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Spatial heterogeneity of soil chemical properties in a lowland tropical moist forest, Panama

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Abstract. We evaluated spatial heterogeneity for pH and a comprehensive set of nutrient and trace elements in surface (0–0.1 m depth) and subsurface (0.3–0.4 m depth) soils across 26.6 ha of old-growth, lowland, tropical moist forest, established on a highly weathered soil in Panama. Little is known about spatial heterogeneity patterns of soil properties in tropical forest soils. Soil was moderately acidic (pH 5.28) with low concentrations of exchangeable base cations (13.4 $\mathrm{cmol_c/kg}$), Bray-extractable PO_4 (2.2 mg/kg), KCl-extractable NO_3 (5.0 mg/kg), and KCl-extractable NH_4 (15.5 mg/kg). The coefficient of variation for soil properties ranged from 24% to >200%, with a median value of 84%. Geostatistical analysis revealed spatial dependence at a scale of 10–100 m for most of the soil properties; however, pH, NH_4, Al, and B had spatial dependence at a scale up to 350 m. Best-fit models to individual variograms included random, exponential, spherical, Gaussian, linear, and power functions, indicating many different spatial patterns among the set of soil properties. Correlation among individual elements was poor, indicating independent patterns. Our results show complex spatial patterns in soil chemical properties and provide a basis for future investigations on soil–plant relationships and soil nutrient niche differentiation.

Additional keywords: base cations, geostatistical analysis, nutrients, spatial variability, trace elements, variogram.

Introduction

Despite increased efforts during the past 30 or so years to quantify and interpret spatial heterogeneity of soil properties (Heuvelink and Webster 2001), we have limited understanding of spatial heterogeneity in tropical forest soils. Research has lagged in tropical forests, in part because many early researchers simply assumed that intense leaching depleted the soil profile of nearly all nutrient elements, except nitrogen (N), destroyed clay minerals by selective loss of silicon (Si), and led to soil colloids composed of mostly insoluble oxides of iron (Fe) and aluminum (Al) with little sorption capacity (Richter and Babbar 1991). Here, we describe spatial heterogeneity in soil chemical properties at the local scale (defined as tens of hectares) in an old-growth, lowland, tropical moist forest.

Many ecological and biogeochemical studies in tropical forests occur at the local scale, because it is an area large enough to obtain demographic information on individual trees species and to provide long-term information on forest composition so that future changes can be detected (Condit 1995; Losos and Leigh 2004). High diversity of tree species at the local scale shows concomitant chemical and structural diversity in the forest canopy (Townsend *et al.* 2007). Whether canopy diversity translates into soil chemical heterogeneity is less clear. According to ecosystem theory (Vitousek 1982), plant–soil feedback maintains fertile and infertile soils. For example, infertile soils support plants with high nutrient-use efficiency and nutrient-poor litter, which decomposes slowly, maintaining low soil nutrient availability. However, Townsend *et al.* (2008) question whether high species diversity in tropical forests might alter soil nutrient patterns to a greater degree than is seen in other biomes.

Geostatistical analysis is a powerful way to describe and quantify spatial dependence of resources and can be applied at multiple scales. The approach is based on the statistical theory of autocorrelation, and spatial dependence is quantified using variography (Sauer *et al.* 2006). The magnitude of spatial dependence in soil properties across tens of hectares of relatively uniform tropical forest is unclear, but it is potentially important ecologically (cf. John *et al.* 2007). Moreover, most geostatistical studies focus on a few soil properties, whereas a comprehensive set is needed to understand soil fertility.

We evaluate spatial heterogeneity for a comprehensive set of nutrient and trace elements at 2 soil depths across 26.6 ha of old-growth, lowland, tropical moist forest in Panama. We quantified the 2 components of spatial heterogeneity: (*1*) variability (in relation to the mean or median), and (*2*) dependence or pattern. By considering several chemical properties we evaluate heterogeneity as a function of element mobility and plant growth processes. For instance, we expected less variability for relatively mobile chemical elements than for less mobile

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elements. Research at the fine scale, especially in arid and semi-arid regions, has shown that plant growth enhances variability by creating and maintaining nutrient elements in patches, whereas chemical elements controlled primarily by geochemical processes show less spatial variability (Schlesinger *et al.* 1996; Gallardo and Parama 2007). However, we hypothesised that plant growth processes would lessen variability at the local scale in tropical forests. We examined 2 depth intervals in the soil assuming that plant growth processes played a stronger role in the surface 0–0.1 m depth interval than in the subsurface 0.3–0.4 m depth interval. Our study area had some topographic variability. We delineated topographic habitats and examined correlations between chemical element concentrations and habitats. Overall, we observed more complexity in spatial variability and spatial patterns of soil chemical properties than expected.

Materials and methods

Site details

The project area is a 38.4-ha rectangle of lowland, tropical moist forest located on the Gigante Peninsula, Republic of Panama, ~1 km inland from the shore of Gatun Lake, which forms the Panama Canal waterway. The centre of the plot is at 9°6′30.7″N, 79°50′36.9″W and *c.* 80 m above sea level. The northern border of the plot is 5 km south of the southern border of the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI). Gigante Peninsula and BCI form part of the Barro Colorado Nature Monument (BCNM), administered by the Smithsonian Tropical Research Institute (Leigh 1999).

Climate at the BCNM is moist tropical with a 4-month dry season. The majority of the annual rainfall (mean *c.* 2600 mm) occurs during the rainy season from May through mid-December. Monthly mean temperature is 27°C in April and 26°C in the rest of the year. Relative humidity is >75%. Soils at the BCNM are highly weathered and moderately acidic, and have high clay contents. The main soils are Oxisols and Inceptisols. The underlying bedrock in the study area is a resistant andesite flow that overlies a series of nearly flat sedimentary rocks (Johnsson and Stallard 1989). These include volcanic and marine facies of Oligocene-age material. The andesite has a maximum thickness of 85 m, and it is a non-vesicular, phenocrystic andesite with veins and vugs. The main minerals are plagioclase, clinopyroxene, orthopyroxene, and magnetite; the veins and vugs contain quartz, calcite, and zeolite. The regional terrain is highly varied, although the andesite is nearly flat and drained by little incised streams.

The site is covered by late secondary to old-growth tropical moist forest. *Cecropia* is a common genus of pioneer trees in Central America, and only 1 species (*C. insignis*) occurs in the study area, suggesting no recent disturbances.

Sampling and measurements

We established a 26.6-ha, irregularly shaped sample grid (Fig. 1). This grid covered a gentle slope from the north-east corner to the south and west edges with a maximum relief of 36 m. Four small streams drained to the west. The topographic variation avoided pronounced ridges, slopes, valleys, and bottomlands. Within the plot we established 87 base points, spaced every 60 m on the grid. At each base point we placed a 20-m-long transect in a randomly assigned cardinal direction (N, NE, E, SE, etc.) and located 3 additional sampling locations at 2, 8, and 20 m from the base point. We added 14 additional soil samples to increase coverage in selected portions of the study area, for a total of 362 soil-sampling locations. This unaligned grid design allowed us to quantify spatial patterns of soil resources from 2 to ~500 m.

