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Variation in nutrient characteristics of surface soils from the Luquillo Experimental Forest of Puerto Rico: A multivariate perspective

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Abstract

We assessed the effects of landscape features (vegetation type and topography), season, and spatial hierarchy on the nutrient content of surface soils in the Luquillo Experimental Forest (LEF) of Puerto Rico. Considerable spatial variation characterized the soils of the LEF, and differences between replicate sites within each combination of vegetation type (tabonuco vs. palo colorado vs. dwarf vs. pasture) and topographic position (ridge vs valley) accounted for 11–60% of the total variation in soil properties. Nevertheless, mean soil properties differed significantly among vegetation types, between topographic positions, and between seasons (wet vs dry). Differences among vegetation types reflected soil properties (e.g., bulk density, soil moisture, Na, P, C, N, S) that typically are related to biological processes and inputs of water. In forests, differences between topographic positions reflected elements (e.g., Ca, Mg, K, and Al) that typically are associated with geochemical processes; however, the nutrients and elements responsible for topographic differences in dwarf forest were different from those in other forest types. In pastures, differences between topographic positions were associated with the same soil properties responsible for differences among the other vegetation types. Pastures also had reduced N levels and different soil characteristics compared to undisturbed tabonuco forest. The only soil parameter that differed significantly between seasons was soil moisture. Soils of the LEF do not support the contention that N becomes limiting with an increase in elevation, and suggest that absolute pool sizes of N and P are not responsible for the reduction in productivity with elevation.

Introduction

Although tropical forests only cover 7% of the Earth's surface, they contain over half of all biological species (Wilson, 1988). In addition, tropical forests perform key roles in global carbon cycling, and 10^9 tons of CO_2 are released into the atmosphere yearly as a result of changes in tropical landuse (Detwiler and Hall, 1988). Soils of tropical forests exhibit considerable temporal and spatial variability in chemical and physical properties, and consequently can be extremely productive or extremely infertile (Sollins, 1998). This variability has been hypothesized to affect structural and functional characteristics (e.g., diversity and productivity) that change along elevational gradients in tropical forests (Bruijnzeel and Veneklaas, 1998; Chapin, 1980; Grubb, 1971; Vitousek and Denslow, 1987). More specifically, recent research (e.g., Sollins, 1998; Tanner et al., 1988) has implicated soil nutrient limitation as a mechanism responsible for a decrease in forest productivity with elevation.

Soils of tropical montane forests can evince patterns at at least four different spatial scales. First, soils may differ among mountain ranges. Second, soils may differ among vegetation types (usually associated with

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elevation) within a mountain range. Third, soils may differ among topographic positions within a vegetation type. Finally, soils may differ among sites within the same topographic position. Previous work (Johnston, 1992; Silver et al., 1994; Scatena and Lugo, 1995; Willig et al., 1996) in Puerto Rico at the scale of patches (within a particular vegetation type) documented that soil properties, disturbance frequency (both anthropogenic and natural), topography, and vegetation are interrelated. Similarly, work at broader geographic scales (among vegetation types) has documented changes in soil properties among forest types (Silver et al., 1999). However, to our knowledge, no study has systematically sampled tropical soils in a directly comparable fashion to disentangle the effects of site, topographic position, vegetation type, and season on soil nutrient status. The goals of this study are: (1) to determine patterns of soil properties with respect to vegetation type (both lowland and montane forests), topography, and anthropogenic disturbance, and (2) to infer the relative importance of climate, geology, and ecological processes in accounting for these patterns.

