rather than correlations because spatial correlations have been demonstrated to peak at spatial scales unrelated to the actual scale of patterns in the data (Dale 1999; p. 114).

Results

Understorey plant community structure was highly variable both among and within study plots. The first axis of the DCA ordination of the understorey data explained 12% of the variation in the species data, and was highly correlated with canopy cover type. Quadrat scores on the first DCA axis were correlated with increasing deciduous canopy cover and decreasing conifer canopy cover. The second and third axes of the ordination explained 8% and 6% of the variation in the data set respectively, and were not correlated with any canopy cover variables.

Understorey species with positive scores on the first axis were mostly 'early-successional' species characteristic of Aspen stands, including numerous shrubs (*Symphoricarpos occidentalis, Shepherdia canadensis, Viburnum edule, Rosa acicularis*) and herbaceous species (*Thalictrum dasycarpum, Aster ciliolatus, Vicia ameri-*

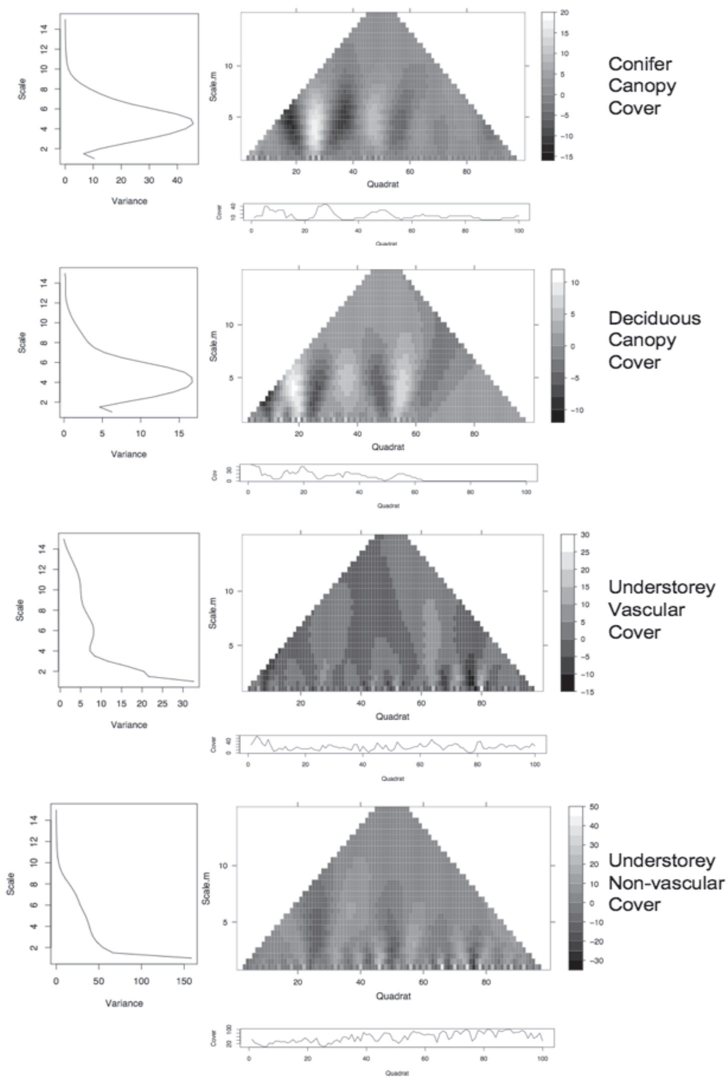

Fig. 1. Abundances (% cover), wavelet transform values and wavelet variances for canopy and understory vegetation along a 50-m transect established in a Mixed stand (*Picea glauca* and *Populus* spp. dominant in the canopy) at the EMEND site in Alberta, Canada. Wavelet transform values are represented by grayscale diagrams, with cell shading indicating wavelet transform values at a given transect position and spatial scale, ranging from black (negative wavelet scores or 'gaps') to white (positive wavelet scores or 'patches'). A wavelet variance peak at a given spatial scale indicates the presence of non-random spatial structures (gaps or patches) at that scale.

canum, Epilobium angustifolium, Delphinium glaucum, Fragaria virginiana, Achillea millefolium). Species with negative scores on the first axis were mostly 'late-successional' species characteristic of Conifer and Mixed stands, including numerous low shrubs (*Linnaea borealis, Ledum groenlandicum, Vaccinium vitis-idaea*), herbs (*Lycopodium* spec., *Equisetum* spec., *Goodyera repens, Maianthemum canadense, Habenaria orbiculata, Galium triflorum, Arnica cordifolia, Mitella nuda, Pyrola secunda, Moneses uniflora*), and moss species (*Ptilium crista-castrensis, Hylocomium splendens, Dicranum* spec., *Pleurozium schreberi*). Mean vascular plant cover, understorey species richness and diversity, and ordination scores were higher overall in Aspen plots, while non-vascular plant cover was higher overall in Mixed and Conifer plots.

