

Changes in the spatial variation of soil properties following shifting cultivation in a Mexican tropical dry forest

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Abstract The role of secondary vegetation in restoring soil fertility during shifting cultivation in the tropics is well known. Yet the effect of secondary succession on the spatial patterns of soil properties has received little attention. To determine whether changes in the plant community as a result of shifting cultivation affect the scale of spatial dependence for biologically important soil nutrients, we sampled three dry tropical forest stands in Campeche, Mexico. These stands represented a gradient of cultivation history: one mature forest stand, a forest fallow that had undergone one cultivation-fallow cycle, and a forest fallow that had undergone two cultivation-fallow cycles. We used an analysis of semivariance to quantify the scale and magnitude of spatial dependence for organic matter content (OM), phosphorus (P), potassium (K), and aluminum (Al) in each stand. The scale of spatial

dependence varied with cultivation history, but the degree of spatial dependence did not differ among stands. In the mature forest P and K were autocorrelated over distances >7.5 m. In the forest fallows 48–88% of the variation in soil P and K was autocorrelated over distances up to 1.1–5.1 m. In contrast, the range of autocorrelation for Al (~2.5 m) did not differ among stands. We conclude that shifting cultivation changes the range of autocorrelation for biologically important soil nutrients at a scale that may influence plant growth. The finer scaled pattern of soil nutrients in forest fallows is likely to persist with continued shifting cultivation, since fallows are cleared every 3–15 years.

Keywords Tropical dry forest · Geostatistics · Mexico · Shifting cultivation · Soil nutrients · Spatial heterogeneity

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Introduction

Resource gradients and environmental heterogeneity are common features of ecological communities (Robertson and Gross 1994). In soils the combined effect of biota and differences in topography, climate, age, and parent material create variation on local to regional scales (Jenny 1941), yet spatial patterns are rarely made explicit in studies of soil properties. Research in tropical

(Fernandes and Sanford 1995; Døckersmith et al. 1999), temperate (Boettcher and Kalisz 1990), and arid (Schlesinger et al. 1996) ecosystems has shown that individual plants have a lasting effect on the chemical distribution of soil nutrients, contributing to the spatial heterogeneity of soil properties at a site. In fact, the impact of secondary vegetation on soil fertility is the basis of shifting cultivation in the tropics (Nye and Greenland 1960; Brown and Lugo 1990; Døckersmith et al. 1999). Despite its influence on soil chemistry following cultivation, little is known about how secondary succession might also affect the spatial distribution of soil nutrients, or how spatial patterns may change with repeated disturbance and regrowth, as occurs in shifting cultivation.

If plants are an important source of heterogeneity in soil properties, large changes in the plant community, like those that occur during cultivation and succession, should produce changes in soil heterogeneity. Plants' ability to create, maintain and exploit spatial heterogeneity may be a factor affecting species succession (Stark 1994) and the establishment and survival of seedlings (Huante et al. 1995; Lawrence 2003). Therefore, the scale and extent of spatial heterogeneity in soil properties may influence species composition, distribution, and performance and possibly ecosystem-level processes in secondary forests (Robertson and Gross 1994; Gallardo 2003). If the spatial distribution of nutrients evolves over many cycles of disturbance and recovery, the species composition of secondary forests may continue to change (Lawrence et al. 2005).

The objective of this study was to determine whether repeated disturbance from shifting cultivation affects the distribution of soil properties in a Mexican tropical dry forest. Our initial hypotheses were that (1) changes in the size and structure of the plant community caused by forest clearing and regrowth would be accompanied by changes in the scale of soil variability; and (2) changes in soil spatial patterns associated with shifting cultivation would be most clearly reflected in biologically important elements (e.g. phosphorus). Therefore, we expected the scale of spatial patterning for biologically important soil nutrients to be smaller in secondary than in mature forest stands. To explore spatial patterns

in soil properties, we intensively sampled three forest stands in an *ejido* in Campeche, Mexico. These included two secondary forest stands that were the same successional age but had different cultivation histories. A third stand, a mature forest that had not been cultivated in recent memory, was included for comparison. Because of the proposed connection between vegetation and spatial patterning in the soil, we surveyed the vegetation at these sites in addition to sampling soil properties. Using geostatistical measures of spatial variability, we described the degree and extent of spatial variability present at the study sites for different soil properties.

Methods

Study area

In May 2003 fieldwork was conducted in El Refugio (18°49' N, 89°27' W), an *ejido* located along the northeastern boundary of the Calakmul Biosphere Reserve in Campeche, Mexico. This area is part of a karstic upland, characterized by rolling limestone hills 20–60 m high (Turner 1974). Soils are shallow and calcareous with a high pH because of the calcium-carbonate-rich parent material. El Refugio has a mean annual temperature of 24.4°C and receives ca. 890 mm of rain annually although precipitation is highly variable both seasonally and interannually. The typical dry season begins between November and January and lasts from 5 to 7 months (Lawrence and Foster 2002). Due to the pronounced dry season, the dominant vegetation in this region is characteristic of a tropical dry forest.

As part of the Southern Yucatan Peninsula Region (SYPR), El Refugio has a long history of human use and occupation, making it a particularly relevant area for studying the effects of human disturbance. During the Maya period (ca. 1000 B.C.–1000 A.D.) much of the SYPR was subject to large-scale intensive agriculture and widespread deforestation (Turner 1974; Turner et al. 2001). The most recent period of intense use began at the start of the 20th century when the government opened the region to chicle extraction. Between the 1930s and the 1960s the timber

industry boomed, but by the 1980s the most economically valuable species, mahogany and Spanish cedar, had been almost completely eliminated (Turner et al. 2001; Klepeis 2004). Currently, conversion of forest for agriculture is the leading cause of deforestation. Beginning in the late 1960s, government sponsorship of the *ejido* system (communal land tenure) encouraged an influx of settlers from other regions in Mexico. The area continues to attract new settlers to engage in subsistence production of maize and increasingly the cultivation of jalapeños for market (Keys 2005).