Methods

Study area

The Luquillo Experimental Forest (LEF) is a site in the Long-Term Ecological Research (LTER) network of the National Science Foundation (Figure 1, Franklin et al., 1990). The LEF is located in the northeast corner of Puerto Rico and comprises three major vegetation types (tabonuco, colorado, and dwarf forests) as a consequence of elevational changes in climate and soil characteristics (see Brown et al., 1983). The tabonuco forest (subtropical wet forest life zone [Ewel & Whitmore, 1973]) is found below 600 m. It is dominated by *Dacryodes excelsa* (tabonuco) and occupies nearly 70% of the LEF. Soils are Ultisols, belonging to the Humatus - Zarzal - Cristal complex (Johnston, 1992). Above the average cloud condensation level (600 m) is the colorado forest (lower montane wet forest), which covers about 17% of the LEF. *Cyrilla racemiflora* (palo colorado) is the dominant tree in this zone. Because of abrupt changes in topography and substrate, tabonuco and colorado forests are often adjacent to each other. Dwarf forest (lower montane rain forest), with short, gnarled vegetation, occurs on peaks and ridges above 750 m. It is dominated by *Tabebuia rigida* and *Ocotea spathulata*, but occupies only 2% of the LEF. Almost pure stands of the sierra palm (*Prestoea montana*) are interspersed across the entire elevational gradient. They cover 11% of the LEF and are associated with poorly drained soils.

Abandoned pastures that were used for cattle grazing lie adjacent to forest at lower elevations in the LEF. Pasture sites have similar bedrock geology and climate to that of adjacent tabonuco forest. These sites were cleared prior to 1936 and abandoned by 1988 (Zou and Gonzalez, 1997). Since abandonment, they have developed into an early successional community, dominated by grasses, ferns, and vines. Soils are Oxisols with high clay content, belonging to the Zarzal series.

Sample collection

Within pastures and each of the forest types, three topographic positions (ridges, slopes, and valleys) correspond to important soil properties (Scatena, 1989; Silver et al., 1994; Scatena and Lugo, 1995). Soil samples were collected from each of the two extreme topographic positions (ridge and riparian valley) within pasture, tabonuco forest, palo colorado forest, and dwarf forest. Within each ecosystem, two ridge and two riparian valley sites were selected, and six samples were taken from each site. In valleys, samples were taken adjacent to stream channels. This led to a total of 96 locations (12 replicates $\times$ 2 topographic positions $\times$ 4 ecosystem types) which were sampled in the dry (March) and in the wet (late June) season of 1998. At each location, 24 replicate soil cores (diameter = 1.91 cm, depth = 10 cm) were taken from a 1 m circle and mixed, leading to one homogenized sample per location.

Laboratory analyses

Soil samples were taken to the laboratory at the International Institute of Tropical Forestry within 48 h of collection, and soil nutrients were analyzed on air-dried soils. Soil pH was measured in a 1:1 soil:1 *N* KCl solution with a combination electrode. Exchangeable Ca, Mg, Na, and Al were extracted using 1 *N* KCl. Exchangeable Fe, Mn, K, and P were determined using a modified Olsen's method (Hunter, 1982), with a Beckman plasma emission spectrometer (Spectra Span V) used to analyze soil extracts. Total N, C, and S were determined using a CNS LECO-2000, with the procedure recommended by Tabatabai and Bremmer (1991). All data except pH were log-transformed.

