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SPATIAL VARIABILITY OF SOIL ORGANISMS, pH, MOISTURE, O-HORIZON DEPTH, AND TEMPERATURE IN DIFFERENTIATED CONIFER STANDS IN THE WESTERN CASCADES, OREGON

by

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A THESIS

Presented to the Department of Geography
and the Honors College of the University of Oregon
in partial fulfillment of the requirments
for the degree of
Bachelor of Arts
June 1993

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An Abstract of the Thesis of

Christian Erik Torgersen for the degree of Bachelor of Arts

in the Department of Geography to be taken June 1993

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Geostatistical tools, the semi-variogram and correlogram, were applied in an ecological setting to test for differences in spatial heterogeneity patterns of soil microarthropods, nematodes, pH, moisture content, O-horizon depth, and temperature in two contrasting forest stands. Two adjacent research plots, with varied densities of old-growth and 80-year re-growth trees, were selected in coniferous forest near Blue River in the Western Cascades of Oregon. One plot consisted of a heterogeneous mix of age classes with a high density of old-growth trees; the other plot contained homogeneous re-growth with a low density of old-growth trees. Means and standard deviations of soil properties and organism counts were similar in both plots. Spatial analysis results, however, revealed distinguishable differences between treatment areas. Short range (5-8 m) patch-to-patch patterns, especially in pH, moisture, O-horizon, and faunal census, were more pronounced in the re-growth homogeneous plot, whereas long range patterns (17-22 m) were more pronounced in the old-growth heterogeneous plot.

ACKNOWLEDGEMENTS

I attribute the success of this research to the generosity in time and effort of the many people who worked side by side with me through the exciting, but often tedious, process of scientific research. From sweltering days in the field, to mind-numbing hours peering through the microscope or staring at the computer screen, all these people donated their energy to bring this thesis to completion, and they all deserve due recognition. I extend my gratitude to each of the 1992 Research Experiences for Undergraduates students who collected my field data (the dirty work). Sincere thanks also go to Carolyn Krueger for her help in the last minute preparations of the manuscript. I also wish to thank Julia A. Jones for the ingenuity and patience with which she master-minded the project. To Andy Moldenke I owe the utmost of gratitude for the many years he has spent teaching me about the forest soil, and for the guidance he has given me which has undoubtedly influenced my decision to continue ecological research. The project was supported in part by a stipend from the National Science Foundation Research Experiences for Undergraduates Program and the Department of Biology at Oregon State University.

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I. INTRODUCTION

The forests of the Pacific Northwest are known for their tall stands of moss-covered old-growth Douglas-fir, hemlock and cedar surrounded by a lush understory of ferns and shrubs thriving in the maritime climate. This unique ecosystem above the ground is associated with a myriad of complex biological processes in and beneath the forest floor. Diverse arrays of invertebrates such as spiders, insects, worms, mites, and terrestrial molluscs form an interwoven food web which is the foundation of forest soil production (Moldenke 1990).

The long-term health of the forest depends on nutrient cycling processes in the upper organic and inorganic layers of the soil, the O and A horizons. The growth of trees, shrubs and other surface vegetation is determined by the biological and chemical characteristics of the soil. Plants rely on bacteria, fungi and invertebrates to break down dead organic material into usable forms through the process of decomposition. With their extensive networks of roots, woody plants have an ecological impact on soil physical structure and chemical content, which, in turn, affects the communities of soil organisms.

In the last several years, scientific and public interest in the ecological significance of old-growth forests of the Pacific Northwest has reached a peak, particularly as a result of the controversy between conservationists and Oregon's logging industry concerning the preservation of old-growth timber stands as habitat for the endangered northern spotted owl. Questions have

arisen about whether other species and communities exist uniquely in the old-growth environment. For example, what ecological components besides trees distinguish an old-growth forest from a younger re-growth stand? How may three-hundred to six-hundred year old trees influence the flora and fauna both in tree canopies and in the soil within the trees' branching root networks? Questions such as these need to be addressed in a time when incomplete understanding of the forest's regeneration capacity could lead to mismanagement and subsequent depletion of biological diversity and economic resources in Pacific Northwest forests.

Project Purpose

In this study, the objective was to determine and understand what distinguishes the ecosystems of differentiated coniferous forest stands from one another in terms of spatial patterns of soil organisms, pH, moisture, temperature and O-horizon depth within the soil environment. Specifically, the research project was designed to examine spatial pattern and assess the associations of old-growth and re-growth trees with the physical, biological, and chemical structure of the soil. Geostatistical methods as well as basic statistics were applied to describe contrasting forest stands. Two compositionally different research plots were examined: a predominantly old-growth stand consisting of a heterogeneous mix of young and old conifers; and a homogeneous, predominantly re-growth stand approximately 80 years of age.

Motivation to examine the spatial dimension of soil properties and invertebrates in connection with conifer stand composition came from a

similar study by D. Perry (pers. comm.), T. Bell, and T. Spies of the Forest Sciences Department at Oregon State University. Perry, Bell, and Spies tested for spatial autocorrelation of soil carbon, nitrogen, microbial biomass, and canopy cover with semi-variograms in old-growth forest stands in the Western Cascades. The unpublished results of their study revealed correlation between the spatial variability patterns of these three soil characteristics. Soil carbon, nitrogen, and canopy cover exhibited similar spatial patterns over an inter-sampling point distance of approximately 30 m. Patterns of microbial biomass also showed correlation, but to a lesser degree.

The research by Perry, Bell, and Spies raised questions about the effects of trees on the spatial patterns of soil properties. My research addressed the question of whether different conifer stand compositions would each reveal a unique spatial signature within the soil environment. This thesis presents the results of a pilot study in which this hypothesis was tested, by comparing the spatial patterns of soil organisms, pH, moisture, temperature, and O-horizon depth in two adjacent forest stands of contrasting age.

Background

The Forest Soil Environment

The most obvious and immediately inspiring characteristics of old-growth forests in the Pacific Northwest are certainly the trees, shrubs, and plants that grow out of a deceivingly nondescript mat of needles and twigs--the forest floor. However, within this rich mixture of decaying matter live vast numbers of arthropods that form the most diverse part of the forest

ecosystem. Coniferous forest soils in western Oregon contain some of the richest and most diverse terrestrial complexes of soil-dwelling arthropods in the world (Petersen and Luxton, 1982). Oribatid mites (150,000/m^2) and springtails (50,000/m^2) are the most abundant soil arthropods in Oregon's western forests. One square foot of old-growth forest soil can contain more than 200 species (Moldenke and Lattin, 1990a).

The long-term health of a forest ultimately depends on the biological dynamics in the soil that aid the process of organic matter decomposition and nutrient transformation. Acquisition of nutrients and water through tree roots is influenced by the metabolic activity of fungi and bacteria in the soil (Moldenke, 1990). Symbiotic associations between mycorrhizal fungi and plant roots occur at the interface between root and soil and facilitate uptake of nutrients from the soil into the root (Feldman, 1988). Soil invertebrates larger than the microbial scale such as mites, centipedes, and millipedes play an irreplaceable role in soil production, physical structure, and chemical content. Arthropod faeces make up the bulk of particulate matter in the soil organic layer, while arthropod burrowing activities aerate the soil, making it accessible to root penetration and water absorption (Rusek, 1986; Andrew Moldenke, pers. comm.). Microcosm experiments by Teuben and Roelofsma (1990) testing the influence of soil arthropods on coniferous litter decomposition found that isopods and collembolla, two very common and abundant soil arthropods, enhanced microbial activity and concentrations of exchangeable nitrate, ammonium, and phosphate. The presence of soil fauna is generally assumed to benefit plants by increasing the amount of available nutrients for root uptake. Setala and Huhta (1991) have shown in laboratory

experiments that soil fauna exert a positive influence on birch seedling growth. Root biomass of the seedlings was as much as 70% greater in the presence of nematodes and microarthropods.

Soil invertebrates are integrally tied to their environment. They produce the soil in which they live and are also subject to changes in the forest environment as a whole. Soil ecosystems, and especially their faunal components, are highly sensitive to successional stage changes following forest utilization and management practices, such as logging and burning. Studies by Moldenke and Lattin (1990) have found that clearcut-and-burn practices reduce total arthropods by approximately 90%. Many species that are characteristic of an old-growth environment do not appear in cut forest stands for 20-40 years following disturbance (Moldenke and Fichter, 1988; McIver et al. 1992). Soil arthropods function as biological indicators of forest type and successional stage (Moldenke 1990), making them a vital variable in the assessment of forest composition and its relationship to the soil spatial structure.

Spatial Analysis of Ecological Phenomena

Analysis of spatial pattern and geostatistics are relatively new additions in the field of ecology, yet their popularity is rapidly increasing as techniques are developed to describe the spatial dimension of natural phenomena. Statistical tools such as *t* and *F* tests and analysis of variance (ANOVA) are commonly applied in ecology and function on the basic assumption that individual data points exist independent of one another and are distributed identically. However, observations of dynamic natural

systems reveal that, more often than not, spatial and temporal dependance are major factors affecting ecological relationships (Legendre and Fortin, 1989; Rossi et al. 1992). Spatial dependence, also called autocorrelation, refers to the tendency of data to be more similar the closer they are to one another, and different as the distance between them, or lag distance, increases. The same concept can also be applied temporally in a similar manner, i.e. the variability of sample measurements will increase with time between sampling intervals.

Spatial pattern analysis has become an accepted method for assessing spatial heterogeneity of chemical and mineral content, moisture, and pH in the soil environment (Goodchild and Mark, 1987; Yost et al. 1982; Webster and Oliver, 1990; Mausbach and Wilding, 1991). Soils are spatially complex, with discontinuities between homogeneous zones that create patchy gradients and structures (Legendre and Fortin, 1989). Many different gradients at varied scales have the potential to affect soil spatial structure in intricate ways. Such complexities in heterogeneity are augmented when the spatial structure observed in a given ecological situation is the reflection, not the cause, of different underlying processes that generated it (Borcard et al. 1992). Possible explanations of spatial structure in soils range from large scale associations with surface topography and plant roots (Robertson et al. 1988) to minute spatial scales generated by the interactions between individual microorganisms. Anderson (1988) describes soil biological processes as "a hierarchy of successive levels of organization where macro-, meso- and microfauna influence one another at different scales in the habitat

mosaic." Integration of plant roots into the system introduces yet another spatial component to the hierarchy (Figure 1).

Amidst such a myriad of scales of interaction, how then can one even attempt to parcel out pattern in the soil environment? In this study of soil properties in two contrasting forest stands, two standard methods of geostatistics are used to assess spatial pattern: the semi-variogram and the correlogram. Abundant examples in the current literature describe the theory and application of spatial statistical methods in pedological and ecological settings (Burgess and Webster, 1980; Burrough 1983a, 1983b; Isaaks and Srivastava, 1989; Legendre and Fortin, 1989; Rossi et al. 1992).

Burrough (1983a, 1983b) describes the spatial pattern of soil properties as self-similar, in terms of fractal concepts. Self-similarity means that each portion of a spatial pattern is considered a reduced-scale image of the whole (Mandelbrot, 1967), much like the crystalline structure of points on a snowflake becomes ever finer with increased magnification. The semi-variogram, a plot of sample variance as a function of lag distance (i.e. the distance between sample points in a geographical area), can be used to estimate the fractal dimension of a particular data set (Burrough 1983a, 1983b; Webster and Oliver, 1990) and to determine whether the data are spatially autocorrelated. Correlograms also test the spatial heterogeneity of data as a function of lag distance, but as the name suggests, positive or negative *correlation* is the basis by which spacing, or patch-to-patch distance, between similar and dissimilar samples is measured (Legendre and Fortin, 1989). Significant positive autocorrelation values at a particular lag distance indicate the presence of similar patches of phenomena separated by

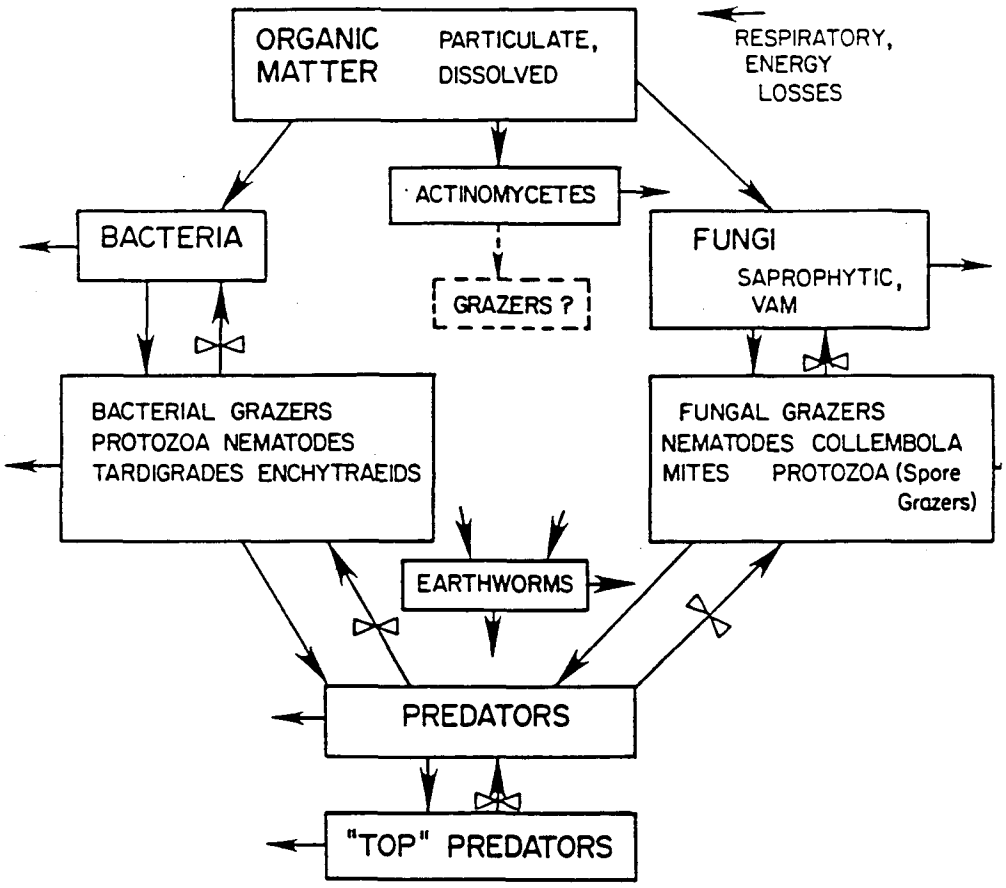


Figure 1. Conceptual model of breakdown of particulate and soluble organic matter in soil ecosystems. Vertical arrows show respiratory energy losses; and arrows with ⋈ show return, information-feedback from trophic levels on lower ones (from Coleman, 1986).

that distance. Negative autocorrelation values for a particular lag distance indicate the presence of patches separated by contrasting inter-patch zones at that lag distance. A plot of positive and negative peaks at relatively the same interval suggests that the variable being tested is distributed uniformly in an alternating patchwork of similar and dissimilar zones (see Legendre and Fortin 1989). Spatial analysis can assess and describe these complex patterns. However, it is up to the ecologist to identify the driving forces creating them.

