PLOT-SCALE SPATIAL STRUCTURE AND VARIABILITY OF FOREST FLOOR PROPERTIES IN AN OLD GROWTH STAND OF COASTAL BRITISH COLUMBIA

by

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Title of Project

Plot-scale spatial structure and variability of forest floor properties in an old growth stand of coastal British Columbia

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Abstract

The spatial structure of physical and chemical forest floor properties can be difficult to quantify, because a large number of biotic and abiotic environmental variables contribute to their distribution. In this study, I investigated the spatial structure of selected forest floor properties at the plot scale (range of meters) in a coastal old-growth stand in southwestern British Columbia. I also explored methods of quantifying the amount of variation according to different environmental variables, with a focus on the understory hardwood species vine maple (*Acer circinatum* Pursh.). I used spatial autocorrelation analysis to quantify the patterns of distribution of specific forest floor properties. In addition, I applied a variance partitioning method based on redundancy analysis to determine whether selected spatial and local environmental variables contributed to the observed variation in forest floor properties. I found that eight out of ten properties exhibited some degree of spatial autocorrelation over a four to ten meter range, with pH, total N, available Ca and available K showing the strongest spatial dependence. All variables that exhibited spatial autocorrelation were anisotropically distributed. Variance partitioning results showed that environmental variables explained 31.7% of the total variation. Of this variation, 11.9% could be assessed by the spatial descriptors alone, indicating that these descriptors act as surrogates for unmeasured underlying processes. Local variables contributed 11.2% to the total explained variation, with forest floor type, presence of CWD, bulk density and the presence of slope at sampling locations contributing to the greatest extent. A large amount of variation (68.2%) remained unexplained. Ordination results indicate that while canopy extent of vine maple had little influence on the distribution of forest floor properties, moder forest floor, as determined by the presence of vine maple, was one of the primary local factors that affected variability. These results indicate that vine maple can impact forest floor variability, but that it may need to be present for longer time periods before its influence on forest floor properties becomes obvious.

Keywords: forest floor properties, spatial autocorrelation, variance partitioning, vine maple.

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1. INTRODUCTION

For many decades, soil scientists and surveyors viewed the soil landscape as homogeneous patches, where changes in soil properties occurred abruptly at the boundaries of soil types (Burrough, 1993). Such a conceptual model negated the need for a quantitative understanding of soil variability, and consequently, information regarding soil heterogeneity was scattered. Over the last twenty years, however, research in the area of soil variability has grown extensively, and current experimental evidence indicates that soil properties are not homogeneous, but are subject to spatial variation at many scales (Riha et al. 1986, Qian and Klinka 1995, Ehrenfeld et al. 1997). These findings have led to the development of a new conceptual model, one which is based on the assumption that values of soil properties vary gradually over the landscape, and which recognizes that variation within boundaries may be considerable. Pronounced heterogeneity is particularly common in forest soils, where high lateral variability can occur to below the centimeter sampling scale (Qian and Klinka 1995). A number of recent studies have addressed forest soil variability (Courtin et al. 1983; Correa and Reichardt 1989, Rahman et al. 1996), and several more have specifically focused on variability of the forest floor (Arp and Krause 1984, Carter and Lowe 1986, Nukvist and Skyllberg 1989, Klinka et al. 1990, Grigal et al. 1991, Van Wesemael and Veer 1992, Bringmark and Bringmark 1995, Qian and Klinka 1995, Emmer 1997, Emmer 1998).

1.1. Analysis of Forest Floor Spatial Structure

Quantification of forest floor variability poses a particular challenge, because physical and chemical properties at a particular site are the result of biotic and abiotic processes that operate at a variety of spatial and temporal scales. As a result of variability in factors such as geological substrate, type of vegetation, disturbance history, and microclimatic spatial differences, forest floor properties can change drastically over very small distances, making it difficult to quantify forest floor properties into precise averages.

Many past statistical analyses of soil variability treated forest floor variability as a random process and analyzed spatial structure with classical statistical methods, which assume that observations are random and spatially independent. However, inferential statistical methods treat values of a variable in terms of relative magnitude only, and do not quantify the variability of soil parameters with respect to spatial arrangement (Goderya 1998). Consequently, classical statistical methods do not provide any information about the variation of soil properties with distance, which is essential for an understanding of the patterns of soil properties across the landscape.

Because experimental evidence shows that soil properties vary gradually across the landscape, a new hypothesis has emerged which postulates that values of variables, which are close to each other in space (or time), will be more similar than those farther apart . This phenomenon of spatial dependence or autocorrelation has been increasingly investigated with the application of spatial statistical (Cliff and Ord 1981) and geostatistical (Journel and Hujbregts 1978) tools. Using these tools, a number of recent studies have addressed the spatial structure of the forest floor at scales ranging from centimeters to kilometers (Qian and Klinka 1995, Bruckner et al. 1999, Bednorz et al. 2000, Lister et al. 2000). In general, these studies found that forest floor properties were spatially dependent within a range of 50 cm to 1.5 m; however, Lister et al. (2000), investigated long-range forest floor spatial structure in a monospecific pine plantation, and measured an average range of spatial autocorrelation of about 58 m.

While autocorrelation analysis makes it possible to test for the presence of spatial structure, it cannot be used to measure the amount of variation explained by this structure or by different types of environmental variables (e.g., vegetation). To determine such relative contributions to total variability, the variance partitioning approach of Borcard et al. (1992) can be used. This method has been applied by Pelletier et al. (1999) in conjunction with various spatial analyses to examine the influence of tree species on forest floor properties in a mixed species stand.

1.2. Influence of Tree Species on Forest Floor Variability

To explain spatial heterogeneity in the forest floor, two different models can be applied: the abiotic control model, in which abiotic factors such as climate, topography, parent material and disturbance history act as the primary causes of lateral variability, and the biotic control model, in which types of vegetation and soil organisms are responsible for the observed type and extent of heterogeneity (Pelletier et al. 1999). A third possibility is that neither model acts exclusively, but that spatial patterns are determined by some combination of the two models (Emmer 1998). Because I was predominantly interested in investigating species-specific influences of trees on the spatial distribution of forest floor nutrients, my research design was based on the biotic control model.

The spatial influence of tree species on forest floor properties is particularly important in the context of mixed species management. A quantitative description of spatial variation can help to elucidate important underlying mechanisms in the function of forest ecosystems, and aid in specifying areas of special importance when perturbations of the ecosystem occur (Riha et al. 1986). However, spatial influence of tree species is not easily quantified, because covariants, such as soil type, climate, aspect, slope and tree age are difficult to control over space.

Many studies have investigated species-specific effects on forest floor properties (Challinor 1968, van Cleve and Noonan 1971, Alban 1982, France et al. 1989, Turner et al. 1993, Vesterdal and Raulund-Rasmussen 1998, Finzi et al. 1998a, 1998b), and several more have dealt specifically with the spatial influence of tree species on nutrient distributions (Riha et al. 1986, Nykvist and Skyllberg 1989, Klinka et al. 1990, van Wesemael and Veer 1992, Rhoades 1997, Pelletier et al. 1999). Many of these studies support the state factor model of Jenny (1941), showing that the effect of climate, parent material and site history interact with the direct effects of trees at both microsite[1] and landscape scales (Lohmeyer and von Zezschwitz 1982, Riha et al. 1986), and that forest floor properties and tree species vary spatially in response to gradients in environmental or historical factors (Emmer 1997). Current research indicates that spatial variability of forest soil properties occurs on several different scales (Grigal et al. 1991, Qian and Klinka 1995, Bednorz et al. 2000), and that forest floor heterogeneity under the forest canopy results from spatial and temporal effect of trees (Finzi et al. 1998a, 1998b, Lister et al. 2000).

Studies investigating the effects of tree species on forest floor heterogeneity have produced differing results. While the effects of forest vegetation can be fairly uniform in single species stands (Riha et al. 1986), in a mixed species stand, the relative role of a species in controlling forest floor properties is difficult to isolate from the effects of other species or gradients in the physical environment (Klinka et al. 1990, Emmer 1997). In addition, species effects cannot be easily aggregated into hardwood versus conifer effects. In mixed species stands, individual trees may affect soil conditions differently than surrounding vegetation (Zinke 1962). This mixed influence often results in a mosaic of conditions, and the effect on forest floor properties may often exceed the life of an individual tree.

It is clear from the above discussion that trees have the ability to influence forest floor properties across spatial scales. However, because these effects are often confounded by biotic and abiotic environmental factors, it is difficult to assess the contribution of tree species and individual trees to the overall spatial heterogeneity of the forest floor. A main goal of my study

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[1] defined as a portion of a site that is uniform in microtopography and surface soil materials

was to explore methods of quantifying the amount of variation explained by different tree species, with a focus on the understory hardwood species vine maple (*Acer circinatum* Pursh.).

1.3. The Role of Hardwoods in the Distribution of Forest Floor Properties

As awareness increases that biodiversity plays an important role in the function of forest ecosystems (Hansen et al. 1991), the effect of single trees on soil properties has become the subject of a more wide spread debate (Crampton 1984, Pallant and Riha 1990, Beniamino et al. 1991, Rhoades 1997). Historically in the Pacific Northwest, non-timber species, such as alder, maple, poplar and other hardwoods were removed from conifer plantations because of their potential for rapid growth and high nutrient requirements (Haeussler et al. 1990). However, the removal of such species could have unintended ecological consequences. For example, the nitrogen-fixing species red alder (A*lnus rubra* Bong.) increases soil nitrogen and phosphorous (Binkley et al. 1992, Giardina et al. 1995), and improves soil fertility sufficiently to warrant consideration in forest management strategies aimed at improving site fertility (Tarrant and Trappe 1971, Binkley 1983, Brozek 1990, Hart et al. 1997). Most other common hardwood species in British Columbia (BC) do not fix nitrogen; however, studies have shown that over the course of several rotations, certain species may positively influence soil properties enough to offset impacts as competitors, and to justify selective retention as components of commercial conifer stands (Ogden and Schmidt 1997, Wardman and Schmidt 1997, Tashe and Schmidt 2001).