Multiscale analyses

Spatial patterns of boreal mixed-wood forest canopy and understorey vegetation were quite variable within and among transects and plot types, but several general trends were apparent. Canopy conifers were uncommon in the Aspen plots, and when present they exhibited spatial patterns (wavelet variance peaks) at scales of around 2.5-5 m, consistent with the presence of small and isolated conifer trees in these plots (Fig. 2). In Mixed and Conifer plots, conifer canopy cover was much more common and generally showed patchiness at spatial scales of ca. 5 m in Mixed plots and 5-10 m in Conifer plots. Conversely, canopy deciduous tree cover was most common in the Aspen plots where spatial patterns were found at a wide range of spatial scales, with several transects showing spatial patterns at very small spatial scales (< 2.5 m), while spatial patterns at scales from 5-10 m were more common in Mixed and Conifer plots.

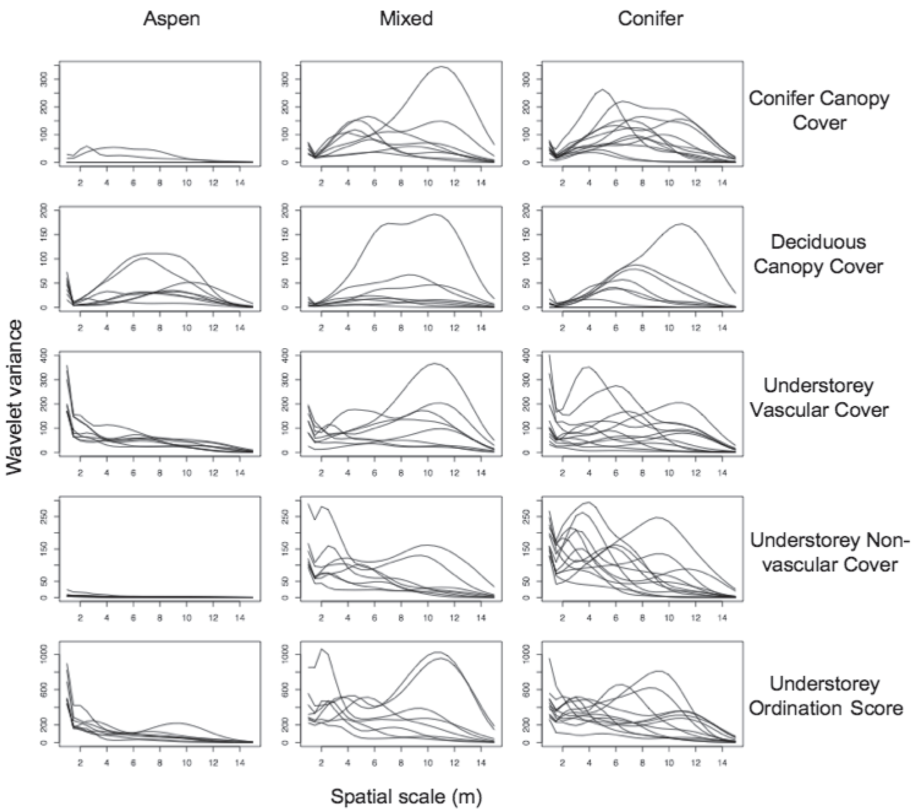

Fig. 2. Wavelet variances versus spatial scale for canopy and understory vegetation in three forest stand types (Aspen, Mixed and Conifer) at the EMEND site in Alberta, Canada. Peaks and shoulders in the wavelet variance at a given spatial scale indicate non-random spatial structures (patches or gaps) at that spatial scale.