Farmers in this region practice shifting cultivation. After the slash-and-burn clearing of a tract of land, they cultivate it for several years, then abandon it, allowing secondary vegetation to grow until they are ready to clear and cultivate that parcel again. The process begins each year in March, when farmers clear a 1–2 ha plot. Cut vegetation is burned after having dried in the field for 3–6 weeks. Following the fire, stumps, logs, or large branches that have not been fully consumed remain in the field, but no trees are left standing. Once the field has been prepared in this manner, farmers use a 2 m-long stick to create small holes for the kernels, which are usually planted less than half a meter apart. These fields, known locally as *milpa*, may occasionally be weeded but they do not receive pesticides or fertilizers. After a field has been cultivated, it is abandoned, typically for 3–15 years, until the farmer decides to clear it again and the process starts over (Eaton and Lawrence 2006). A complete cultivation-fallow cycle encompasses clearing, cultivation, and a fallow period.

Within El Refugio, three forest stands were selected to represent a gradient of cultivation history while minimizing differences in successional age. Based on interviews with local farmers, we selected two 8-year old secondary forest fallows that had been used exclusively to cultivate maize without the input of chemical fertilizers. One secondary forest stand had undergone only one cultivation-fallow cycle (subsequently referred to as ‘one-fallow’ forest). It had been cleared from mature forest, farmed for two consecutive years, and then abandoned 8 years prior to sampling. The second forest fallow had

experienced two cultivation-fallow cycles (‘two-fallow’ forest). After being cleared from mature forest, it was cultivated for three consecutive years, and lay fallow for 6–7 years. Then it was cleared again, cultivated for another 3 years, and had been fallow for 8 years. The third stand, a mature forest, was managed by the same *ejidatario* who farmed the two-fallow forest and these two stands were separated by less than 1 km. Like the stands that have been converted to agriculture, all mature forest stands in El Refugio may have been selectively logged in the past 40–100 years, but none have been cultivated in recent memory. Therefore, though this stand may have been selectively logged, it represents a pre-cultivation state and serves as a good comparison for the agriculturally disturbed stands (Read and Lawrence, 2003). There is little soil disturbance associated with the no-till agriculture practiced in El Refugio, so differences in soil nutrients between mature and secondary forests are largely due to the impact of fire, harvest, and regrowth.

Field sampling and laboratory analysis

Two plots were established within each of the three forest stands (mature, one-fallow, two-fallow). In each plot, we laid out two orthogonal 15-m transects that intersected in the middle. Each transect was divided into meter-long segments and within each segment soil samples were collected at two or three randomly selected points. Soil samples (7.5 cm diameter corer) of the top 5 cm were taken at 40 points along each transect ($n = 80$). In order to include two plots per stand, we chose this sampling design rather than the nested-grid design used in some other studies of soil spatial patterns (e.g. Gross et al. 1995). Nutrients that are most limiting to plant growth (e.g. P and K) are more concentrated in the topsoil and their vertical distribution is primarily controlled by plant cycling (Jobbágy and Jackson 2001). Thus, our measurements were restricted to the top 5 cm because this depth is more likely to reflect changes in aboveground inputs to the soil. Because of the hypothesized relationship between vegetation and soil heterogeneity, the location, species, and dbh (diameter at breast height, measured at 1.3 m) were

recorded for all trees along the transects with dbh >1 cm. Trees >5 cm dbh were documented within a 6 × 15 m rectangle bisected longitudinally by each transect (total sampling areas 144 m²/plot); stems 1–5 cm dbh were recorded within a 1 × 15 m rectangle bisected longitudinally by each transect (total sampling area 29 m²/plot). We expect this sampling design to capture heterogeneity in these stands because they tend to be small (≤2 ha) and low-statured (mean height 7.6 m for mature forest trees 5–10 cm dbh, 12.6 m for mature forest trees >10 cm dbh, Vester et al. 2007). Moreover, in all three forest stands included in this study, mean interstem distance is <2.25 m for stems >5 cm dbh and <1.5 m for stems 1–5 cm dbh (Table 4).

After sampling, soils were air dried, then passed through a 2 mm sieve. Soil samples were analyzed by Brookside Laboratories (New Knoxville, OH) for Mehlich III extractable Ca, Mg, K, P, S, Mn, Cu, Zn, B, Fe, and Al (by Inductively Coupled Plasma Spectrometry). Soil organic matter content (OM) was determined by loss on ignition (LOI) at 360°C; soil pH was determined in a 1:1 H₂O solution; and total cation exchange capacity (TEC) was calculated using the summation method (M. Flock, personal communication). LOI has a tendency to overestimate soil organic matter because of the loss of CO₂ from carbonates and of structural water from clays (Frogbrook and Oliver 2001; De Vos et al. 2005). However, LOI was performed on our samples at 360°C, which should minimize the effect of these losses since carbonates are stable at temperatures <500°C (De Vos et al. 2005) and the greatest loss of structural water occurs at >450°C (Varvel et al. 2002; De Vos et al. 2005). Moreover, studies have shown that the spatial patterns calculated from different soil organic carbon determination methods are similar, even if the magnitude of the values these methods produce is different (Frogbrook and Oliver 2001; Ping and Dobermann 2006).

Statistical analysis

To determine the general distribution of nutrients at each plot, the mean, standard deviation, standard error, variance, and coefficient of vari-

ation were calculated for each soil property at each of the 6 plots using SAS (version 8.2, SAS Institute Inc., Cary, NC). One-way analysis of variance (ANOVA) was used to compare soil properties between stands and between plots. A post hoc comparison of means following a significant ANOVA ($P < 0.05$) was done with a Tukey's studentized range test.