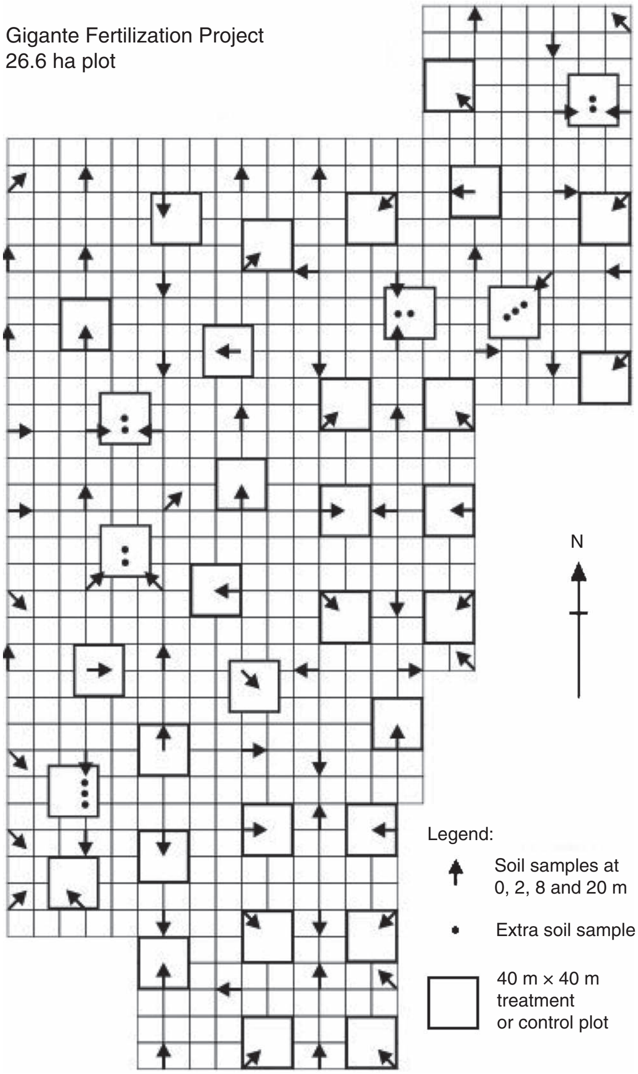

Fig. 1. Map of the study area. Grid lines represent 20-m intervals. Arrows indicate soil-sampling locations. The 40 by 40 m treatment plots were used for a forest fertilisation study, initiated after the soil sampling presented here.

Soil samples were collected during the later part of the wet season in Panama (September and November). Rainfall patterns were normal during the soil-collection period, although a very strong El Niño began soon after that (January 1998). A surface sample was collected with a hand trowel from 0–0.1 m depth, excluding litter and debris at the upper surface. Three scoops of soil from within 0.5 m of the sample point were bulked and a 300-g sample of this bulked soil was collected. When a surface sample was collected, an incubation tube (PVC pipe 15cm long, 5 cm diameter) was driven into the soil until the base of the tube reached a depth of 10 cm. The top of the tube was covered to keep out rainwater but to allow gas exchange between the inside and outside of the tube. The soil cores within the incubation tubes were allowed to incubate *in situ* before being collected 30–35 days later, and a portion of the soil was used to estimate rates of net N mineralisation and net nitrification. Upon removing each incubation tube, a deeper soil sample (0.3–0.4 m depth) was collected with a Dutch auger.

All soil samples were collected into plastic Whirl-pak® bags for transportation from the study site to the laboratory on BCI or in Panama City. Transportation from the field to the laboratory never required >6 h. Bags were kept in a cold room for a maximum of 36 h before laboratory processing.

Soil samples were divided into portions for various analyses. Field-moist portions were used for soil moisture determination and extractions of inorganic N and phosphorus (PO_4). Portions were air-dried at 50°C, pulverised, and sieved through a mesh screen to remove rocks and were used for pH determination and exchangeable chemical elements.

The percent of soil moisture was estimated by the change in mass before and again after oven drying at 105°C for 48 h. Soil pH was measured by mixing a slurry of 4 g of air-dried soil with 8 mL distilled water (reported as pH_{H_2O}), and also after adding 6 drops of 2 M $CaCl_2$ solution to the slurry (pH_{salt}). Soil pH_{H_2O} measures the amount of free acidity, and pH_{salt} includes exchangeable acidity.

Nitrogen was extracted from 2 g of fresh soil overnight in 20 mL of 2 M KCl. Phosphorus was extracted from 1 g of fresh soil by shaking vigorously for 1 min in 7 mL of Bray's P1 extraction solution (0.03 N NH_4F and 0.025 N HCl; Bray and Kurtz 1945) and centrifuged. Base cations (Ca, Mg, Na, K) and several trace elements (Al, B, Co, Cu, Fe, Mn, Mo, Ni, Si, Se, Zn) were extracted from 5 g of air-dried soil for 30 min on a shaker table in 100 mL 1 M NH_4Cl. Extraction solutions were collected into polyethylene sample bottles and stored in a cold room for no longer than 2 weeks before analysis. Concentrations of NH_4 and NO_3 were determined colourimetrically by continuous flow analyses. Concentrations of PO_4 were determined colourimetrically, and all other chemical elements were determined by inductively coupled plasma (ICP) mass spectrometry.

Data analyses

Values for NH_4, NO_3, PO_4, base cations, and trace elements are reported as mg/kg dry soil. Values for rates of change of NH_4 and NO_3 are reported as net N mineralisation (NO_3 plus NH_4) and net N nitrification (NO_3). In each case the concentration at the surface before incubation (t_o) is subtracted from the concentration in the incubation tube after incubation (t_1) and expressed as mg N mineralised per kg dry soil per day.

Parametric summary statistics for each nutrient were calculated using Data Desk (Version 6.2 for Mac OS, Ithaca, NY). We used a paired *t*-test to analyse differences for each soil chemical property in surface (0–0.1 m depth interval) *v.* corresponding deeper (0.3–0.4 m depth interval) soil. We examined associations among individual chemical properties by computing principal components (PCs). Data were transformed to *z*-scores before analysis. The final PCs were unrotated and include only the first 3 PCs because PCs greater than PC3 individually accounted for <10% of the variation.

We used geostatistical analysis to quantify the spatial dependence of each soil nutrient (S+ software, Version 7. Insightful Inc., Seattle, WA). This analysis produces variograms, which reveal random and structured aspects of spatial dependence in a dataset of multiple samples collected at increasing distances from each other (the lag interval). The variogram plots the semivariance statistic γ(h) for a range of distance intervals h:

$$\gamma(h) = 1/2N(h)\sum[z(s_i) - z(s_i + h)]^2$$

where γ(h) is the semivariance, N(h) is the number of observation pairs separated by a distance h, $z(s_i)$ is the value of the variable of interest at location s_i, and $z(s_i + h)$ is its value at a location at distance h from s_i. Semivariance was calculated using log-transformed data.

We use the proportion of model sample variance (Co + C; known as the sill) explained by structural variance C as a normalised measure of spatial dependence for each soil property; as C/(Co + C) approaches a value of 1, more of the spatial structure has been explained by the variogram; as the ratio approaches 0, apparent spatial dependence is small (Trangmer *et al.* 1985). A small value indicates large measurement error or spatial dependence at a scale smaller than the smallest distance between sampling points (Co, known as the nugget), 2 m in our case. In variograms with no sill, spatial dependence might occur at distances greater than that sampled. The distance at which the variogram reaches the sill is known as the range.

We fit mathematical models to the each variogram: linear, exponential, spherical, Gaussian, and power (McBratney and Webster 1986), using the weighted least-squares method by Cressie (1991), except the power model, which is fitted using ordinary nonlinear least-squares. The exponential, spherical, and Gaussian models are bounded, i.e. they have a sill, and describe fairly distinct patches of large and small concentrations. The linear and power models do not have a range or sill, and thus they indicate trends, often reflecting continuous gradients in concentrations across the study area.

