

# Temporal changes in spatial patterns of soil moisture following disturbance: an experimental approach

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## Summary

**1** We quantified changes in spatial heterogeneity of soil moisture over 2.5 years in a *Pinus elliottii* Engelm. forest, following disturbance and succession. We harvested or girdled upper canopy trees and measured three components of heterogeneity – global (non-spatial) variability, spatial dependence and temporal persistence – in replicate plots, using sample points arrayed at a fine scale (0.5–6 m) nested within a coarser scale (5–60 m).

**2** Global variability increased after disturbance and then declined, eventually returning to the level recorded in an undisturbed plot. Harvesting resulted in greater, more rapid and more prolonged changes in global variability than girdling.

**3** Geostatistical parameters for measuring spatial dependence were largely unaffected by disturbance. Spatial dependence was, however, quite variable across replicate plots and was stronger at the finer sampling scale.

**4** Spearman rank correlations showed that the spatial pattern of soil moisture had greater long-term persistence in the undisturbed and girdled plots than in the harvested plots.

**5** Some elements of spatial heterogeneity appear to vary over time in a predictable manner. Detection of temporal trends may be improved if multiple components of heterogeneity are quantified, more than one scale of observation is used, replicate plots are employed and sole reliance on geostatistics is avoided.

*Key-words:* girdling, geostatistics, *Pinus elliottii*, scale, whole-tree harvesting

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## Introduction

During the past three decades, we have seen many advances in our understanding of environmental heterogeneity and its ecological consequences (Hutchings *et al.* 2000). In terrestrial plant communities, for example, soil resource heterogeneity influences plant growth and competitive interactions (Einsmann *et al.* 1999; Fransen *et al.* 2001), the coexistence of species and species diversity (Levin 1974; Grime 1979; Bell *et al.* 2000), and spatial patterns of species distribution (Snaydon 1962; Palmer 1990; Nicotra *et al.* 1999). Plants also alter spatial patterns of soil properties (Hendrickson &

Robinson 1984; Breshears *et al.* 1997; Finzi *et al.* 1998a, 1998b), leading to dynamic interactions between fine-scale patterns within vegetation and soil and, theoretically, to close correlation between the two.

Measured correlations between soil and vegetation patterns are often weaker than theory suggests, however, because spatial patterns change through time, and rates of change are not the same for all variables (e.g. compare Gross *et al.* 1995; Ryel *et al.* 1996; van den Pol-van Dasselaar *et al.* 1998; Cain *et al.* 1999; Farley & Fitter 1999). Soil resource patterns in particular can change quickly, leading to noise in the data that decreases apparent correlation with the relatively more stable patterns in vegetation (Ehrenfeld *et al.* 1997; Robertson *et al.* 1997). A further impediment to relating soil and vegetation properties is the fact that few studies have measured spatial patterns at more than one point in time. Thus, the processes that control spatial patterning are not yet well understood.

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To quantify temporal trends in spatial patterns, the components of heterogeneity, and parameters used to measure them, must be defined (Li & Reynolds 1995; Cooper *et al.* 1997). In this study, we selected global variability, spatial dependence and temporal persistence as indicators of spatial heterogeneity and its dynamics. These measures have been used in other studies of ecological heterogeneity (Goovaerts & Chiang 1993; Jackson & Caldwell 1993a, 1993b; Gross *et al.* 1995; Miller *et al.* 1995; Schlesinger *et al.* 1996; Robertson *et al.* 1997; Pastor *et al.* 1998; Nicotra *et al.* 1999). Global variability is expressed by the variance of an ecological variable within a given sampling area (Bell *et al.* 1993; Li & Reynolds 1995). Spatial dependence is usually characterized by two semivariogram parameters: SH% and range. SH% is the proportion of the total variability due to spatial factors, while range is the distance over which values of the measured variable are spatially autocorrelated (Journel & Huijbregts 1978; Robertson & Gross 1994; Li & Reynolds 1995). Temporal persistence, the repeatability of the same patterns in time, can be measured by correlating data collected at one time with data collected from the same measurement points at other times (Kachanoski & de Jong 1988; Goovaerts & Chiang 1993).

After heterogeneity components and parameters are defined, a sampling design is needed that matches the spatial and temporal scales of the parameters being measured (Addicott *et al.* 1987; Wiens 1989; Miller *et al.* 1995). Environmental variability may change as spatial scale changes, or show nested patterns (Bell *et al.* 1993; Robertson *et al.* 1997; Pastor *et al.* 1998). Therefore, soil resource heterogeneity in natural communities should be examined at multiple scales. Another aspect of sampling relates to plot replication. Because large numbers of samples are needed to construct a single semivariogram, most studies of heterogeneity have used a single plot per community type. The possibility that spatial structure is not uniform within a single community has not been adequately tested (Halvorson *et al.* 1994; Nicotra *et al.* 1999).