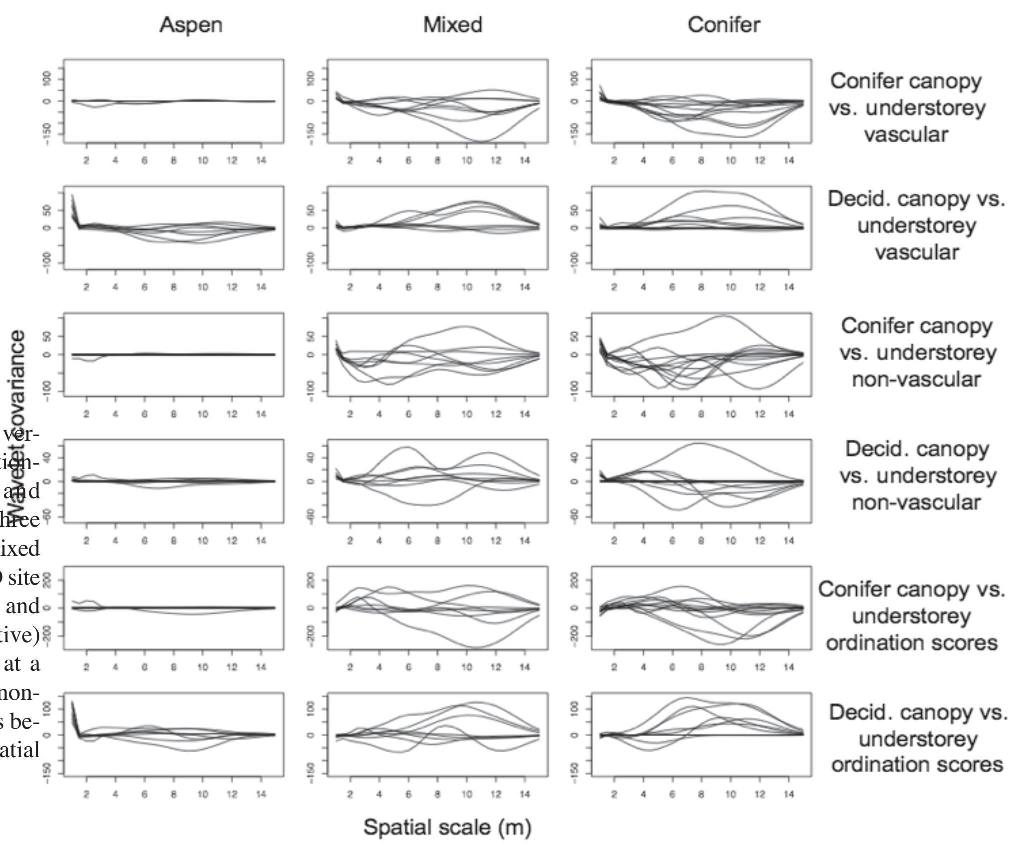

Fig. 3. Wavelet covariances versus spatial scale for relationships between canopy and understory vegetation in three forest stand types (Aspen, Mixed and Conifer) at the EMEND site in Alberta, Canada. Peaks and shoulders (negative or positive) in the wavelet covariance at a given spatial scale indicate non-random spatial associations between variables at that spatial scale.

Understorey vascular plant cover and ordination scores showed a clear trend of increasing spatial scale along the gradient of increasing conifer canopy cover (Fig. 2). Understorey non-vascular plant cover was uncommon in Aspen plots and occurred in small patches in these plots. In Mixed and Conifer plots, non-vascular cover was much more common and generally showed spatial patterns at all spatial scales examined.

Patterns of wavelet covariance between canopy and understorey vegetation (Fig. 3) were highly variable among transects and plot types. Understorey vascular plant cover was generally negatively related to conifer canopy cover and positively related to deciduous canopy cover in Mixed and Conifer stands at spatial scales of 5-15 m. Non-vascular plant cover showed less consistent associations with canopy cover, although negative relationships between canopy conifer cover and understorey non-vascular plant cover were more common at larger spatial scales in Mixed and Conifer plots. Understorey ordination scores generally showed patterns of spatial association with canopy cover similar to those found for vascular plant cover, being more often negatively related with conifer canopy cover and positively related with deciduous canopy cover, but with a great deal of variation in this general trend. Understorey vascular and non-vascular plant cover were positively associated with canopy cover at very small spatial scales (< 2.5 m), while understorey ordination scores showed positive covariances with deciduous canopy cover at these spatial scales in Aspen plots and negative covariances with both coniferous and deciduous canopy cover at these scales in Mixed and Conifer plots.

Discussion

The within-stand distributions of boreal mixed-wood canopy and understorey vegetation were patchy at several spatial scales. Many of the patterns and associations we observed were found only at certain spatial scales, and the nature and strength of canopy-understorey relationships varied among plots, transects, and with the spatial scale of observation. For example, the mean correlation between understorey non-vascular plant cover and conifer canopy cover in the raw data was positive (Pearson's $r = 0.40$, $N = 28$ transects, $P < 0.01$), and understorey non-vascular plant cover was frequently positively related to conifer canopy cover at small spatial scales, but negatively related to conifer canopy cover at larger spatial scales. A multi-scale approach to the analysis of ecological data can provide insights that would be overlooked by analyses carried out at a single spatial scale (Wiens 1989).