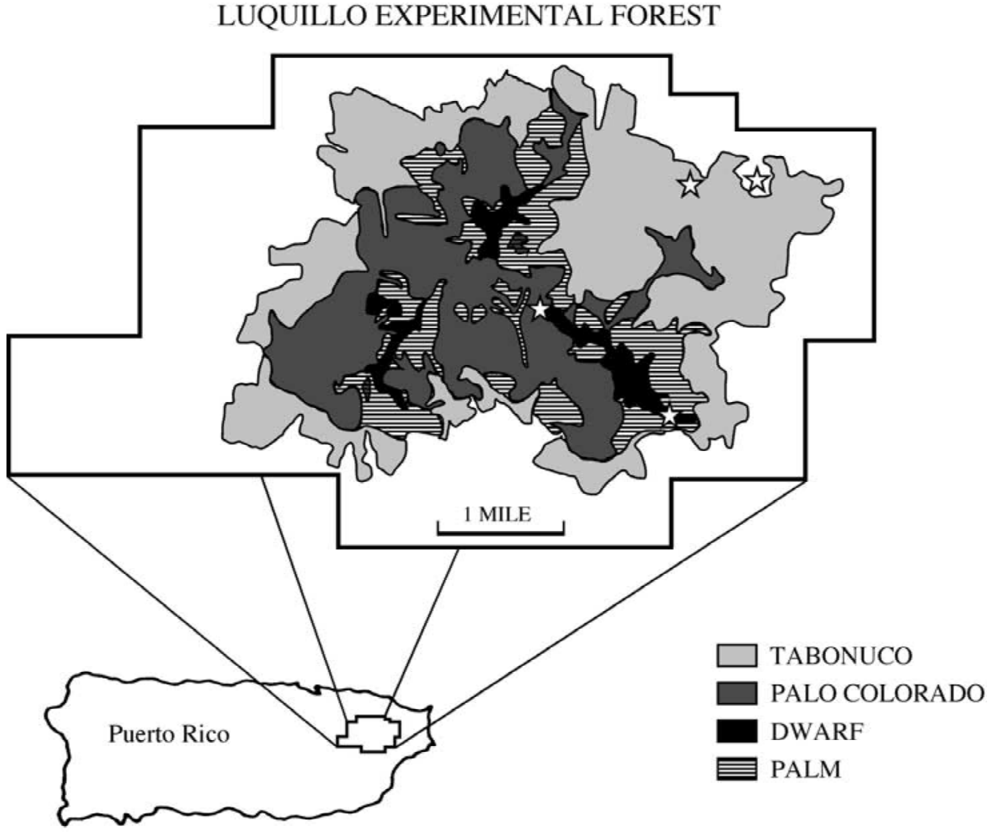

Figure 1. Diagram of the Luquillo Experimental Forest of Puerto Rico. Stars represent the location of study areas within each of the forest types.

Statistical analyses

All statistical analyses were conducted in SPSS (SPSS, 1990) unless otherwise noted. A factorial design was used to evaluate forest heterogeneity. The treatment factor *vegetation type* comprises four categorical levels: Tabonuco, palo colorado, and dwarf forests, as well as pasture. The effects of vegetation type, topography, and season on *central tendencies* of soil characteristics were assessed using nested, three-way multivariate analysis of variance (MANOVA). Sites ($n = 2$) were nested within each combination of vegetation type, topography, and season. Principal components analysis (PCA) on the correlation matrix of soil characteristics was performed to facilitate the interpretation of MANOVA results. Results were portrayed graphically in two dimensions by plotting 95% confidence ellipses around centroids based on combinations of vegetation type and topography for each season separately. Particular pairs of centroids were considered significantly different when confidence ellipses did not overlap.

The effects of vegetation type, topography, and season on *variability* of soil characteristics were assessed using a multivariate extension of Levene's test (Manly, 1994). For Levene's test, data were transformed to absolute deviations from site medians and then analyzed via nested, three-way MANOVA. Univariate ANOVAs with Bonferroni's sequential adjustment (Rice, 1989) were used to corroborate multivariate results concerning variability, and to determine which soil characteristics contributed to multivariate differences.

Correlations between all possible pairs of soil properties were represented by a matrix of Pearson correlation coefficients for each of 16 sites in the dry season as well as in the wet season. Hierarchical Mantel analyses (Manly, 1994) were used to assess if the relationships (patterns of correlation) between soil properties were similar with regard to site, topographic position, vegetation type, and season. Mantel analyses were conducted using Matlab v 4.0 (Matlab, 1995).

Results

Central tendencies

Despite a significant added variance component due to sites (3-way, nested MANOVA: nested factor, $P < 0.001$), mean values of soil properties differed with respect to vegetation types, topographic position, and season (3-way, nested MANOVA: Season, $P = 0.005$; vegetation type $\times$ topography, $P = 0.005$). Differences between seasons were consistent regardless of vegetation type or topography, and reflected differences in soil moisture and bulk density (data not shown). In contrast, differences between topographic positions depended on vegetation type.