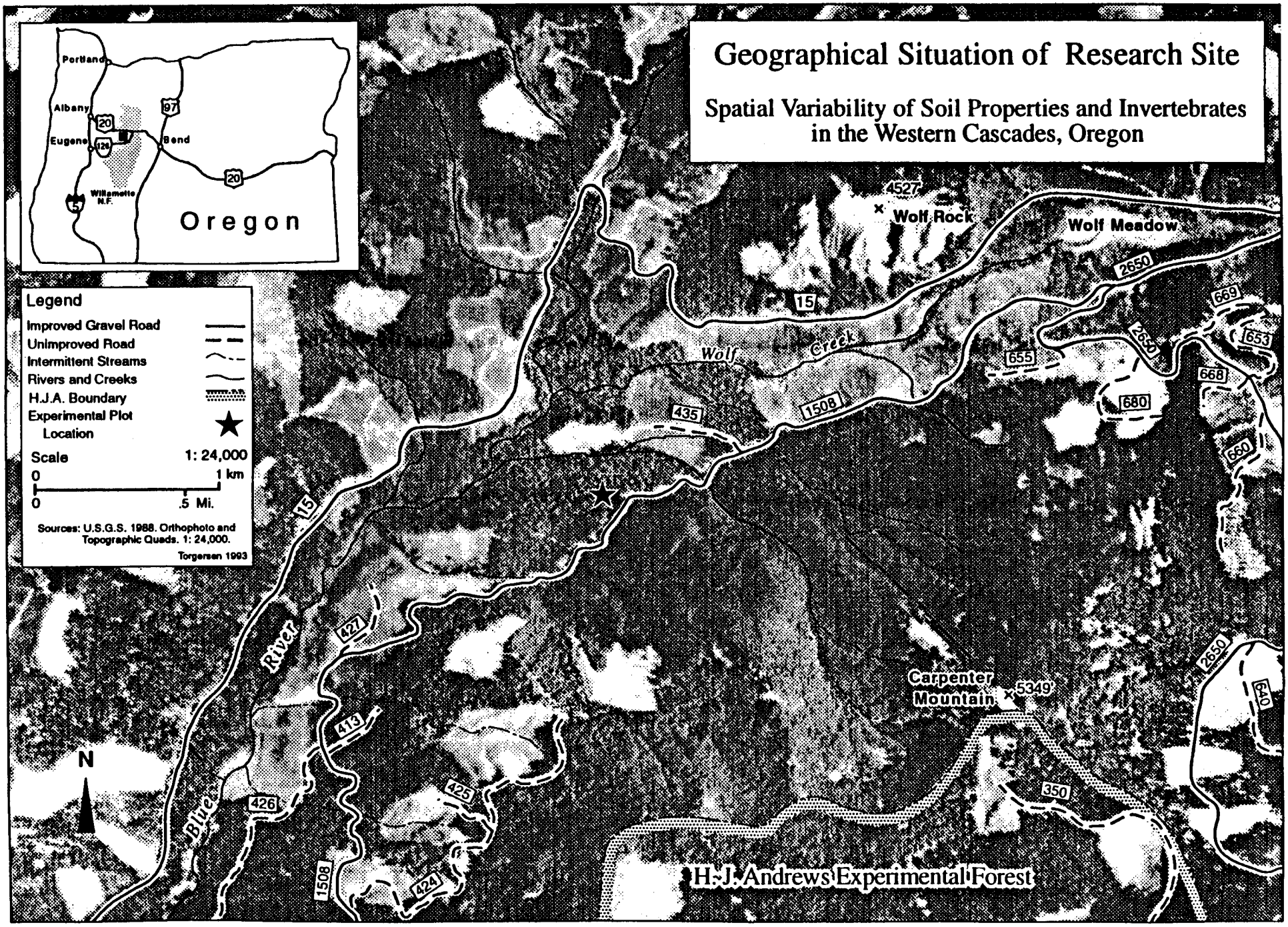
Statistical methods of geographical analysis present a unique picture of the spatial organization of biological phenomena. They test for subtleties that might otherwise go unnoticed using other statistical methods. In contrast to non-areal statistics such as central tendency (means, medians, and modes) and measurement of dispersion (standard deviation and variance), semi-variograms and correlograms allow the examination of the *spatial organization* of contrasting forest stands. In this study of soil organisms and properties, both basic statistics and spatial statistical methods were used to assess the similarities and differences between two compositionally different coniferous forest plots.

II. MATERIALS AND METHODS

Site Description

Research was conducted during late June 1992 outside the northwestern edge of the H.J. Andrews Experimental Forest (HJA), in the Blue River Ranger District, in Oregon's Western Cascade Mountains (122°09'46"W, 44°13'30"N) (Map 1). The HJA is a Long-Term Research Site set aside by the National Science Foundation for interdisciplinary ecological research. It is representative of Northwest coniferous forest habitats with mixed stands of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) with old dominant trees commonly exceeding 400 years in age. In mature conifer stands, gap and understory vegetation consists primarily of rhododendron (*Rhododendron macrophyllum*) patches and young conifers (Dyrness et al. 1974). The forest floor is covered by a thick moss layer and large accumulations of detrital matter such as needles and coarse woody debris.

Climatic conditions in the western Cascade Mountains are typically mild and moist in the winter months, and warm and dry in the summer, with temperatures moderated particularly in the winter by maritime air. Mean annual precipitation between 1951 and 1980 was approximately 220 cm (87 in), with the most precipitation falling in the winter months. The mean maximum summer temperatures over this time period reached as high as


Geographical Situation of Research Site
Spatial Variability of Soil Properties and Invertebrates in the Western Cascades, Oregon
Portland
Albany
Eugene
Bend
Willamette N.F.
Oregon
Legend
Improved Gravel Road
Unimproved Road
Intermittent Streams
Rivers and Creeks
H.J.A. Boundary
Experimental Plot Location
Scale 1: 24,000
0 1 km
0 .5 Mi.
Sources: U.S.G.S. 1988. Orthophoto and Topographic Quads. 1: 24,000.
Torgersen 1993
N
Wolf Rock
4527
Wolf Meadow
Wolf Creek
Blue River
Carpenter Mountain
5349
H.J. Andrews Experimental Forest
15
2650
669
653
655
668
680
660
435
1508
427
413
425
426
424
350
640

Map 1.

28°C (84°F) in July and August and as low as -1°C (30°F) in December and January (McKee and Bierlmaier, 1987).

The research plot is situated at an elevation of approximately 884 m (2900 feet) on a northwest facing slope of about 10 degrees. This particular plot is referred to by T. Spies and M. Goslin (pers. comm.) as a retrospective stand because of its unique burn history and distinctive character. Approximately 80 years ago, the stand experienced a naturally induced burn. The fire passed through the stand at differentiated intensities, leaving higher densities of living old-growth trees in some areas, and lower densities in others (Spies and Goslin, pers. comm.). Currently the stand is a patchwork of composition types: homogeneous, predominantly re-growth forest with a low density of remnant trees; and heterogeneous, primarily old-growth forest with a high density of remnant trees. Re-growth homogeneous areas are characterized by close tree-to-tree spacing, low incoming insolation through a relatively closed canopy, and small gaps. In contrast, old-growth heterogeneous areas frequently are characterized by large gaps that were created by falling remnant trees and receive direct sunlight and rainfall through a patchy forest canopy. Open spaces created by fallen trees are commonly colonized by clumps of rhododendron understory. Tree spacing and age class variation are greater in old-growth heterogeneous areas. The heterogeneous, high-density old-growth sections could be considered mature analogs to modern forestry cuts which selectively leave standing old-growth trees as opposed to clear-cutting (Gillis, 1990). Forest scientists can view this particular stand retrospectively and determine, in principle, what these current selective cuts with mixed densities of old-growth and re-growth will

look like in 80 years. Although there are clearly dissimilarities between a burned forest, such as the research area, and a logged forest, this stand is nevertheless useful as a theoretical model of the spatio-ecological effects of mixed heterogeneous remnant old-growth and homogeneous re-growth conifer forests on soil properties and organisms.

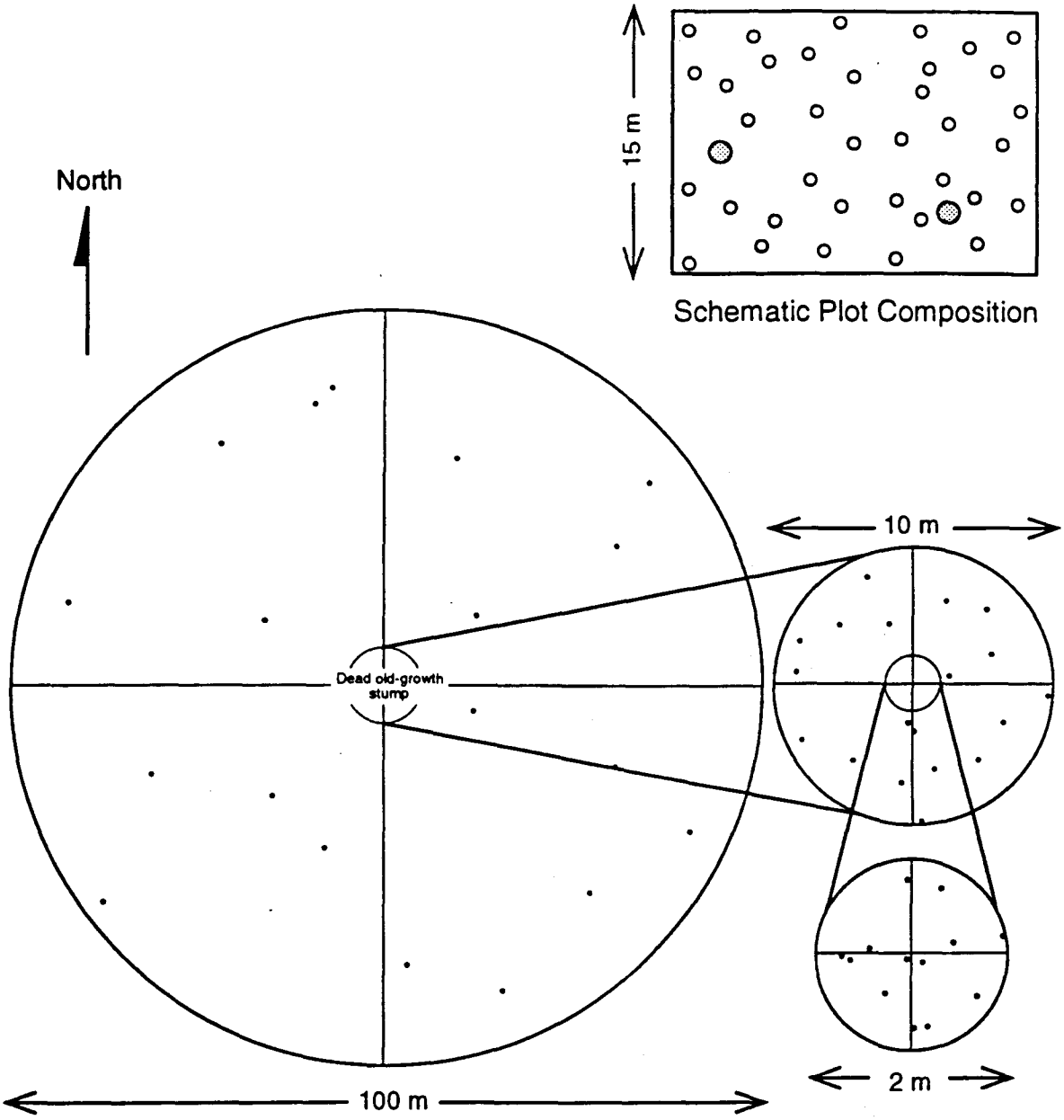
As a research site for the comparison of soil organisms and properties in contrasting forest environments, this stand is particularly useful because it allows for the selection of two adjacent, yet compositionally different, study plots: one with heterogeneous tree spacing, large gap size and a high density of remnant old-growth, and the other consisting predominantly of homogeneous-aged, closely spaced 80-year re-growth. Hypothetically, the only difference between the two plots in the spatial organization of soil properties and fauna should be the result of the treatment areas' contrasting compositional characteristics.

Field Methods

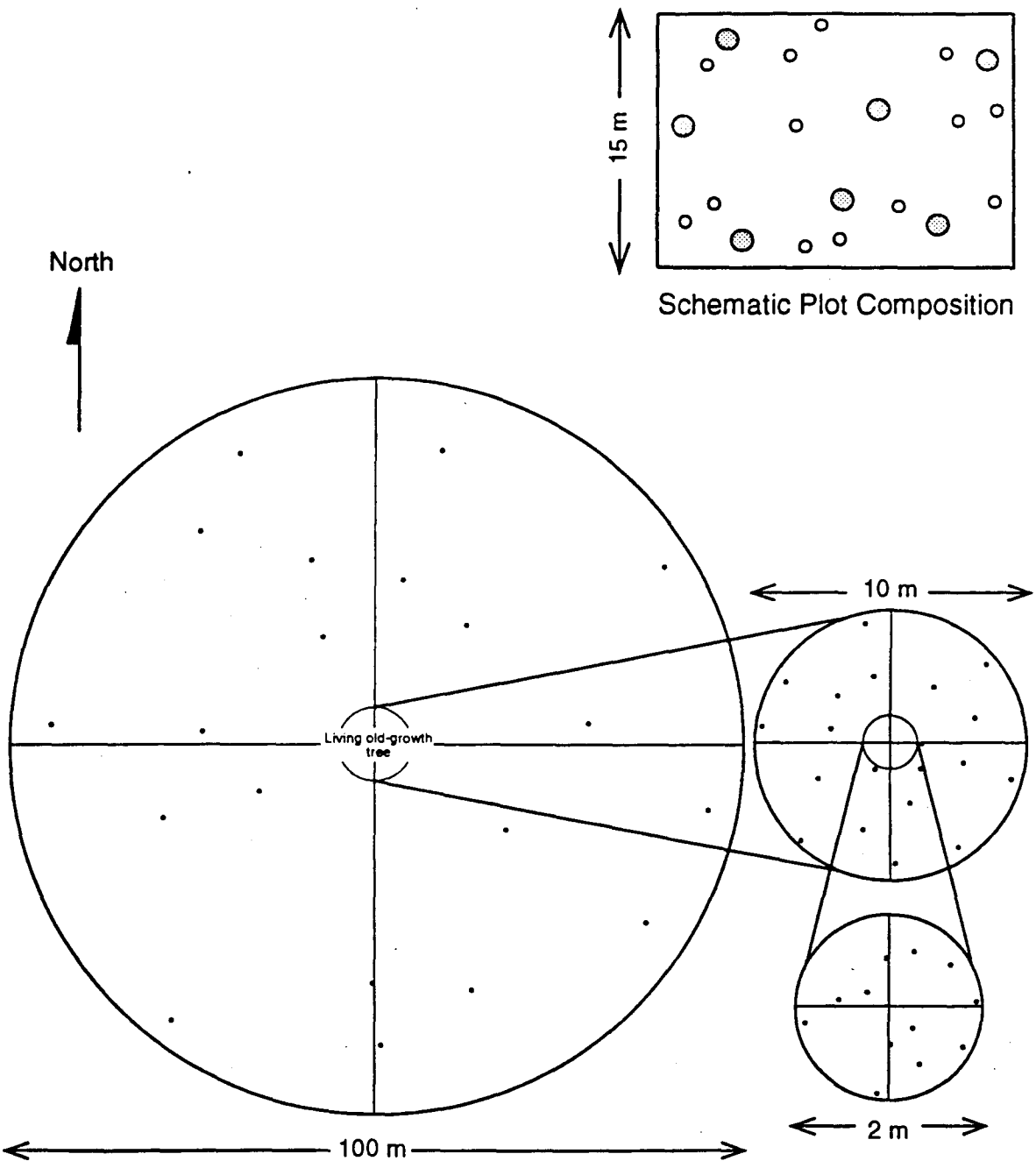
Two circular plots, 100 meters in diameter, were situated adjacently. The first plot, a heterogeneous mixture of old- and re-growth conifers with a high density of remnant trees, was centered around one living old-growth Douglas-fir tree. The second plot, with a relatively homogeneous composition of re-growth, was centered around a decaying old-growth stump. The old-growth heterogeneous plot contained 52 data collection points and the re-growth homogeneous plot contained 51. Sample point locations were generated using randomized grids with cell sizes of 20, 2, and 0.5 m (J.A. Jones, pers. comm). Point locations were converted from

Cartesian to polar coordinates designated by an azimuth in degrees from true North and distance from a center point. The sample points in each plot were organized in nested spatial scales: the first inner 2 meter diameter circle with 12 points, the second inner 10 meter diameter circle with 20 points, and the outer 100 meter diameter circle with 20 points (Maps 2 and 3). The nested spatial design tests for autocorrelation at three scales in order to represent the wide range of patch distances that could be influenced by the spatial organization of vegetation and soils in the forest environment. Such a design produces many more closely-spaced points but is the most efficient way to sample for an anisotropic pattern that may occur at a wide range of scales from 0.5 to 30 m (J.A. Jones, pers. comm.).