Ecological habitats were identified by 3 topographic parameters, viz. elevation, slope, and convexity for each 20 by 20 m portion of the study area. The mean elevations at the 4 corners of each 20 by 20 m portion gave the quadrat's elevation. We calculated slope following Harms *et al.* (2001), and convexity was the quadrat's mean elevation relative to the mean elevation of its contiguous neighbour quadrats. Positive values indicate convex surfaces; negative values indicate concave surfaces.

Results

Soil variability

Soil in the 0–0.1 m depth interval (Table 1) was moderately acidic, and the sum of exchangeable base cations averaged 13.4 $cmol_c$/kg, consisting of Ca (62%) and Mg (34%) with minor contributions from K (2.5%) and Na (1.4%). Nitrogen was predominantly NH_4 rather than NO_3, and net nitrification

Table 1. Summary statistics for pH, concentrations of exchangeable chemical elements (mg/kg), and N transformation rates (mg/kg.day) in soil at Gigante, Panama ($n = 362$)

	0–0.1 m				0.3–0.4 m			
	Mean	s.d.	CV (%)	Median	Mean	s.d.	CV (%)	Median
pH_{H_2O}	5.26	0.51	113	5.45	5.25	0.44	62	5.15
pH_{salt}	4.53	0.51	115	4.72	4.35	0.58	71	4.11
NO_3	5.03	2.73	54	4.59				
NH_4	15.5	9.5	61	13.3				
Net N min.	0.22	0.55	252	0.18				
Net nitrif.	0.42	0.42	101	0.33				
PO_4	2.2	1.6	76	1.8	0.2	0.36	178	0.05
Base cations								
K	131	67	50	117	54	54	101	40
Na	44	10	24	41	33	13	41	30
Ca	1690	843	50	1499	572	476	83	444
Mg	553	254	44	503	352	249	71	273
Trace elements								
Al	20	37	181	11	238	255	107	163
B	0.9	0.38	42	0.86	0.82	0.37	45	0.78
Co	0.57	0.53	92	0.42	0.67	0.66	98	0.48
Cu	0.79	2.29	290	0.3	0.64	0.82	127	0.41
Fe	4.5	5.6	125	2.9	1	1.3	122	0.62
Mn	157	107	68	147	59	56	95	44
Mo	0.11	0.25	230	0.01	0.03	0.08	291	0.01
Ni	0.83	0.51	62	0.78	1.04	0.57	55	0.94
Se	0.12	0.21	171	0.01	0.12	0.18	150	0.1
Si	28	8.9	32	28	25	9.4	37	24
Zn	1.4	1.7	120	1	0.72	0.66	92	0.56

rates were 2-fold larger than net N mineralisation rates. Concentrations were significantly different between the 0–0.1 and 0.3–0.4 m depth intervals (Table 1) (paired *t*-tests, d.f. = 362, $P < 0.001$), except for pH_{H_2O} ($P = 0.3206$) and Cu ($P = 0.5197$), which showed no difference in concentrations between depth intervals. Most of the chemical elements had greater concentrations in the 0–0.1 m depth interval than 0.3–0.4 m; the exceptions were concentrations of Al, Co, and Ni, which increased with depth.

The coefficient of variation (CV) for soil properties in the study area (Table 1) ranged from relatively invariant for Na (24%) and Si (32%) in the 0–0.1 m depth interval to several components with CV values >200%. The median CV among chemical elements in the 0–0.1 m depth interval was 84%, and thus NO_3, NH_4, PO_4, base cations, Mn, Si, and B had CV values less than the median. In contrast, pH, most of the micronutrients, and N transformation rates were more variable than the median. The CV values for base cations, Mn, and Mo were greater in the 0.3–0.4 than in 0–0.1 m depth interval, whereas the other components were more spatially variable in the 0–0.1 m depth interval or had equal variability in both depth intervals.

Three PCs explained only 50% of the variation in soil properties in the 0–0.1 m depth interval. The first PC had high positive loadings (>0.50) on pH and Ca and high negative loadings (<–0.50) on Co and Ni. The second PC had high negative loadings on Al, Fe, Mg, Na, and Si. The third PC had high negative loadings on B and N transformation rates. Three PCs explained 53% of the variation in soil chemical properties in the 0.3–0.4 m depth interval; however, the high loadings were somewhat different than those in the surface depth interval. The fist PC had high positive loadings on pH and high negative loadings on Al, Cu, and Ni. The second PC had high negative loadings on Ca and Mg, whereas the third PC had high positive loadings on Co and Mn.

Spatial dependence

The range of spatial dependence for chemical properties in the 0–0.1 m depth interval (Table 2) was as small as 13 m for Na, 30–88 m for a host of soil components, and >100 m for pH, NH_4 and net N mineralisation rate, Al, and B. The proportion of total variance that was spatially dependent (defined as $C/(C_0 + C)$) varied from <25% for Se and Mo, to 25–75% for a host of soil components, and >75% for Na, Mn, and Ni. The range of spatial dependence in the 0.3–0.4 m depth interval (Table 3) was 20–67 m for Se, Fe, Mn, Zn, Co, Ni, Al, and B, and >250 m for Na, Ca, Mg, and Cu. The proportion of total variance that was spatially dependent was >50%, except for 33% spatial dependence for Se.

One particular model did not provide best fit to each variogram for soil chemical elements in the 0–0.1 m depth interval (Table 2). Rather, best-fit models (largest R^2 value) were exponential in 10 cases, Gaussian in 5 cases, spherical in 4 cases, and power models fit in 3 cases. An exponential model provided best fit to the variogram for base cations, except for Mg with a power model. Although an exponential model fitted the variogram for NO_3 and net nitrification rate, a Gaussian model fitted the data for NH_4 and net N mineralisation. In the 0.3–0.4 m depth interval, no one type of model provided the best fit to variogram for each soil resource (Table 3). Here, best-fit models

Table 2. Variogram parameters for pH, concentrations of exchangeable chemical elements, and N transformation rates in the 0–0.1 m depth interval

The smallest lag distance was 2 m. Models are exponential (Exp.), spherical (Sph.), Gaussian (Gau.), and power (Pow.)

	Model	Sill (Co + C)	Nugget (Co)	Range (m)	C/(Co + C)
pH_{H_2O}	Exp.	0.31	0.13	177.2	0.56
pH_{salt}	Sph.	0.29	0.16	378.1	0.45
NO_3	Exp.	7.98	5.04	74.2	0.37
NH_4	Gau.	85.25	50.27	111.3	0.41
Net N min.	Gau.	0.32	0.22	153.5	0.32
Net nitrif.	Exp.	0.17	0.12	65.1	0.31
PO_4	Exp.	2.89	1.12	61	0.61
Base cations					
K	Exp.	4592.81	2083.5	47.6	0.55
Na	Exp.	98.66	17.61	13	0.82
Ca	Exp.	67 6486	33 1524	50.8	0.51
Mg	Pow.				
Trace elements					
Al	Sph.	1554.42	722.78	101.2	0.54
B	Sph.	0.17	0.07	377.4	0.61
Co	Exp.	0.28	0.08	37.7	0.71
Cu	Gau.	4.44	2.16	31.9	0.51
Fe	Pow.				
Mn	Exp.	10420.9	2356.18	41.4	0.77
Mo	Gau.	0.063	0.058	72.6	0.09
Ni	Sph.	0.29	0.06	29	0.79
Se	Exp.	0.047	0.038	88.1	0.2
Si	Pow.				
Zn	Gau.	2.99	1.66	32	0.44

were spherical in 5 cases and Gaussian in 4 cases, whereas exponential and power models fitted in each of 3 cases. Notably, K and Mo showed no spatial dependence in the 0.3–0.4 m depth interval. Only the variogram for Na and Si had the same type of model fit in both depth intervals.