The first principal component (PC1) accounted for 44.0% of the total variation in soil characteristics among samples, and reflected differences in bulk density, soil moisture, Na, P, C, N, and S (Figure 2A). In contrast, PC2 accounted for 24.4% of the total variation, reflecting the influence of Ca, Mg, K, pH, and Al (Figure 2A). Because the interactions between vegetation type and topography were consistent in both seasons (i.e., no 3-way interaction), only results for the dry season are illustrated for PCA. PC1 was the axis of differentiation among forest types, regardless of topographic position (Figure 2B); whereas, PC2 was the axis of differentiation between topographic positions in the three forests. Nonetheless, the trends in tabonuco and palo colorado forest differed from those in dwarf forest. In tabonuco and palo colorado, PC2 values were greater for valleys (greater pH and Ca, less Al). In dwarf forest, PC2 values were greater for ridges. In pastures, however, ridges and valleys differed with respect to PC1, with valleys having higher soil moisture and P and lower bulk density.

An increase in C to N ratios with elevation was particularly striking and consistent across topographic settings. Ratios of C to N increased significantly from pasture (lowest elevations) to dwarf forest (highest elevations)(3-way, nested ANOVA: Vegetation Type, $P < 0.001$; Figure 2C). In addition, C to N ratios in the wet season were significantly higher than those in the dry season (3-way, nested ANOVA: Season, $P = 0.018$). No significant 2 or 3-way interactions suggest that all differences were consistent with respect to other factors.

Variability

Variability of soil properties among locations within a site differed significantly among vegetation types (Table 1), with dwarf forest tending to have higher variation among sampling locations. These differences among vegetation zones were unaffected by topography, season, or their interaction. Bonferroni's sequential adjustment indicated that of the 14 soil properties examined, C, S, soil moisture, and bulk density contributed significantly to multivariate differences. Variabilities in soil moisture and bulk density were related to forest type, and variabilities in C and S were related to an interaction between forest type and topography. Variabilities in Al, Ca, Fe, and K were not related to any of the categorical factors.

Correlations

Despite differences in the central tendencies and dispersions of soil characteristics with respect to vegetation type, topography, and season, the pattern of correlation between characteristics was uniform (Figure 3). At the smallest spatial scale, patterns of correlation between soil characteristics were similar (at least approached significance in 12 of 16 analyses) in replicate sites within most combinations of topography, vegetation type, and season. At the next highest spatial scale (topographic positions within combinations of vegetation type and season), the similarities in patterns of correlation were even more prevalent, with all 18 analyses at least approaching significance. Finally, at the largest spatial scale, all analyses comparing patterns of correlations between vegetation zones (6 of 6) were significant.

Discussion

Variability in soils

Combining replicate cores at each location minimized the effect of microspatial variation. Nevertheless, vegetation types in the LEF are characterized by a high degree of site variation, and differences between sites accounted for 11–60% of the total variation in soil parameters. Sites accounted for more than 48% of the total variation in soil parameters that are related to geochemical processes (e.g., pH, 60%; Ca, 49%; Al, 58%; Fe, 51%). In contrast, sites accounted for much less variation in soil parameters that are related to in-