In this study, we examine temporal and spatial heterogeneity of a single resource – soil moisture – in a coastal plain forest in South Carolina, United States of America (USA). The main objectives were to: (i) quantify temporal patterns of global variability, spatial dependence and persistence of soil moisture; (ii) determine whether these patterns are changed by disturbance, and, if so, how they change as plant biomass increases during early stages of post-disturbance succession; and (iii) determine how use of multiple components of heterogeneity, multiple spatial scales of measurement and replicate plots might influence results and conclusions. We chose an early successional system for the study because temporal changes in ecological processes are particularly great, and therefore most likely to influence soil heterogeneity at this stage. Immediately after a forest is disturbed, plants lose some control over soil resource uptake, but this control

is soon regained as biomass re-grows (Canham & Marks 1985; Mou *et al.* 1993). We chose to measure soil moisture because it is among the most variable soil factors in space and time. Its temporal variation at both daily and annual scales has been explicitly observed in the field and studied theoretically (Campbell 1977; Hillel 1982).

Our hypotheses were that: (i) global variability in soil moisture would increase after disturbance and then decrease with the re-establishment of vegetation; (ii) spatial patterns of soil moisture would become finer-grained (i.e. there would be smaller patch sizes) after disturbance, due to vegetation removal and increased patchiness of the forest floor, and then become more coarse-grained as vegetation re-grows; (iii) persistence of spatial patterns would be lower in disturbed than in undisturbed plots, due to the influences of disturbance and post-disturbance development; and (iv) more intense disturbances would lead to greater, more rapid and more prolonged changes in both global variability and spatial patterns of soil moisture.

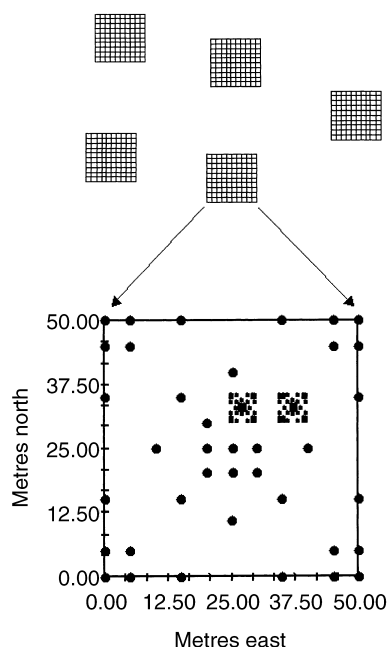
## Methods

### STUDY SITE

This study was conducted in a 40-year-old slash pine plantation located at the US Department of Energy's Savannah River Site near Aiken, South Carolina, USA. The climate is subtropical with mean July maximum, January minimum and annual temperatures of 27 °C, 9 °C and 24 °C, respectively. The mean annual precipitation (113 cm) is relatively evenly distributed throughout the year (South Carolina State Climatology Office, 1998). The soils are well-drained Dothan sandy loam (kaolinitic, thermic Plinthic Kandudult) with a low nutrient-holding capacity and a low organic matter content (Rogers 1988). Soils were relatively uniform in bulk density and texture across the site (Lister 1998). The site was a pasture prior to the establishment of the plantation in 1958 and was probably used for row crop production at some time between 1900 and 1950 (Rogers 1988). Prescribed burning was used to control forest floor fuel load in 1988 and 1993. The fires burnt relatively evenly throughout the stand. The study site has low topographic relief and an understorey that is homogeneous in species composition. The dominant overstorey species is slash pine, which comprised 82.5% of the pre-disturbance stand with total basal area of 37.3 m<sup>2</sup> ha<sup>-1</sup> (Lister *et al.* 2000), with several oaks (*Quercus* spp.), waxmyrtle (*Myrica cerifera* L.) and black cherry (*Prunus serotina* Ehrh.) also common (Lister *et al.* 2000).