Vine maple is a common deciduous understory species in southwestern coastal BC, whose influence on soil fertility has been investigated in two recent papers. Ogden and Schmidt (1997) examined the influence of vine maple on site productivity in an 80-year old forest of western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western redcedar (*Thuja plicata*). They found that the forest floor below vine maple contained higher concentrations of certain bases (i.e., calcium, magnesium and potassium), as well as higher pH levels. The surface mineral soil horizons under vine maple had significantly higher pH levels and higher total nitrogen concentrations. However, despite higher base concentrations in the forest floor under vine maple, mean total amounts of nutrients did not differ significantly between vine maple and conifer plots. Because the contribution of vine maple litter was relatively small compared to the large contribution of conifer litter, the authors concluded that vine maple may require long time periods to significantly influence soil properties (Ogden and Schmidt 1997).

Tashe and Schmidt (2001) studied vine maple to determine whether its presence enhanced site fertility in mature coastal forests in southwestern BC. The authors studied a 75-year old and a 130-year old stand, and found that four and five out of eight measured nutrients were significantly greater or had a weak tendency to be greater for forest floors of vine maple plots compared to conifer plots. The authors suggested that because of differences in nutrient concentrations of vine maple and conifer litter, vine maple was able to improve nutrient availability to the benefit of adjacent Douglas-fir.

1.4. Research Objectives and Hypotheses

Previous studies have shown that vine maple can influence forest floor properties on the local level through input of litterfall with high nutrient concentrations (Ogden and Schmidt 1997, Tashe and Schmidt 2001). The purpose of this study was to investigate the spatial extent of vine maple influence on forest floor properties. My research goal was to determine whether the distribution of forest floor properties in a specific research plot was spatially structured along a gradient determined by the position of vine maple and its canopy extent. In addition, I wanted to examine other biotic and abiotic environmental variables that could contribute to spatial heterogeneity, and to quantify their influence according to the amount of variation they explained.

In this study, I characterized the spatial structure of eight chemical and two physical forest floor properties. The chemical properties measured were: pH, total carbon (TC), total nitrogen (TN), mineralizable nitrogen (mN), and available phosphorous (P), calcium (Ca), potassium (K) and magnesium (Mg). The forest floor physical properties measured were moisture content (MC) and bulk density (BD). To quantify factors that may contribute to the variation in forest floor chemical properties, I collected data for twelve environmental variables. These variables included spatial descriptors (the geographic x and y coordinates of sampling locations), and local descriptors, both abiotic and biotic. Abiotic descriptors included measurements of forest floor moisture and bulk density, and qualitative determination of rockiness (presence/absence of coarse fragments). Slope was also included as an abiotic variable; however, since the small size of the sample plot made quantitative inclination measurements extremely difficult, I simplified the descriptor of slope to one of presence or absence at sampling locations. Biotic descriptors included the classification of forest floor order at sampling locations, presence of coarse woody debris (CWD), and determination of species-specific and total canopy cover at sampling locations (i.e., samples below western hemlock, western redcedar or vine maple canopy, and samples not below any canopy).

My objectives for this study were (1) to investigate the spatial structure of forest floor properties (chemical and physical) at the plot scale (range of meters); (2) to quantify these patterns using spatial statistical techniques; (3) to quantify the amount of variation that could be explained by the presence of vine maple using variance partitioning; and (4) to quantify the additional spatial variation that could be explained by other, easily measured, environmental variables.

2. METHODS

2.1. Research Site

I conducted the study in the Lower Seymour Conservation Reserve (LSCR) north of Vancouver in the Coast Range of southwestern British Columbia (49°37′N, 123°5′W). The area I examined falls within the Submontane Very Wet Maritime variant (CWHvm1) of the Coastal Western Hemlock (CWH) biogeoclimatic zone (Green and Klinka 1994). Mean annual precipitation in the CWHvm1 subzone is 2787 mm, which occurs mostly as rain from October to March, with less than 15% falling as snow (Pojar et al. 1991). The mean annual temperature in the region is 8.2°C (Pojar et al. 1991).

The study area is located within an old growth stand that was estimated to be at least 700 years old (J. Gaspar, Pers. Comm.), and consists of a range of regeneration stages and different moisture regimes. The forest within the site is dominated by western hemlock, western redcedar and Pacific silver fir (*Abies amabilis*), with isolated occurrences of Pacific yew (*Taxus brevifolia*). The understory consists predominantly of regenerating western hemlock, red huckleberry (*Vaccinium parvifolium*), swordfern (*Polystichum munitum*) and deer fern (*Blechnum spicant*).

2.2. Plot Selection

I used the following criteria for plot selection:

a) The area within the plot could not be adjacent to stream edges or in an obvious debris flow area; and

b) The plot had to contain at least one well-established vine maple clone.

The plot was located approximately 300 m above sea level, with a westerly aspect and slopes varying from 0° to 22°. It contained two live vine maple clones: a large clone that I chose for plot center, and a smaller clone to the north with limited canopy cover. The plot had abundant CWD, it contained several co-dominant western hemlocks, and it was bounded in the east and south by large, dominant western redcedars. The central vine maple clone was situated on a flat (non-sloping) bench running north-south, approximately 2.5 m wide and 10 m long.

2.3. Sampling Design

I devised a sampling design that was centered on the vine maple clone and focused the most intense sampling in the vicinity of the clone to ensure that I collected enough samples to detect even a weak spatial pattern. Previous studies have shown that systematic designs can distort or miss spatial structure depending on the sample spacing (Fortin et al. 1989). I therefore chose a sampling design that, in addition to systematic samples, also included random samples (Figure 1). By collecting information at several spatial scales, I hoped to ensure that samples were not out of phase with any spatial structure.

I established eight sampling transects that were centered (0 meters) in the middle of the vine maple clone and extended 10 m away from the clone at bearings 0, 45, 90, 135, 180, 225, 270, and 315 degrees from magnetic north. I collected forest floor samples (F and H horizons) along these transects at distances of 0.25, 0.50, 1, 2, 4, 6, 8, and 10 meters, and at random sampling locations within a 10 m radius of the vine maple clone (Figure 1).

At each sampling point, I collected two samples from intact forest floor and scraped fresh litter from the top of each sample. I excavated all forest floor material to the forest floor–mineral soil interface using a 10 x 10 cm template. I measured the forest floor depth as the average of eight measurements of the sides of each excavated sample. If I could not sample a point along a transect due to the presence of rocks or live roots, I excluded the location and substituted an extra random point. Similarly, if a random sampling point proved inadequate, it was replaced by the next random distance and bearing. In total, I collected 119 samples (65 systematic and 54 random).

2.4. Humus Form and Mineral Soil Classification

I described the humus form at each sampling location according to the classification system of Green et al. (1993), and noted presence/absence of CWD at sampling locations, as well as the depth to which CWD extended in the forest floor (F or H horizon). I measured the thickness of each horizon in situ, and classified the horizons of the humus form profile in the field. I subsequently classified the humus forms according to profile descriptions. I recorded abundance of mycelia and fecal pellets following the system of Green et al. (1993). Depth of H layers (particularly for ligneous horizons) frequently made it difficult to determine the presence of A horizons, but where possible, I noted depth of Ah or Ae horizons for each sample.

I classified the soil type according to the Canadian System of Soil Classification (Agriculture Canada Expert Committee on Soil Survey 1987). Results indicated that the soil type, an orthic humo-ferric podzol, was consistent across the site.

2.5. Canopy Extent

I quantified canopy extent by measuring the vertical projections of the conifer and vine maple canopies to the ground at five locations for each canopy. I subsequently produced maps of species-specific canopy cover using ArcView GIS (1999) (Figure 2). I determined which type of canopy each sample was located beneath (vine maple, dominant/co-dominant western hemlock, or dominant/co-dominant western red cedar). If samples fell below the canopies of more than one tree species, I analyzed them separately for the effects of each tree species.

2.6. Vine Maple Extent

In addition to the live vine maple clone located in the center of the plot, my plot contained two dead clones: one just outside of the plot boundary, which had been felled in the summer of 1999 to conduct a dendrochronologial analysis (Schmidt et al. unpublished results), and one in the south-east corner of the plot which consisted of a rootball and several large stems in advanced stages of decay. A large portion of the former clone had fallen within plot boundaries, and had contributed a substantial quantity of leaf litter to the forest floor in 1999-2000. Because both clones exerted a potential influence on forest floor properties through the input of leaf litter, I included the location of these vine maples in my analysis. To determine which samples may have been affected by the clones, I estimated the extent of vine maple influence by the positions of the rootballs and the locations of any stems that I could positively identify as vine maple based on bark residue (Figure 2).

2.7. Physical and Chemical Forest Floor Properties

I carried out the analysis of forest floor physical properties (moisture content and bulk density) at Simon Fraser University using one set of forest floor samples. All chemical analyses were conducted on the second set of samples by Pacific Soil Analysis Inc. (Richmond, BC).

To determine forest floor moisture content, I weighed all samples after collection, dried them in an oven at 70°C for 48 hours, and then re-weighed the samples. I calculated gravimetric moisture content as (wet wt – dry wt)/(dry wt) and expressed it as grams of water per grams of dry forest floor. I calculated bulk density (BD) as dry weight/sample volume, using the volume of forest floor from field measurements. Bulk density is expressed as grams of forest floor per cubic centimetre of sample.