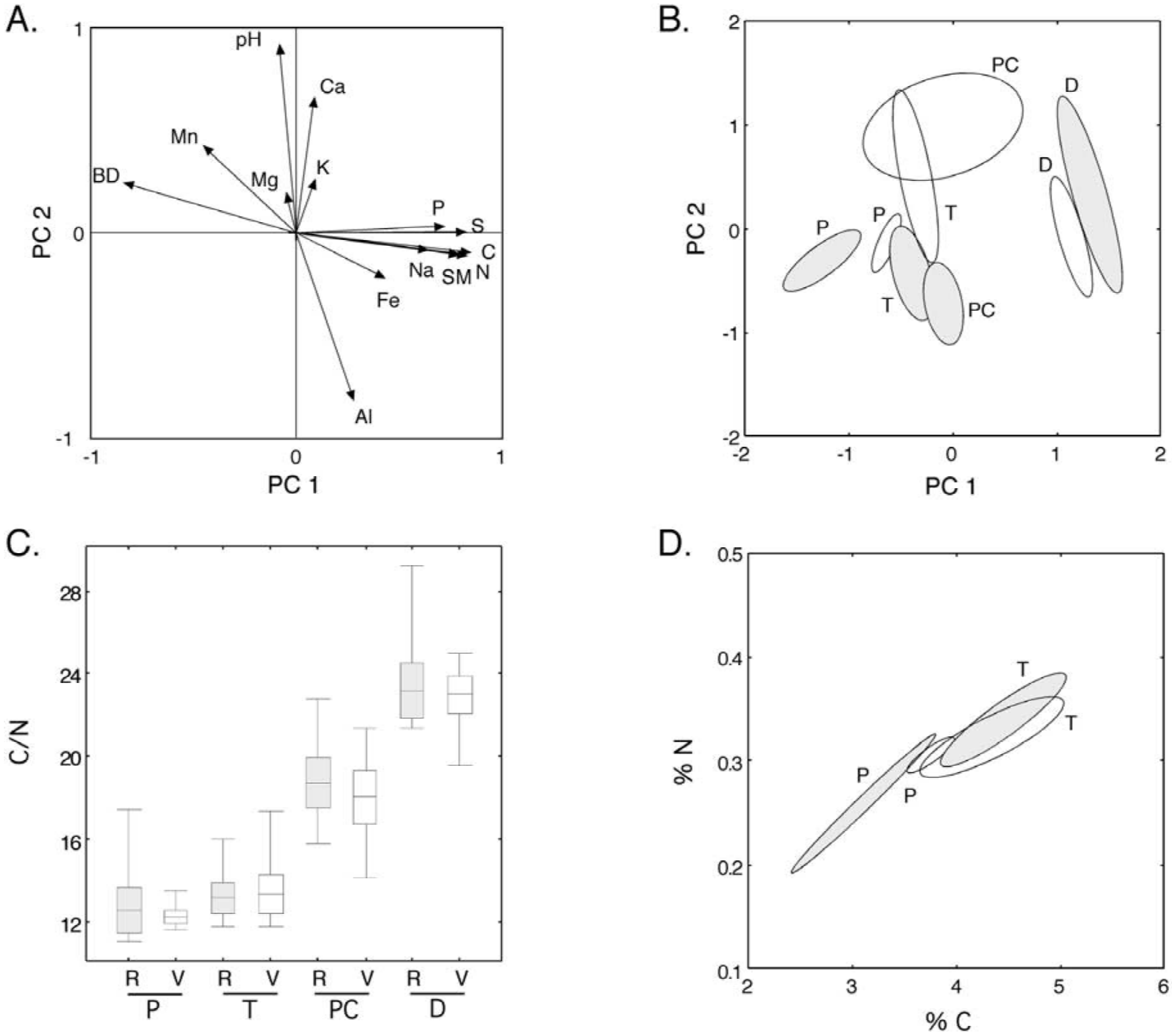

Figure 2. (A) Correlations of soil properties (pH; Al [meq/100 g]; Ca, K, Mg, Na, P, Fe, Mn [mg/g]; C, N, S, soil moisture [%]; and bulk density [g/cm^3]) with PC axes. All variables except pH were ln–transformed. (B) Graphical portrayal of each topographic position within vegetation types based on PCA of soil properties. Ellipses are 95% confidence intervals around centroids. Letters denote vegetation types (P = pasture, T = tabonuco, PC = palo colorado, D = dwarf). Open ellipses represent valleys; shaded are ridges. (C) C to N ratios by topography in each vegetation type. Lines denote the range of data, and boxes span 2 standard errors of the mean. Open boxes represent valleys; closed are ridges. (D) The effect of clearcutting and pasture management on C and N in tabonuco soils. Soils were sampled 60 years after clearing, and 10 years after pasture abandonment. Ellipses are 95% confidence intervals around centroids. Open ellipses represent valleys; shaded are ridges. Letters denote vegetation types (P = pasture, T = tabonuco).

puts of water or ecological and biological processes (e.g., C, 11%; N, 22%; S, 13%; soil moisture, 20%). Sites within vegetation types of the LEF experience similar rainfall as well as similar patterns in the uptake and release of nutrients by plants and microbes. Thus, differences between sites in soil properties are related to geology or geomorphology more than to inputs of water or other ecological processes.