We used variography to describe the spatial distribution of OM, P, K, and Al at each site. Organic matter, P, and K were selected because they are important for plant growth and their movement in the soil is, to varying degrees, biologically controlled. Aluminum was chosen because it is not essential to plant nutrition and its movement in the soil is geochemically controlled. A semivariogram (also known as a variogram) is a graphic representation of spatial autocorrelation that is made by plotting the semivariance for several distance intervals (Robertson and Gross 1994). The semivariance is calculated as:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{N(h)} [z(x_i) - z(x_i + h)]^2$$

where, $\gamma(h)$ is the semivariance, h is the distance interval or lag, $N(h)$ is the total number of pairs separated by distance h , $z(x_i)$ is the value of the specified property at location x_i , and $z(x_i + h)$ is the value of that property at the location $x_i + h$ (Kaluzny et al. 1998). The distance interval (h) can represent either an exact distance (e.g. 20 cm), or a class of distances, (e.g. 10–30 cm).

Spatial autocorrelation is based on the idea that samples taken close together are more likely to have similar values than those that are further apart. If variance does not change with distance, the semivariogram is relatively flat. When spatial autocorrelation occurs the semivariance is small at short lag intervals, indicating that samples separated by a short distance are more similar, and increases as samples become further apart and less similar (Rossi et al. 1992). Eventually the semivariance may rise to some asymptote, the sill ($C + C_0$), that approximates the population variance. The range (A_0) is the distance at which the semivariogram reaches the sill and it describes the distance over which spatial autocorrelation is expressed. Theoretically there should be no

variance at 0 lag distance because samples are perfectly autocorrelated with themselves. However at very short lag distances, semivariance can deviate substantially from zero. The semivariance calculated at lag distances close to 0 (or more typically, projected to the y-axis) is called the nugget variance (C_0) and represents either experimental error or variability that occurs at a scale smaller than the sampling interval. Finally, the ratio of the spatially structured variance to the sample variance ($C/C + C_0$) reveals the degree of spatial dependence. As outlined by Robertson and Gross (1994), the ecologically significant functions of a semivariance analysis of soil resources are to determine whether spatial dependence or patchiness exists for a resource, how distinct the patches are, and at what scale they occur.

S+ Spatial Stats (Version 1.5, Insightful Corporation, Seattle, Washington) was used to construct semivariograms and fit models to data for OM, P, K, and Al. Before fitting models to the semivariograms the data was checked for normality and stationarity. Data that deviated from normality was transformed for the analysis of semivariance. We also checked the data for anisotropy and made directional variograms where appropriate. When the analysis of stationarity revealed a trend in the data along one sampling axis, we chose to make two directional semivariograms rather than one omnidirectional variogram that could be distorted by the trended data. Directional semivariograms made when the assumption of stationarity may have been violated have been noted. We used the lag interval that produced the best semivariogram, therefore the lag intervals range from 20 to 50 cm, distances that are substantially less than the typical inter-tree distance. The analysis extends to a maximum distance of 7.5 m, which is approximately half the distance between the largest lag pair (Rossi et al. 1992). Given the different lag intervals used and the mix of omnidirectional and directional semivariograms, the maximum and minimum number of pairs for each semivariance analysis varies. The minimum number of pairs ranged from 7 to 56 (mean = 20). The maximum number of pairs ranged from 21 to 220 (mean = 99; see Appendix 1 for a complete list of minimum and maximum pairs). We used unweighted nonlinear least

squares analysis to fit variogram models. For goodness of fit and ease of comparison, we applied spherical models to the semivariograms except where a linear model was more appropriate. We have chosen to focus on spherical models because they have been found to be a good fit to semivariograms of soil properties (Webster 1985; Schlesinger et al. 1996). A linear model indicates that there is spatial autocorrelation in the dataset, but that the range of autocorrelation is greater than the maximum lag distance (7.5 m). If neither a spherical nor a linear model fit the semivariogram, it was characterized as random. Cross-validation was used to evaluate how well variogram models estimated known values from the sample population, (GS+, version 7, Gamma Design Software, Plainwell, MI). All correlation coefficients between cross-validation estimates and actual values for spherical models are significant with 99% confidence.

Results

Soils

Variation among stands

Comparing soil properties between the three forest stands and between the six plots shows that the mature forest and the two-fallow forest near by have similar soil nutrient concentrations (ANOVA, $P > 0.05$) (Table 1). With higher pH, more OM, greater S, Ca, K, and lower Mn, Al, and Fe concentrations (Table 1), these two stands appear more fertile than the one-fallow forest located about 2 km away. Organic matter content was greatest in the mature forest stand (15.0%), while P (25.9 $\mu\text{g/g}$) and K (385.1 $\mu\text{g/g}$) were greatest in the two-fallow forest. The one-fallow forest had nearly 7 times as much Al as the other two stands.

Variation within stands

The coefficient of variation (CV) functions as an indicator of variability in each plot (Schlesinger et al. 1996). Generally, CVs from these sites are relatively low indicating that most of the variables

Table 1 The mean concentration of soil properties (0–5 cm) for each of three stands of tropical dry forest in Campeche, Mexico

	Mature forest <i>n</i> = 2	One-fallow <i>n</i> = 2	Two-fallow <i>n</i> = 2
<i>Soil properties</i>			
Al	68.3 ^a	469.7 ^b	48.3 ^c
Na	38.8 ^a	40.0 ^a	26.1 ^b
OM (%)	15.0 ^a	8.7 ^b	12.6 ^c
PH	7.9 ^a	7.5 ^b	8.0 ^c
TEC (M.E./ 100 g)	56.5 ^a	40.6 ^b	82.7 ^c
<i>Macronutrients</i>			
Ca	10,547 ^a	7,344 ^b	15,570 ^c
K	243.7 ^a	166.3 ^b	385.1 ^c
Mg	362.0 ^a	392.5 ^b	446.5 ^c
P	14.1 ^a	12.1 ^b	25.9 ^c
S	38.7 ^a	32.6 ^b	40.4 ^a
<i>Micronutrients</i>			
B	2.9 ^a	1.2 ^b	2.0 ^c
Cu	2.0 ^a	1.9 ^a	1.3 ^b
Fe	12.1 ^a	40.1 ^b	7.4 ^c
Mn	83.3 ^a	115.1 ^b	41.3 ^c
Zn	1.4 ^a	1.3 ^a	1.9 ^b