Active forest floor pH was measured on a radiometer pH meter in a 1:4 forest floor to 0.01 Mole (M) calcium chloride ($CaCl_2$) solution (Black et al. 1965). Total carbon concentrations (g C/kg forest floor) were measured on a Leco Induction Furnace (Bremner and Tabatabai 1971). Total nitrogen (g N/kg forest floor) was determined by a semi-micro Kjedahl digestion, followed by a colourimetric analysis on a Technicon Autoanalyzer (Jackson 1958, Black et al. 1965). Mineralizable N (mN) was measured after anaerobic incubation for 2 weeks at 30°C (Waring and Bremner 1964), followed by colourimetric analysis on a Technicon Autoanalyzer. Quantities are given in milligrams of mineralizable nitrogen per kilogram of forest floor. A Bray P_1 extraction followed by ammonium molybdate and ascorbic acid colour development determined available phosphorous (mg P/kg forest floor) (Bray and Kurtz 1945, Jackson 1958, Black et al. 1965). A 1:50 forest floor to 1 Normal (N) ammonium acetate (NH_4OAc) extraction left undisturbed for one hour was analyzed on an atomic absorption spectrophotometer to determine available Ca, Mg, and K (cmol kg^{-1}) (Greweling and Peech 1965).

2.8. Data Analysis

2.8.1. Spatial Autocorrelation Analysis

I used spatial autocorrelation analysis (Cliff and Ord 1981) to test for the presence of spatial structure of forest floor nutrients in the study plot, and to determine whether the observed spatial structure, if present, was statistically significant. Spatial autocorrelation analysis (SAA) quantifies the degree of spatial dependence of values of a variable. A variable is autocorrelated when it is possible to predict the value of this variable at unsampled locations from known values at sampled locations whose spatial positions are also known (Legendre and Fortin 1989). In

SAA, the spatial intensity and scale of a quantitative variable can be estimated by means of spatial autocorrelation coefficients (Legendre and Fortin 1989), which compute the degree of autocorrelation as a function of location. The most common coefficient is Moran's *I*, which is based on the computation of cross-products of centered data, and is comparable to a Pearson's correlation coefficient (Fortin et al. 1989). Graphs of autocorrelation coefficients against distance classes (termed *correlograms*) can provide information about the spatial zone of influence of the variable (Fortin 1999).

Spatial autocorrelation can be positive or negative, depending on whether nearby values are similar to each other (+ correlation) or take on different values (- correlation). The autocorrelation sign, as well as the shape of the correlogram, can give insights into the processes that may be generating the observed spatial pattern (Legendre and Fortin 1989).

A key assumption of SAA is that of *stationarity*, that is, the property under investigation must be spatially stationary, such that each location is described by the same probability distribution (Goderya 1998). This stationarity assumption implies that the data are normally distributed, and have the same mean, variance and isotropy (i.e., the same intensity in all directions) throughout the study plot (Fortin 1999). SAA is more sensitive to non-stationary data than other spatial statistical methods (e.g., geostatistics); however, despite this higher sensitivity, SAA can be extremely useful in analyzing soil variability, in particular since the computation of autocorrelation coefficients makes possible the analysis of directionality or *anisotropy*[2] in the spatial patterns (Legendre and Fortin 1989).

While SAA has been used extensively in ecology (e.g., Fortin and Legendre 1989, Asselin et al. 2001), it is used less frequently in soil science, where geostatistical methods are more

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[2] the degree to which a signal extends further in one direction than into another

common (Burrough 1993, Qian and Klinka 1995, Goovaerts 1998). However, the use of SAA in soil variability studies is becoming more prevalent, as shown by recent literature examples (Torgensen et al. 1995, Cain et al. 1999, Roberts and Jones 2000).

I chose to use SAA, because this method allows for significance testing of individual correlation coefficients, and of the whole correlogram. Individual coefficients are tested for statistical significance at the $\alpha = 5\%$ level, based on the null hypothesis that there is no significant spatial autocorrelation (i.e., $M(I) = 0$). To determine the significance of the whole correlogram, the *Bonferroni* method (Oden 1984) is used, which takes into account that individual coefficients are not independent from one another (Fortin 1999), and approximates the adjusted significance probability while having multiple distance classes (DC). A correlogram is globally significant at the $\alpha = 5\%$ level when it contains at least one coefficient that is significant at the Bonferroni corrected level $\alpha' = 5\%/\text{number of simultaneous tests}$ (Legendre and Fortin 1989). As a result of this adjusted significance level, a correlogram may not be globally significant at the Bonferroni corrected α' level, even though it contains individual coefficients that are significant at the $\alpha = 5\%$ level.

Prior to SAA, I assessed all quantitative data for normality and skewness, and normalized data through square-root or $\log_{10}$ transformations where necessary. Of the ten forest floor properties I investigated, only total C, available P and pH exhibited deviations from normality. I normalized available P through a square-root transformation, and I removed two outliers[3] from the total C data, since the presence of outliers can suppress genuine spatial structures (Roberts and Jones 2000). I did not transform the pH data, because the distribution was not strongly

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[3] defined as observations three or more standard deviations from the average

skewed, and I therefore assumed that the spatial structure would not be unduly distorted through use of the raw data.

Because correlation coefficients compare values for pairs of point, I divided the data into twenty equidistant classes of one meter (the average sampling step in the field) prior to the analysis. I carried out the computation of spatial autocorrelation coefficients and correlograms using the spatial statistics program PASSAGE (Rosenberg 2001) by computing Moran's *I* correlograms for all variables. To identify variables in my data set with anisotropic spatial structures, I computed uni-directional bearing correlograms (Rosenberg 2000) with Moran's *I* coefficient, using eight geographic directions separated by 22.5° and twenty distance classes of one meter each. I chose geographic directions to mimic the field sampling design – every second increment is equal to one division (45°) between transects in the field.

2.8.2. Variance Partitioning

I made use of variance partitioning using partial redundancy analysis to examine the relative environmental and spatial influences on the spatial variability of forest floor chemical properties (Borcard et al. 1992). Variance partitioning allows for the integration of space as a predictive variable by dividing sources of variation in a set of dependent variables into pure environmental, spatially structured environmental, pure spatial and unexplained classes. Redundancy analysis (RDA) constrains ordination axes to be linear combinations of the supplied set of environmental variables, thereby measuring the amount of variation in the dependent variables (forest floor properties, in this case) that can be explained by the set of environmental variables. Environmental variables are all the independent variables (spatial, biotic and abiotic) that are thought to contribute to the variation in the dependent variables. RDA is generally used when it is expected that the responses of the dependent variables to conditions are linear. This assumption was reasonable in my case, because the study was conducted on a small spatial scale and sampled only small segments of the ecological gradients.

I present the results of the RDA analyses in a percent-variation bar graph, which shows the fraction of the variation in forest floor properties that is explained either by local variables alone, or is due to the inherent spatial structure of the properties. In addition, results are presented in biplots, which provide information about the relative type and magnitude of influence that specific environmental variables exert over forest floor properties. Arrows provide a picture of correlations: arrows pointing roughly in the same direction indicate a high positive correlation, while arrows pointing in opposite directions indicate high negative correlations. Variables whose arrows cross at right angles have a near zero correlation (ter Braak and Prentice 1988). While neither ordination axis is comprised solely of one variable, the relative correlations provide information about which variables define the axes. Arrow length also provides useful information – the longer the arrow, the more confident one can be about the inferred correlation.

When preparing the data for analysis, I followed the procedure of Palmer (1993), who suggests logarithmic transformations for soil nutrient data when no physiological data is available on the responses of dependent variables to resource gradients. I carried out all variance partitioning analyses using the RDA procedure in CANOCO (ter Braak 1998).

3. RESULTS

3.1. Forest Floor Summary Statistics and Humus Form Classification

Global variability of forest floor properties, as measured by the coefficient of variation, (CV%), ranged from 6.2% to 44.3% (Table 1). The CVs indicate a trend of low variability around mean pH and TC, and a high variability around mean BD and available P. The remaining forest floor properties exhibited moderate variability around the mean. To provide an overview of the statistical distributions of the forest floor properties, Table 1 also lists minimum and maximum values, means, and standard deviations.

Classification of the humus form (Green et al. 1993) at each sampling location showed that 68% of samples were of the mor order, and 32% could be classified as moder. I found that the latter order occurred most frequently in the vicinity of vine maple. Specifically, moder forest floor was present predominantly in the vicinity of the central live vine maple and one dead vine maple clone.

3.2. Spatial Autocorrelation Analysis

Eight out of ten forest floor variables produced Moran's *I* correlograms that were globally significant at the Bonferroni corrected level ($\alpha' = 0.0025$). Four chemical properties (pH, total N, and available Ca and K) exhibited a strong degree of spatial autocorrelation (Figure 3). MC, TC, mN and available Mg were weakly autocorrelated, and BD and available P showed no significant spatial autocorrelation (Figure 4). The average range of positive autocorrelation was between 4 to 6 meters, while negative autocorrelation occurred between distances of 8 to10 m on average. MC had the shortest spatial ranges of positive autocorrelation (2-3 m), while Ca and K showed long spatial autocorrelation ranges (6-8 m and 10-12 m, respectively).

The directional autocorrelation analysis indicated that spatial patterns do not extend equally in all directions (Figure 5). Variables with strong spatial autocorrelation in the all-directional analysis (i.e., pH, Ca, K, TN) clearly showed the presence of anisotropy in their spatial structures. For these variables, positive spatial dependence generally extended further in south-easterly and north-westerly directions than in other directions. For example, available Ca (Figure 5a) shows a longer range of positive spatial autocorrelation from 112.5° to 180° (up to DC 9) than from 45° to 90° (up to DC 6). Values for pH (Figure 5b) shows a similar trend – the positively autocorrelated spatial pattern extends to higher distance classes between 112.5° and 157.5° (up to DC 9) than between 0° and 90° (up to DC 6). Available K also exhibited spatial anisotropy: Figure 5c clearly indicates that positive spatial dependence has longer ranges at 0°, 22.5°, and 135° to 180°, and that certain directions show no clustering at all (e.g., the east-west direction). Directional correlograms for TN (not shown) demonstrate that this variable has a longest range of positive autocorrelation at 0°/180° (up to DC 7), and the shortest range at 90°/270° (up to DC 3). Variables with weak autocorrelation in the all-directional correlograms exhibited few to zero directional trends (e.g., available Mg, Figure 5d).