Topographic differences

Although there were significant differences in soils between sites, adjacent soils in different topographic positions within a watershed are connected by the downslope transfer of mass and nutrients. Previous research in the tabonuco forest has used the catena concept to describe the spatial variability in soils with respect to topography (Johnston, 1992; Scatena, 1989;

Table 1. Results from a multivariate extension of Levene's comparison of variability for a suite of 14 soil characteristics. Soil properties were transformed to absolute deviations from site medians, and then analyzed via three-way ANOVA and MANOVA (Wilks' lambda). Sites ($n = 2$) were nested within each combination of forest (i.e., vegetation type), topography, and season. Units for available elements are Mg/g dry soil, except for Al which is meq/100 g. Total elements (C, N, S) are percentages. Bonferroni's sequential adjustment corroborates the overall significance of the MANOVA and identifies 4 of the 14 variables that contribute to multivariate differences

Soil Property	*P*-values								
	Total df = 31	Forest df = 3	Topography df = 1	Season df = 1	F × T df = 3	F × S df = 3	T × S df = 1	F × T × S df = 3	Site in (F × T × S) df = 16
ln (Al)	0.678	0.359	0.757	0.267	0.358	0.880	0.603	0.701	0.073
ln (Ca)	0.673	0.272	0.724	0.167	0.679	0.760	0.724	0.690	0.296
ln (Fe)	0.674	0.803	0.751	0.473	0.241	0.568	0.198	0.888	0.356
ln (K)	0.440	0.971	0.643	0.927	0.100	0.285	0.674	0.343	0.397
ln (Mg)	0.517	0.516	0.121	0.940	0.273	0.936	0.904	0.266	0.029
ln (Mn)	0.671	0.158	0.490	0.581	0.339	0.963	0.966	0.974	<0.001
ln (Na)	0.336	0.034	0.203	0.286	0.709	0.481	0.926	0.986	0.539
ln (P)	0.152	0.458	0.317	0.327	0.015	0.518	0.508	0.507	0.611
ln (C)	<0.001*	<0.001	0.356	0.223	0.003	0.693	0.748	0.463	0.545
ln (N)	0.007	0.003	0.651	0.404	0.006	0.981	0.484	0.834	0.425
ln (S)	<0.001*	<0.001	0.006	0.446	<0.001	0.631	0.766	0.962	0.944
pH	0.113	0.008	0.093	0.726	0.378	0.702	0.858	0.795	0.056
ln (soil moisture)	<0.001*	0.070	0.201	<0.001	0.265	0.003	0.524	0.970	0.273
ln (bulk density)	<0.001*	<0.001	0.975	0.688	0.187	0.949	0.886	0.279	0.792
MANOVA		0.006	0.656	0.272	0.353	0.670	0.826	0.826	<0.001

*Denotes significance after Bonferroni's Sequential Adjustment (P−values are prior to adjustment).

Silver et al., 1994). This research suggests that the catena concept may have broad applicability to all the forest types of the LEF. However, the biogeochemical processes responsible for topographic differences in soils may differ between vegetation types. In the tabonuco forest, two related mechanisms may cause the higher exchangeable cation content of riparian valleys (Silver et al., 1994). First, the lateral flow of nutrient-rich waters removes cations from ridges and deposits them in valleys. Second, the accumulation of Fe oxides on ridges blocks a significant proportion of exchange sites; whereas, flooding and poor drainage in valleys promotes the removal of Fe coatings from soil particles. Results from this study support the operation of these mechanisms within both tabonuco and palo colorado forests. Concentrations of both Ca and Mg were significantly higher in valleys than on ridges. In addition, PC2 was primarily responsible for separating ridges (low scores) from valleys (high scores) in tabonuco and palo colorado forests (Figure 2B). Ca and Mg were associated positively, and Fe was associated negatively with PC2.