Two plots per stand were sampled. Statistically significant differences sites are represented with lowercase letters (a–c). All differences are significant at the $P < 0.0001$ level. Unless otherwise noted units are ($\mu\text{g/g}$)

had similar concentrations throughout a plot (Table 2). In the mature and two-fallow forest, CVs were highest for Al, Zn, and Fe, and <25% for the remaining soil properties. Aluminum was the most variable soil property, with a CV of 73.6% in the two-fallow forest. Across all three sites the CVs for P, K, and OM were <35% and relatively low. Using spearman rank-correlation coefficients, we found strong positive correlations among pH, S, Ca, and Mg and among Al, Fe, and Mn ($P \leq 0.0006$ with a bonferroni adjustment for multiple comparisons).

Spatial variation

The degree of spatial variability ($C/C + C_0$) differed little among sites or soil properties. In all three stands 62%–85% of the variance in OM, 58%–88% of the variance in P, 48%–65% of the variance in K was spatially dependent, and 53%–76% of the variance in Al (Table 3). Replicate plots showed similar degrees of spatial variability for OM and K in the one-fallow forest, and similar degrees of spatial variability for OM in the two-fallow forest. While cultivation history did

Table 2 The coefficient of variation [(SD+mean) \times 100%] of soil properties (0–5 cm) for each plot sampled in three stands of tropical dry forest in Campeche, Mexico

	Mature forest <i>n</i> = 80	Mature forest <i>n</i> = 80	One-fallow <i>n</i> = 80	One-fallow <i>n</i> = 80	Two-fallow <i>n</i> = 77	Two-fallow <i>n</i> = 81
<i>Soil properties</i>						
Al	46.9	36.0	19.9	17.0	56.0	73.6
Na	10.3	18.0	22.6	20.5	17.3	16.2
OM	21.0	17.4	19.9	26.4	20.0	18.0
PH	1.2	0.7	4.2	4.9	1.4	0.8
TEC	15.2	7.9	29.3	13.2	15.4	13.5
<i>Macronutrients</i>						
Ca	16.8	8.1	31.7	13.9	16.6	13.8
K	22.0	23.7	32.1	33.4	15.7	17.4
Mg	13.7	15.1	15.3	13.3	14.3	14.0
P	12.3	13.9	21.4	15.9	12.6	15.0
S	9.1	6.8	31.6	18.4	10.9	17.9
<i>Micronutrients</i>						
B	16.8	13.7	26.7	13.8	19.5	12.0
Cu	34.8	28.4	18.7	24.0	20.6	16.7
Fe	50.1	38.6	22.9	24.7	22.2	63.2
Mn	23.1	20.9	21.5	48.2	18.5	21.5
Zn	38.3	40.0	30.3	29.5	49.4	19.6

Table 3 Summary of the semivariogram model parameters for OM, P, K, Al from three tropical dry forest stands

Variate	Site	Model	Nugget (C_0)	Sill ($C_0 + C$)	Range (cm)	$C/(C_0 + C)$	r^2	Correlation coefficient
OM	Mature (0°)	L ^a	1.97	–	>750	–	0.71	–
	(90°)	S	0.71	4.81	552	0.85	0.48	0.70
	Mature (0°)	L ^a	4.04	–	>750	–	0.40	–
	(90°)	R	–	–	–	–	–	–
	One-fallow	S	0.42	3.77	243	0.62	0.61	0.53
	One-fallow	S	1.65	5.02	513	0.67	0.73	0.69
	Two-fallow	S	2.02	6.38	394	0.68	0.68	0.63
P	Two-fallow	S	1.47	5.8	573	0.75	0.73	0.58
	Mature	L	1.2	–	>750	–	0.18	–
	Mature	L	3.05	–	>750	–	0.38	–
	One-fallow (0°)	S	1.29	3.04	459	0.58	0.29	0.41
	(90°)	R	–	–	–	–	–	–
	One-fallow	S	1.02	3.91	383	0.74	0.91	0.69
	Two-fallow	S	0.47	4.06	113	0.88	0.74	0.36
K	Two-fallow	S	10.46	33.62	305	0.69	0.79	0.60
	Mature (0°)	L	100	–	>750	–	0.61	–
	(90°)	L	960	–	>750	–	0.61	–
	Mature	L	385	–	>750	–	0.87	–
	One-fallow	S	924	2,280	459	0.59	0.57	0.55
	One-fallow	S	1,723	4,414	183	0.61	0.83	0.48
	Two-fallow	S	1,906	5,447	508	0.65	0.68	0.65
Al	Two-fallow	S	1,584	3,075	363	0.48	0.57	0.50
	Mature (0°)	S	0.043	0.156	244	0.72	0.43	0.82
	(90°)	L ^a	0.049	–	>750	–	0.51	–
	Mature	S	0.038	0.096	345	0.60	0.66	0.71
	One-fallow	S	0.026	0.055	398	0.53	0.63	0.58
	One-fallow	S	0.008	0.023	142	0.66	0.94	0.55
	Two-fallow (0°)	S	0.049	0.204	242	0.76	0.81	0.90
	(90°)	L ^a	0.062	–	>750	–	0.32	–
	Two-fallow	S	0.107	0.212	143	0.50	0.85	0.46

Plots with two entries were anisotropic for that variate and separate semivariograms for each sampling axis have been created. ^a Indicates a trend in the data. L = linear model, S = spherical model, and R = random model. A linear model indicates that there is spatial autocorrelation in the dataset, but that the range of autocorrelation is greater than the maximum lag distance (7.5 m). The cross-validation correlation coefficient is a measure of how well spherical semivariogram models estimate sample values; all cross-validation correlation coefficients are significant ($P < 0.01$)

not appear to affect the degree of spatial dependence, the range of autocorrelation differed between forest stands.