3.3. Variance Partitioning Analysis

Partitioning the variation of forest floor properties provided details on the amount of variation explained by each set of environmental variables (spatial and local), and gave a measure of the total variation in forest floor chemical properties that could be explained by four ordination axes (Figure 6). Local environmental variables accounted for 11.3% of the explained variation. This percentage accounts for the variation in forest floor properties that can be explained by environmental descriptors independently of any spatial structures. Inherent spatial patterns (i.e., pure spatial effects) in the forest floor properties accounted for 11.9% of the total explained variation. There was also some amount of shared variation between environment and space (8.5%); this percentage accounts for a common spatial structuring that was extracted by both local and spatial environmental variables. In total, the amount of explained variation was 31.7% (local, spatial and shared). The majority of variation (68.3%) could not be explained by either spatial or local environmental variables (Figure 6).

Biplots of forest floor chemical properties and environmental variables (Figure 7) provide information about how individual properties are affected by specific environmental and spatial descriptors. Figure 7a describes the influence of spatial descriptors (as supplied by the x- and y-coordinates) on the variation of forest floor properties. Correlation coefficients between the x and y-coordinates and axis 1 in Figure 7a indicate that the first ordination axis is strongly defined by the x-coordinate ($r = 0.69$), with a weaker contribution by the y-coordinate ($r = -0.26$). Spatial variation of this axis is therefore driven by processes that operate in the direction of the x-coordinate, which runs parallel to the slope of the site. Variation in the second axis is primarily driven by the y-coordinate ($r = -0.59$), but the x-coordinate also contributes to defining the axis ($r = -0.37$). Consequently, spatial variation of this axis is defined by processes that operate in the direction of the y-coordinate, or perpendicular to the slope.

Because pH, Ca and K show relatively strong correlations to the first axis ($r = 0.42$, 0.53, and -0.36, respectively) (Figure 7a), these properties vary spatially through the site along the x-coordinate. Variation in the distribution of TN, on the other hand, is influenced by spatial processes that occur in the direction of the y-coordinate, as indicated by its correlation to the second axis ($r = -0.31$). The remaining variables are less affected by the spatial factors that define the first two ordination axes, as indicated by the shorter arrows. It is interesting to note that available P is highly correlated with the third ordination axis ($r = -0.90$; not shown in Figure 7), while available Mg and mN are correlated with the fourth axis ($r= 0.69$ and 0.49, respectively; not shown in Figure 7). However, because only two environmental variables were used in the analysis (the x- and y-coordinates), axes 3 and 4 are unconstrained. It is therefore not possible to determine which variables define the variability in these axes, only that it is caused by information not accounted for in the spatial matrix.

Biplots obtained from the analysis of local environmental variables (Figure 7b) indicate that forest floor BD ($r = 0.46$) and slope ($r = 0.37$) define the variation in the first axis, while moder forest floor and the presence of CWD at sampling sites drive variation in the second axis (r = 0.62 and 0.42; respectively). Other variables contribute to a lesser extent, such as hemlock canopy (r = -0.30 with the first axis), vine maple extent (r = -0.24 with the first axis), and cedar canopy (r = 0.24 with the second axis).

4. DISCUSSION

4.1. Forest Floor Summary Statistics

Mean values and coefficients of variation (CV) of forest floor properties (Table 1) corresponded well to those normally found in coniferous forest floor associated with a podzolic soil (Lowe 1972, Quesnel and Lavkulich 1980, Arp and Krause 1984, Carter and Lowe 1986, Grigal et al. 1991, Bruckner et al. 1999, Pelletier et al. 1999, Lister et al. 2000). Global variation was smallest for TC and pH, which is in accord with results of Qian and Klinka (1995), who carried out studies of forest floor variability at five sites in coastal British Columbia. Variation in BD and available P was higher than that reported in other studies conducted in podzolic soils (Carter and Lowe 1986, Pelletier et al. 1999).

4.2. Spatial Autocorrelation Analysis

Eight out of ten forest floor properties were not distributed randomly across the site, but displayed varying degrees of spatial structure. All properties that produced globally significant correlograms showed a similar spatial trend of positive spatial autocorrelation at short distances and negative autocorrelation at longer distances. This result suggests that within a spatial range of approximately 5 m, a given forest floor property at this site will show similar values. Values of the same property will be negatively related at locations separated by more than 8 meters. The ranges of spatial dependence are longer than those reported in the literature (Qian and Klinka 1995, Bruckner et al. 1999). Bruckner et al. (1999) reported ranges of spatial pattern of roughly one meter for all forest floor variables studied, while Qian and Klinka found that spatial structure ranged from 0.5 m to 1.2 m for forest floor properties. A possible cause for this difference in spatial structure could be the disturbance history of the stand under investigation.

Most previous studies carried out spatial autocorrelation analysis in second growth stands which have experienced significant disturbance in the form of logging. For example, Bruckner et al. (1999) investigated spatial structure in a managed, 40-year old stand of even-aged Norway spruce, while Qian and Klinka (1995) studied two sites of unmanaged, 75-year old second-growth. The latter authors also investigated the spatial structure of forest floor properties in an unmanaged, uneven-aged old-growth stand, and found that spatial continuity in this undisturbed site was greater than in the disturbed sites. This finding is not surprising, since a broad scale disturbance, such as logging, can disrupt forest floor structure (physical and spatial), especially if site preparation is involved. Disruption of forest floor structure could affect long-range spatial dependence, and spatial autocorrelation may take several decades to re-establish. In second growth plantations, initial spatial structuring of forest floor properties would likely occur through litterfall and stemflow from individual trees (Zinke 1962), which are highly localized processes. Younger plantations and naturally regenerated second growth should therefore show the type of short range spatial structure measured by Bruckner et al. (1999).

I conducted my study in a stand of late transition coastal old-growth forest (Spies 1997), which does not have a history of recent large scale disturbance. Forests in the old-growth seral stage are subject to small scale patchy disturbances, such as death of individual trees; consequently, any recent disturbance to the forest floor in my site has likely been caused by localized phenomena. In the absence of large scale disturbance, the forest floor will remain largely intact, and processes that contribute to the distribution of forest floor properties can act over longer temporal scales. It is conceivable that such continual influence will cause forest floor properties to show greater spatial dependence, as spatial structures extend over greater areas.

Variables with significant spatial structure, including pH, TC and TN, available Ca, K and Mg, and forest floor MC (Figures 3, 4) had very similar all-directional correlograms. These similarities indicate that relatively small differences exist in the spatial continuity of these properties. The pattern of positive autocorrelation at short distance and negative autocorrelation at larger distances is indicative of a spatial gradient (Legendre and Fortin 1989) that causes microsites[4] close to each other to be significantly more similar, on average, than microsites further apart. While this gradient is likely a result of spatial structuring processes acting on the distribution of forest floor properties, it is difficult to determine causal factors without further studies of the spatial distribution of forest floor properties at other sites. Biotic factors, such as vegetation may be imposing spatial structure; alternatively underlying, unmeasured environmental factors, such as activity of soil fauna or microtopography may influence forest floor properties while displaying relatively small scale spatial patterns over neighbouring microsites.

While the autocorrelation trend was similar for all significant correlograms, the shape and magnitude of autocorrelation varied with each individual property. These differential "signatures" indicate that each property has a slightly different spatial pattern. A similar observation was made by Qian and Klinka (1995), who proposed that the development of such individual patterns may be imposed by the property itself, or by the disturbance history of the site.

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[4] defined as a portion of a site that is uniform in microtopography and surface soil materials

Some variables showed weak or no spatial autocorrelation (e.g., available P and BD). This lack of spatial dependence may result from a sampling step that is too large or too small to adequately capture the spatial structure of these properties. However, the mixed systematic-random sampling design that I implemented should have served to minimize this problem. A more likely explanation is that the spatial signal of these variables is simply too weak to produce significant autocorrelation coefficients with the given number of samples.

Variables that exhibited strong autocorrelation in the all-directional analysis (i.e., pH, Ca, K and total N) showed obvious directionality in the analysis of anisotropy. Whether this type of directionality in the spatial structure is commonplace is difficult to substantiate, because literature on the spatial patterns of forest floor properties is scarce. Bruckner et al. (1999) found that some forest floor properties exhibited directionality, specifically moisture content and mineralizeable N, while pH was isotropic; however, these results may not be strictly comparable. Because the authors sampled along two transects, they did not compute uni-directional correlograms, but rather compared the two directions that were measured. None of the variables in my study exhibited isotropic behaviour; the distribution was either strongly anisotropic or the directional analysis produced weakly anisotropic patterns (e.g. available Mg, Figure 5d).

4.3. Variance Partitioning

Results of the variance partitioning analyses indicate that the environmental variables and spatial variables each explain approximately 20% of the variation in the forest floor properties (Figure 6), and that the amount of explained variation is globally significant (*P* = 0.005). Just under half of the variation explained by the environmental variables is spatially structured (8.5%), indicating that it can also be explained by the geographic coordinates of the samples. This common variation could be caused by local environmental variables imposing a spatial pattern on the forest floor properties (e.g., impact of canopy throughfall, Zinke 1962). Alternatively, this shared variation could be non-causal, i.e., an external spatial structuring process may be affecting environmental variables and forest floor properties in a similar manner, resulting in a common spatial structuring (Borcard et al. 1992).

The fact that spatial descriptors and environmental variables contribute almost equally to explaining the variation in forest floor properties shows that spatial structuring processes play an important role in the distribution of nutrients in these forest soils. Spatial descriptors alone accounted for 11.9% of the total explained variation, indicating that certain underlying processes exist for which these descriptors act as surrogates. While I cannot identify these processes from the available data, the results indicate that they are, in part, independent of the measured environmental variables.