Mapping the variations in concentrations of each chemical property across the study area revealed several spatially explicit patterns. For example, soil pH (Fig. 2) showed fairly large patches of near-neutral values in the west and extreme north-east portion of the study area *v.* fairly large patches of acidic soil pH towards the south-east and in the area between the near-neutral values. The negative correlation between pH and Al was evident with large patches of higher Al concentrations towards the south and lower Al concentrations in the extreme north-east. For N (Fig. 3), NH_4 had large patches of lower concentrations in the north-east corner of the study area that graded into large patches of high concentrations in the centre of the study, whereas rates of net N mineralisation were greater in the north-east corner and lower in the centre. In contrast, patches of lower NO_3 concentrations were prevalent in the southern portion of the plot *v.* patches of greater concentrations north. Net nitrification had scattered patches of greater and lesser concentrations across a matrix of moderate values.

The exchangeable base cations (Fig. 4) had relatively small patches, except for Mg with banding of concentrations from lesser values in the north-east to greater values in the south-west. Calcium had patches of higher concentrations along the western portion of the plot and patches of lower concentrations towards the north-east. In contrast, Na and K had small patches of lower and higher concentrations scattered across the plot.

Table 3. Variogram parameters for pH and concentrations of exchangeable chemical elements in the 0.3–0.4 m depth interval

The smallest lag distance was 2 m. Models are random (Ran.), exponential (Exp.), spherical (Sph.), Gaussian (Gau.), and power (Pow.)

	Model	Sill (Co + C)	Nugget (Co)	Range (m)	C/(Co + C)
pH_{H_2O}	Pow.				
pH_{salt}	Pow.				
Base cations					
K	Ran.				
Na	Exp.	717.32	119.01	585.2	0.83
Ca	Sph.	265 450	121 511	402.6	0.54
Mg	Exp.	98072.4	24423.7	504.5	0.75
Trace elements					
Al	Exp.	57 343	0	22.2	1.0
B	Gau.	0.16	0.08	66.9	0.51
Co	Gau.	0.48	0.1	23.9	0.78
Cu	Sph.	0.67	0.33	253.1	0.51
Fe	Gau.	1.85	0.53	50.9	0.71
Mn	Sph.	3437.66	420.53	31.3	0.88
Mo	Ran.				
Ni	Gau.	0.34	0.09	28.7	0.72
Se	Sph.	0.026	0.017	26.2	0.33
Si	Pow.				
Zn	Sph.	0.44	0.18	57.5	0.6

Trace elements (e.g. B, Co, and Mn) generally had higher concentrations towards the north-east and south-west, whereas patches with lower concentrations were prominent in the centre of the study area (Fig. 5). In contrast, Mo had intermingling patches of higher and lower concentrations in the south. The power model fit to the variograms for Fe (Fig. 2) was evident as a band of lower concentrations in the north-eastern portion of the study area followed by bands of higher and moderate concentrations towards the south-west. Phosphorus (Fig. 2) showed a mixed spatial pattern with patches of higher concentrations in the southern portion and across the northern tier, whereas patches with lower concentrations were congregated towards the west central and extreme northern portions.

Topographic variability had several significant correlations with different soil chemical properties (Table 4). The strongest correlations were negative relationships between elevation and NH_4, Mg, Fe, and Si. These correlations, except for NH_4, were stronger in the 0.3–0.4 m depth interval than in surface soil. Although correlation coefficients >0.050 were statistically significant ($P < 0.05$), correlations were usually weak as indicated by small values.

Discussion

The mean concentration of exchangeable Ca was greater than expected for a highly weathered soil (Uehara and Gillman 1981), whereas the mean concentration of exchangeable K less than typical. We attribute these findings to the Ca-rich and K-poor parent material in central Panama (Ronov and Yaroshevsky 1972; Donnelly *et al.* 1990). Concentrations of exchangeable Al are usually determined in 1 M KCl, although concentrations in

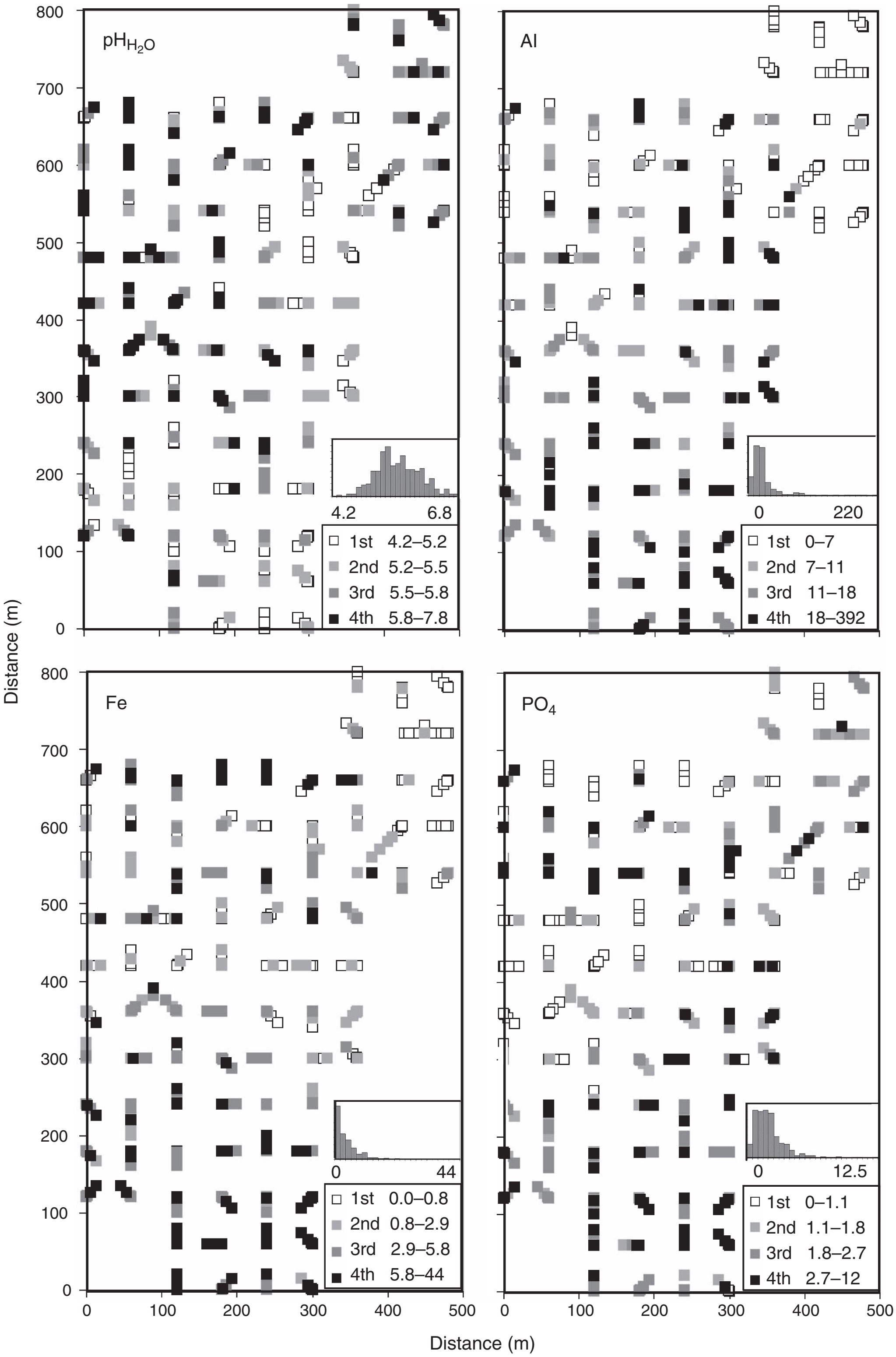

Fig. 2. Distribution of soil pH measured in water, exchangeable aluminium and iron, and Bray-extractable PO$_4$ from 0–0.1 m depth interval at Gigante, Panama. Dot shades correspond to quartiles of values. A histogram of values also is shown.