In the mature forest, semivariograms for both P and K were linear, indicating that soil P and K were autocorrelated over a distance >7.5 m in both plots (Figs. 1, 2). A linear model indicates that there is spatial autocorrelation in the dataset, but that the range of the spatial autocorrelation is larger than the longest lag distance. There was no consistent spatial pattern for OM. In one of the mature forest plots, a directional semivariogram showed the range of autocorrelation for OM was 5.5 m; at the other plot a directional semivario-

gram showed the variance in OM was random, indicating that OM was not spatially structured over the scale of analysis (Table 3). In contrast, Al exhibited a clear pattern in the mature forest. Al was autocorrelated over distances of 2.4 and 3.5 m in the two mature forest plots (Fig. 3). The nugget-to-sill ratios of these semivariograms indicated that 28%–40% of variance occurred at <0.3 m.

In the forest fallows P and K were spatially autocorrelated over shorter distances than in the mature forest. At the one-fallow forest, the range of autocorrelation for P was 3.8 m in one plot and 4.6 m in the other. Spatially structured

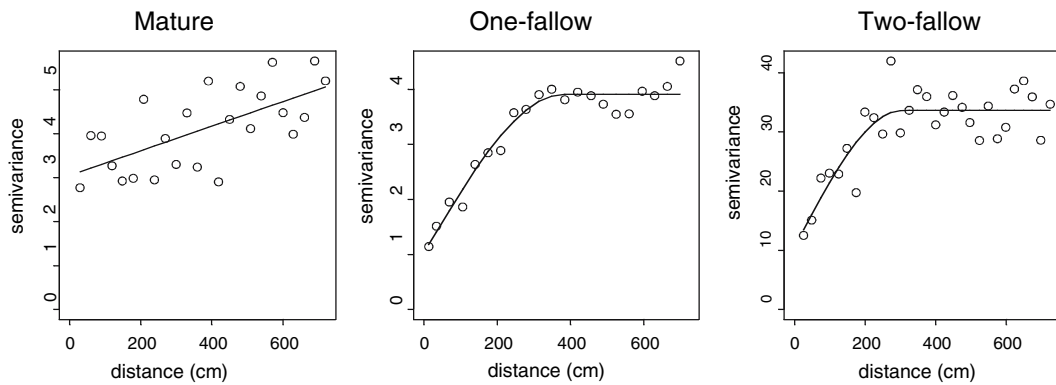


Fig. 1 Semivariograms for P from mature forest and forest fallows with different cultivation histories in a Mexican tropical dry forest

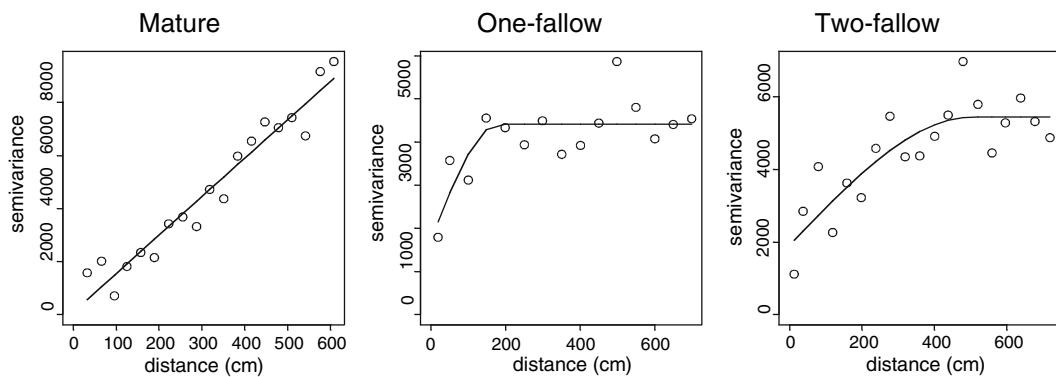


Fig. 2 Semivariograms for K from mature forest and forest fallows with different cultivation histories in a Mexican tropical dry forest

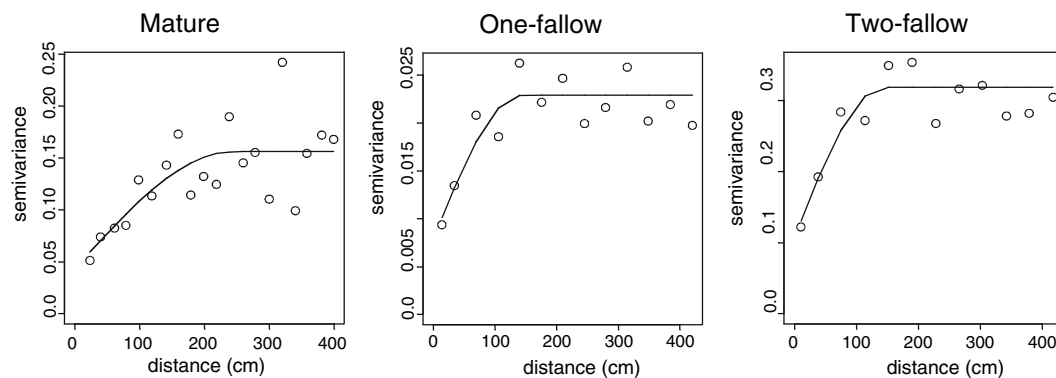


Fig. 3 Semivariograms for Al from mature forest and forest fallows with different cultivation histories in a Mexican tropical dry forest

variance occurred over a shorter distance at the two-fallow site, where P had a range of autocorrelation of 1.1 and 3.1 m (Fig. 1). K exhibited a similar pattern: spatial autocorrelation occurred over distances of 1.8 and 4.6 m in the

one-fallow stand and over 3.6 and 5.1 m in the two-fallow stand (Fig. 2).