About one third of the total explained variation is due to local effects of the environmental variables on forest floor properties. Of these local variables, the most significant contributions are due to the presence of moder forest floor and CWD, followed by forest floor BD and the presence of a slope at sampling locations (Figure 7b). These results indicate that forest floor type, as determined by the presence of vine maple, is an important component in the overall variability of the forest floor. The influence of vine maple on forest floor variability will be discussed in more detail in Section 4.4.

The importance of CWD as a determinant of forest floor variability is supported by two recent studies (Klinka et al. 1995, Kayahara et al. 1996). Klinka et al. (1995) investigated the role of CWD in determining the distribution of forest floor nutrients, and found that in Douglas-fir dominated stands, there were significant differences between the nutrient status of wood-containing forest floor and that of forest floor without CWD. While the influence of CWD on forest soils was highly site specific, the spatial pattern of CWD in a site accounted for much of the variation in the chemical properties of the mineral soil. A study by Kayahara et al. (1996) found that properties of lignic and alignic forest floors were significantly different, specifically in pH, total C and N, mineralizable N, available P and extractable Mg, K and Ca.

After forest floor type and presence of CWD, BD and slope at sampling locations were the most important local environmental variables that contributed to variability in forest floor properties. Unfortunately, there are no studies to date that address the impact of bulk density on the distribution of forest floor properties, and information on the influence of slope on nutrient distribution is limited. Because slope position influences the transport of water-soluble nutrients (Rhoades and Binkley 1992, Fisher and Binkley 2000), the presence of a slope within a forest stand will likely contribute to spatial variation. Very few studies have addressed the effects of slope on forest floor properties (Bruckner et al. 1999); most focus instead on the impact of slope on nutrient distribution in the mineral soil (Rhoades and Binkley 1992, Gonzalez and Zak 1994, Enoki et al. 1996). Whether dealing with forest floor or mineral soil, however, research into the effects of slope has produced mixed results. Two studies found no relationship between slope and the spatial structure of mineralizable N (Bruckner et al. 1999, Gonzalez and Zak 1994), pH and organic C (Gonzalez and Zak 1994). However, Rhoades and Binkley (1992) found that slope strongly influenced the extent of nitrogen availability into adjacent stands, and Enoki et al. (1996) found that sloping sites had an effect on the distribution of moisture content and amounts of organic C. Variance partitioning results from this study indicate that slope does play a role in the variability of forest floor properties, but that other spatial and local environmental variables affect this variability more strongly.

A large amount of the variation (68.3%) in forest floor properties remains unexplained (Figure 6), which can be common in ecological data (Asselin et al. 2000). The high amount of unexplained variation indicates ecological processes may be occurring at scales smaller than the measurement scale (i.e., the step between sampled sites was inadequate for capturing dominant processes) (Borcard et al. 1992, Pelletier et al. 1999, Asselin et al. 2001). Alternatively, processes that created the observed variability may no longer be active, but the soil retains the consequences of these influences (Hammer 1998). In addition, I may have overlooked certain key structuring elements, such as the type and distribution of soil organisms, which will affect the variability of forest floor properties through rates of litter decomposition and soil turnover (Fisher and Binkley 2000). Additionally (or alternatively), microtopographic conditions could have affected the observed variability. Microtopography can have considerable influence on soil moisture and temperature over the seasons (Peterson et al. 1990), and may therefore directly or indirectly affect variability of other forest floor properties. Finally, it is possible that the simple spatial descriptors I used were insufficient for describing certain spatial structures, and that these structures would have been better accounted for by the use of more complex functions (e.g., trend surface equations; Pelletier et al. 1999). However, even with more complex descriptors, the combination of large and small-scale processes may still have confounded the variables' signals.

There is a clear relationship between results of the variance partitioning and the spatial autocorrelation analyses. The variation in those forest floor properties that show strong spatial autocorrelation (i.e., TN, pH, available Ca and available K) is driven primarily by spatial processes (Figure 7a). Properties that exhibited little or no spatial dependence (e.g., available Mg, mN) produced short arrows in the biplot of spatial scores (Figure 7a), indicating that the distribution of these variables is not strongly affected by space.

Because variation in the first ordination axis is predominantly driven by the x-coordinate (r = 0.69), the correlations of pH, available Ca and K to the first axis indicate that processes driving the distribution of these properties likely operate in the direction of the x-coordinate, or parallel to the slope. Since pH is a measure of hydrogen ion concentration, and available Ca and K are present in ionic form in the forest floor, one spatial process that may be responsible for the variation in these properties is the movement of these cations downslope over time through leaching and diffusion (Brady and Weil 2002). It is surprising that available Mg did not exhibit similar correlations; however, since this cation did also not exhibit strong spatial autocorrelation, it is likely that spatial processes do not contribute extensively to the distribution of this nutrient.

The distribution of TN appears to be influenced by processes that operate perpendicular to the slope, as shown by the correlation to the second axis, which is defined by the y-coordinate (r = -0.59). The concentration of TN in the forest floor is generally determined by the type of materials that make up the forest floor, such as wood, species-specific litterfall and fine roots (Fisher and Binkley 2000). There appears to be no direct connection between TN concentration and presence of CWD or species-specific canopy (Figure 7b). TN is most abundant in the northwest corner of the plot, and least abundant in the southwest corner, a distribution which supports a structuring process operating perpendicular to the east-west slope of the site, but further research is needed to determine which specific spatial processes may be affecting the distribution of TN.

The relationship between chemical properties of the forest floor and local environmental variables (Figure 7b) indicates that variability in mN and available P can be attributed to local processes. Variation in the former is affected by the presence of moder forest floor type, while levels of available P are primarily related to BD. The availability of K and Mg in the forest floor are positively correlated with the presence of rock, and negatively correlated with the presence of cedar canopy, and sampling locations where a slope is present. Available K is a particularly interesting property, since it appears to be affected by both spatial and local processes, as shown by the relatively long arrows on both biplots. TC, on the other hand, is not affected strongly by either process (i.e., TC shows short arrows in both biplots).

4.4. Vine Maple Influence on Forest Floor Variability

In this analysis, I used the presence of moder forest floor as a surrogate for vine maple influence on forest floor development. Moder forest floors generally develop in forest stands which yield easily decomposed litter, typically from deciduous over- or understory vegetation (Green et al. 1993). The forest floor in my site was predominantly of the mor order, as is common in coniferous forests growing on podzolic soils (Fisher and Binkley 2000); however, in the vicinity of vine maple, I frequently classified the forest floor as moder. While moder forest floor extends further than the canopy of the live vine maple and the approximate extent of influence of the dead clone, the clonal nature of this shrub makes it possible that vine maple has been present in this section of the site for quite some time, thus influencing forest floor development through annual litterfall and litter decomposition. These findings are in accordance with other studies (Odgen and Schmidt 1997, Tashe and Schmidt 2001) which suggest that vine maple growing within conifer forest may significantly affect some forest soil properties, especially if it is present in the site over longer time periods.

Ordination results indicate that while the canopy extent of vine maple had little influence on the distribution of forest floor properties, moder forest floor was one of the primary local factors that affected variability. Moder forest floor is highly correlated with the second ordination axis ($r = 0.62$), and it specifically affects the distribution of mN (Figure 7b). Since deciduous leaf litter decomposes faster than conifer litter (Ogden and Schmidt 1997, Fried et al. 1989), and rates of gross N mineralization can be higher in deciduous forests than in conifer forests (Campbell and Gower 2000), the relationship between moder forest floor and mN suggests that vine maple may have an impact on nutrient distribution.

5. RESEARCH AND MANAGEMENT IMPLICATIONS

Broadleaf trees have traditionally been viewed as weeds in conifer-dominated forests of the Pacific Northwest (Klinka et al. 1991), but increased recognition of their contribution to the diversity and sustainability of British Columbia's forest ecosystems is resulting in greater utilization of deciduous tree species (Thomas 1999). Broadleaf species, such as vine maple, are desirable ecosystem components that add to structural and species diversity, and, as recent research has shown (Tashe and Schmidt 2001), vine maple is also able to improve nutrient availability to the benefit of adjacent conifers through its nutrient-rich litterfall.

My study was focused on the plot scale, and because results were not replicated, they cannot be readily extended to the stand level or landscape scale. However, for the coastal old-growth site under investigation, results have shown that forest floor type, as determined by the influence of the broadleaf species vine maple, is an important environmental descriptor of variability in forest floor chemical properties. Because the development of moder forest floor was more pronounced in the vicinity of older vine maple clones (dead and recently felled), it is possible that the species may need to be present for extended periods of time before its contribution to forest floor variability becomes pronounced enough to be detected.

The findings of this study raise questions about the importance of microscale forest floor variability on the plot scale for managed forest stands. Forest managers recognize that any particular site in a forest is a complex of microsites, and that some of these microsites may be more appropriate for tree establishment than others (Stathers et al. 1991). However, while site quality is used as a criterion for tree species selection, causes of microscale environmental variation are largely ignored by existing soil management practices. Current criteria for microsite selection are basic and are limited to avoiding wet depressions, unstable microsites, and areas containing decaying wood (Krasowski and Elder 2000). Because early tree growth often reflects microsite conditions, and can result in a large degree of variability in early tree growth (Stathers et al. 1991), a better understanding of forest soil variability would allow managers to base site selection decisions on soil variability descriptors. When seedlings are planted systematically, the spacing is unrelated to microscale nutrient variation; consequently, areas of higher nutrient concentrations may be missed. With a better understanding of the factors that contribute to the variability of forest soil properties, planting can still occur at a particular density, but with microsite selection, it would be possible to align planting spots with soil variability.