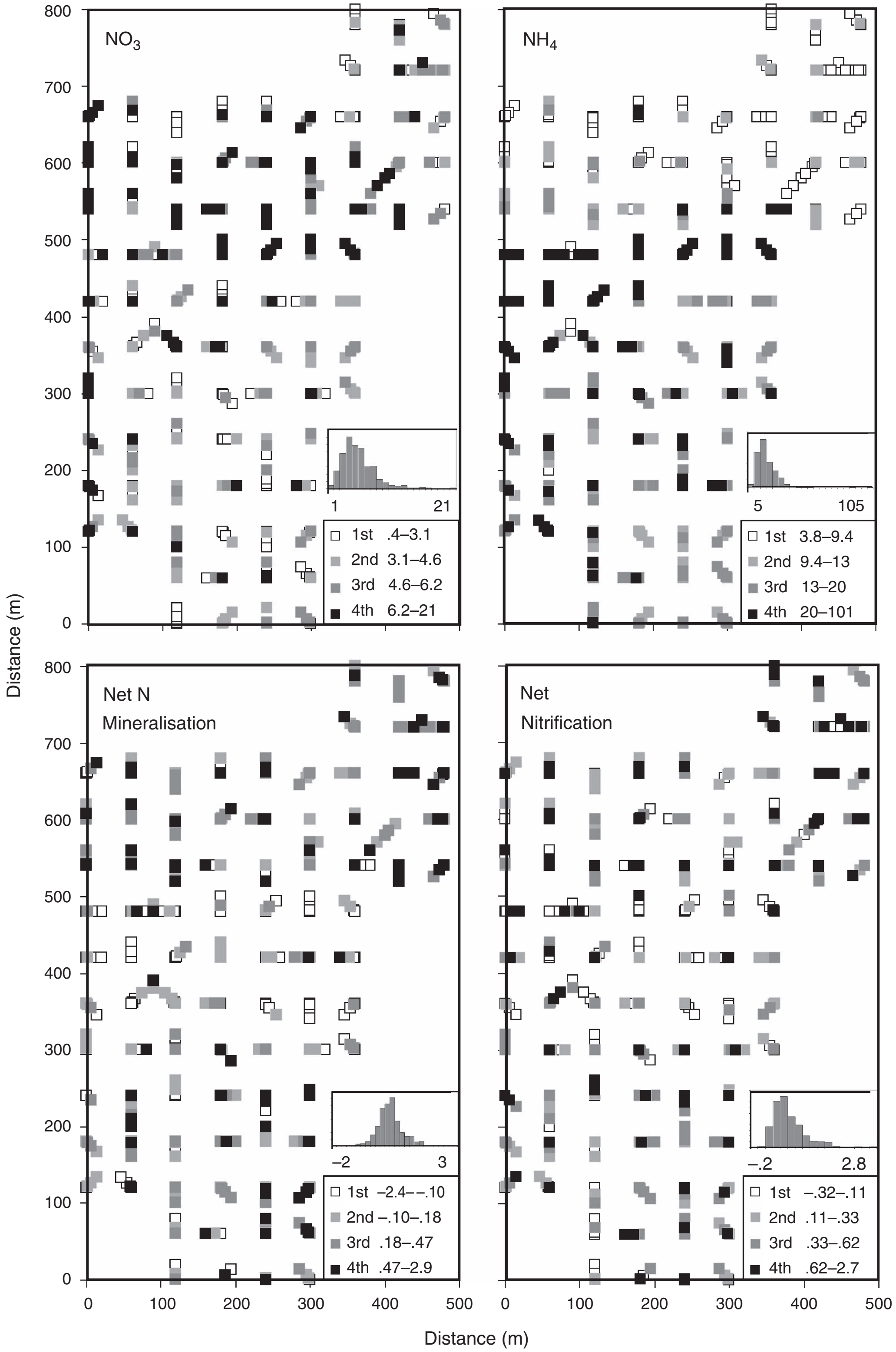

Fig. 3. Distribution of NO$_3$ and NH$_4$ (mg/kg) and N transformation rates (mg/kg.day) in soil from the 0–0.1 m depth interval at Gigante, Panama. Dot shades correspond to quartiles of values. A histogram of values also is shown.