In the one-fallow forest, OM was autocorrelated over distances of up to 2.4 and 5.1 m and up to 3.9 and 5.7 m in the two-fallow forest

Table 4 Vegetation characteristics of three dry tropical forest stands (mean of two plots per stand, with the exception of 8 year two-fallow for which we have data for only one plot)

Forest type	No. species	Stem density (stems/m ²)	Average inter-stem distance (m ² /stems) ^{1/2}	Basal area (m ² /ha)
<i>Stems 1–5 cm dbh</i>				
Mature	12	0.53	1.41	2.50
8 year One-fallow	16	1.79	0.76	8.91
8 year Two-fallow	10	1.28	0.88	4.05
<i>Stems >5 cm dbh</i>				
Mature	23	0.24	2.04	44.09
8 year One-fallow	4	0.01	10.0	0.51
8 year Two-fallow	11	0.20	2.24	15.34
<i>All stems</i>				
Mature	29	0.75	1.15	46.58
8 year One-fallow	17	1.80	0.75	9.41
8 year Two-fallow	14	1.48	0.82	19.39

Stems 1–5 cm dbh were sampled in a 29 m² area; stems ≥5 cm dbh were sampled in an 144 m² area. Basal area was calculated using every stem recorded. When calculating stem density each tree was considered as one stem, even when a single tree had several stems

(Table 3). While the scale of autocorrelation for OM, P, and K differs between the mature forest and the forest fallows, among the forest fallows the pattern of spatial dependence does not appear to differ much despite the differences in their cultivation histories. Only AI had a range of autocorrelation similar to that found in the mature forest. In the one-fallow forest, AI was autocorrelated over distances of 1.4 and 4.0 m, and in the two-fallow forest, over 1.4 and 2.4 m (Fig. 3).

Vegetation

The vegetation of the three sites differed substantially (Table 4). We recorded 17 species in the one-fallow forest, 14 species in the two-fallow forest, and 29 species in the mature forest. Of the 5 most frequent species at each site, only one species, *Psidium sartorianum*, was common to all three sites. Although there is only one other species ('Bomopch', common name) shared by all three sites, all pairwise combinations of the sites share several species. Basal area (>1 cm) was greatest in the mature forest (46.6 m²/ha), followed by the two-fallow (19.4 m²/ha) and one-fallow (9.4 m²/ha) sites. Driving the difference in basal area among our three sites is the dearth of trees >5 cm dbh in the one-fallow forest, where we recorded a stem density of only 0.01 stems/m² between 5 and 10 cm dbh and no stems ≥10 cm

dbh. In contrast, the two-fallow forest had 0.12 stems/m² between 5 and 10 cm dbh and 0.08 stems/m² between 10 and 20 cm dbh. The mature forest had 0.20 stems/m² with dbh >20 cm. The one-fallow forest had the highest number of stems <5 cm (Table 4). Including all stems, the density of the one- and two-fallow forests are similar (1.80 vs. 1.48 stems/m²) and approximately twice that of mature forest (0.75 stems/m²).

The range of autocorrelation for both K and P is lowest in stands with high stem density or low basal area. In our plots, the ranges of these soil nutrients increase with greater basal area; they also increase with lower stem density. In contrast, the range of autocorrelation for OM and AI does not appear related to basal area, small stem density, or total stem density (Table 4).

Discussion

Geostatistics augments the ability of parametric statistics to compare spatial dependence between and within forest stands. On the one hand, parametric statistics indicate that the location of forest stands in El Refugio influences the magnitude of nutrient concentrations (Table 1). Similarly, comparing CVs between sites reveals that geographic location is a better indicator of variability in each plot than disturbance history

(Table 2). On the other hand, a geostatistical analysis suggests that cultivation history has a greater effect than geographic proximity on the spatial pattern of nutrients within a stand (Figs. 1, 2).

The pattern of soil properties in El Refugio—soil resources that are spatially dependent from 0.2 m to more than 7.5 m—is within the range reported for other forests. In a temperate old growth forest, Lechowicz and Bell (1991) found that pH, NO_3 , and K were all spatially correlated at distances less than 2 m. In a Nicaraguan wet tropical forest, P was autocorrelated over distances up to 7–11.6 m and K was autocorrelated over distances up to 3.8–10.8 m (Blair 2005). Gonzalez and Zak (1994) found that organic C, N transformations, and available P were all spatially dependent at ≤ 24 m in a secondary tropical dry forest. They concluded that much of the spatial variation in this system was fine-scale and likely to be driven by individual trees. The nugget variance in their study was quite high (55%–74% of the sample variance), indicating that a large portion of the sample variance occurs at scale smaller than their shortest lag distance (4 m) (Schlesinger et al. 1996). Results from our study, done with much shorter lag intervals (0.2–0.5 m), also indicate fine-scale spatial patterning in secondary dry tropical forests. For instance, 58%–88% of the total variation in P was spatially dependent from 0.2 to 4.6 m.

In the three forest stands we studied, cultivation history did not appear to affect the degree of spatial dependence in soil properties (Table 3). However, the process of shifting cultivation reduced the scale of variability of both P and K (Figs. 1 and 2). For example, P had a range greater than ≥ 7.5 m in the mature forest compared to a range of 1.1–3.1 m in the one-fallow forest, and 3.8–4.6 m in the two-fallow forest. Shorter ranges of autocorrelation for both P and K in the forest fallows are likely due to the smaller tree canopies in these stands. Vegetative cover influences the spatial distribution of soil nutrients, through litter deposition and decomposition, stemflow, and throughfall (Lechowicz and Bell 1991; Døckersmith et al. 1999). In addition, plants affect soil nutrients through the decomposition of root litter, the release of root exudates, and root turnover (Vitousek and Sanford 1986;

Døckersmith et al. 1999; Blair 2005), although these belowground processes are not addressed specifically by this research.