### PLOT ESTABLISHMENT

Five one-hectare plots were randomly placed in the forest. In March 1997 a 50 × 50 m permanent survey plot was established in the central portion of each plot, with



**Fig. 1** Design for measuring soil moisture heterogeneity. In each of five plots, 41 points were located on the intersections of a  $5 \times 5$  m grid, using a configuration to optimize semivariogram analysis with a minimum sampling interval of 5 m. The same sampling layout was also applied within each of two randomly chosen cells, but with a minimum sampling interval of 0.5 m.

a 25-m buffer zone on each side, and was divided into 100 grid cells of  $5 \times 5$  m. Coarse-scale sampling locations were systematically established at 41 of the grid intersections (Fig. 1) following Halvorson *et al.* (1994). Within each survey plot, two grid cells were randomly chosen and further divided into 100 microgrids of  $0.5 \times 0.5$  m that were sampled at a fine-scale using the same 41-point layout as the coarse scale (Fig. 1). This nested sampling system allowed us to examine spatial variations at scales from 0.5 to 60 m using geostatistics with a relatively balanced distribution of sample pairs at all distance lags, and sufficient number of pairs per lag class. Coarse-scale sampling locations remained unchanged throughout the study period. Fine-scale plots were randomly relocated each year (i.e. in early 1998 and early 1999) to minimize the effects of previous sampling disturbance.

#### DISTURBANCE TREATMENT

In late May 1997 a commercial harvest was applied to two randomly selected plots (H1 and H2), girdling to a further two (G1 and G2) and the remaining plot (undisturbed) was left as a reference. In H1 and H2, trees of all sizes were cut and removed from the site but some slash (branches and needles) remained, including a 40-m<sup>2</sup> area with 60-cm deep slash in H1 that later resulted in greater soil moisture variability in this plot. In G1 and G2 all pine trees whose crowns were in the main canopy (> 25 cm in d.b.h.) were girdled and the

herbicide triclopyr (44% active ingredient in water; Garlon 3A, Dow Chemical Co., Midland, Missouri, USA) was applied to the girdling cuts; all pines in the understorey were felled by chainsaw and left in place and all hardwoods were left undisturbed.

#### SOIL MOISTURE MEASUREMENT

Soil moisture was measured using time domain reflectometry (TDR, Topp *et al.* 1980; Topp & Davis 1985) with a Tektronix model 1502C cable tester system (Tektronix Inc., Wilsonville, Oregon, USA). A pair of 21-cm long stainless steel rods was installed in the soil at each sampling location to measure moisture (% by volume) in the top 20 cm of soil. TDR trace shapes were visually inspected following the procedure of Gray & Spies (1995). Measurements were obtained shortly before the disturbance treatments (10 May 1997) and on eight occasions between November 1997 and October 1999. Samples were taken at least 2 days after a rain event and at approximately similar hours during the day. A TDR calibration curve was constructed in the laboratory using samples of natural soil following the procedure of Topp *et al.* (1980). We adopted the linear equation for sandy loam soil (core 7) by Gray & Spies (1995) because it most accurately predicted soil moisture for our samples. Soil bulk density may have been slightly different after different disturbance treatments, but this is unlikely to influence the calibration equations (Gray & Spies 1995).

#### STATISTICAL ANALYSIS

We assessed global variability by calculating mean, variance and coefficient of variation (CV) of soil moisture for each coarse- and fine-scale plot at each sample date. For each date we used ANOVA to examine the differences between plot means and variance at the coarse scale, and differences in variance between a coarse-scale plot and its two embedded fine-scale plots. Coarse- and fine-scale plots often shared some sampling points. We included shared points in the coarse-scale data and excluded them from the fine-scale data before conducting the ANOVAs. As our sampling was systematic, the ANOVA results were only used to highlight patterns in the data, rather than to test specific hypotheses. We also looked for temporal patterns in global variability by dividing the mean, variance and CV in each disturbed plot by the same statistics measured in the undisturbed plot. Deviations from the expected ratio of 1.0 were taken as evidence of changes in global variability.

Spatial patterns of soil moisture were examined using semivariance analysis. Semivariogram modelling requires the data to be stationary, i.e. to lack spatial trend (Journel & Huijbregts 1978; Rossi *et al.* 1992). We used trend surface analysis (TSA) to detect and remove trends in the coarse-scale data prior to semivariance analysis following Davis (1986). We did not perform TSA on the fine-scale data because stationarity is

better approximated at fine scales (Journel & Huijbregts 1978).

Semivariograms were modelled using GS+ version 3.11.12 (Gamma Design, Plainwell, Missouri, USA). When semivariograms were erratic, data were inspected and spatial outliers were deleted following the procedure of Isaaks & Srivastava (1989). Our data generally followed a normal distribution, with few extreme values and spatial outliers. The choices of lag distance were based on a balance between equal lag distance and equal numbers of pairs for each lag (Zheng & Silliman 2000). Isotropic semivariograms were computed but there were insufficient numbers of sample pairs to produce directional semivariograms.