Data collection and sampling was completed over a three hour period on June 27, 1992. Sample points were located with measuring tape, to determine distance from center point, and compass, to measure azimuth in degrees from a North bearing. Prior to soil coring, large branches, twigs, and woody vegetation were partially cleared to facilitate sampling. Two adjacent volumetric soil cores were taken at each observation point with a 5 cm x 10 cm cylindrical corer and placed in zip-sealing plastic bags to be stored later at 2°C (35°F) until faunal extraction and analysis following procedures designed by A. Moldenke and C. Roberts (Oregon State University). The cores commonly included both O and A soil horizons, i.e. both organic (detritus, moss, humus) and mineral soil layers; the amount of mineral soil collection depended on depth of organic matter since cores were uniformly 10 cm deep. The first sample was used for chemical analysis (moisture content and pH) and the second for arthropod (insects, mites,



Map 2. Sampling design and point distribution in the re-growth homogeneous plot, containing a low density of old-growth trees. Sample points (n=51) were generated using randomized grids with cell sizes of 20, 2, and 0.5 m. They were located using polar coordinates from a center point (a dead old-growth stump). Schematic stand composition (◎) old-growth conifer, (o) re-growth conifer.



Map 3. Sampling design and point distribution in the old-growth heterogeneous plot, containing a high density of old-growth trees. Sample points (n=52) were generated using randomized grids with cell sizes of 20, 2, and 0.5 m. They were located using polar coordinates from a center point (a living old-growth tree). Schematic stand composition (◎) old-growth conifer, (o) re-growth conifer.

spiders, springtails, etc.) and nematode extraction. Studies by Whitford et al. (1981) indicate that faunal densities are likely to vary diurnally; however, the depth sampled is likely to have encompassed most of these migrations at such favorable temperature and moisture conditions. Notes on O-horizon depth, litter composition and surrounding vegetation were taken during soil sample collection. Temperature was measured with a field thermocouple at 10 cm depth at each observation point in late afternoon on the same day. The samples were weighed in bags the next day in the research facilities of the HJA.

Laboratory Analysis

Analysis of soil moisture and pH was conducted at the Forest Soil Laboratory (O.S.U.). Soil water content was determined gravimetrically: sub-samples of approximately 25 grams were weighed from soil samples set aside for chemical analysis, placed in tin evaporation cups, and dried in an oven for 24 hours at 105°C. Percent water content was calculated by dividing the difference in sample weight before and after oven-drying by the sample weight after drying.

Soil pH in water was measured by adding 60 ml of double de-ionized water to 15 g sub-samples in plastic cups, mixing, and then letting samples settle for 24 hours. The samples were shaken a final time and two pH measurements were taken with a glass electrode Corning electronic pH meter. The average of two pH readings was then calculated to minimize equipment and within-sample variation.

Soil Organism Extraction

Extraction, identification and abundance counts of soil fauna from remaining samples took place two to three weeks following collection in the field at the Forest Insect Laboratory, O.S.U (microarthropods) and at the research facilities in HJA (nematodes). Volumetric samples reserved for mircoarthropod extraction were removed from refrigerated storage and placed in modified MacFadyen high-gradient moisture extraction funnels (Freckman et al. 1986; Merchant and Crossley, 1970; Moldenke, 1993). A high-gradient extractor has a heat lamp positioned over the surface of the soil sample, and the bottom surface, which is retained by a mesh, is exposed to a cool, moist environment to which the organisms migrate downward into a collection vessel containing a mixture of water and fungicide (cyclohexamide 2 g/L). The soil samples remained in extraction funnels for eleven days. After this first phase of the extraction process, the collection vessel containing the organisms suspended in solution was removed and refrigerated at 2° C. The first container was then replaced by a dry one, and extraction of the remaining fauna progressed for four more days. Both collection subsamples were then combined and refrigerated prior to faunal identification and census.

To facilitate counting, the collections were rinsed into glass vials with water, and 1 to 2 ml of mineral oil was added to separate fauna from heavier dirt particles. Upon shaking, the lipophilic microarthropods become suspended in the oil layer and, hence, can be more easily recognized. Some of the organisms, which are lipophobic, remain in the water column and must later be differentiated from other dense soil debris (Moldenke, 1993).

All extracted microarthropods from each observation point were identified and counted visually with a microscope, and then categorized into guilds by size and functional feeding group, i.e. fungivores, herbivores and predators. Taxonomic accuracy in the identification of the soil organisms was highly dependent on the abundance of organisms in immature stages since many of the early metamorphic forms have not yet been described. The census and identification process was also occasionally confounded by excess soil debris which can fall into the collection vessel, obstructing the view through the microscope.

Nematodes (minute soil-dwelling worms) were extracted at the HJA field station from soil samples remaining after pH and water content testing using the Baermann water column filter technique (Baermann, 1917). A nematode filter consists of a plastic funnel, fine cloth mesh, and a glass collection vial; the soil sample is placed in the funnel on the cloth mesh which reduces soil accumulation in collection vial. Water is added to partially suspend the soil and allow nematodes to wriggle downward through the mesh and into the vial. One or, if possible, two subsamples each weighing 20 grams were taken from each soil sample and left at ambient temperature in extractors for forty-eight hours. The total census of nematodes was conducted the following day by pouring and washing contents of each collection vial onto a grid-marked petri dish and counting the individuals in each quadrant. When two extractions per sample were taken, the subsample totals were averaged. Nematode density was expressed as number per dry gram of soil.

Statistical Analysis

Totals for census, species richness, and conversion to biomass were calculated for faunal functional groups, as were descriptive statistics for O-horizon depth, temperature, soil moisture, and pH, from raw data entered into a Quattro Pro 4.0 spreadsheet (Borland Inc.). Using spreadsheet software, bivariate correlation with regression analysis was tested between soil properties, total fauna, biomass and average nematode density.

Prior to spatial statistical analysis, potential confounding large scale spatial surface trends (anisotropy) were assessed along north-south and west-east axes. Such trends might result from the overall orientation of plots on gradients of slope or moisture and tend to mask finer scale spatial structures quantified by the semi-variograms, causing misinterpretation and inaccuracy in analysis (Webster and Oliver, 1990; Legendre and Fortin, 1989).

Semi-variograms and correlograms (Legendre and Fortin, 1989) testing for patterns of spatial variability in pH, temperature, O-horizon depth, soil moisture, nematode density and faunal census of biomass were produced for each plot. The raw semi-variance is a function of the overall variance in the data set. To make the comparison of plots with different variables easier, the semi-variograms were standardized by dividing the semi-variance at each distance class by the overall sample variance following Rossi et al. (1992). The autocorrelation coefficient, *Moran's I*, was calculated in correlograms to measure autocorrelation. Semi-variance and autocorrelation were plotted as a function of increasing distance classes up to 30 m to produce semi-variograms and correlograms, respectively. Measurements of variance and correlation at distances greater than 2/3 of the

sampling radius (i.e. 30 m) were disregarded because the number of pairs of points used in computation decreases as distance increases (Legendre and Fortin, 1989). Semi-variograms and correlograms were generated according to methods and formulae outlined in Legendre and Fortin (1989). Computation was completed on the Sun Workstation in the U.S.F.S. Forestry Sciences Laboratory, Corvallis, Oregon using C programs written by B. Marks and J.A. Jones.

The first series of semi-variograms exhibited erroneous peaks in variability at mid-range lag distances for soil fauna and properties in the old-growth plot. The first computer program that generated the semi-variograms used equal sample sizes for each distance class rather than equal distance classes, resulting in an uneven distribution of calculated variance/autocorrelation coefficients by distance. The statistical program was corrected.

III. RESULTS

Descriptive Statistics

The faunal census and biomass data, and the soil property means both reflect statistical similarity between the two compositionally different study plots (Tables 1 and 2). Total counts of microarthropods for the old- and re-growth plots were 16,747 and 16,683 (per 20 liters of soil), respectively (Table 2 and Figure 2). Collectively, 125 different taxa of microarthropods were found in both plots. Broken down into functional groups, this species richness figure represents 12 species of Collembolla, 52 oribatid mites, 9 predaceous mites, 2 fungivorous prostigmatid mites, 7 herbaceous mesoarthropods, 25 predaceous mesoarthropods, and 18 kinds of fungivorous mesoarthropods. Species richness figures for the old- and re-growth plots are 103 and 106, respectively.

The biomass data for microarthropod guild composition were also similar across the two plots, with the exception of much higher biomass, especially of fungivorous mesoarthropods, such as click beetle larvae (Elateridae), in the old-growth plot. The difference in total biomass figures between the two plots, 641 mg in the re-growth and 928 mg in the old-growth, is most likely connected with the higher numbers of fungivorous mesoarthropods found in the old-growth soil samples (Table 2 and Figure 3). These organisms, such as the click beetle larvae, although not very densely

distributed, are some of the largest arthropods in body size and make up a disproportionately large percentage of soil arthropod biomass.

The average density of nematodes/gram of soil differed between the two plots, with a mean of 2.21 in the old-growth heterogeneous plot and 1.39 in the re-growth homogeneous plot. However, standard deviation statistics indicated no significant difference between the two treatment areas (Table 2).

The two forest plots have similar values for all soil properties. The mean values and standard deviation (s) and coefficient of variance (CV) of temperature, O-horizon depth and pH in the old- and re-growth plots are nearly identical in the two plots. Percent soil moisture is somewhat higher in the re-growth plot, yet once again the high standard deviation values in both plots restrict assumptions on moisture content in the contrasting soil environments (Table 1 and Figure 4).

Bivariate correlations and regression analysis between the four soil properties, faunal census, biomass and average nematode density revealed no distinct relationships. The strongest correlation (r^2= 0.32) was observed between pH and water content, where acidity increased with greater soil moisture. Tests for Bonferroni adjusted significance were not conducted.

There are some indications that the lower pH values are also directly correlated with woody debris content in the samples. Comparison of pH means between samples taken near, in contrast to distant from decaying logs revealed lower pH values for samples associated with decaying wood. This assumption is also supported by tests that exhibited positive correlation between pH value and sample weight prior to drying. Sample weight is

largely dependent on woody debris versus heavy mineral soil content, such that lighter samples tend to contain more decaying organic matter.

Analysis of Spatial Pattern

Tests for anisotropy revealed slight increasing gradients to the southwest in soil moisture and microarthropod biomass data in both plots. The pH in the old-growth plot also decreased to the west, most likely in conjunction with the moisture gradient to the southwest (Figures 5 and 6). These trends may reflect an underlying environmental gradient towards a partially dry streambed southwest of the plots. Although perceptible, these spatial trends were considered to have an insignificant ($r^2 < 0.1$) effect on semi-variograms, and no attempt was made to correct for them (Figures 5-11).

Although average invertebrate numbers and soil properties are nearly identical in both plots, their spatial patterns are different. Semi-variogram and correlogram results indicate contrasting patterns of short and long range spatial heterogeneity at two distance classes in the two plots. Spatial autocorrelation analysis revealed more pronounced short range (approximately 7 m) variability in the predominantly re-growth plot than in the plot containing a high density of old-growth conifers. Long range variability at approximately 20 m, indicating greater patch-to-patch spacing, were better defined in the high density old-growth plot.

pH

Measurements of soil pH ranged from 3.8 to 5.5 with a mean of 4.9 (s=0.5, CV=0.1) in the old-growth plot, and 3.6 to 6.0, mean 4.7 (s=0.6, CV=0.1), in the re-growth homogeneous stand (Table 1). Semi-variograms of soil pH indicate that the property is spatially autocorrelated in both plots. Standardized semi-variance increases from low variability at a 0 m lag to a peak at 20 m (Figures 12a and 12b). Short range heterogeneity is lower (semi-variance = 1.2 at 10 m) than long range variability (semi-variance = 2.4 at 21 m) in the old-growth heterogeneous plot (12b), whereas the re-growth study area (12a) has standardized semi-variance of 1.5 at 8 m and 1.8 at 20 m.

Correlograms provide a more informative picture of the spatial autocorrelation of pH in the two study areas. The old-growth heterogeneous plot (Figures 12b, 12d) shows little or no variation at distances < 20 m, and suggests widely spaced (17 m) smaller patches. Less short range variation in this plot suggests that there is little influence in the old-growth heterogeneous plot from short inter-patch spacing. In contrast, the re-growth homogeneous plot shows more short range variation at 5-6 m (Figure 12a), significant small patches with a diameter <1-2 m, spaced at approximately 10 m, with 5 m from patch center to inter-patch space. For clarification, high positive correlation (Moran's I>0) indicates patches of similar pH values separated by that distance, and, conversely, negative correlation (Moran's I<0) indicates a different patch of pH values.

Soil Moisture

Values of percent soil moisture by weight ranged from 11-60% with a mean of 34% (s=10, CV=0.3) in the old-growth heterogeneous plot, and 19-67%, mean 43% (s=10, CV=0.3), in the homogeneous re-growth stand (Table 1). Semi-variograms and correlograms 13a,b,c,d demonstrate that soil moisture is strongly spatially autocorrelated with similar underlying patterns of heterogeneity existing in both plots. Discordances, however, are apparent especially in correlograms 13c and 13d which show differentiated significance of short and long range patterning between the two plots.

Semi-variograms 13a and 13b exhibit analogous patterns of relatively low variability at short distance classes that increase to a peak at $\pm$20 m and then drops off at 30 m. Short range variance (0-9 m) is less pronounced in the old-growth heterogeneous stand; however, peaks in this plot at +20 m distances exceed those in the homogeneous re-growth plot. Correlograms 13c and 13d support the general shape of their paired semi-variograms, yet yield more information on the contrasting nature of spatial pattern of soil moisture in the two study plots. In Figure 13c the negative correlation (Moran's I= -0.6) at an approximate 7 m distance class illustrates pronounced inter-patch heterogeneity and is followed by peaks in moisture homogeneity at 14, 21 and 28 m lags, thereby signifying the influence of a patch-to-patch distance of 7 m. The corresponding correlogram (13d) for the old-growth plot shows a less significant negative correlation (Moran's I= -0.3) at 7 m lags. The sharp peaks at 20 m in semi-variogram 13b, which suggest the effect of greater between-patch spacing, are not significantly defined in correlogram 13d.

O-Horizon Depth

Basic statistics for O-horizon depth in the two study areas differ only slightly. However, analysis of their spatial dimensions shows that they are, indeed, quite dissimilar. Patterns in short range patch-to-patch spacing are more pronounced in the re-growth homogeneous plot. The range of depths for the old-growth heterogeneous plot was 0-8 cm, with a mean of 2.8 cm (s=1.7, CV=0.3). For the re-growth homogeneous stand, range was 0-5 cm, with a mean of 3.0 cm (s=1.3, CV=0.3) (Table 1). Semi-variogram results between the two plots are strikingly different (Figures 14a,b). Both figures portray spatial autocorrelation of O-horizon depth, yet their patterns are nearly the inverse of one another. Semi-variogram 14a exhibits high variance (CV=1.9) at short distance classes up to approximately 7 m, and relatively low variance at +20 lag distances. In contrast, semi-variogram 14b has low variance values in the short range that increase to a peak at approximately 20 m.

Correlograms of soil O-horizon depths, like the semi-variograms, differ significantly between plots (Figures 14c,d). Correlogram 14c of the homogeneous re-growth area displays peak positive correlation at approximately 7 meters. Short range inter-patch spacing of approximately 7 m is well-defined in the re-growth study area. An anomalously high peak in positive correlation (Moran's I=0.6) occurs at 15 meters in the old-growth heterogeneous plot, resembling the rise in variance displayed by its paired semi-variogram 14a. Such a dramatic increase in correlation is an indication of strong underlying spatial pattern at an approximate 16 m scale.