Canopy coniferous evergreen and deciduous broad-leaved trees differed in their influences on the distribution of understorey vegetation. Canopy-understorey relationships were more common in Mixed and Conifer plots where conifers dominate the canopy (Fig. 3). In Aspen plots, understorey vascular plant cover was higher under canopy gaps, as evidenced by the predominantly negative covariances between canopy cover and vascular plant cover in these plots. Conversely, in Mixed and Conifer plots understorey vascular plants were generally positively associated with deciduous canopy cover at spatial scales of 5-15 m, but negatively associated with conifer canopy cover at the same spatial scales. This trend is probably related to the ability of canopy conifers to reduce light levels well below those found under canopy deciduous trees (Canham et al. 1994; Lieffers & Stadt 1994), as well as the differences in leaf litter deposition, soil nutrients and moisture availability under canopy conifers versus canopy deciduous trees (Pelletier et al. 1999; Saetre 1999). The average crown radii of coniferous and deciduous trees in mature boreal mixed-wood stands are generally similar (e.g. *Populus tremuloides* mean radius = 2 m, *Picea glauca* mean radius = 1.5 m; Stadt et al. 2005), and so differences in crown size between coniferous and deciduous trees are not likely as a cause of the different spatial relationships of these trees with understorey vegetation.

Succession in boreal mixed-wood forests often proceeds from initial dominance of a stand by shade-intolerant deciduous broad-leaved species towards increasing canopy dominance by shade-tolerant evergreen coniferous species (Dix & Swan 1971; Bergeron 2000), although in some cases, stands may remain dominated by deciduous canopy species for an extended period of time (Cumming et al. 2000). Aspen plots contained much more homogenous understorey communities, with higher mean cover and a more homogenous community composition throughout the plots. In Mixed and Conifer plots, understorey community cover and composition was much more heterogenous and patchily distributed, and the scale of patchiness was larger than in the Aspen plots. Understorey vascular plant cover was much higher under canopy gaps in these plots and under deciduous trees, while non-vascular plant cover (composed mostly of feather mosses) changed from the isolated patches found under conifers in the Aspen plots, to large patches found throughout the plot. Understorey community composition in canopy gaps in the Mixed and Conifer plots is similar to the community composition found in Aspen plots, as shown by the positive ordination scores found in both Aspen plots, and in regions of low canopy cover or deciduous canopy cover in Mixed and Conifer plots. However, spatial associations between canopy and understorey were highly variable, with many exceptions to these general trends.

These results are consistent with previous findings that change in understorey community composition during succession in boreal forests is driven by changes in the spatial arrangement of existing understorey species patches (Watt 1947; Shafi & Yarranton 1973; Fortin et al. 1999; van der Maarel 1996), rather than by total replacement of species as predicted by a relay floristics model of succession (Egler 1954). Most boreal understorey species are found in a range of stand types and stand successional ages, but their relative abundances and spatial distributions change as environmental conditions in the understorey are modified by canopy and soil development (Shafi & Yarranton 1973; de Grandpré et al. 1993; Fortin et al. 1999).

In the Aspen plots in this study, understorey plant cover consisted of small patches of vascular plants, with community composition also patchy at small spatial scales (Fig. 2). In forests where conifer canopy cover is higher, vascular plant cover is greatly reduced except in patches of high cover found under canopy gaps, while moss cover is more homogenous and feather mosses are found throughout the plot. Our results suggest that changes in canopy composition and environmental conditions in boreal forests create a pattern of understorey community change during secondary succession that is similar to the pattern of nucleation and patch expansion seen in other ecosystems undergoing primary and secondary succession (Yarranton & Morrison 1974; Dale & Blundon 1990, 1991).

Conclusions

Boreal mixed-wood canopy and understorey vegetation are patchily distributed at a range of within-stand spatial scales. The spatial distribution of understorey vegetation was generally patchier at larger spatial scales in Mixed and Conifer forests with increased conifer presence in the canopy, and conifer and deciduous trees differed in their spatial relationships with understorey vegetation. Understorey vascular plant cover was predominantly negatively associated with deciduous canopy cover in Aspen plots, but positively associated with deciduous canopy cover and negatively associated with conifer canopy cover at spatial scales of 5-15 m in Mixed and Conifer plots.

Estimates of canopy cover are a surrogate measure for the influence of the canopy on the understorey environment. We did not address the specific mechanisms which caused the observed relationships between canopy and understorey vegetation. Many factors other than canopy structure and composition play a role in structuring boreal understorey plant communities. Further studies which examine environmental variables other than canopy cover would be useful for determining the processes which gave rise to the patterns and relationships we observed, as well as accounting for variation in the spatial patterns of understorey vegetation that could not be explained by canopy cover.

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