Semivariance parameters used to characterize spatial dependence include goodness-of-fit ( $R^2$ ), nugget ( $C_0$ ), sill ( $C + C_0$ ) (where  $C$  is the variability due to spatial dependence) and range (Isaaks & Srivastava 1989; Rossi *et al.* 1992; Robertson & Gross 1994). SH% ( $C / (C + C_0) \times 100\%$ ), a proportion of variance due to spatial dependence, has been used to indicate the structural variability in a spatial data set (Li & Reynolds 1995). A semivariogram with a high  $R^2$  and a high SH% indicates a strong spatial structure (i.e. it has a high degree of spatial dependence). Range is used to indicate the spatial pattern of variability. A smaller range may suggest a finer-grained spatial pattern. If the samples are completely uncorrelated, the semivariogram will exhibit a so-called nugget effect.

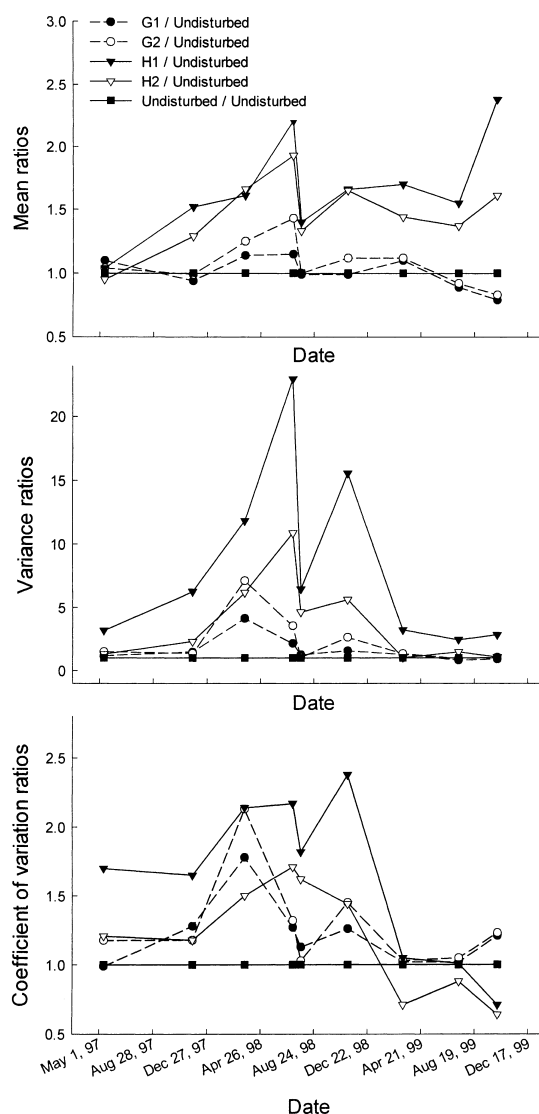
To evaluate effects of plot replication and scale on analyses of spatial dependence, we conducted separate semivariance analyses for each plot at each scale. We also conducted semivariance analyses after combining both scales within each plot. Combining the replicate plots within each treatment would not have been valid as their semivariograms were not similar (Halvorson *et al.* 1994).

We assessed temporal persistence by calculating Spearman rank correlation coefficients (CC) between soil moisture values on different sampling dates (Kachanoski & de Jong 1988; Goovaerts & Chiang 1993) with lower or negative CC values expected if disturbance or succession influences on soil moisture are strong. At the coarse scale, CCs were calculated for each plot between all possible pairs of sampling dates. Locations of fine-scale plots changed yearly and CCs were therefore calculated within each year (1998 and 1999 only, plots were relocated after the disturbances in 1997). All statistical tests were performed using SAS version 8 (SAS Institute, Cary, North Carolina, USA).

## Results

### TEMPORAL CHANGES IN GLOBAL VARIABILITY

Prior to disturbance, mean soil moisture measured at the coarse scale was similar in all five plots, but increased after both treatments, sooner and more



**Fig. 2** Temporal changes in mean, variance and CV of soil moisture at the coarse scale (5–60 m) expressed by the ratios of mean, variance and CV of soil moisture in each plot divided by those in the undisturbed plot.

markedly in harvested than in girdled plots (Fig. 2). Mean soil moisture of the girdled plots then rapidly decreased to and remained at the level of the undisturbed plot, whereas in the harvested plots it remained high (Fig. 2).