Temperature

Both basic statistics and spatial analysis revealed very little difference between measurements of temperature in the two compositionally contrasting treatment areas. Temperature values ranged from 11 to 21 C° with a mean of 15.4 C° (s=1.6, CV=0.1) in the old-growth heterogeneous area. Results from the re-growth plot vary only slightly with a mean of 15.6 C° (s=1.4, CV=0.1) (Table 1). Semi-variograms 15a,b and 8a exhibit nearly identical spatial patterns of high short range heterogeneity, after which variance increases gradually to a relatively low (CV=1.3) peak at 20 m. Peak short range variance in the re-growth plot at 2 meters (CV=3.8) exceeds that in the old-growth heterogeneous plot at similar lags (CV=3.2). The patterns of high variance at short range, and low variance at longer lags that are demonstrated by these semi-variograms differ markedly from the other variogram results in this study.

Correlograms 15c and 15d mirror semi-variogram results, such that the strongest patterning is present at shorter lag distances. Inter-patch spacing in correlogram 15c is only slightly less (as the peak of positive correlation at 3 m reflects) in the re-growth homogeneous plot compared to the positive peak at 5 m in correlogram 15d of the old-growth heterogeneous plot. The re-growth homogeneous area, however, has slightly more defined short range patterns of variability with positive and negative peaks in correlation of 0.26 and -0.37.

Soil Fauna

Spatial analysis indicates underlying autocorrelation among data for microarthropod census, biomass and nematode density in both treatment areas. Patterns of short range heterogeneity are only slightly more pronounced in correlograms from the re-growth homogeneous plot, except in the case of nematode density which is more variable at short distance classes in the old-growth homogeneous treatment area. In general, spatial analysis results of the soil faunal properties were difficult to interpret without calculating confidence intervals that show significance levels.

Basic statistics of microarthropod census are strikingly similar in both plots. A total of 16,747 individuals were collected from 52 samples at the old-growth heterogeneous site, with a sample range of 49-750, and mean of 322 (s=180, CV=0.6). In comparison, the re-growth homogeneous plot, consisting of 51 samples, yielded 16,683 individuals, with a sample mean of 327 (s=200, CV=0.6) (Table 2). Semi-variogram results for faunal census are differentiated between plots. Figure 16a exhibits peak heterogeneity (CV=1.3) at 4 m lag after which variance levels remain relatively constant and increase only after 20 m. A steep slope of increasing variability is portrayed in the old-growth heterogeneous plot, semi-variogram 16b. Variance rises to a higher peak (CV=1.9) at approximately 21 m. Correlograms 16c and 16d indicate significant negative correlation (Moran's I= -0.4) at short inter-patch distances (4 m) in the re-growth homogeneous plot, and less pronounced short range positive and negative patterns in the old-growth treatment area. Correlogram 16c also shows high (Moran's I= 0.4) positive correlation at 15 m, which is lacking in 16d. The old-growth

heterogeneous plot (16d), however, has a sharp peak in negative correlation (Moran's I= -0.5) at an approximate 23 m inter-patch distance. Aside from more defined short range patterning in the re-growth homogeneous plot, and possibly marked long range patch spacing in the old-growth plot, results of spatial analysis for faunal census are difficult to interpret due to their irregularity.

Biomass results are more variable than soil property and census data (old-growth CV=0.7 and re-growth CV=0.9). Maximum and minimum biomass figures for the old-growth heterogeneous plot ranged from 0.4 mg to 50 mg per sample with a mean of 18 mg (s=13). The re-growth homogeneous numbers ranged from 2 mg to 53 mg with a mean of 13 mg (s=11) (Table 2). Spatial analysis results are very irregular between plots, and the biomass results bear little resemblance to census patterns. Semi-variogram 17a exhibits decreasing heterogeneity with distance, whereas 17b of the old-growth heterogeneous plot demonstrates increasing variability with distance. Correlogram 17d representing the old-growth plot has consistent positive and negative correlation of equal magnitude (Moran's I= 0.3) at 7 m and 15 m lags, indicating an approximate 7 m patch-to-patch spacing. Such patterning is not present in correlogram 17c, although a higher peak in negative correlation (Moran's I= -0.5) does occur at 4 m lag distance. After 20 m, correlation in 17c reaches 0.0, thereby mirroring its paired semi-variogram 17a with low heterogeneity at high lag distances.

Nematode numbers are the most variable of the three faunal measurement classes. The density of nematodes per sample ranged from 0 to 10, with a mean of 2.2 (s=2.4, CV=1.1) per gram of soil in the old-growth

heterogeneous plot, and from 0 to 11, with a mean of 1.4 (s=2.2, CV=1.6) in the re-growth homogeneous study area (Table 2). Analysis of the spatial dimension of nematode numbers revealed more significant short range (approximately 7 m) patterning in the old-growth heterogeneous plot. Semi-variograms 18a and 18b reflect different underlying spatial structures in the two contrasting treatment areas. Variance increases steeply from 0 m to a prominent peak at 7 m in 18b, whereas in 18a, heterogeneity decreases from relatively high initial variability at 0 m (CV=1.7) to a trough at 4 m. Both semi-variograms exhibit sharp decreases in variance at >10 m and reach a trough at 20 m. Correlograms 18c and 18d indicate much clearer patterns of negative correlation at 7 m (Moran's I= -0.6), 20 m (Moran's I= -0.4) and 30 m (Moran's I= -0.6) in the old-growth heterogeneous plot (14b). Interestingly, relatively smaller and probably less significant peaks in positive correlation occur at 10, 20, and 30 m lag intervals in the re-growth correlogram 18c. This suggests that patch-to-patch (or inter-patch to inter-patch) spacing is perhaps similar in the two stand compositions, yet more distinct in the old-growth heterogeneous treatment area. The more defined short range patterning in the old-growth heterogeneous plot is anomalous compared to results for all properties tested in which short range spatial structure was relatively more expressed in the re-growth homogeneous plot.

Table 1. Means and standard deviations of soil properties in two adjacent plots, a heterogeneous composition of old- and re-growth conifers, and a homogeneous, predominantly re-growth stand, in the Blue River Drainage of the Western Cascades, Oregon. Soil moisture is percentage by weight.

Soil property		old-growth heterogenous	re-growth homogeneous
	n	52	51
pH	range	3.8-5.5	3.6-6.0
	mean	4.9	4.7
	std.dev.	0.5	0.6
	C.V.	0.1	0.1
moisture (%)	range	11-60	19-67
	mean	34	43
	std.dev.	10	10
	C.V.	0.3	0.3
O-horizon	range	0-8	0-5
depth (cm)	mean	2.8	3
	std.dev.	1.7	1.3
	C.V.	0.6	0.4
temperature (C)	range	10.5-20.4	12.3-19.0
	mean	15.4	15.6
	std.dev.	1.6	1.4
	C.V.	0.1	0.1

Table 2. Abundances of soil fauna by guild in two adjacent plots, a heterogeneous composition of old- and re-growth conifers, and a homogeneous, predominantly re-growth stand, in the Blue River Drainage of the Western Cascades, Oregon. Arthropod numbers are individuals collected from old-growth (n=52) and re-growth (n=51) plots.

		old-growth heterogenous		re-growth homogeneous	
Faunal Group		census	biomass(mg)	census	biomass(mg)
Totals					
Arthropods					
springtails		3213	40	2410	33
oribatids		9153	112	9816	107
predaceous mites		218	18	319	25
prostigmatid mites		3899	1	3872	1
herbivorous mesoarthropods		35	24	27	15
predaceous mesoarthropods		115	98	167	155
fungivorous mesoarthropods		114	635	72	306
Grand Totals		16747	928	16683	641
No. of species		103		109	
Faunal Density					
Arthropods (per ml soil)	range	49-750	0.4-50	30-886	2-53
	mean	322	18	327	13
	std.dev.	180	13	200	11
	C.V.	0.6	0.7	0.6	0.9
Nematodes (no./g soil)					
	range	0-10		0-11	
	mean	2.2		1.4	
	std.dev.	2.4		2.2	
	C.V.	1.1		1.6	

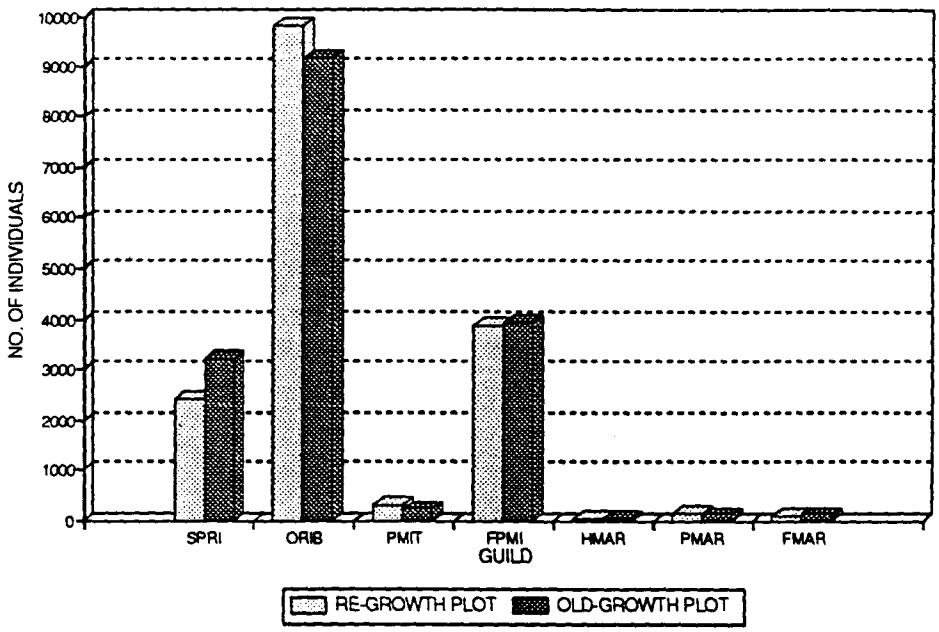


Figure 2. Total faunal counts. Composition by guild. From two experimental plots: an old-growth heterogeneous stand with a high density of old-growth trees; and a re-growth homogeneous stand with a low density of old-growth trees. (SPRI) springtails, (ORIB) oribatid mites, (PMIT) predaceous mites, (FPMI) fungivorous prostigmatid mites, (HMAR) herbivorous meso-arthropods, (PMAR) predaceous mesoarthropods, (FMAR) fungivorous mesoarthropods.

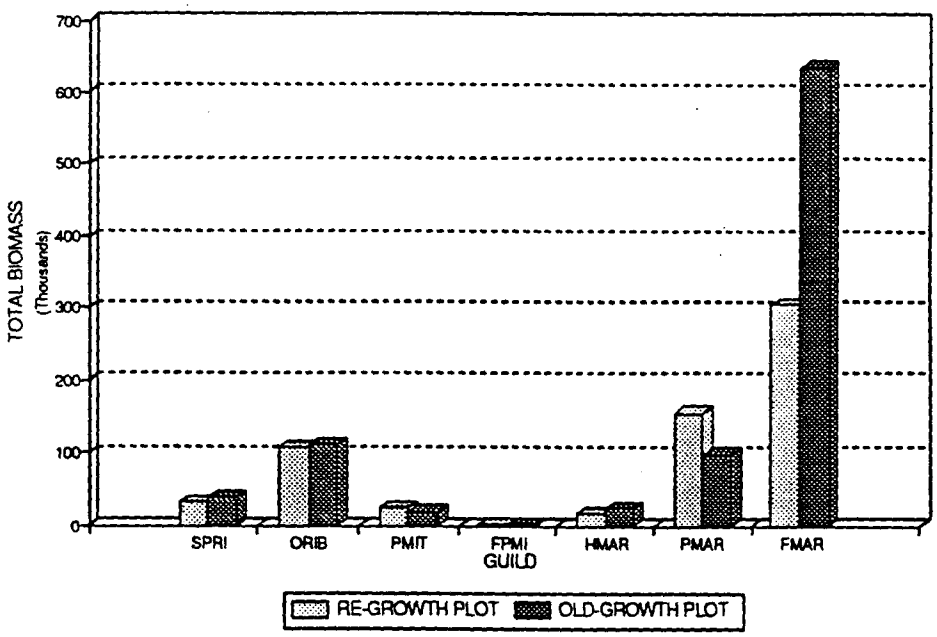


Figure 3. Total faunal biomass. Composition by guild. From two experimental plots: an old-growth heterogeneous stand with a high density of old-growth trees; and a re-growth homogeneous stand with a low density of old-growth trees. (SPRI) springtails, (ORIB) oribatid mites, (PMIT) predaceous mites, (FPMI) fungivorous prostigmatid mites, (HMAR) herbivorous meso-arthropods, (PMAR) predaceous mesoarthropods, (FMAR) fungivorous mesoarthropods.

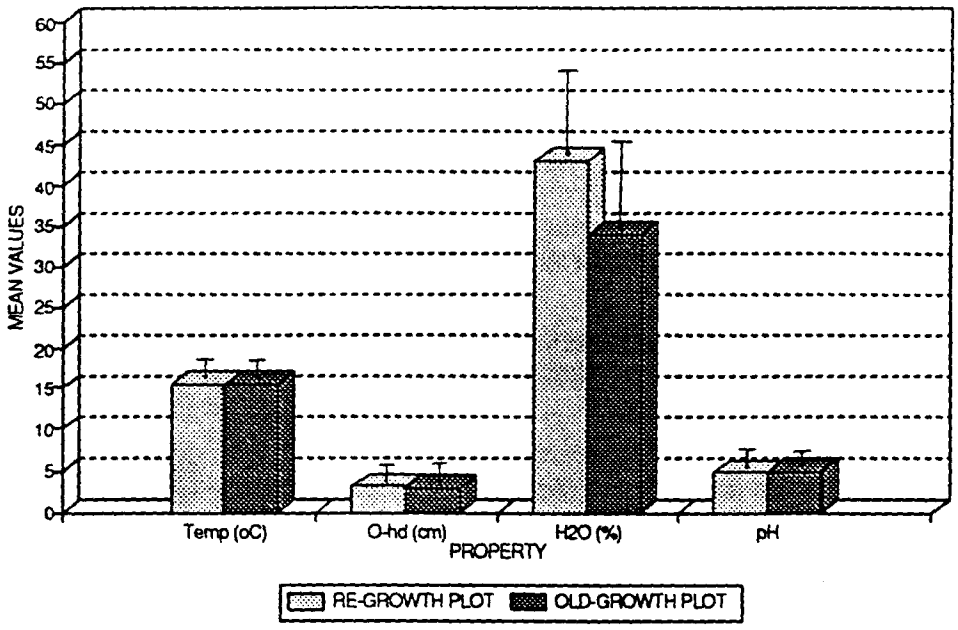


Figure 4. Soil property means. From two experimental plots: an old-growth heterogeneous stand with a high density of old-growth trees; and a re-growth homogeneous stand with a low density of old-growth trees. Error bars show standard deviation.