While OM did not exhibit a consistent pattern of spatial dependence over the scale of analysis in the mature forest, the variability in OM was described well by spherical models at both secondary forest sites (Table 3). Following slash-and-burn clearing, the spacing of mature forest trees would influence the location of aboveground inputs from woody debris and belowground inputs from decomposing roots. In milpas and young forest fallows woody debris plays an important role, making up 88% of total aboveground biomass in milpas and 30% of total aboveground biomass in 6–11 year old forest fallows (Eaton and Lawrence 2006). These localized organic inputs from both above- and belowground sources may contribute to spatial patterning in soil organic matter after trees have been cut and burned in preparation for cultivation (Døckersmith et al. 1999). The role of vegetation (and surficial processes in the soil) in creating spatial patterns are probably especially relevant to this study because we sampled only the top 5 cm of soil, a depth likely to reflect changes in aboveground inputs to the soil (Jobbágy and Jackson 2001).

We expected to compare the one-fallow and two-fallow stands to see what if any changes there were to the scale of spatial dependence after a second cultivation-fallow cycle. However the differences in the structure of vegetation between the 8-year old one-fallow and 8-year old two-fallow stand make it difficult to analyze the effect of repeated cultivation on spatial patterns (Table 4). Despite the structural differences between these stands, the basal areas calculated at the two sites—9.4 m^2/ha for one-fallow forest and 19.4 m^2/ha for the two-fallow—correspond well to the range (5.9–34.3 m^2/ha) for secondary forests recorded in a study of biomass recovery in the SYPR that used 500 m^2 plots to characterize forest structure (Read and Lawrence 2003).

In addition to the effects that plants are expected to have on the spatial distribution of soil nutrients, other factors associated with shifting cultivation may also influence spatial heterogeneity following disturbance. Robertson et al. (1993), studying a cultivated and uncultivated

field in southwest Michigan, found that although the magnitude of spatial dependence remained relatively constant for all soil properties, the scale of autocorrelation was quite different: the range of most soil properties was greater by a factor of 3 or more in the cultivated field, a pattern they attribute to repeated tillage, which is a “smearing out” process. Similarly disturbance influenced the scale, but not the degree, of spatial patterning at our study site. Because farmers in El Refugio use dibble sticks to plant, the changes in the range of autocorrelation that we observed are more likely the result of changes in vegetation than of physical disturbances associated with cultivation. Fire may also affect the spatial patterns of soil nutrients. In a tropical wet forest, burning was found to reduce the patch size of P, N, K, and C (Blair 2005). Blair (2005) attributes soil spatial patterns in the unburned plots to the above- and belowground effects of plants on soil and those in burned plots to changes in the plant community as well as to the effects of fire. Our results indicate that after slash-and-burn clearing, 2–3 years of cultivation, and 8 years of fallow the spatial pattern of biologically cycled soil properties is markedly different from that of the mature forest (Figs. 1, 2). Moreover at these sites, where a new cultivation-fallow cycle begins every 3–15 years (Eaton and Lawrence 2006), it is unlikely that the coarser pattern found in the mature forest will be restored as long as shifting cultivation persists in these locations. Further study of currently cultivated fields and forest fallows of different ages is needed to determine the relative influence of plant above- and belowground impacts, cultivation, and burning on the spatial heterogeneity of soil properties in forest fallows.

At our study site Al, which is not required by plants and is potentially toxic (Aber and Melillo 2001), had the most consistent range of autocorrelation (ca. 2.5 m) of the soil constituents we considered, suggesting that its spatial distribution was not altered by forest clearing and burning, the growth of secondary vegetation, or transport processes (Fig. 3). That Al showed a similar range of autocorrelation in all three forest stands, while P, K, and OM, differed among stands, supports the hypothesis that fallow vegetation plays a role in restructuring the spatial pattern of

essential factors of soil fertility. However, if physical processes completely controlled the movement of Al we would expect to see either a random distribution or a distribution markedly different from those soil properties strongly influenced by biotic processes (e.g. Schlesinger et al. 1996, Holmes et al. 2005). In this case, Al may be passively cycled by trees (e.g. Markewitz and Richter 1998) and heavily influenced by geochemical process in the soil. Additionally, the low mobility of Al oxides in hot and humid climates (Brady and Weil 1999) may explain the persistence of its spatial distribution through two cycles of disturbance and recovery.

Several other studies have also concluded that biologically essential elements respond differently to changes in the plant community than nonessential elements because of the different processes (biological vs. geochemical) controlling their movement (Schlesinger et al. 1996; Gallardo 2003). Poor correspondence between the range of autocorrelation of soil texture and that of P, C, and N, in a Caribbean dry tropical forests led Gonzalez and Zak (1994) to conclude that plant community structure rather than physical soil processes are driving the spatial patterning of essential nutrients in that system. Schlesinger et al. (1996) attributed the concentration of the most limiting nutrients (N, P, and K) beneath desert shrubs to the concentration of biotic processes and biogeochemical cycling beneath shrub canopies. In the dry tropical forest stands of El Refugio, where canopy cover is less discontinuous than in a shrubland, it is likely that individual trees affect the spatial pattern of soil nutrients (Døcker-smith et al. 1999), but that the extent of canopy cover, mean canopy size, and the distribution and density of tree stems probably also influence the way in which trees contribute to spatial patterns.

Our initial hypothesis was two-fold: we hypothesized, first, that spatial changes in the plant community, like those that occur during succession, would produce corresponding changes in the spatial distribution of soil nutrients in the same direction (e.g. larger plants, larger scale of autocorrelation), and second, that because of the biotic processes that link plants to the soil, the spatial distribution of biologically important soil nutrients would reflect changes in the plant

community more clearly than non-essential elements. While our first hypothesis assumes that plant size is the most important determinant of the scale of soil nutrient variability, implicit in our second hypothesis is the idea that nutrient cycling processes are also an important factor. After considering our results, we have realized that the explanatory power of differences in nutrient cycling is not limited to explaining the differences between biologically and geochemically cycled nutrients. For instance, to interpret within stand differences in the range of P and K we suggest that it is important to consider differences in how and at what rate these nutrients are cycled in addition to canopy size and stem density. Because K is rapidly leached from leaf surfaces, throughfall and stemflow as well as litterfall are important components of K cycling (Schlesinger 1997; Campo et al. 2000), and are likely to contribute to spatial patterning. Phosphorus is not so readily leached from plant surfaces, so litterfall is likely to dominate the signature of tree effects on spatial patterns in the soil (Campo et al. 2001). Additionally we expect that the range of autocorrelation for soil nutrients with faster turnover times will be more closely coupled to canopy size than those that move through the soil reservoir more slowly. That is to say, the longer leaf litter remains at the surface, the more that diffusional (bioturbation, capillary flow, or molecular diffu-

sion in porewater) or advective (sheetflow or near-surface ground water flow) processes will modify the spatial signal of the tree canopy, impacting the range. These hypotheses, however, remain to be tested (Fig. 4).