Before disturbance, both variance and CV of soil moisture measured at the coarse scale were greater in one of the plots (H1) (Fig. 2), probably due to a slight downward slope towards the south-eastern corner where there was also a large slash pile. After disturbance, variance increased in all treated plots before returning to the undisturbed level, with a smaller increase and faster recovery after girdling (Fig. 2). CV increased to a similar extent after both disturbance treatments and then declined, peaking earlier in girdled plots (Fig. 2). The two replicate plots of each treatment showed similar temporal changes (Fig. 2).

**Table 1** Ratios of soil moisture variance between a coarse-scale plot and its two nested fine-scale plots (a & b) at each sampling date. \*Variance of the coarse-scale plot is significantly different from that of a nested fine-scale plot (*F*-tests,  $\alpha = 0.05$ ). All sampling dates except 10 May 1997 are post-disturbance

Plot (coarse/fine)	1997		1998				1999			
	10 May	24 November	21 March	7 July	25 July	7 November	11 March	14 July	9 October	Mean
Girdled (1/a)	0.44*	1.37	0.69	0.19*	0.61	0.42*	0.71	1.12	1.20	0.79
Girdled (1/b)	0.89	0.75	1.30	1.19	1.29	1.72	1.38	1.02	1.65	1.29
Girdled (2/a)	0.64	1.05	0.90	0.48*	0.34*	0.74	0.86	1.11	0.83	0.79
Girdled (2/b)	1.02	0.98	3.61*	0.61	0.77	1.20	1.08	2.05*	0.70	1.38
Harvested (1/a)	1.98*	1.81*	4.75*	2.07*	3.33*	3.54*	1.45	1.91*	2.01*	2.61
Harvested (1/b)	3.28*	2.67*	7.74*	1.96*	2.47*	5.36*	2.52*	2.31*	2.97*	3.50
Harvested (2/a)	1.23	1.37	2.36*	1.77	4.12*	2.30*	0.54*	1.44	1.61	1.94
Harvested (2/b)	0.77	0.94	4.01*	1.34	2.49*	1.06	0.91	0.70	1.96*	1.68
Undisturbed (/a)	1.20	0.79	0.44*	0.15*	0.54*	0.88	1.24	0.96	1.60	0.83
Undisturbed (/b)	1.42	0.77	0.78	0.29*	0.60	0.48*	0.89	0.74	1.07	0.70

**Table 2** Summary of trend and semivariogram analyses for soil moisture at the coarse scale (5–60 m). Trends were either first- or second-order. Significance levels of these trends were indicated as: \* $< 0.05$ , \*\* $< 0.001$ , \*\*\* $< 0.0001$ . A lack of trend was indicated by a ‘–’. Semivariogram parameters (range, SH%,  $R^2$ ) were obtained after data were de-trended. The best model fit to the data based on least squares is: S = spherical, N = nugget, L = linear, and is shown after  $R^2$  values. Where a nugget model was found, all three parameters are undefined and therefore marked with ‘--’

Plot	Parameter	Date								
		05/10/97	24/11/1997	21/3/1998	07/07/98	25/7/1998	11/07/98	03/11/99	14/7/1999	10/09/99
G1	Trend	--	--	1st***	--	--	--	2nd*	--	--
	Range (m)	35	--	--	--	--	--	--	--	--
	SH%	78	--	--	--	--	--	--	--	--
	$R^2$ /Model	0.66/S	N	N	N	N	N	N	N	N
G2	Trend	--	--	1st***	--	--	--	--	--	--
	Range (m)	22	--	--	--	--	--	45	--	52
	SH%	66	--	--	--	--	--	95	--	78
	$R^2$ /Model	0.33/S	N	N	N	N	N	0.66/S	N	0.76/S
H1	Trend	--	2nd**	2nd***	2nd***	2nd***	2nd***	2nd***	2nd**	2nd**
	Range (m)	62	--	--	--	--	--	--	--	--
	SH%	65	--	--	--	--	--	--	--	--
	$R^2$ /Model	0.39/L	N	N	N	N	N	N	N	N
H2	Trend	--	1st***	1st***	--	--	--	1st***	--	--
	Range (m)	--	--	--	--	--	--	--	--	--
	SH%	--	--	--	--	--	--	--	--	--
	$R^2$ /Model	N	N	N	N	N	N	N	N	N
U0	Trend	--	--	--	--	--	--	--	--	--
	Range (m)	8	--	8	--	--	--	--	--	--
	SH%	83	--	89	--	--	--	--	--	--
	$R^2$ /Model	0.24/S	--	0.39/S	--	--	--	--	--	--

For all treatments, mean, variance and CV of soil moisture at the fine scale followed similar temporal patterns to those at the coarse scale, with means being most consistent (data not shown). The difference between means of the two scales was within 10% of the coarse-scale values in 13, 16, 8, 6 and 10 out of 18 cases in H1, H2, G1, G2 and undisturbed, respectively (details not shown). The greatest differences between scales occurred in the harvested plots where variance was often more than twice as great at the coarse scale, especially up to 18 months after felling (Table 1). In the girdled and undisturbed plots, variances at the coarse scale were similar to or less than variances at the fine

scale throughout the post-disturbance sampling period (Table 1). CVs were generally greater at the coarse scale than at the fine scale in the disturbed plots but there were no marked differences in the undisturbed plot (data not shown).