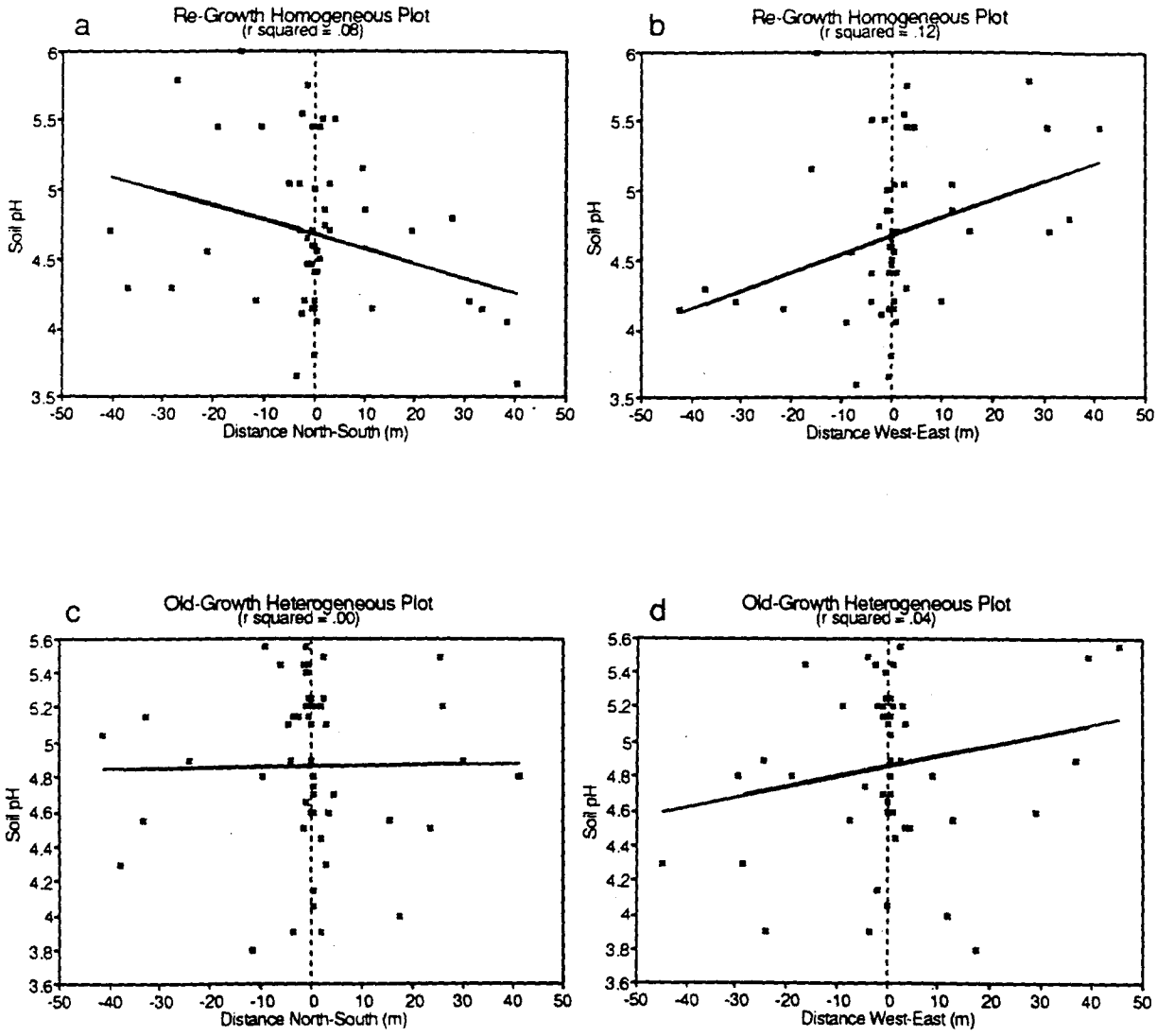


Figure 5. Surface trend bias checks of pH for anisotropy in two differentiated conifer stands. (a) re-growth homogeneous plot, north-south axis. (b) re-growth homogeneous plot, east-west axis. (c) old-growth heterogeneous plot, north-south axis. (d) old-growth heterogeneous plot, east-west axis.

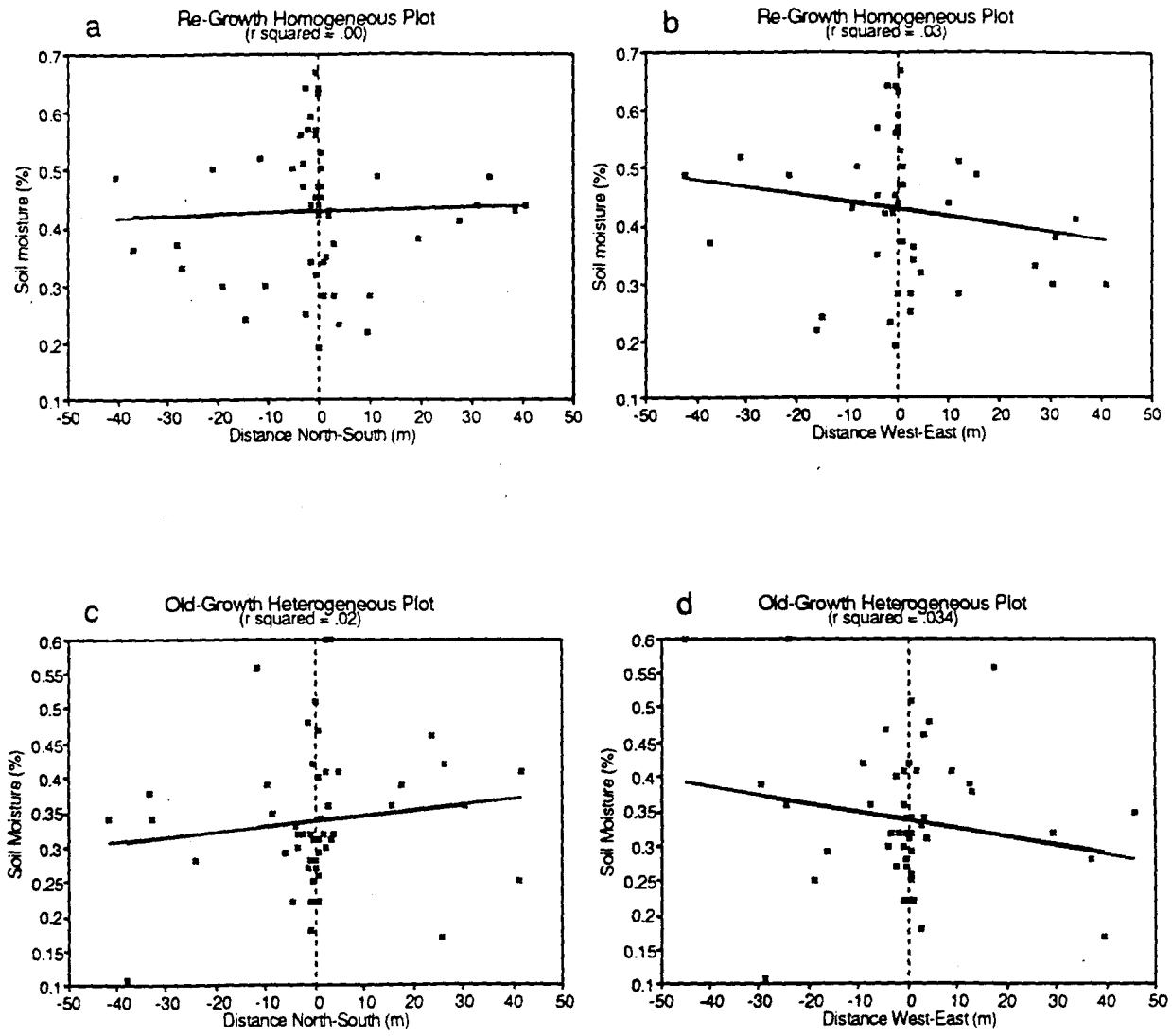


Figure 6. Surface trend bias checks of soil moisture (%) for anisotropy in two differentiated conifer stands. (a) re-growth homogeneous plot, north-south axis. (b) re-growth homogeneous plot, east-west axis. (c) old-growth heterogeneous plot, north-south axis. (d) old-growth heterogeneous plot, east-west axis.

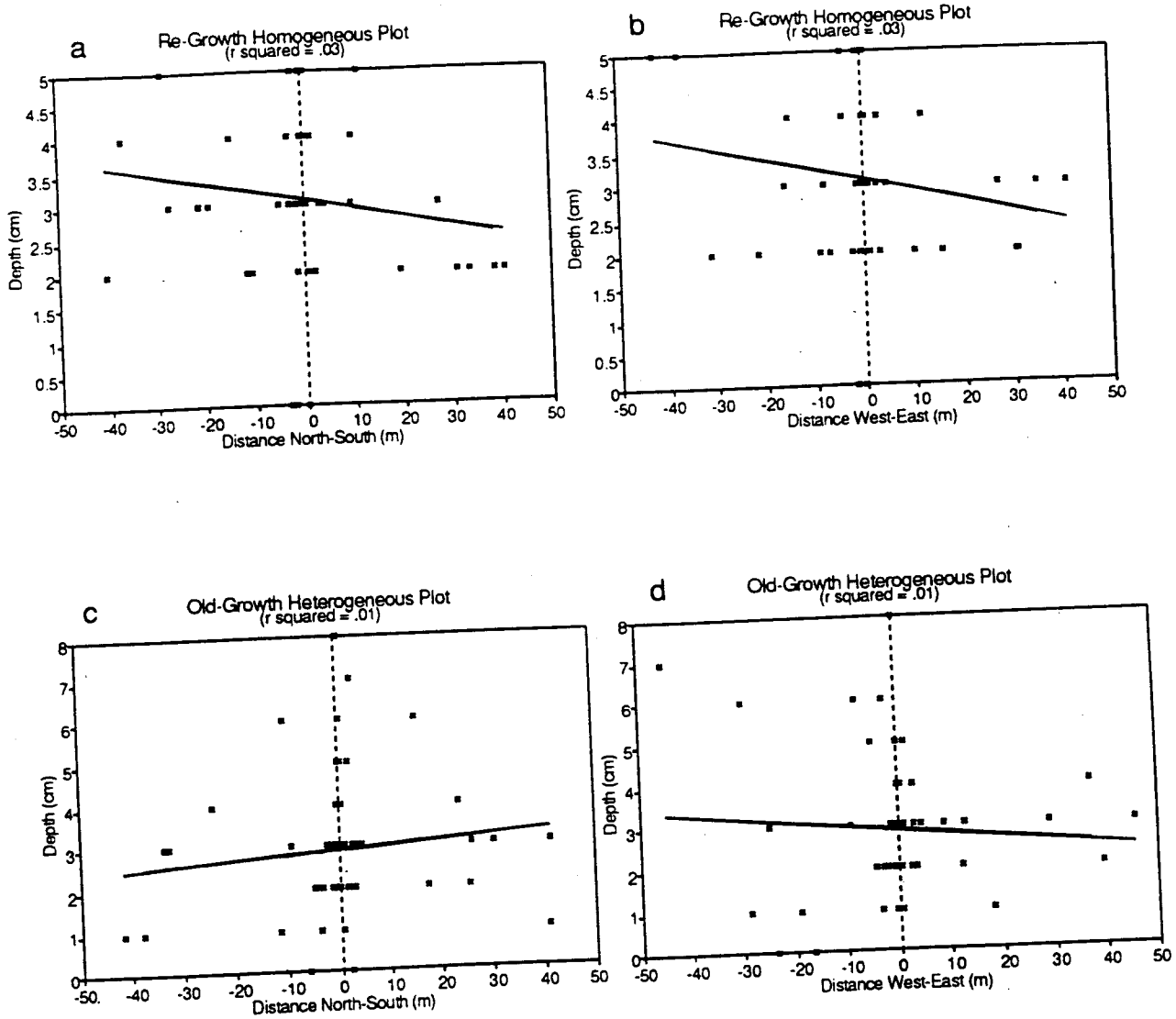


Figure 7. Surface trend bias checks of O-horizon depth for anisotropy in two differentiated conifer stands. (a) re-growth homogeneous plot, north-south axis. (b) re-growth homogeneous plot, east-west axis. (c) old-growth heterogeneous plot, north-south axis. (d) old-growth heterogeneous plot, east-west axis.

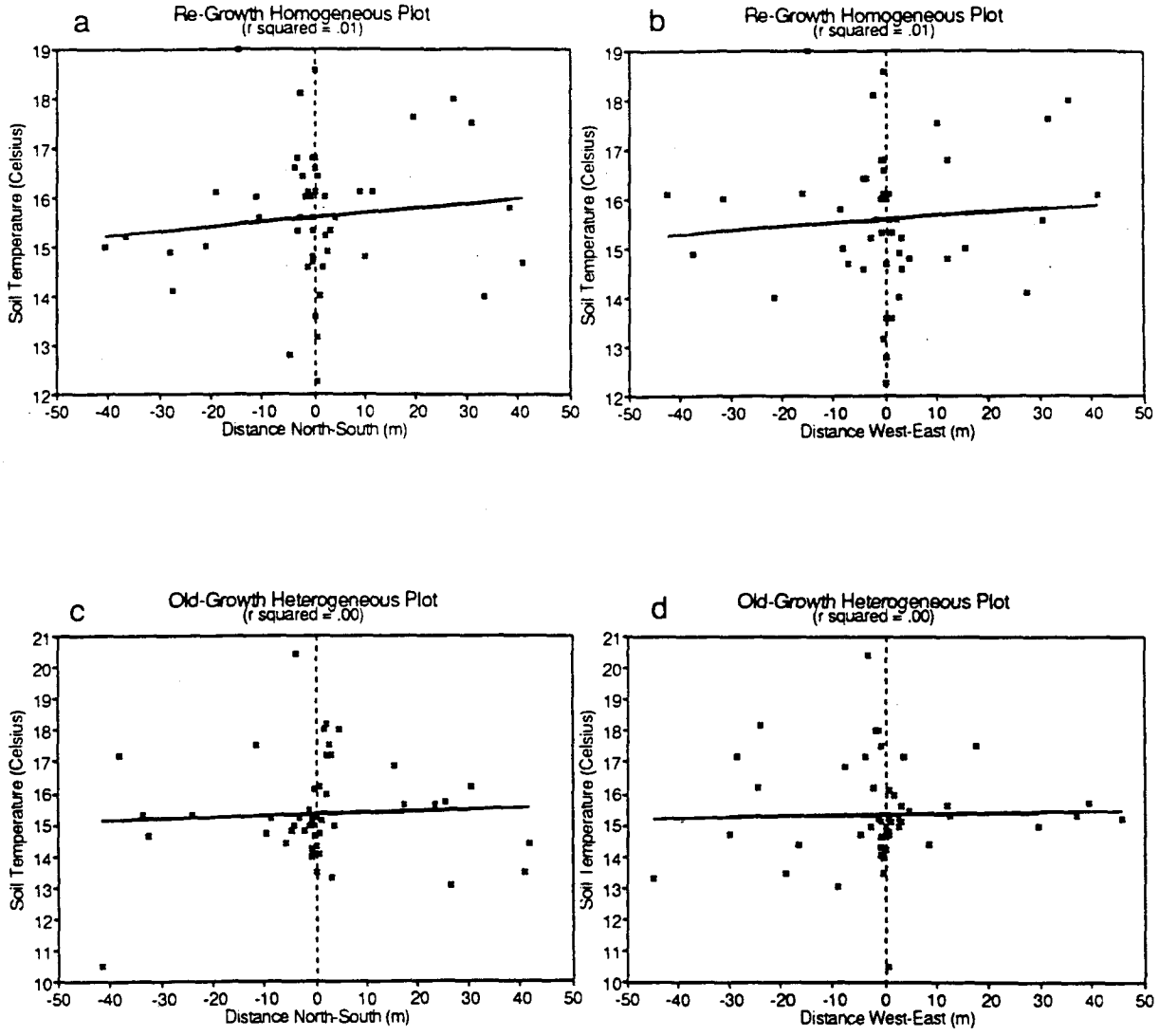


Figure 8. Surface trend bias checks of soil temperature for anisotropy in two differentiated conifer stands. (a) re-growth homogeneous plot, north-south axis. (b) re-growth homogeneous plot, east-west axis. (c) old-growth heterogeneous plot, north-south axis. (d) old-growth heterogeneous plot, east-west axis.