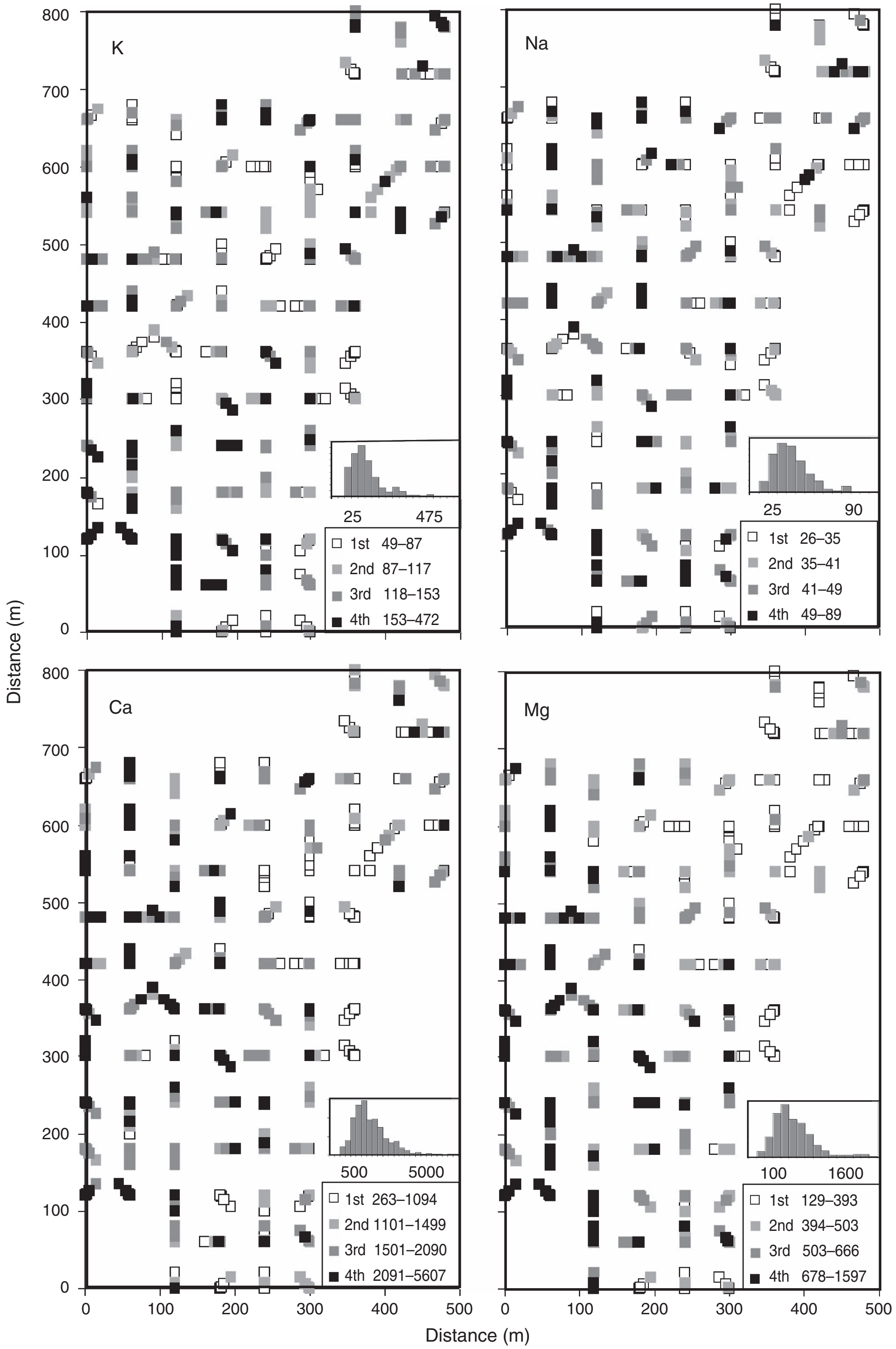

Fig. 4. Distribution of exchangeable base cations (mg/kg) in soil from the 0–0.1 m depth interval at Gigante, Panama. Dot shades correspond to quartiles of values. A histogram of values also is shown.

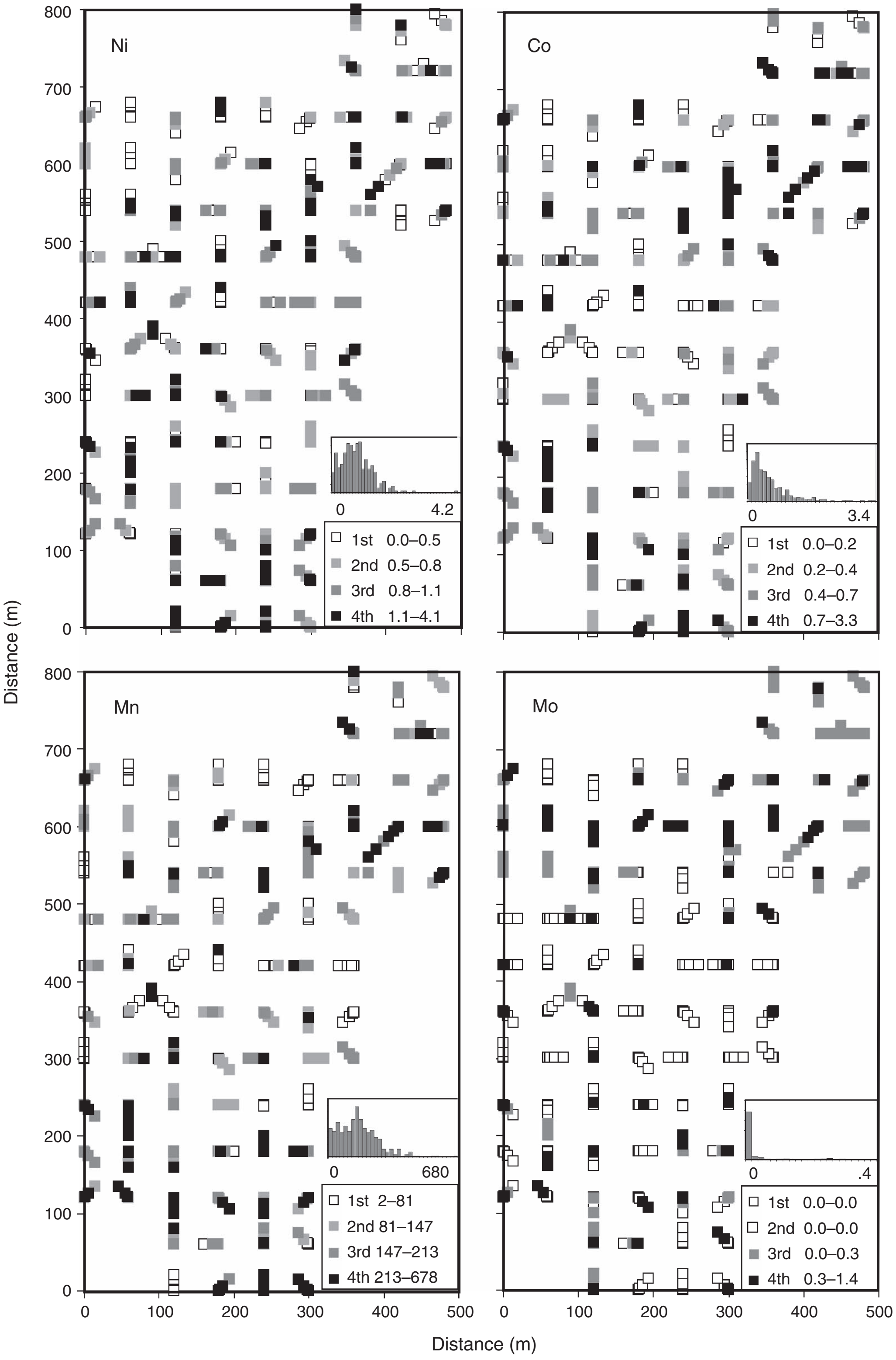

Fig. 5. Distribution of exchangeable nickel, cobalt, manganese, and molybdenum (mg/kg) in soil from the 0–0.1 m depth interval at Gigante, Panama. Dot shades correspond to quartiles of values. A histogram of values also is shown.

Table 4. Kendall correlation coefficients for pH, concentrations of exchangeable chemical elements, and N transformation rates *v.* topographic factors (elevation, slope), soil wetness (at the time of collection), and pH

For clarity, values between –0.05 and 0.05 are left blank

	0–0.1 m				0.3–0.4 m			
	Elev.	Slope	Soil wet.	pH	Elev.	Slope	Soil wet.	pH
pH_{H_2O}	–0.09	0.17		0.1		0.14	–0.07	1.0
pH_{salt}	–0.07	0.12		0.83	0.17	0.08	–0.13	0.67
NO_3	0.09		–0.06	0.08				
NH_4	–0.24	–0.05	0.15	0.1				
Net N min.	0.14			–0.11				
Net nitrif.	0.1			–0.07				
PO_4		–0.12	0.03	–0.19		0.07		0.16
Base cations								
K	–0.11		0.14	0.16	–0.2		0.14	
Na	–0.18		0.22	0.12	–0.2	–0.09	0.11	–0.1
Ca	–0.2	0.08	0.22	0.51	–0.2	0.08	0.1	0.35
Mg	–0.4		0.27	0.21	–0.44		0.2	0.14
Trace elements								
Al			0.11	–0.38	0.13	–0.05	0.16	–0.61
B		–0.05	0.16		–0.06		0.06	0.2
Co	0.1	–0.12	–0.14	–0.55	0.08		–0.16	–0.19
Cu	0.25	0.07	–0.08		–0.23	–0.1	0.21	–0.4
Fe	–0.26	–0.05	0.23	–0.16			0.1	–0.25
Mn		–0.11	–0.1	–0.42	0.06		–0.1	–0.07
Mo		–0.12			–0.04		0.06	–0.1
Ni				–0.55	–0.27	–0.06	0.16	–0.35
Se	–	–0.11		–0.17	0.21		–0.12	
Si	–0.27		0.26		–0.4		0.22	–0.17
Zn	0.07	–0.05	0.09	–0.38	–0.34	–0.13	0.19	–0.31

1 M NH_4Cl are quite comparable (Ponette *et al.* 1996). Little exchangeable Al occurred in the 0–0.1 m depth interval. In contrast, concentrations of exchangeable Al in the subsurface soil were potentially toxic to plant growth, as suggested by a molar ratio of exchangeable base cations (mean 6.1 $cmol_c$/kg) to exchangeable Al (mean 2.7 $cmol_c$/kg) of <10 : 1 (Cronan and Grigal 1995). Mean concentrations of KCl-extractable NO_3 and NH_4, as well as mean rates of net N mineralisation and net nitrification, were low to moderate for tropical forest soils (Vitousek and Matson 1988). In contrast, mean concentrations of Bray-extractable PO_4 were close to the level that limits plant growth in tropical soils (Denslow *et al.* 1987).