#### TEMPORAL CHANGES IN SPATIAL PATTERN

At the coarse scale, spatial dependence was detected in four of the five plots prior to disturbance (Table 2). Semivariogram ranges for these four plots were between 8 and 62 m and the strength of spatial dependence was moderate to rather high (i.e. SH%  $\geq 65\%$  and

**Table 3** Summary of semivariogram analysis for soil moisture at the fine scale (0.5–6 m). Semivariogram parameters (range, SH%,  $R^2$ ) were obtained with original data (not de-trended data). The second and third columns indicate the number of times that soil moisture was spatially dependent. The last three columns indicate the minimum and the maximum values of semivariogram parameters

Treatment (Plot)	Pre-disturbance (1)	Post-disturbance (8)	SH% (min, max)	Range (min, max)	$R^2$ (min, max)
G1a	1	6	(43, 100)	(2.0, 12.1)	(0.30, 0.81)
G1b	0	6	(50, 85)	(1.6, 12.5)	(0.33, 0.67)
G2a	1	8	(85, 100)	(0.8, 13.2)	(0.30, 0.92)
G2b	0	5	(58, 100)	(1.3, 7.0)	(0.31, 0.81)
H1a	1	5	(61, 95)	(4.7, 12.5)	(0.51, 0.93)
H1b	1	7	(55, 97)	(1.3, 15.8)	(0.30, 0.89)
H2a	1	8	(50, 100)	(1.3, 13.4)	(0.36, 0.85)
H2b	1	5	(73, 100)	(1.4, 17.5)	(0.31, 0.92)
Undisturbed a	0	7	(71, 100)	(2.1, 7.8)	(0.37, 0.90)
Undisturbed b	1	7	(50, 100)	(1.3, 9.2)	(0.30, 0.89)

**Table 4** Spearman rank correlation coefficients (CC) between the pre-disturbance data set (10 May 1997) and post-disturbance data sets at the coarse scale (5–60 m). Significance level: \* < 0.05, \*\* < 0.01, \*\*\* < 0.001

Plot	Pre-11/97	Pre-3/98	Pre-7/7/98	Pre-25/7/98	Pre-11/98	Pre-3/99	Pre-7/99	Pre-10/99
G1	0.43**	0.39*	0.24	0.69***	0.34*	0.59***	0.55***	0.51***
G2	0.43**	0.36*	0.07	0.39*	0.29	0.50**	0.39*	0.37*
H1	0.17	0.04	0.12	0.05	0.05	0.18	-0.1	0.2
H2	0.23	-0.28	0.14	-0.02	0.31	0.27	-0.05	0.21
Undisturbed	0.49**	0.21	0.35*	0.37*	0.17	0.44**	0.25	0.63***

$R^2 \geq 0.24$ ). After disturbance, spatial dependence was rarely detected, except twice in plot G2 and once in the undisturbed plot (Table 2). However, spatial trends were found eight times in H1, three times in H2, twice in G1 and once in G2.

More spatial structure was detected at the fine scale. Seven (of 10) fine-scale plots had various degrees of spatial dependence before disturbance (Table 3). The semivariograms for these plots produced range estimates varying from 1.4 to 13.4 m, SH% estimates from 55% to 85% and  $R^2$  from 0.36 to 0.81 (data not shown). There were often large differences between the two replicates in each large plot. After disturbance, soil moisture was still spatially dependent in most of the fine-scale plots at most sampling dates (Table 3). Temporal patterns corresponding to disturbance treatments were not found.

#### TEMPORAL PERSISTENCE OF SPATIAL PATTERN

Temporal persistence analysis of coarse-scale data showed that spatial patterns of soil moisture were disrupted by harvesting, but not by girdling. Soil moisture before disturbance was often significantly correlated with soil moisture up to 2.5 years after disturbance in the two girdled plots and in the undisturbed plot, but not in the harvested plots (Table 4).