The majority of forest floor properties in my study site showed moderate to strong autocorrelation, and variability in these properties was strongly influenced by spatial processes. I suggest that this study be extended to investigate the distribution of forest floor properties at multiple sites and over a larger spatial range to determine whether autocorrelation ranges are consistent. Sites should include old-growth, second growth and recently harvested areas. Such replication would provide a picture of macronutrient distribution in the forest floor under various site conditions, and allow managers to utilize the spatial dependence of forest floor properties to optimize planting locations in harvested blocks.

Replicated studies would also provide more insight into the types of spatial processes and environmental variables that contribute to the observed variation. The influence of other deciduous, non-nitrogen fixing tree species, such as big leaf maple (*Acer macrophyllum* Pursh), could be investigated in future studies to determine whether the development of moder forest floor makes a similar contribution to variability as in the case of vine maple. This type of research is necessary before definite conclusions can be drawn about the impact of non-nitrogen fixing species on forest floor variability. Further studies should also incorporate a more extensive selection of environmental variables, including type and distribution of soil fauna, microtopography, and a more comprehensive classification of understory vegetation in an effort to decrease the amount of unexplained variation. Information derived from this type of research could be utilized to "recreate" late seral stage conditions in a younger stand by incorporating those variables that contribute more significantly to the observed variability in old-growth stands. Thus, spatial variability could be incorporated explicitly into forest management to enhance the range of values a stand managed for.

While the importance of spatial relationships in ecosystem function is being recognized increasingly in ecology (Kareiva 1994, Levin 1992, Pacala and Deutschman 1995), silvicultural prescriptions were, until recently, still largely aspatial (e.g., BC Ministry of Forests 1994). Late seral stage stands were harvested largely through clear-cutting and were replaced by even-aged, monospecific plantations with the objective of optimizing production of timber (Smith 1986). The spatial distribution of trees in these stands was often determined on the basis of light requirements for maximum growth of commercially important tree species. However, as shown by Pacala et al. (1995), the spatial structure of individual trees does not affect growth rates of trees alone; it can also significantly affect the function of a forest as an ecosystem. Although the authors do no deal with tree-soil effects, they address the critical importance of spatial "details" as determinants of ecosystem functions by modeling forest response to elevated CO_2 levels. The authors show that a forest with vertical structure (i.e., size structure), but no horizontal heterogeneity (e.g., canopy gaps) would likely store fifty percent less of the above- and below-ground biomass, and fifty percent less undecomposed organic matter.

These results indicate that spatial interactions are essential elements in determining total biomass accumulation and changes in community composition. Thus, even with only a partial understanding of environmental factors that contribute to soil variability, progressive management approaches should incorporate spatial structure in the forest stand by application of non-traditional harvest systems and the incorporation of ecosystem components that add to stand heterogeneity.

With recent advances in the variable retention harvest system (Franklin et al. 1997), managers have been provided with a tool to manage for multiple objectives more effectively, and are increasingly addressing issues of structural complexity and maintenance of biodiversity in forest ecosystems (BC Ministry of Forests 2001). With this new management system, the issue of spatial pattern and variability becomes more important, because management must now occur at several spatial scales. Because each species within an ecosystem sees the environment at its own scales of time and space, there is no one "correct" scale at which to manage the forest ecosystem (Levin 1992). Rather, to manage effectively for a variety of values at various scales, a better understanding of the patterns that contribute to ecosystem function is required. These patterns need to be quantified and described in order to determine the mechanisms that create and maintain them.

This study was aimed at investigating patterns in a specific part for the forest ecosystem, namely the soil mosaic. By quantifying the spatial structure of selected forest floor properties on the plot scale, and examining factors that contribute to the variability in these properties, I took an initial step towards identifying mechanisms that affect the distribution of soil nutrients. While forest soils are highly variable, this study shows that at least some of this variation can be quantified and attributed to specific environmental influences through the application of spatial and multivariate statistical techniques. Extending this work to other sites and/or to larger spatial scales will provide a better understanding of spatial patterns, variability and processes that maintain soil functions in the forest ecosystem. Such information should enable managers to better address issues of structural complexity and maintenance of biodiversity in forest ecosystems.

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Table 1 Summary statistics for forest floor physical and chemical properties

	Units	**Minimum**	**Maximum**	**Mean**	**SD**	**CV (%)**
Moisture Content	g g^{-1}	1.15	4.37	2.76	0.48	17.3
Bulk Density	g cm^{-3}	0.03	0.33	0.10	0.04	43.8
pH		3.1	4.5	3.7	0.3	7.1
Total Carbon	g kg^{-1}	330.4	550.0	490.8	30.1	6.2
Total Nitrogen	g kg^{-1}	11.0	19.6	15.4	1.6	10.7
Mineralizable Nitrogen	mg kg^{-1}	310	1215	620	149	24.1
Available Phosphorous	mg kg^{-1}	1	41	17	6	44.3
Available Potassium	cmol kg^{-1}	0.38	1.6	0.87	0.22	25.4
Available Calcium	cmol kg^{-1}	6.7	31.3	16.1	5.0	30.7
Available Magnesium	cmol kg^{-1}	1.3	3.3	2.1	0.43	20.5

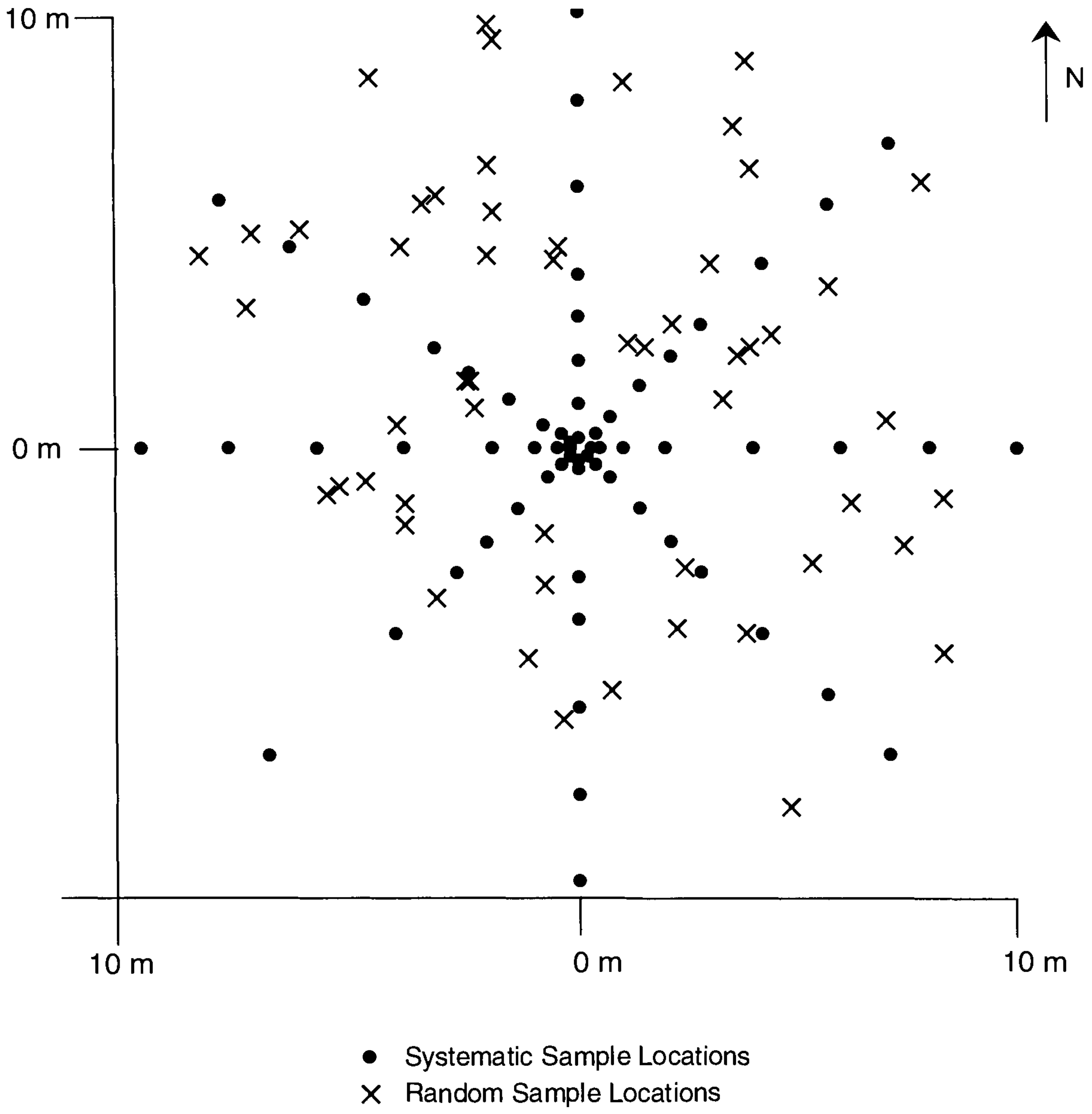

Fig. 1 Sampling locations of systematic and random points. Locations that could not be sampled due to the presence of rock or live roots are excluded.