Neutral NH_4Cl solutions have not been used widely to estimate amounts of trace elements (Menzies *et al.* 2007), even though NH_4Cl is the extractant of choice to predict plant growth, at least for crop plants (Takeda *et al.* 2006). For instance, mean amounts of exchangeable B would be adequate for crop growth (Shuman 2005). In contrast, the mean amount of exchangeable Mn is well above average, and the largest concentrations would be toxic to crop plants. Mean concentrations of exchangeable Ni also were large, about typical of that in less-weathered temperate forest soils (Luwe 1995). Levels of exchangeable Si in our study area are extremely small even for highly weathered soils (Fox 1982), indicating selective loss of soluble Si. Natural soils typically have very small concentrations of exchangeable Mo, and our soils were no exception, with mean levels well below the critical value for crop growth (Shuman 2005).

Spatial variability

The magnitude of variation in soil properties was somewhat greater than might be expected for 26 ha of relatively uniform tropical forest. Wilding (1985) suggests 3 distinct classes of variability for soil properties based on CV values: 0–15% indicates little variability; 16–35% indicates moderate variability;, and >36% indicates high variability. In our case, CV values were mostly >50%, and some elements had CVs >200%. Indeed, variability in the 0–0.1 m depth interval was similar to that observed in surface soils that crossed several different types of soil in Puerto Rico (Silver *et al.* 1994). In contrast, CVs were as large as 857% in subsurface soils in Puerto Rico, whereas they were only marginally larger in subsurface soils in our study area. Holmes *et al.* (2005) reported CVs of 18–225% in surface soils (0–0.05 m depth) and 13–513% in subsurface soils (deeper than 0.25 m) over a very large (195 000 km^2) area in tropical Brazil. Therefore, we conclude soil chemical properties are highly variable at the local scale in our study site.

Many studies have reported that soil pH is the least variable soil property (Mulla and McBratney 2000), whereas soil pH had the median CV for variability in our study area. We calculated summary statistics for pH using H^+ concentrations, not pH values *per se*, which likely explains the increased degree of variability. Most studies do not indicate whether summary statistics for pH used pH values or H^+ concentration, and this would explain discrepancies among studies.

Chemical elements in the 0–0.1 m depth with CVs less than the median CV included the macronutrients N and P, exchangeable base cations, B, Mn, Ni, and Si. Most of these are nutrients with strong biological cycles of repeated uptake from soil by plants, return in litterfall, and release via organic matter decomposition. Boron and Mn, in particular, have strong biological cycles despite being micronutrients (Kabata-Pendias 2001). Nickel is essential for legumes (Eskew *et al.* 1983), which dominate the tree flora in Panama. Although Si is not a plant nutrient *per se*, studies in Hawaii show modest uptake by tropical forest trees (Derry *et al.* 2005).

The extreme amounts of rain in tropical forests suggest a possible explanation for small CVs. Some of the nutrients listed above are considered to be fairly mobile in acidic soil solutions. For example, adsorption of base cations is less at acidic pH. Boron occurs as undissociated boric acid or as an oxyanion and is water-soluble. Although Ni and Mn tend to form insoluble complexes, these are less prevalent at acidic pH, whereas Si also occurs as a mobile oxyanion at acidic pH. Therefore, our results show that spatial variability depends not only on biological processes, but also on physical properties and processes that influence nutrient availability and transport.

Concentrations of KCl-extractable NO_3 and NH_4 were considerably less variable than rates of net nitrification and net N mineralisation (Table 1). Other studies at the local scale have found similar CVs for soil N concentrations and N transformation rates (Robertson *et al.* 1997; Wang *et al.* 2007). Presumably, geophysical processes, i.e. water flux, even out nutrient concentrations to a greater degree than microbial processes in tropical forest soils. There is extensive literature on the variation in soil PO_4 concentrations, and nearly all report that PO_4 is among the most variable soil properties. Dobermann *et al.* (1995) suggested that PO_4 concentrations are variable because PO_4 is less mobile in soil than nearly all other solutes, tending to concentrate in patches and resist homogenisation in water flow across the landscape. Although true at the fine scale, the small concentration of readily available PO_4 at the local scale might contribute to the small CV, as very strong biological demand and decomposition homogenise concentrations spatially. For example, low concentrations of Bray-extractable PO_4 are fairly uniform across several different parent materials on Barro Colorado Island, Panama (Yavitt 2000), and at the local scale in a boreal forest in Canada (Bengtson *et al.* 2007).

The similar CVs for exchangeable concentrations of Ca, Mg, and K in the 0–0.1 m depth interval are noteworthy. Baillie and Ashton (1983) suggested that Ca and Mg should be more variable than K in forest soils, as K occurs exclusively on soil organic matter exchange sites, which should vary little, whereas Ca and Mg occur on mineral exchange sites that are less uniform in soil. This has been observed in studies with soils derived from more than 1 parent material (Manderscheid and Matzner 1995; Stutter *et al.* 2004). In contrast, our plot occurred entirely on 1 Andesite parent material, suggesting less variable mineralogy. Greater variability in the 0.3–0.4 m depth interval than the 0–0.1 m depth interval supports the notion that biological cycling through vegetation and litter homogenises concentrations of Ca and Mg in surface soil *v.* less biological control in subsurface soil (Burt and Park 1999).

In contrast, net N mineralisation and several trace elements, Fe, Cu, Mo, and Se, were more variable than the median CV. These chemical elements tend to be immobile in acidic soils (Kabata-Pendias 2001). For instance, Al and Fe have several insoluble forms that concentrate in highly weathered, acidic soils (Uehara and Gillman 1981). Copper is immobile because it forms strong associations with organic matter (Mylavarapu *et al.* 2002). Molybdenum has maximum adsorption to soil minerals at acidic pH (Goldberg and Forster 1998) as does Se (Tyler and Olsson 2001).

Given the myriad of potential relationships among individual soil chemical constituents in such a large dataset, we used PCA to provide insight into patterns. The strong effect of pH in both depth intervals is not surprising given the important role that pH plays in soil chemistry. In other moderately acidic but less-weathered soils, PCA reveals a close clustering of the acid cations (H, Al, and Fe) *v.* a cluster of the base cations (Ca, Mg, Na, and K) (Ohno *et al.* 2007). In our case, H and Ca predominated over the others, even though Al had a strong influence in the 0.3–0.4 m depth interval, given greater concentration than in surface soil. The strong loading for Ni, Co, Cu, Fe, and Si in various PCs and depth intervals suggests a prominent role for trace elements in soil spatial patterns (Kabata-Pendias 2001). The clustering of B with N transformation rates in the third PC in surface soil is notable, as experimental evidence has shown that B additions can stimulate activity of enzymes involved in net N mineralisation (Ekenler and Tabatabai 2002).