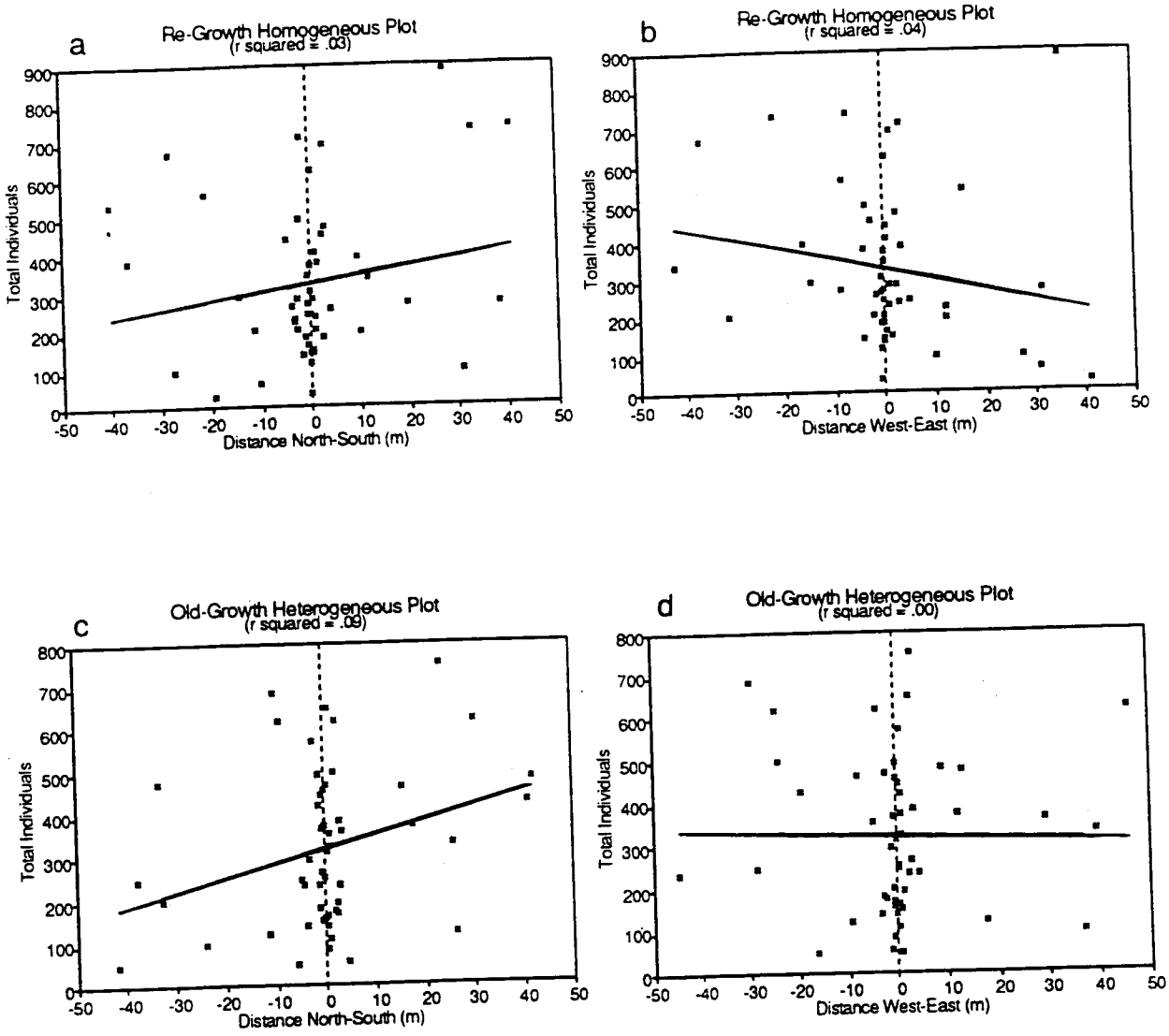


Figure 9. Surface trend bias checks of faunal census for anisotropy in two differentiated conifer stands. (a) re-growth homogeneous plot, north-south axis. (b) re-growth homogeneous plot, east-west axis. (c) old-growth heterogeneous plot, north-south axis. (d) old-growth heterogeneous plot, east-west axis.

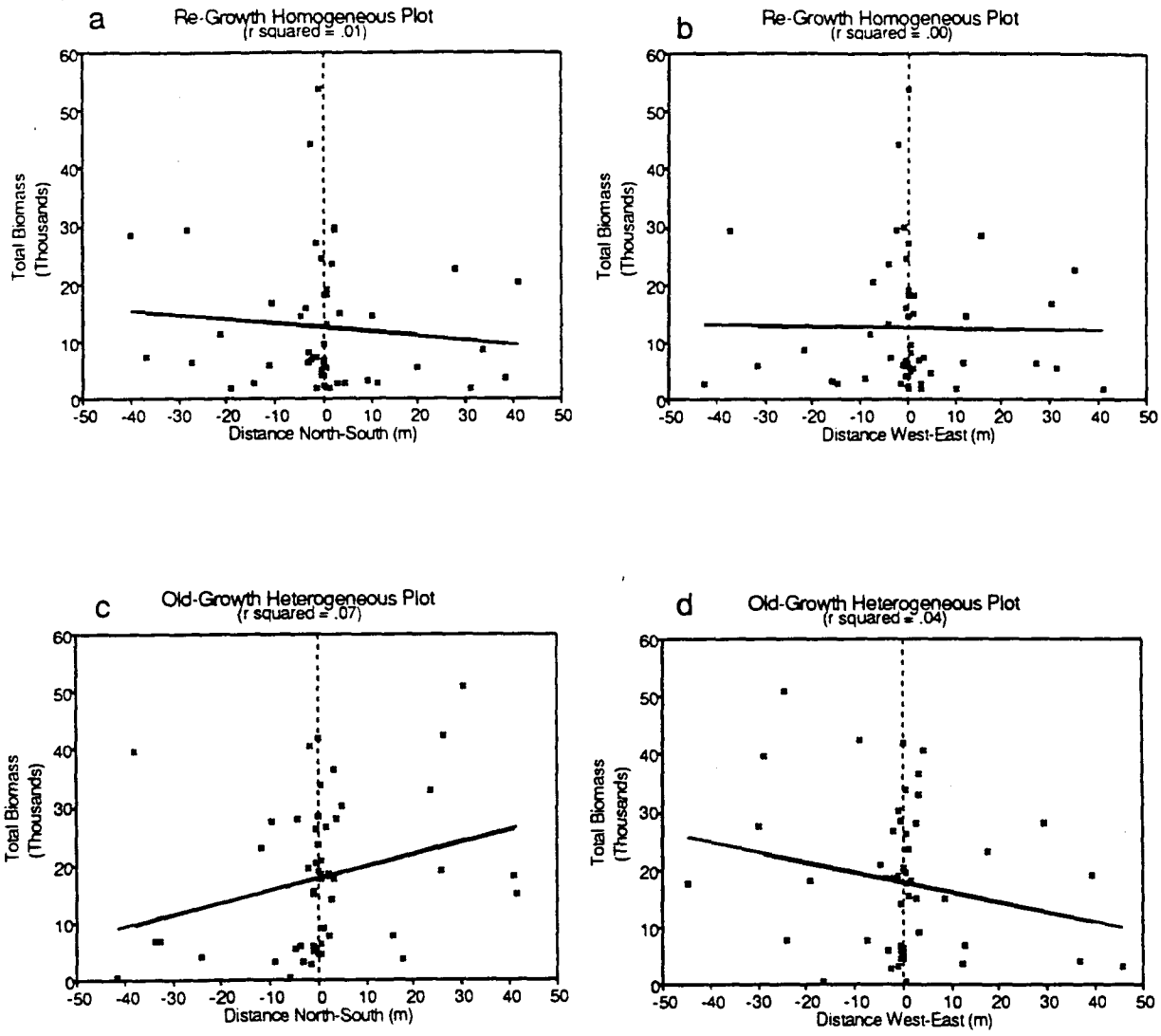


Figure 10. Surface trend bias checks of faunal biomass for anisotropy in two differentiated conifer stands. (a) re-growth homogeneous plot, north-south axis. (b) re-growth homogeneous plot, east-west axis. (c) old-growth heterogeneous plot, north-south axis. (d) old-growth heterogeneous plot, east-west axis.

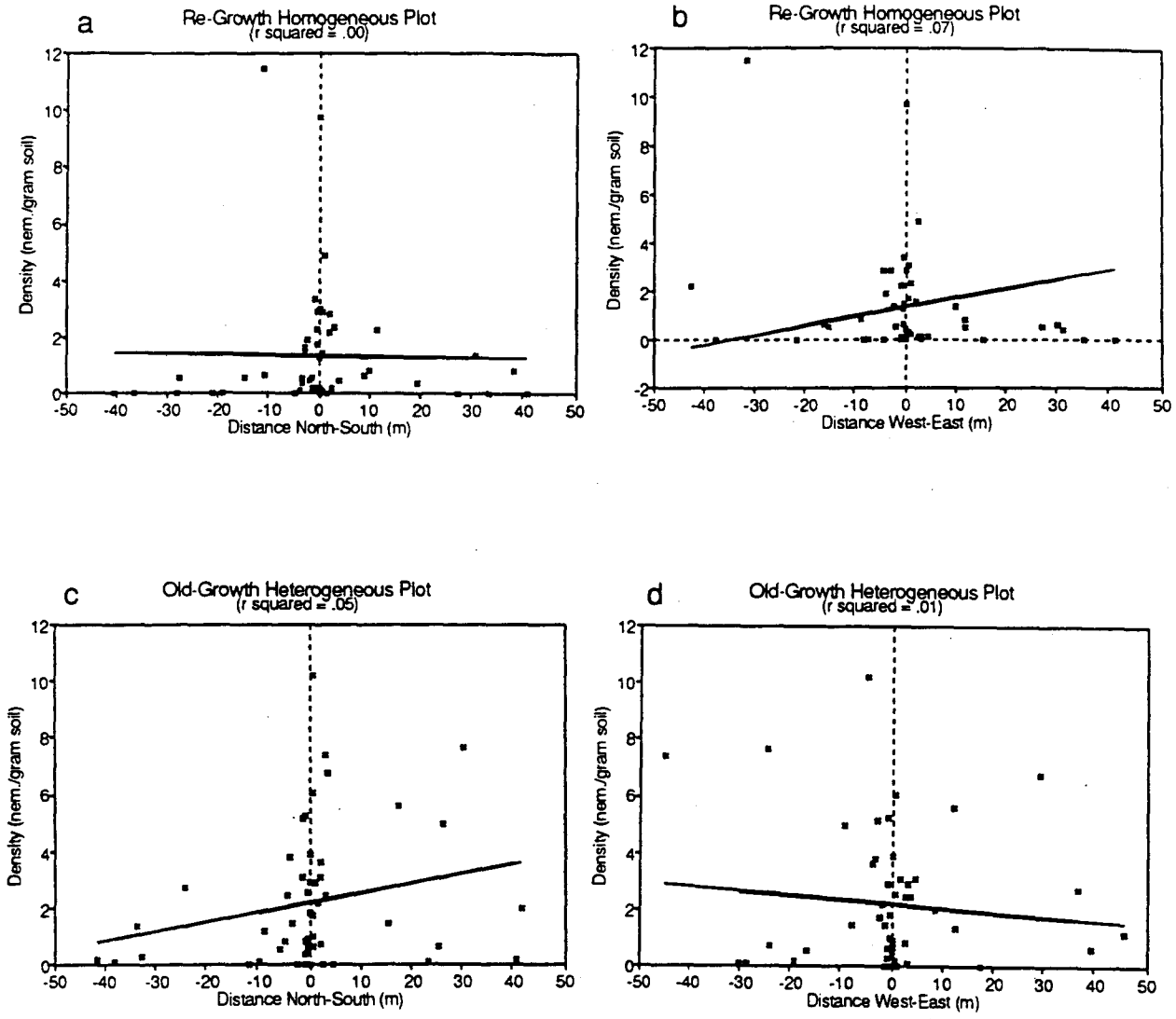


Figure 11. Surface trend bias checks of nematode density for anisotropy in two differentiated conifer stands. (a) re-growth homogeneous plot, north-south axis. (b) re-growth homogeneous plot, east-west axis. (c) old-growth heterogeneous plot, north-south axis. (d) old-growth heterogeneous plot, east-west axis.

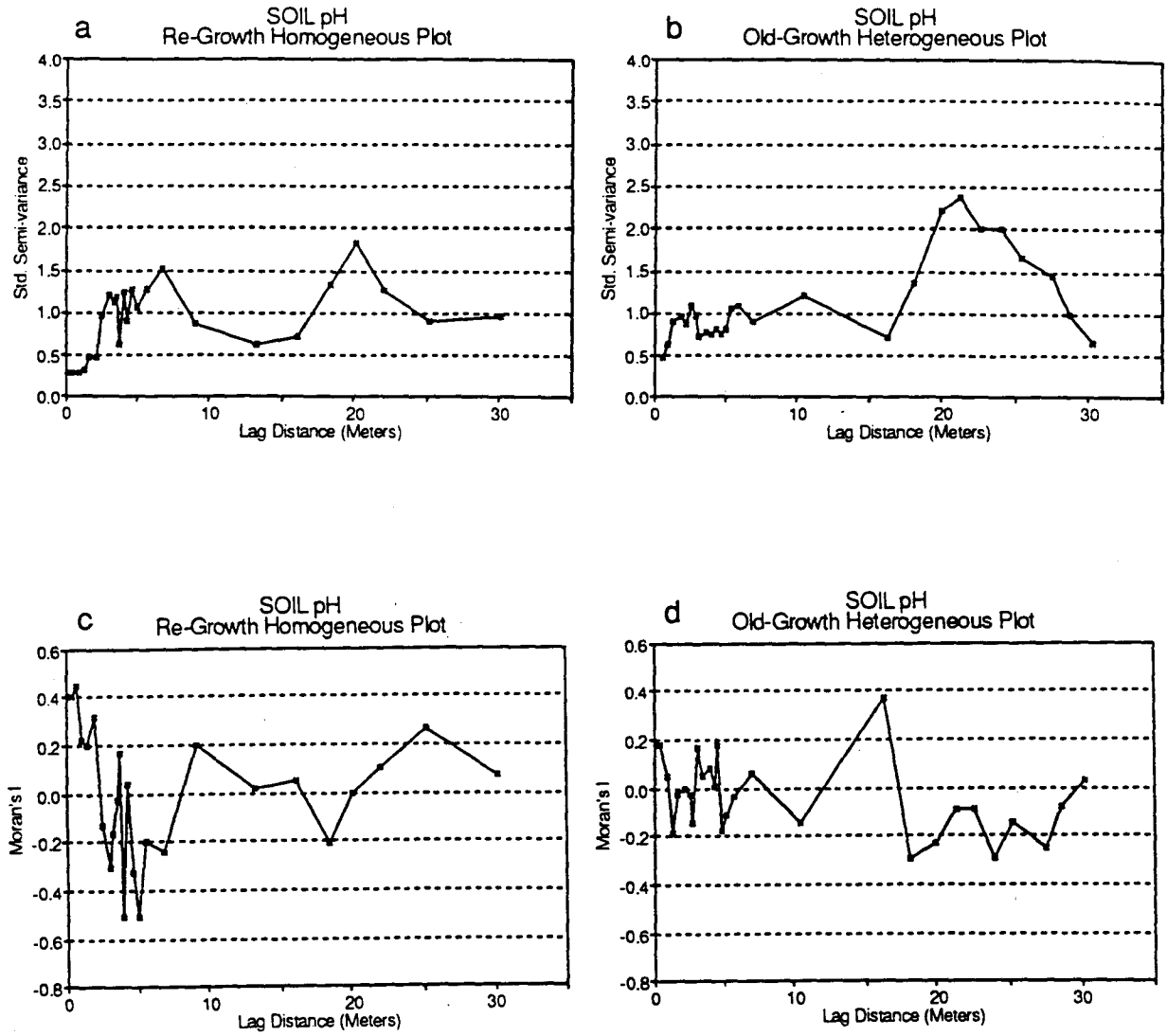


Figure 12. Spatial variability of pH in two differentiated conifer stands: a re-growth homogeneous stand with a low density of old-growth trees; and an old-growth heterogeneous plot with a high density of old-growth trees. (a) re-growth homogeneous plot, semi-variogram. (b) old-growth heterogeneous plot, semi-variogram. (c) re-growth homogeneous plot, correlogram. (d) old-growth heterogeneous plot, correlogram.