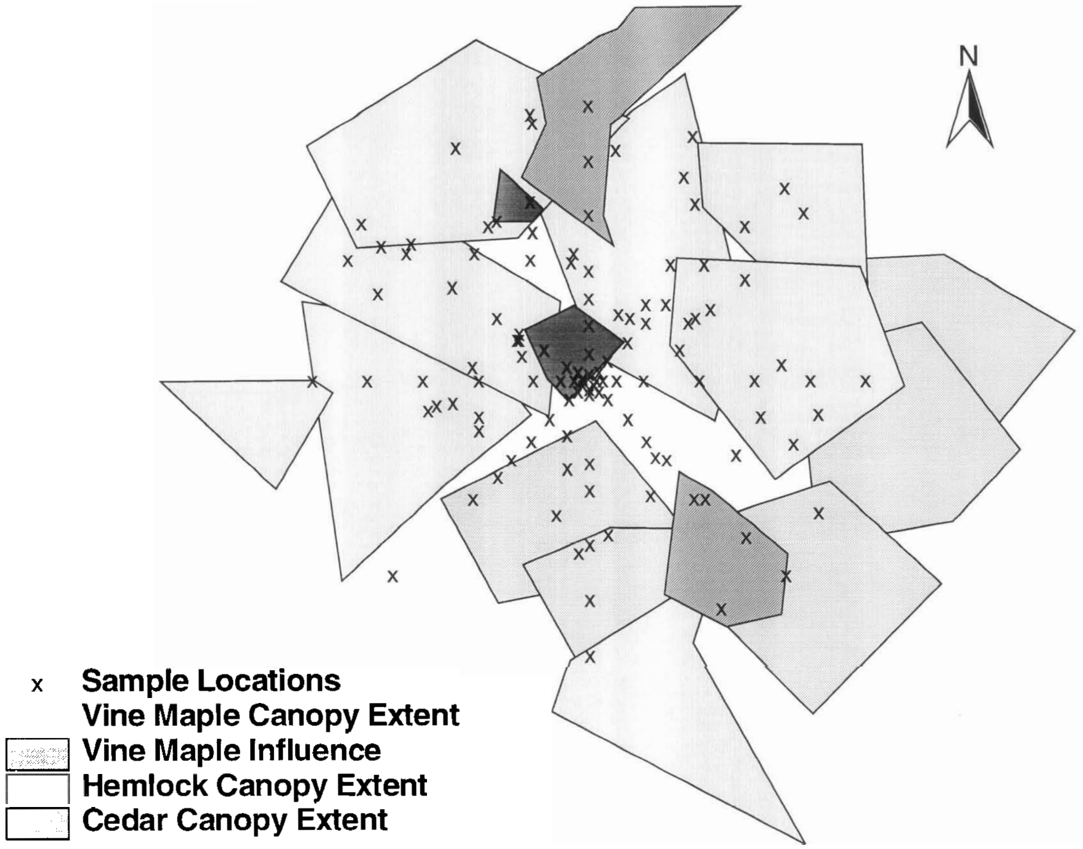

Fig. 2 Map of species-specific canopy cover, produced by measuring vertical projections of the conifer and vine maple canopies to the ground at five locations for each canopy. Extent of vine maple influence was estimated by positions of rootballs and locations of stems that could positively be identified as vine maple based on bark residue.

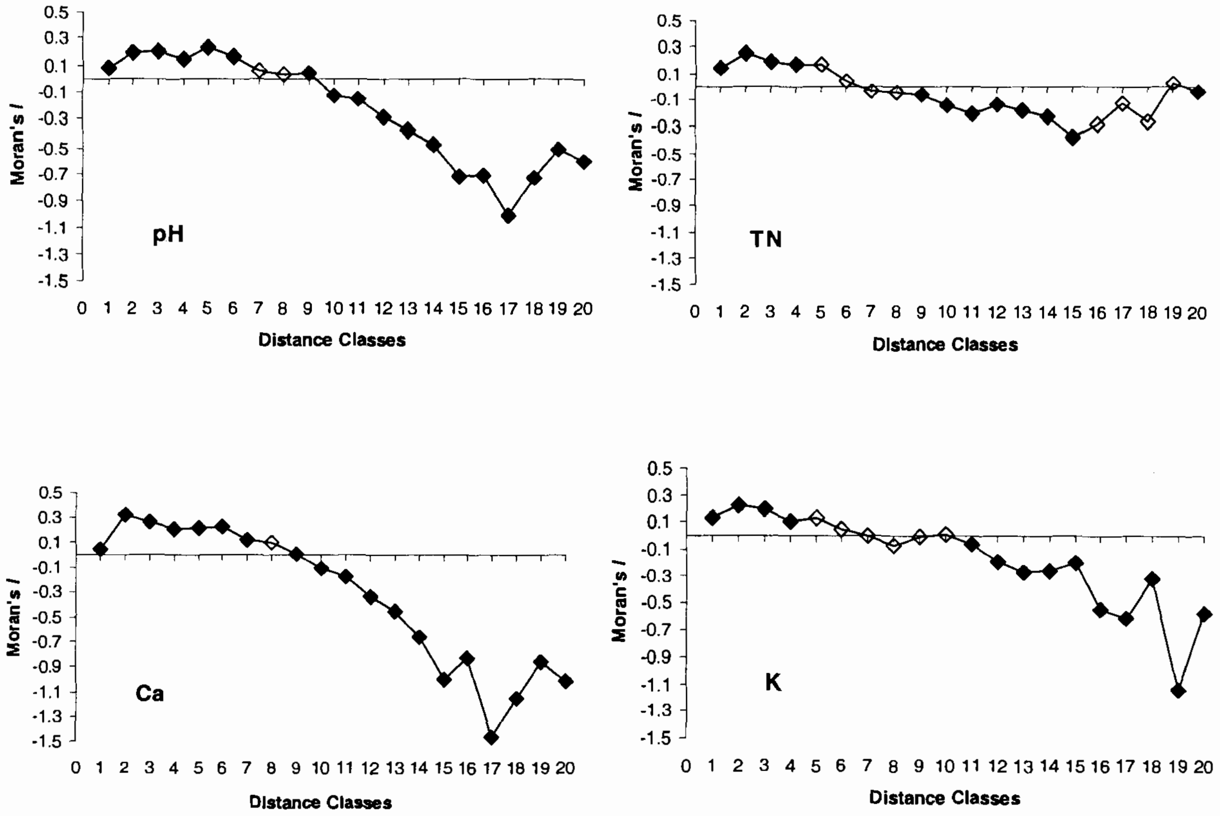

Fig. 3 All-directional spatial correlogram of strongly autocorrelated forest floor variables (pH, total N, available Ca and K). Abscissa: distance classes; the width of distance classes 1-19 is 1 m; the width of distance class 20 is 2 m. Ordinate: Moran's *I* statistic. Black diamonds represent significant values at the $\alpha = 5\%$ level, before applying the Bonferroni correction to test the overall significance of the correlogram; white squares indicate non-significant values.

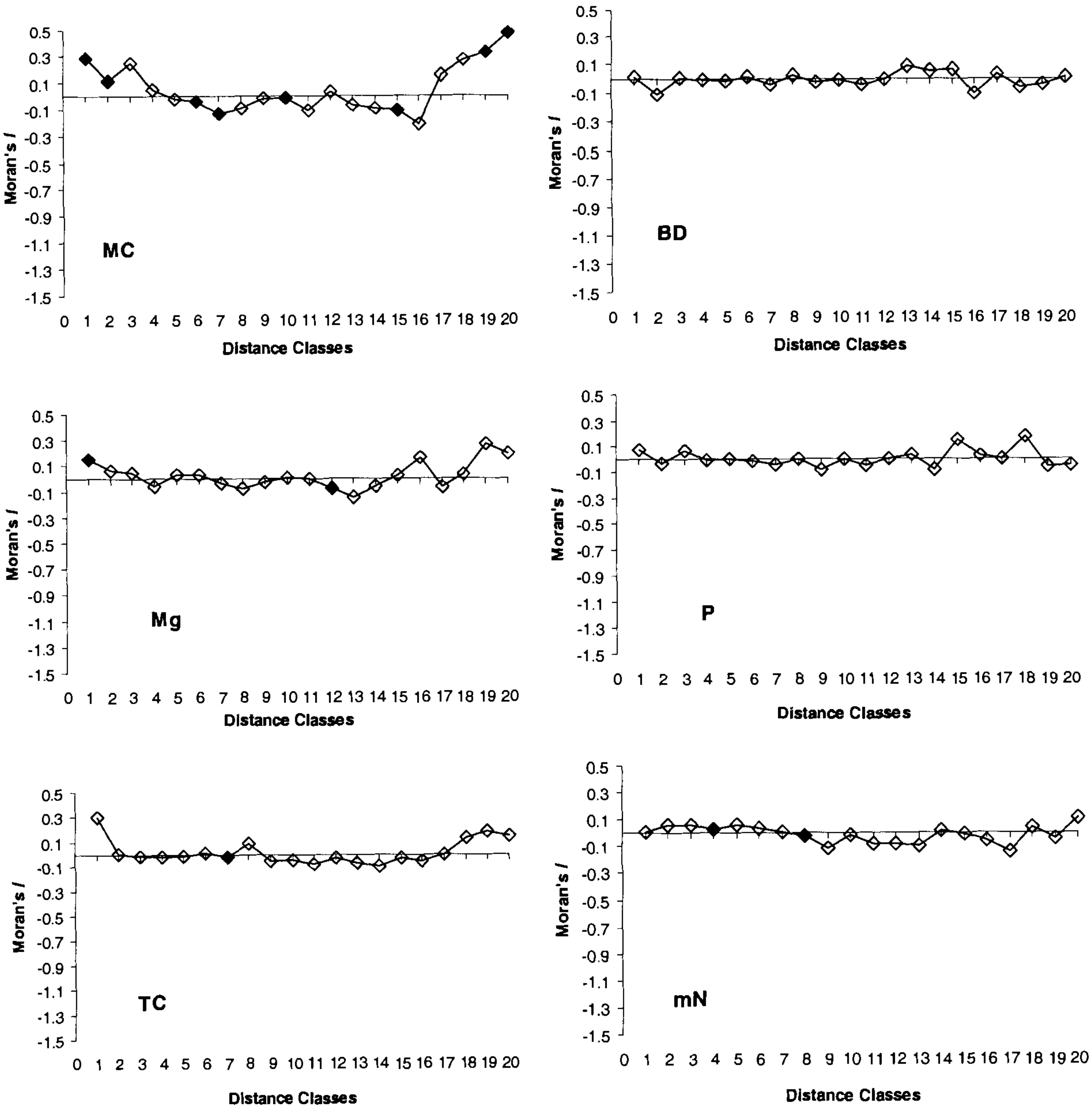

Fig. 4 All-directional spatial correlogram of moisture, bulk density, available magnesium, available phosphorous, total carbon, and mineralizable nitrogen. Abscissa: distance classes; the width of distance classes 1-19 is 1 m; the width of distance class 20 is 2 m. Ordinate: Moran's *I* statistic. Black diamonds represent significant values at the $\alpha = 5\%$ level, before applying the Bonferroni correction to test the overall significance of the correlogram; white squares indicate non-significant values.