Persistence analysis indicated few post-disturbance effects on soil moisture pattern. First, CC values calculated between the pre-disturbance and post-

disturbance samples did not trend upwards or downwards over time in any of the plots, although year to year variation did occur (Table 4). Secondly, when the pre-disturbance data were omitted for examining post-disturbance trends, mean CCs across or within years were approximately the same in three of the four disturbed plots (0.31–0.49) as in the undisturbed plot (0.32–0.44). H1, however, had means ranging between 0.70 and 0.74. Furthermore, we found no clear pattern of increasing or decreasing post-disturbance CCs over time (data not shown). Fine-scale data suggested a weak trend; post-disturbance measures for each fine-scale subplot had mean within-year correlations that were slightly greater for the undisturbed plots (mean of 0.64) than for the harvested (0.56) and girdled (0.58) plots.

## Discussion

#### TEMPORAL CHANGES IN GLOBAL VARIABILITY

As predicted in our first hypothesis, global variability of soil moisture, measured by variance or CV, increased after the disturbances and then declined, returning to the pre-disturbance level within 2 years. During the same period, global variability in the undisturbed plot changed little. The increase immediately after disturbance was probably caused by: (i) increased variability of plant root distribution, creating corresponding variation in local water uptake rates within the soil; and (ii) increased variation in forest floor thickness, enhancing

variation in evaporation rates from the soil surface. The subsequent decline in global variability was probably related to re-establishment of fine roots throughout the soil and redevelopment of a more homogeneous forest floor.

Because disturbances tend to create environmental heterogeneity (Beatty 1984; Pickett & White 1985; Clinton & Baker 2000), the increases in soil moisture variability after harvest and girdling were expected. However, we were surprised by how rapidly global variability returned to pre-disturbance levels, despite the fact that the vegetation changed dramatically from a mature pine forest to an early successional forest dominated by herbs and hardwood sprouts. One explanation for this is that root systems tend to re-establish rapidly in forests after disturbance (Wilcznski & Pickett 1993; Jones *et al.* 1996). When the results of other studies are compared with those reported here, no general patterns of soil moisture variability emerge. Ehrenfeld *et al.* (1997) found little change in CV of soil moisture over a period of 16 months in undisturbed wetland pine forests, yet Ryel *et al.* (1996) found declines in mean and CV of soil moisture within a growing season in sagebrush steppe. Gross *et al.* (1995) measured soil moisture distribution in one forest and two old-field communities, each representing a different stage in succession. They found that CV of soil moisture was greatest in the mid-successional field (29%) and lowest in the early successional field (13%), in contrast to the rapid increase and decline in our study. However, Gross *et al.* (1995) used a space-for-time substitution approach (as opposed to our repeated sampling of the same sites), which may have confounded temporal trends with underlying differences between sampled sites.

Differences in the way which global variability is measured may complicate comparisons of different studies for any measured soil resource. For example, using CV alone, Dent & Grimm (1999) concluded that overall variability of nitrate in a stream increased during succession, but their data suggest that both absolute variability (variance) and mean values decreased dramatically from early succession to middle succession and slightly increased thereafter. The CV data alone in this case may be misleading. This would be true for any study where mean and variance change in different directions or change at different rates.

#### TEMPORAL CHANGES IN SPATIAL PATTERN

Our second hypothesis, that soil moisture would become finer-grained after disturbance and then become coarser-grained, was not supported by the results of TSA and semivariance analysis. At the coarse scale, some spatial dependence, which is a possible indication of patchiness, was observed prior to disturbance but was not detected thereafter (Table 2). Thus, we might conclude that patchiness disappeared after disturbance instead of becoming finer-grained. Spatial

dependence was more frequently observed at the fine scale, but we found no trend for either increased or decreased semivariance range.

Trend surface analysis did not detect spatial trends prior to disturbance in any plot, nor at any time in the undisturbed plot. After disturbance, however, significant trends (TSA,  $P < 0.05$ ) were detected three times in girdled plots and 11 times in harvested plots. We speculate that these patterns reflect underlying soil trends that were masked by the soil water uptake patterns in the mature forest. Bergstrom *et al.* (1998) found that removal of a crop stimulated development of a spatial soil moisture trend in a field with a mean slope of 4%. The crop removal apparently triggered underlying spatial trends in soil moisture that were related to topographic variation or other soil factors. Once vegetation recovered, the spatial trend of soil moisture disappeared. In our study, the greatest number of significant trends (eight) occurred in the H1 plot, possibly because of the influence of a slight slope and the slash pile left in this plot.