Ratios of chemical elements (i.e. stoichiometry) provide further insight into biochemical processes; in particular, they can define critical competitive decision points for plant growth (Ågren 2008). Common ratios include N/P, Ca/K, and Mg/Mn (Jobbágy and Jackson 2001; Kogelmann and Sharpe 2006; Ågren 2008). Median values in our data were fairly typical for soils: 9.8/1 for N/P; 12/1 for Ca/K; and 8/1 for Mg/Mn. However, ranges in theses ratios were fairly broad and indicate gradients in soil fertility. For example, for the N/P ratio, the first quartile indicates P-rich soils (6.3/1) *v.* N-rich soils for the third quartile (19.3/1). Likewise for the Mg/Mn ratio, the first quartile suggests Mn toxicity (4.9/1) *v.* Mg-rich soils for third quartile (17.9). The association of plant species with nutrient availability *per se*, with nutrient ratios of nutrient elements, and with ratios of trace elements remains to be determined.

Spatial dependence

The range in geostatistical analysis indicates the size of patches. The median patch size in surface soils of 65 m is considerably larger than that observed in fine-scale studies of tropical forest soils (Gonzalez and Zak 1994; Blair 2005; Diekmann *et al.* 2007). Although patch sizes in surface soils were generally small compared with the size of the study area, we note that Mg, Fe, and Si had patch sizes larger than the study area. These results emphasise the importance of scale when considering soil chemical properties in tropical forests. The median patch in subsurface soils of 54 m was smaller than that in surface soils. However, the distribution of patch size in subsurface soils was bimodal; values were either <75 m or >250 m, suggesting that controls on the origin and maintenance of patch size differ throughout the soil profile.

Several chemical elements had smaller sized patches in surface than in subsurface soils. These included: pH, exchangeable base cations (except Mg), and trace elements (except B and Fe). Smaller sized patches in surface than in subsurface soils suggest that biological processes play an important role in surface soils *v.* geochemical processes and lateral water flow dominant in subsurface soils. An example is mobile K, which had no spatial dependence in the subsurface soil, but had small-sized patches in the surface soil. There were exceptions to this paradigm, however, as Al, B, and Fe did have larger patches in surface than in subsurface soils. The explanation for this is unclear. Notwithstanding, Wopereis *et al.* (1988) studied the spatial dependence of trace elements at the local scale in a forest soil and observed no spatial dependence. In contrast, Paz *et al.* (1996) and Berndtsson *et al.* (1993) did document small patch size for trace elements at the local scale in agricultural fields.

For N, the range of spatial dependence was larger for NH_4 than for NO_3, and it was larger for net N mineralisation than for net nitrification. Studies at the fine scale have also observed a larger range value for NH_4 than for NO_3 (Gallardo *et al.* 2005). The larger range size for net N mineralisation than for net nitrification might be a characteristic of the local scale, however. One reason is that net N mineralisation depends mostly on a supply of organic N, which presumably has a large range at the local scale, whereas nitrifying bacteria are a more specialised group of microorganisms and might have a more restricted distribution compared with the greater group of microorganisms that account for N mineralisation. We had no *a priori* hypothesis for the range of spatial dependence for PO_4, and our results showed a typical range of <100 m.

The structural variance expressed as a percentage of the total variance allows direct comparison of the relative strength of spatial dependence (Trangmer *et al.* 1985). There are 3 distinct classes of spatial dependence for soil variables: a ratio <25% indicates weak spatial dependence; a ratio 25–75% indicates moderate spatial dependence; and a ratio >75% indicates strong dependence. Given that the median value for the strength of spatial dependence was greater in the 0.3–0.4 m depth interval (71%) than in 0–0.1 m interval (51%), we captured more of the spatial dependency in the 0.3–0.4 m depth interval than in the surface soil. One explanation is the larger nugget variance in surface than in subsurface soils, indicating that we failed to capture all of the fine-scale spatial dependence at a scale of 2 m, the minimum sampling distance.

In geostatistics, mathematical models are fitted to variograms, and different models tell us about the nature of the spatial pattern. For example, spherical models indicate distinct patches of large (or small) concentrations in a matrix of less (or greater concentrations). In contrast, power models indicate gradients across the landscape. Many fine-scale studies fit spherical models (Schlesinger *et al.* 1996; Gallardo 2003; Diekmann *et al.* 2007) or find that either spherical or exponential models provide the best fit (Robertson *et al.* 1993, 1997). The observation that several models provided best fit in our data emphasises the independent nature of spatial patterns among the different chemical elements. For example, Gaussian models imply both small- and large-sized patches within the matrix. Gaussian models rarely provide best fit to data in fine-scale studies, whereas they appear to be more common at the local scale (Delcourt *et al.* 1996; Chien *et al.* 1997). Bengtson *et al.* (2007) evaluated soil resources at the local scale in a boreal forest soil and also observed that random and power models applied in several cases.

Topographic variation had only subtle control over spatial dependence in soil nutrients in our case, and this was mostly the pronounced north-east to south-west elevation gradient that correlated with concentrations of NH_4, Mg, Si, and Fe. At a finer scale, topographic slopes and gullies were not well correlated with spatial dependence. Yavitt (2000) found little variation in PO_4, and Barthold *et al.* (2008) found little variation in concentrations of exchangeable Mg and K across different parent materials on BCI. Furthermore, the lack of correlation between nutrient concentrations and ecological habitats helps explain why more of the plant species in the region show fidelity for nutrient patches (John *et al.* 2007) than for habitats (Harms *et al.* 2001).

Overall, our data revealed a moderate negative relationship between CV values and the degree of structural variability $(C/(C+Co))$ with a Pearson correlation $r = -0.54$. A negative relationship implies that the most variable nutrients, such as Mo and Se, have relatively large nugget variance and considerable fine-scale spatial dependence. In contrast, relatively invariant nutrients, such as Na, have less fine-scale variance. This emphasises that processes at both the fine scale and the local scale contribute to spatial dependence for soil properties in the study area.

Comparison with other studies and implications

We know that soil nutrient availability varies temporally in tropical forests that have distinct wet and dry seasons (Yavitt and Wright 1996). Therefore, comparisons among forests should be made cautiously. Notwithstanding, John *et al.* (2007) examined spatial heterogeneity for soil nutrients in the 50-ha plot on BCI, Panama, 5 km from our study site, for soils collected at the same time of the year, i.e. during the later part of the wet season.

Soil variable loadings were different in the PCA for each study. For example, the strong positive loadings for pH and Ca and negative loading for Ni and Co in our study were not observed for BCI. Rather on BCI, several nutrient elements had roughly equal negative loadings in PC1. Moreover, N and P had strong loadings in PC2 on BCI but not in our results. Therefore, correlations among individual chemical elements were quite different among sites. Moreover, in the geostatistical analysis, ranges were mostly between 85 and 240 m on BCI, which were considerable larger than ranges in our study. Likewise, the degree of spatial dependence was much greater on BCI than in our study, indicating that the same minimum distance between soil samples of 2 m captured more of the fine-scale spatial pattern (i.e. smaller nugget variance).

This comparison indicates an additional amount of spatial heterogeneity at the landscape level for soil chemical properties. Although explanations are unclear, they are not caused by a distinct geochemical gradient in this case, as both plots occur on the same parent material. Since spatial patterns in soil nutrients are recognised as important factors contributing to niche differentiation and diversity of tropical trees (John *et al.* 2007), landscape scale patterns may also contribute to β

diversity in tropical forest composition observed in this portion of Panama (Condit *et al.* 2002). Experiments are needed to establish the origin and maintenance of spatial heterogeneity in soil chemical properties as these may also have important consequences for plant productivity.

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