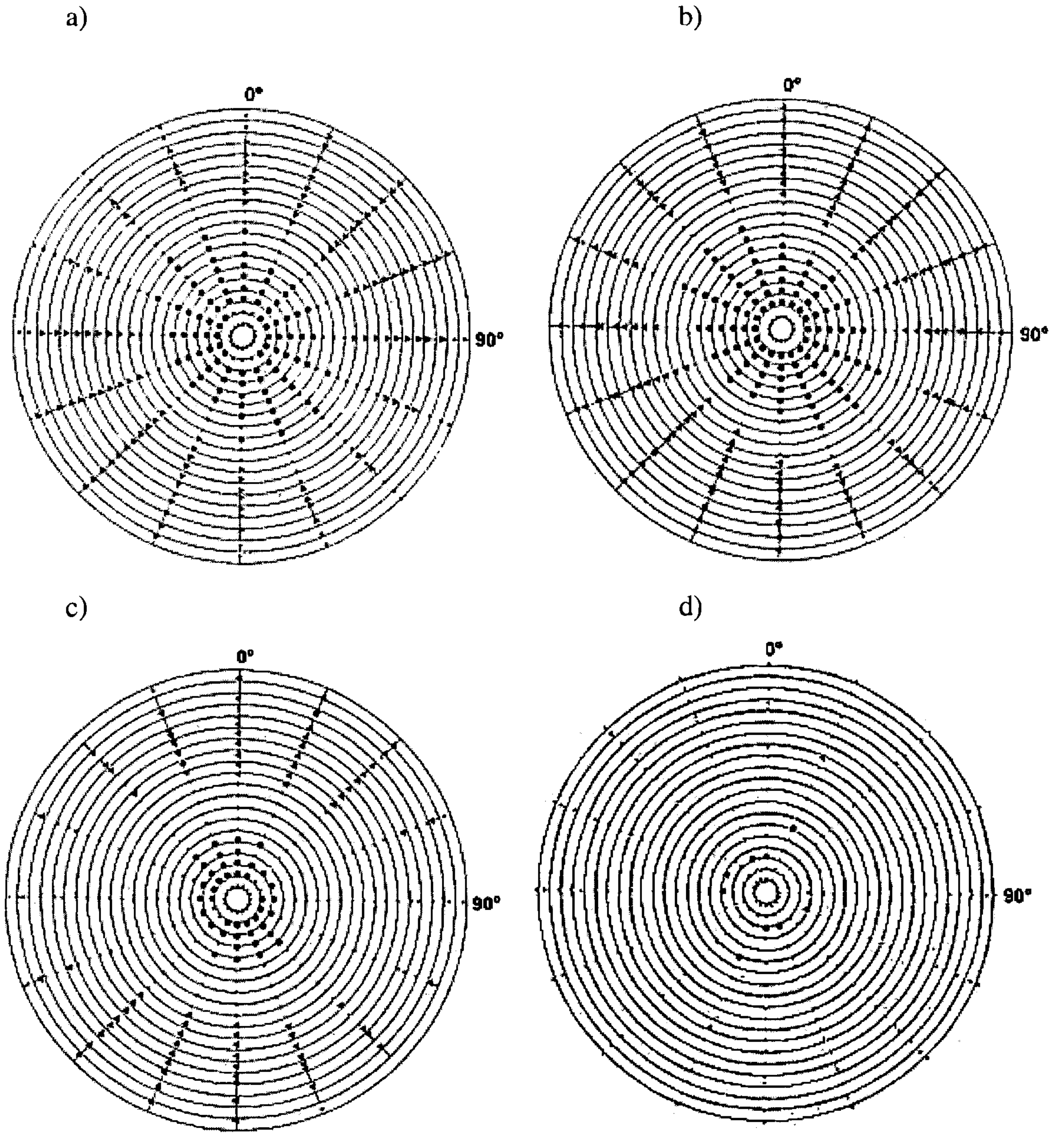

Fig. 5 Uni-directional correlograms of forest floor variables: a) pH, b) available Ca, c) available K, and d) available Mg. Each concentric circle indicates one distance classes; the width of distance classes 1-19 is 1 m; the width of distance class 20 is 2 m. The directions are geographic and mimic the field sampling design; every second increment is equal to one division (45°) between transects in the field. Black circles indicate significant positive autocorrelation values at the $\alpha = 5\%$ level; black triangles indicate significant negative autocorrelation values at the $\alpha = 5\%$ level.

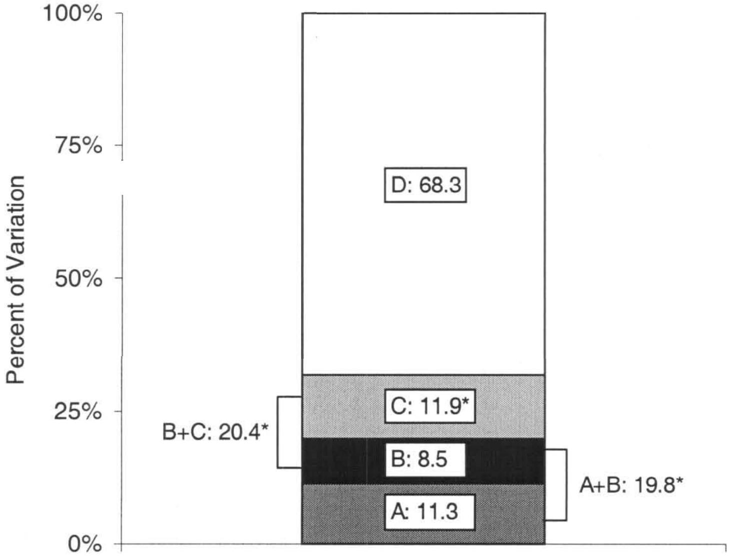

Fig. 6 Variance partitioning of forest floor variation. Fraction (A) is the local component (environmental scores), (B) is the spatially structured environmental component, (C) is the pure spatial component (spatial scores), (D) is the unexplained component. * indicates significance at P = 0.005. Statistical significances are computed with a Monte-Carlo permutation test (199 permutations).

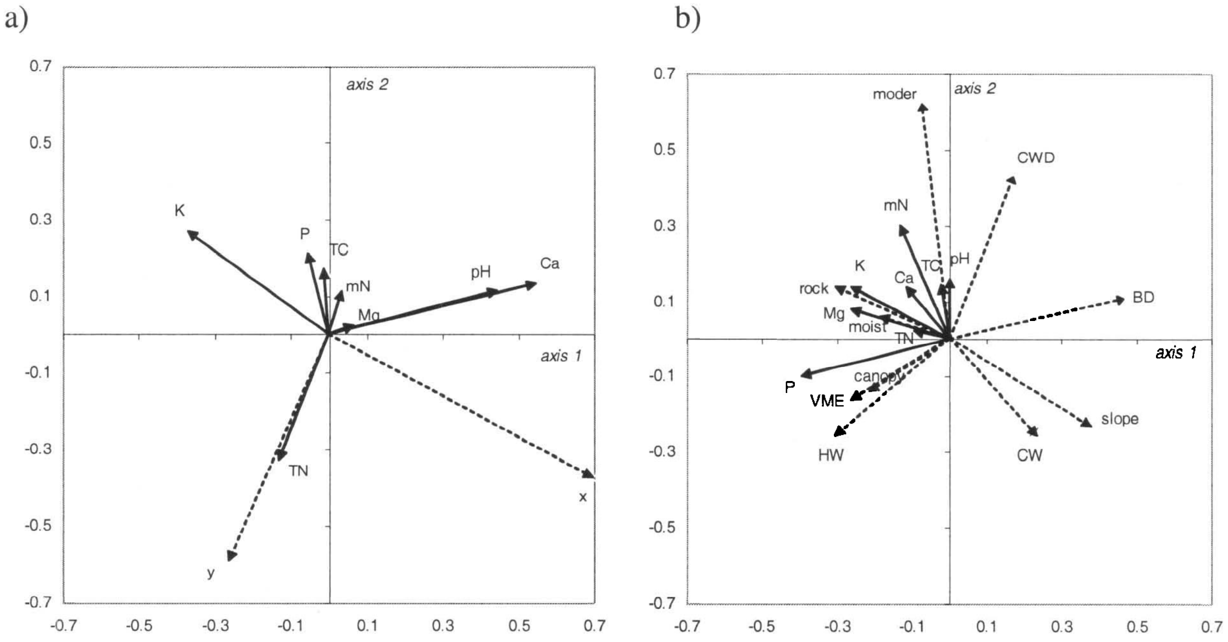

Fig. 7 Ordination biplots of the first two axes of the RDA of a) spatial scores, and b) local scores. The arrows for forest floor properties (solid arrows) and environmental variables

(dashed-line arrows) display the approximate (linear) relationship between forest floor properties and environmental variables. Acute (obtuse) angles indicate positive (negative) correlations. The longer the arrow, the greater the confidence about the inferred correlation. The direction of the x-coordinate is parallel to the slope of the site; the direction of the y-coordinate is perpendicular to the slope of the site. Abbreviations: TC, total carbon; TN, total nitrogen; mN, mineralizable nitrogen; Ca, K, Mg, P, available calcium, magnesium, potassium, phosphorous, respectively; CWD, presence of coarse woody debris; HW, CW, samples under hemlock and cedar canopy, respectively; canopy, samples under any types of canopy; VME, samples under vine maple influence; moist, moisture; BD, bulk density; rock, presence of rock .