There could be a number of reasons why we did not detect a relationship between patchiness and disturbance, even if one existed. First, degree of patchiness and patch size can vary with mean soil moisture (Ryel *et al.* 1996; Western *et al.* 1998; Wendroth *et al.* 1999). However, this should not have been a problem in our study because mean soil moisture levels varied greatly after disturbance (Fig. 2). Secondly, as sampling and data analysis procedures can greatly affect estimation of semivariogram range (Isaaks & Srivastava 1989; Bogaert & Russo 1999; Zheng & Silliman 2000), we might have been unable to detect patchiness using our particular choices of lag distance, number of sample pairs for each lag, and semivariogram regression model. Thirdly, semivariogram analysis may not be robust enough to handle data that have spatial structure at multiple scales (Meisel & Turner 1998). The fact that spatial dependence was more evident at the fine scale in our study suggests that our data may have had this problem. Fourthly, the conceptual connection between semivariogram range and an ecologically meaningful patch has not been established convincingly and more work is needed to determine whether such a functional connection exists.

#### EFFECTS OF DISTURBANCE TYPE

Harvesting disconnected the pre- and post-disturbance soil moisture spatial patterns (Table 4). This supports our third hypothesis that disturbance can make relatively permanent changes to soil moisture distribution. Girdling did not result in a permanent shift in spatial patterns and when compared with harvesting its effects on global variability were shorter in duration (Fig. 2). These results support our fourth hypothesis that greater disturbance intensity would result in greater, more rapid and more prolonged changes in spatial patterns of soil moisture.

The differences in soil moisture response may be due to harvest and natural disturbances, such as windthrow, changing forest floor depth, the degree of mineral soil exposure, microtopography, and bulk density of the mineral soil (Edwards & Ross-Todd 1983; Beatty 1984; Pritchett & Fisher 1987; Liechty *et al.* 1992; Clinton & Baker 2000), whereas girdling (and presumably the bark beetle attacks that were simulated by girdling) cause little immediate disturbance to the forest floor and only later add pine needles and coarse woody debris. A second qualitative difference relates to structure of the vegetation: in our harvest treatment small patches of vegetation became established and these may have maintained or enhanced patchiness, and therefore global variability of soil moisture. In contrast, girdling eliminated the overstorey pines but left a substantial number of hardwoods (*c.* 10% of total basal area) (Lister *et al.* 2000) that may have rapidly extended their root systems and filled the root gaps left by the demise of the pine trees. In addition, many girdled trees lived for several months after the treatment and this may have maintained enough transpiration to reduce the increase in global variability of soil moisture when compared with the harvested plots.

#### INFLUENCES OF SCALE AND PLOT REPLICATION

Scale of measurement had relatively strong impacts on global variability where it interacted with disturbance type and spatial dependence. For example, variability was greater at the coarse scale in the harvested plots, but similar at both scales (or less at the fine scale) in the girdled and undisturbed plots (Table 1). It has been proposed that global variability may increase continually with scale (Bell *et al.* 1993), but our results suggest a more complex relationship at the scales we measured (0.5–60 m). The influence of measurement scale on spatial structure (spatial trend and spatial dependence) was also complex. In general, for semivariograms in individual plots, spatial structure was more prevalent at the fine scale. However, the shapes of semivariograms were complex when data from both scales were pooled.

Our use of plot replication revealed some variation in spatial-temporal patterns of soil moisture. Patterns of spatial dependence are often considered site-specific (e.g. Kelly & Canham 1992; Halvorson *et al.* 1994; Palmer & White 1994; van den Pol-van Dasselaar *et al.* 1998). Our study area would be considered by many to be a 'single site' because it had similar soil conditions and a common history prior to our experimental disturbances. Temporal patterns of global variability were highly repeatable (Fig. 2) but those for spatial dependence were not (Tables 2 and 3). These inconsistencies between replicate plots and the observed temporal changes in spatial patterns (e.g. Table 4) suggest that caution should be taken against making broad generalizations on the ecological significance of spatial pat-

terns based on data from a single plot or at a single sampling date.

#### Conclusions

Spatial heterogeneity is important to many ecological processes, but we have so far lacked consistent methods for measuring it, and more importantly, for relating heterogeneity to ecological processes. Using an experimental approach, we disturbed a forest and thereby set in motion ecological processes (e.g. plant death and regrowth, physical changes in the litter layer) that we assumed would alter spatial patterns of soil moisture. By repeatedly measuring soil moisture spatial patterns in time, we determined that sample variance was a robust measure for quantifying spatial variability. It showed strong dynamic patterns during early succession and differentiated between two types of disturbance. Measures of spatial dependence using geostatistics, however, did not reveal strong or easily interpretable patterns. We do not conclude that the geostatistical approaches are ineffective, but rather suggest that the usefulness of geostatistics in describing spatial patterns remains uncertain.

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