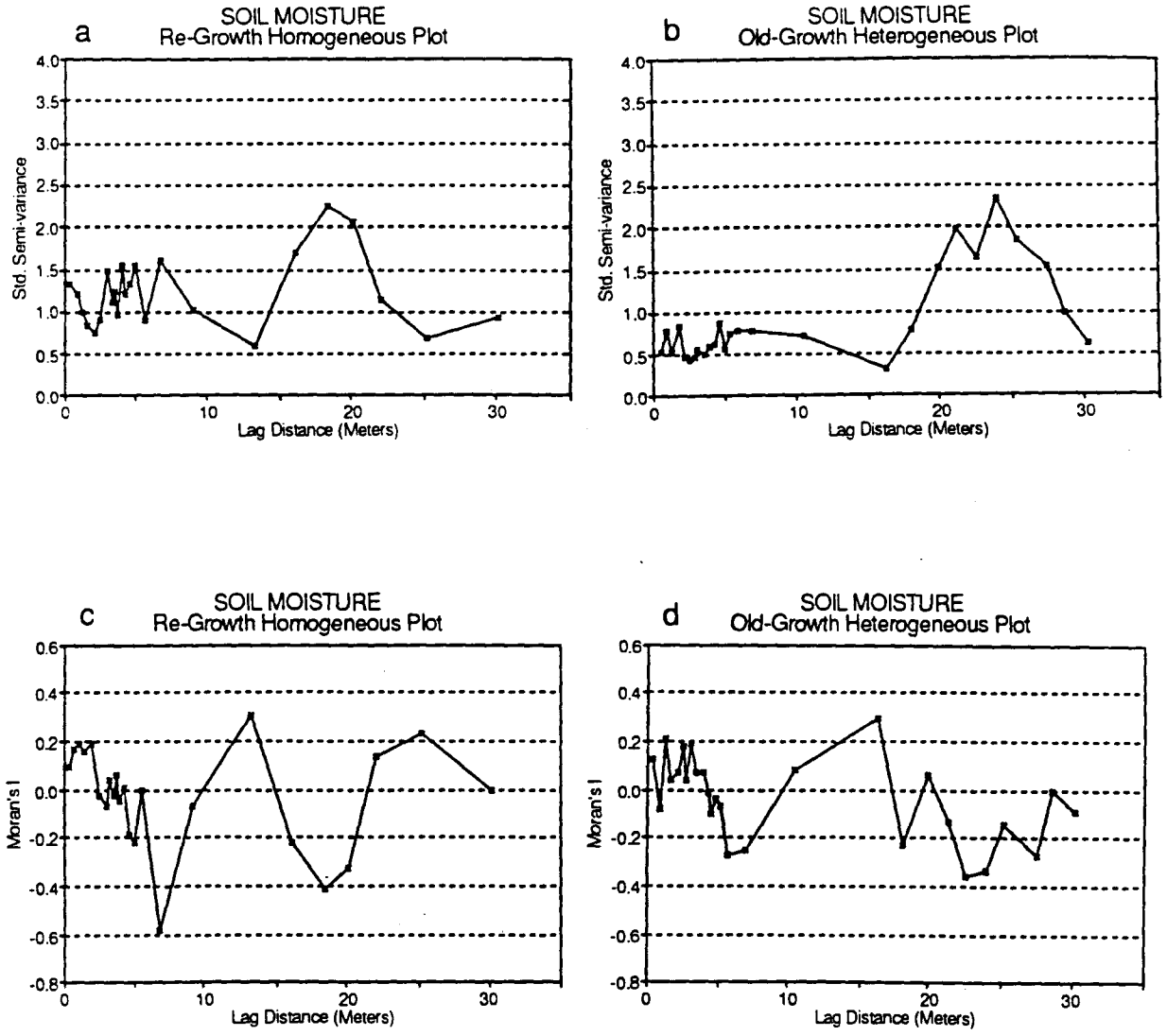


Figure 13. Spatial variability of soil moisture in two differentiated conifer stands: a re-growth homogeneous stand with a low density of old-growth trees; and an old-growth heterogeneous plot with a high density of old-growth trees. (a) re-growth homogeneous plot, semi-variogram. (b) old-growth heterogeneous plot, semi-variogram. (c) re-growth homogeneous plot, correlogram. (d) old-growth heterogeneous plot, correlogram.

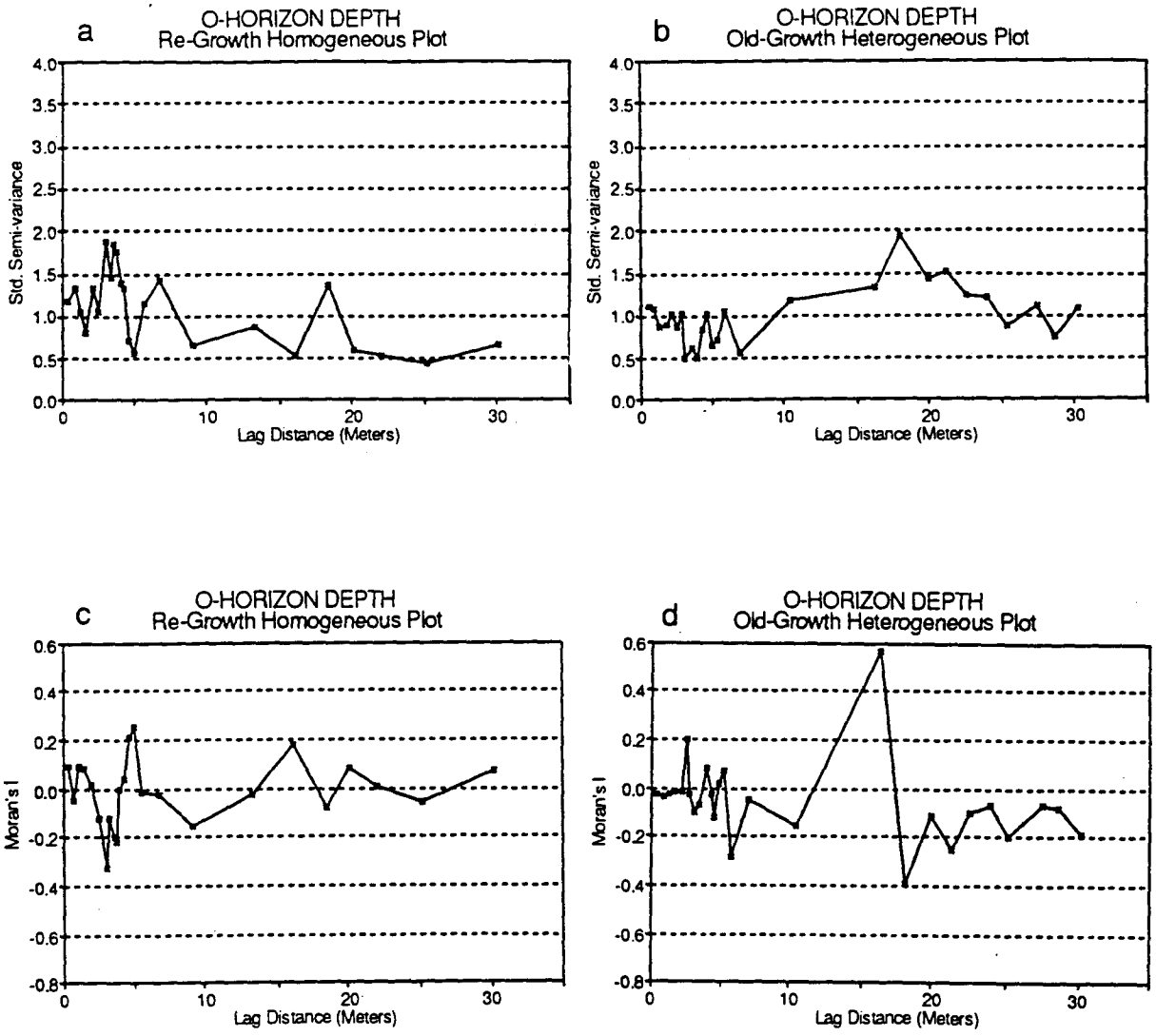


Figure 14. Spatial variability of O-horizon depth in two differentiated conifer stands: a re-growth homogeneous stand with a low density of old-growth trees; and an old-growth heterogeneous plot with a high density of old-growth trees. (a) re-growth homogeneous plot, semi-variogram. (b) old-growth heterogeneous plot, semi-variogram. (c) re-growth homogeneous plot, correlogram. (d) old-growth heterogeneous plot, correlogram.

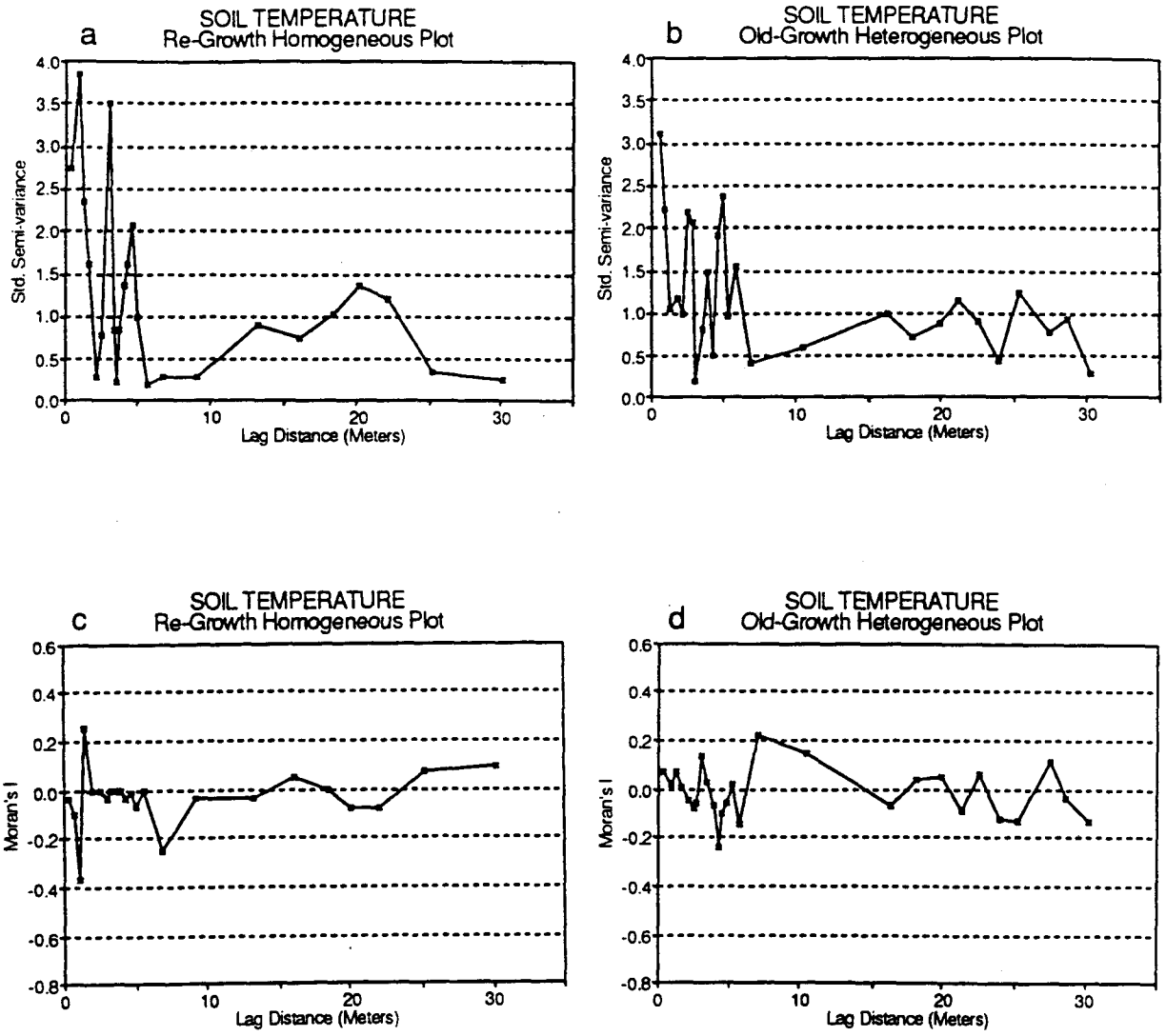


Figure 15. Spatial variability of soil temperature in two differentiated conifer stands: a re-growth homogeneous stand with a low density of old-growth trees; and an old-growth heterogeneous plot with a high density of old-growth trees. (a) re-growth homogeneous plot, semi-variogram. (b) old-growth heterogeneous plot, semi-variogram. (c) re-growth homogeneous plot, correlogram. (d) old-growth heterogeneous plot, correlogram.

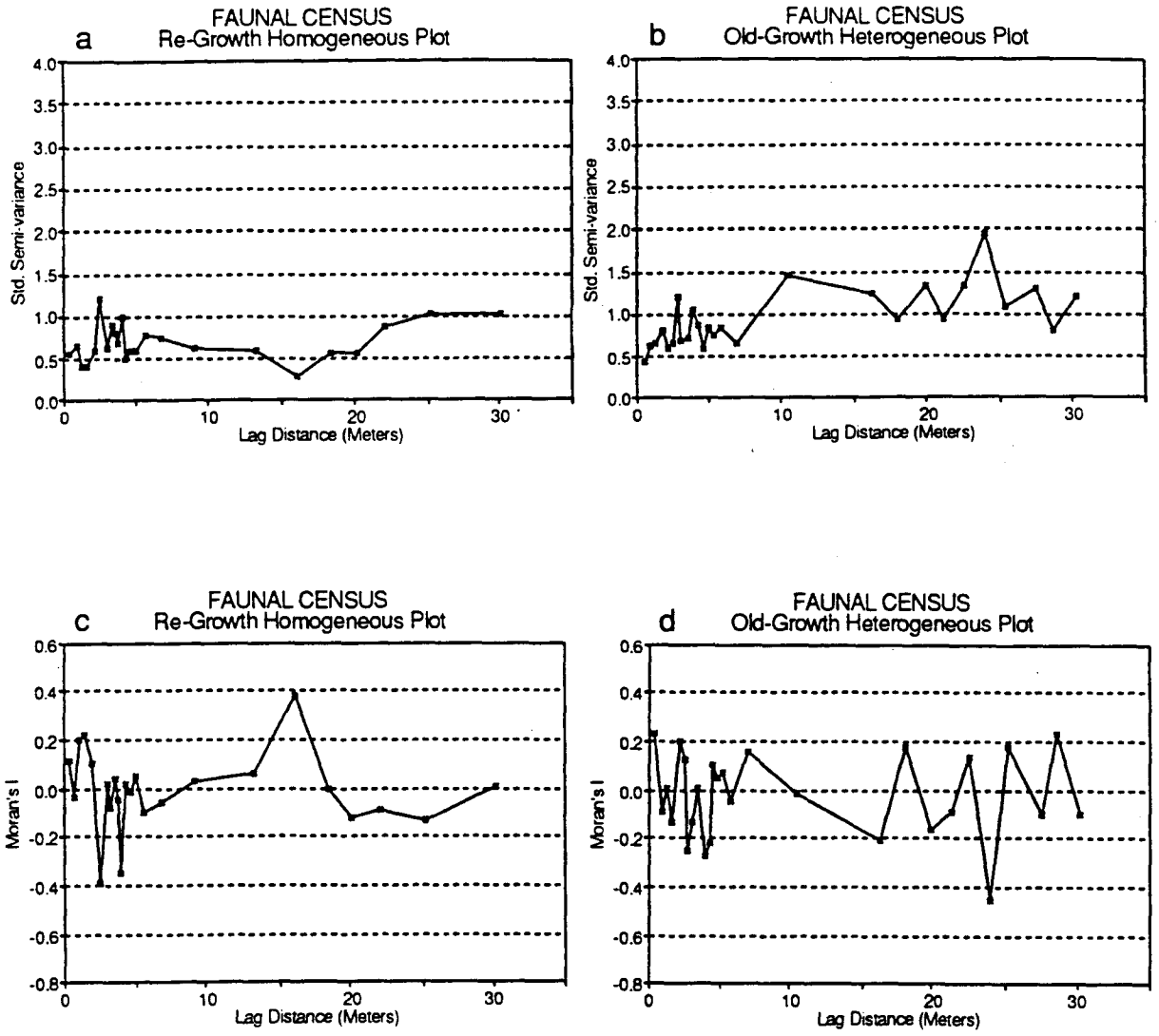


Figure 16. Spatial variability of faunal census in two differentiated conifer stands: a re-growth homogeneous stand with a low density of old-growth trees; and an old-growth heterogeneous plot with a high density of old-growth trees. (a) re-growth homogeneous plot, semi-variogram. (b) old-growth heterogeneous plot, semi-variogram. (c) re-growth homogeneous plot, correlogram. (d) old-growth heterogeneous plot, correlogram.