Given the observed changes to the scale of spatial dependence for P, K, and OM, but not Al, following shifting cultivation, we conclude that the spatial patterns of biologically important soil properties are altered by the slash-and-burn clearing, cultivation, and forest regrowth that comprise shifting cultivation. It is likely that the more fine-scaled pattern of P and K following shifting cultivation is related to changes in vegetative cover, like smaller tree size, reduced basal area, and increased stem density in the forest fallows relative to the mature forest. In addition, we propose that the rate and pathways of nutrient cycling impact the strength and scale of a tree's spatial signal. In forest fallows, OM, P, K, and Al exhibit spatial dependence over a distance of 0.2–5.7 m, a scale that may affect individual growth, and plant population or community structure (Robertson et al. 1993; Dockersmith et al. 1999). Although it is unknown how small-scale environmental heterogeneity affects ecosystem-level processes, studies have shown that resource variability can affect belowground biomass, plant size, competition and mortality in plant populations, and species composition (Day et al. 2003;

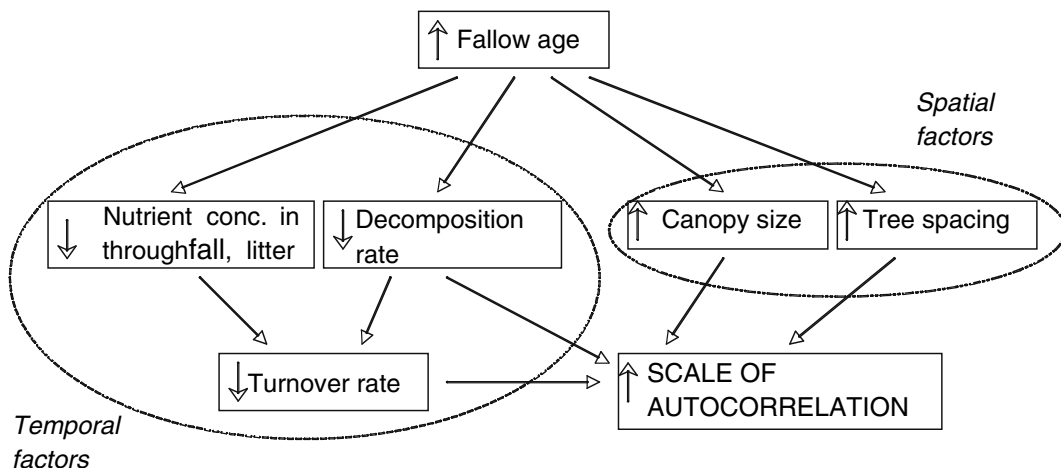


Fig. 4 Hypothesized impact of temporal and spatial factors on the scale of autocorrelation in the top 5 cm of soil in a dry tropical forest. The symbols “↑” and “↓” indicate the direction of change. For instance, lower concentrations of a nutrient in

litterfall would result in longer nutrient turnover times that would, in turn, result in a larger scale of autocorrelation for that nutrient. Increasing time since fallow will result in larger canopies that will result in a coarser distribution of nutrients

Blair and Perfecto 2004; Wijesinghe et al. 2005). These findings suggest that spatial variability in soil resources has the potential to modify competitive interactions within plant communities (Blair 2005). Significantly, the smaller patch sizes we observed in 8-year old forest fallows are likely to be maintained as long as a stand is being actively used for shifting cultivation because local farmers tend to clear forest fallows again after 3–15 years of regrowth.

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Appendix

Appendix 1. Lag interval, minimum and maximum number of pairs, and lag distance at which they occur for each variogram

Site	Lag interval (cm)	Minimum number of pairs		Maximum number of pairs	
		np	Lag distance (cm)	np	Lag distance (cm)
<i>Organic matter</i>					
Mature (0°)	30	15	602	30	31
(90°)	30	11	571	30	119
Mature (0°)	30	10	359	23	239
(90°)	30	14	600	35	88
One-fallow	45	19	16	197	630

Site	Lag interval (cm)	Minimum number of pairs		Maximum number of pairs	
		np	Lag distance (cm)	np	Lag distance (cm)
One-fallow	30	56	30	111	600
Two-fallow	26	46	27	99	493
Two-fallow	34	10	12	151	645
<i>Phosphorus</i>					
Mature	50	37	49	92	650
Mature	30	44	60	112	689
One-fallow (0°)	40	11	15	77	519
(90°)	40	23	159	58	720
One-fallow	35	7	14	157	699
Two-fallow	22	35	23	82	440
Two-fallow	25	40	27	91	675
<i>Potassium</i>					
Mature (0°)	32	18	576	34	32
(90°)	32	11	575	26	93
Mature	28	43	56	94	531
One-fallow	40	18	15	172	681
One-fallow	50	24	19	220	699
Two-fallow	40	12	14	169	720
Two-fallow	25	9	12	138	649
<i>Aluminum</i>					
Mature (0°)	20	12	381	21	119
(90°)	25	12	398	28	123
Mature	40	22	15	127	400
One-fallow	50	20	16	216	700
One-fallow	35	7	14	157	699
Two-fallow	45	10	17	46	89
(0°)					
(90°)	45	11	16	49	90
Two-fallow	38	7	11	131	646

np = number of pairs

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