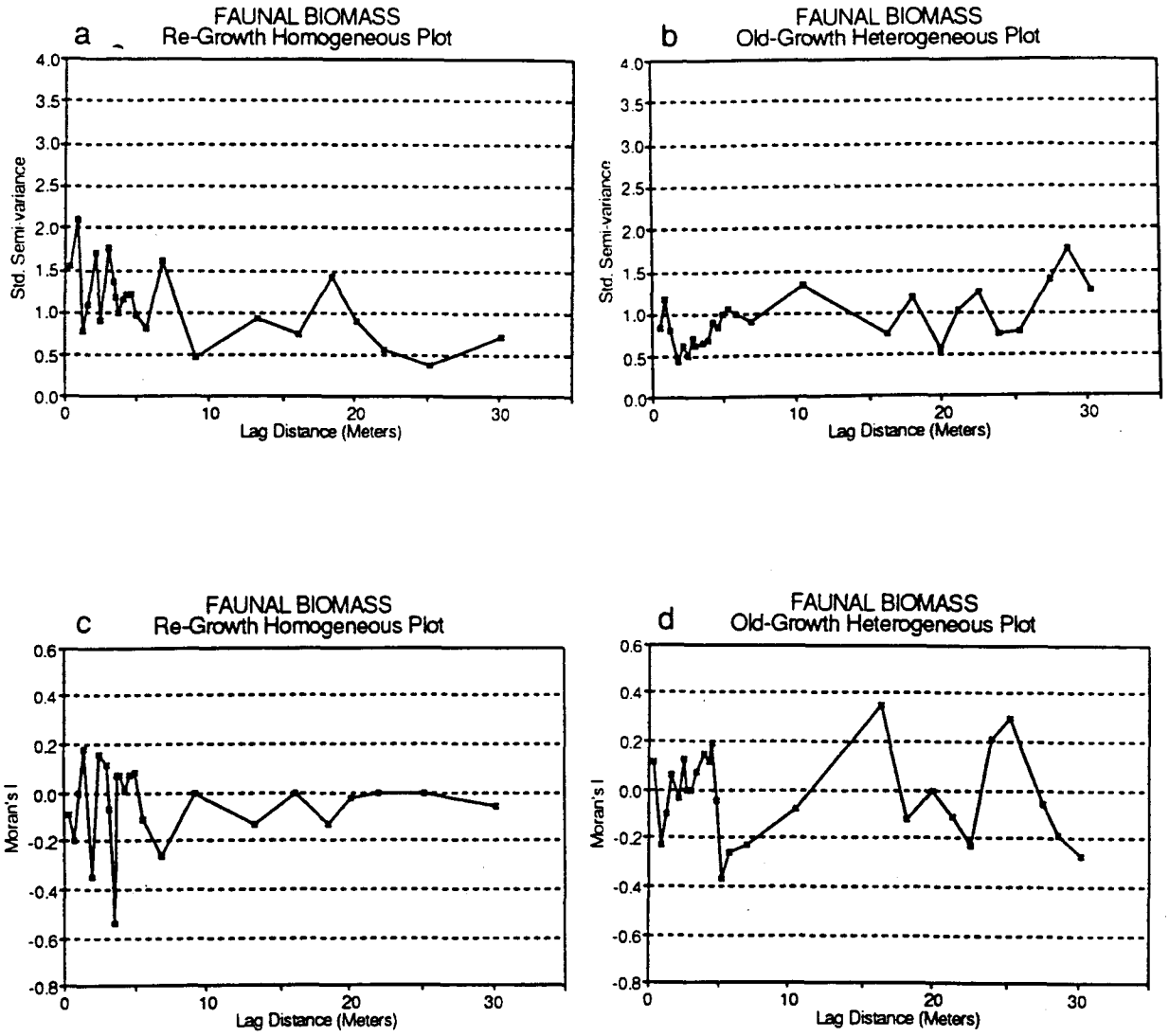


Figure 17. Spatial variability of faunal biomass in two differentiated conifer stands: a re-growth homogeneous stand with a low density of old-growth trees; and an old-growth heterogeneous plot with a high density of old-growth trees. (a) re-growth homogeneous plot, semi-variogram. (b) old-growth heterogeneous plot, semi-variogram. (c) re-growth homogeneous plot, correlogram. (d) old-growth heterogeneous plot, correlogram.

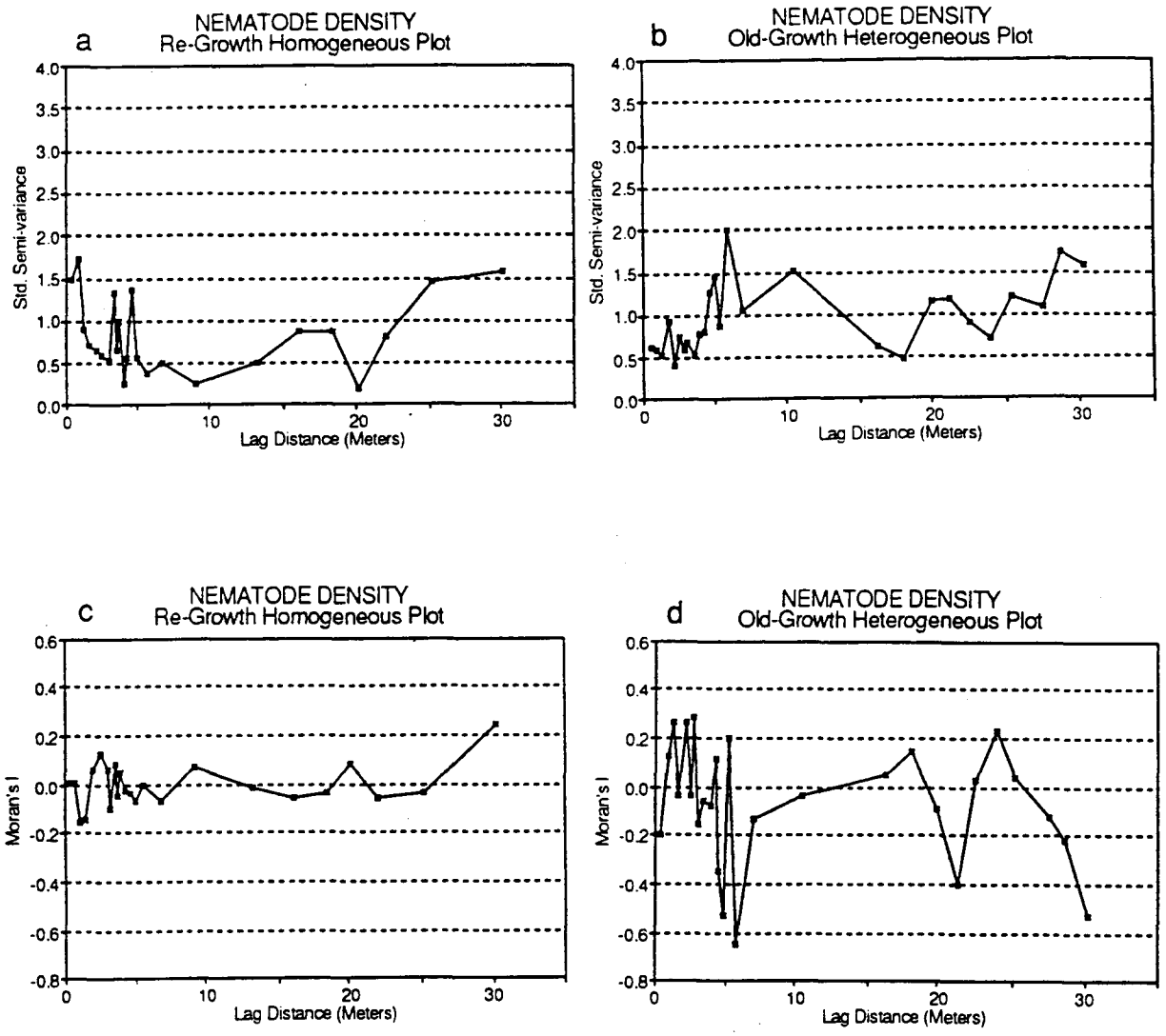


Figure 18. Spatial variability of nematode density in two differentiated conifer stands: a re-growth homogeneous stand with a low density of old-growth trees; and an old-growth heterogeneous plot with a high density of old-growth trees. (a) re-growth homogeneous plot, semi-variogram. (b) old-growth heterogeneous plot, semi-variogram. (c) re-growth homogeneous plot, correlogram. (d) old-growth heterogeneous plot, correlogram.

IV. DISCUSSION

It is particularly interesting in this study that basic statistics (means, standard deviation and coefficient of variance) revealed no significant differences between the two treatment areas, whereas geostatistical methods made the plots' distinguishing characteristics more discernable. Such findings emphasize the value of spatial statistics for picking up otherwise imperceptible ecological relationships. Spatial pattern analysis revealed that soil pH, moisture content, O-horizon depth, temperature, faunal census, biomass and nematode density are autocorrelated in space. The degree of spatial dependence and kind of structure they exhibit, however, differs by soil property and by treatment. Short range variability is the most expressed spatial characteristic in the two treatment areas. Patterns of short range (6-8 m) heterogeneity in soil pH, moisture content and O-horizon are distinctly more apparent in the re-growth homogeneous plot. Faunal numbers and biomass in the same plot reflect analogous, although less uniformly significant, spatial organization. In the old-growth heterogeneous study area, peaks in variability of the same properties occur at similar distances, yet the lower absolute value of their correlation coefficients indicates weaker spatial structuring. Larger scale patch-to-patch spacing, however, at distance classes of 17 to 21 m is the most evident for pH, O-horizon depth, faunal census and biomass in the old-growth heterogeneous plot.

Spatial analysis results of nematode density conflict with the general patterns in the re-growth homogeneous plot of more expressed short range

patterning. Short range patch-to-patch spacing of zones of similar nematode density were weakly defined in the predominantly re-growth plot, whereas in the plot containing a high density of old-growth they were much more developed.

The conforming patterns of spatial structure displayed in both plots especially by soil pH, moisture and 0-horizon, and to a lesser degree faunal census and biomass, are not likely the result of linked causal relationships between the properties since bivariate correlations between all properties were insignificant, with the highest correlation (r^2=0.32) being a positive relationship between soil acidity and moisture content. The resemblance between properties is more likely a reflection of the same universal underlying pattern generated by the spatial organization of different-sized trees in the forest environment.

The forest soil is defined by the patchiness of its habitats created by disturbances such as tree falls, root wad tip-ups and refugia of moisture such as subterranean logs left untouched by passing fires (Moldenke and Lattin, 1990b). The biochemical signature of a tree is imprinted on the local soil ecosystem, even long after the tree blows down or is cut (Moldenke, 1990). It is likely as well that the dead stump of a burned tree continues to influence the soil around it long after a fire. The spatial components of the faunal food web in the soil are integrated by plant and tree roots, such that root morphology determines the scales at which the system functions under different plant nutrient regimes (Anderson, 1988).

In this study, trees and, more generally, forest stand composition appear to be a significant determining factor in the spatial structuring of soil

properties. The re-growth homogeneous plot, with its relatively even-spaced similar-aged conifers, small scale canopy gap structuring, and low density of remnant trees, displays well-defined patterns of short patch-to-patch spacing of soil properties and faunal numbers. Short between-tree distances and small gap size provide one explanation for the prominent short range patterning in the re-growth homogeneous plot.

The plot containing a high density of large old-growth trees intermixed heterogeneously with younger conifers, rhododendron patches, and large gaps has less distinct short range, yet more pronounced long range spatial structure. Older, larger trees have wider canopy radii that affect inputs, such as sunlight, rain, and litter fall (i.e. needles and woody debris), into the soil environment from above; the larger trees' extensive root networks control the uptake of moisture and nutrients from below as well. Longer intervals of tree-to-tree spacing and larger gap size created by large disturbances such as tree falls are very likely related to more significant long range patterning in the old-growth heterogeneous plot.

The orientation of the re-growth homogeneous and old-growth heterogeneous plots around a dead old-growth stump and a living old-growth tree, respectively, as center points must be considered as it affects the results of spatial analysis. The majority of short range distance classes in both plots are represented by samples taken either on the litter skirt of a living tree (old-growth heterogeneous plot) or on the remnant skirt of a dead tree's stump (re-growth homogeneous plot). Although such a manner of plot positioning introduces a non-random element into the data, it has the benefit of providing information on the spatial organization of the stand as a whole,

as well as on the radial influence of an individual tree or stump as a function of distance.

As stated earlier, the objectives of this project were to obtain a basic understanding of the spatial patterns of soil properties and fauna in differentiated conifer stands and test the potential of applying geostatistical methods in soil ecology. The information presented is limited, however, by the size of the sampling population and the representation of forest types. A greater number of study plots in a variety of other compositional forest types, such as non-burned old-growth forest and pure re-growth stands of different ages, would have allowed more comparison between treatment areas and more opportunity to remove any artifacts of sampling design and statistical analysis that might be re-occurrent in the data.

V. CONCLUSION

The results of this study emphasize that biological, chemical and structural properties of the soil are not only spatially dependent, but they exhibit distinct patterning which appears to be related to the compositional character of the forest in which they exist. Geostatistical tools such as semi-variograms and correlograms portray dissimilarities between forest types that basic statistics (mean, standard, deviation and variance) do not reveal. Analysis of spatial heterogeneity has proven a useful measure for assessing biological relationships within the soil. Different canopy size, root morphology, and gap structure are believed to exert varied zones of influence on spatial organization in the soil environment. Short range patterns of heterogeneity in soil pH, moisture content, O-horizon depth, and to a lesser degree, faunal census and biomass were more discernable in predominantly re-growth forest than in a stand containing mostly old-growth trees. Stronger long range patterns were connected with higher densities of old-growth trees and larger gap structure.

In summary, in this study the spatial patterns of soil properties (pH, moisture, O-horizon depth and temperature) and organisms appear to be influenced by different sizes of trees, their spacing and the general forest composition in which they exist. The morphology of spatial patterning is an indicator of forest type. This is reflected in the results of geostatistical analysis. However, this study also revealed that forest stands with high densities of old-growth conifers differ only slightly in terms of basic

statistics when compared to predominantly re-growth stands. Such similarity is an interesting backdrop in the context of spatial pattern analysis, which did reveal distinguishable features between the two forest stand compositions. In the interest of understanding tree-soil interactions, the similarities as well as the differences between the two treatment areas must both be underscored. The results of this study do not provide a basis upon which gross generalizations about the nature of old- and re-growth forests can be made. Any attempts to simplistically pigeon-hole the re-growth or old-growth environments described in this study would be disregarding the complexity inherent in forest soil ecosystems. This research has described the character and spatial aspects of the soil environment in the limited setting of two differing forest stands, and it proposes explanations for the underlying processes and biological systems affecting soil structure. Still, it has only scratched the surface of describing soil ecosystems in old- and re-growth forests as a whole.

Understanding the spatial and non-spatial components of forest soil processes is important. The rich ecosystems of the soil play an irreplaceable role in the maintenance of a healthy forest. With literally thousands of soil creatures turning, fertilizing and aerating the soil around each individual tree (Moldenke, 1990), the whole forest sustains itself through natural nutrient recycling. Maintaining the floral and faunal diversity of these internal interactions is considered by many as the key determinant of productivity and stability in biological systems (Perry et al. 1989). Strong positive feedback through intricate mutual relationships between plants and other organisms buffer the soil system during periods of environmental stress.

Forests need to be protected and enhanced with soil biodiversity in consideration. More studies devoted to obtaining a better understanding of the complex interactions and systems within the forest floor are needed especially as forests come under more and more intense demands for wood products and recreational utilization.

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