Topographic differences within dwarf forest and pastures are distinct from those of tabonuco or palo colorado forest (Figure 2B). Although PC2 distinguished ridges from valleys within dwarf forest, valleys had lower PC2 scores than did ridges. Concentrations of Ca, Mg, and Fe were lower in dwarf valleys whereas soil moisture was higher. Although the downslope movement (i.e., ridge to valley) aspects of the catena concept applies to all forest types, the constituents responsible for topographic differences in dwarf forest are different than those in palo colorado or tabonuco. Moreover, different mechanisms likely are responsible for topographic variation in pasture and dwarf forest compared to other vegetation types. In particular, pasture valleys and ridges were not separated along PC2; thus, the cation-Fe processes cannot account for differences between ridges and valleys in pastures.

Differences in vegetation types

Differences among vegetation types apparently reflect differences in inputs of water or other ecological processes rather than differences in geochemical processes. PC1, which accounted for differences among vegetation types (Figure 2B), reflected variation in bulk density, soil moisture, and concentrations of Na,

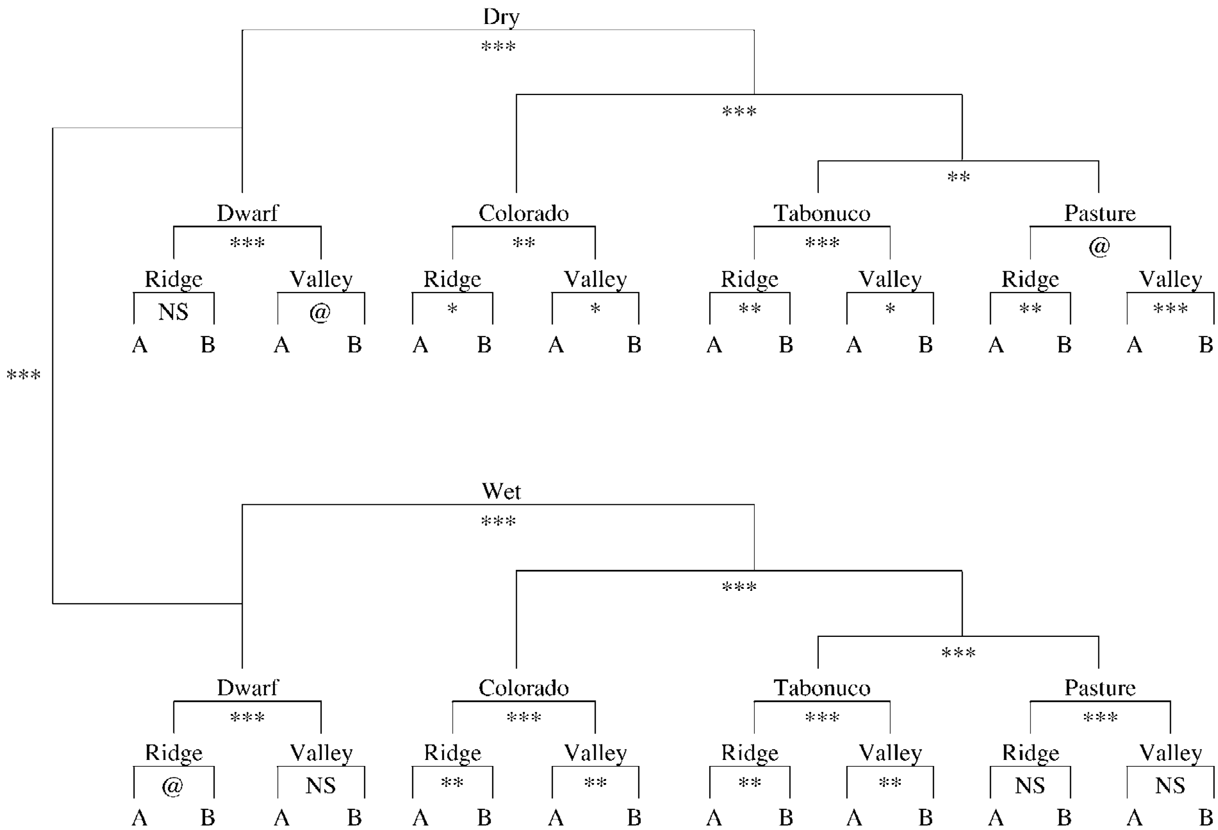

Figure 3. Results of Mantel analyses comparing pairs of correlation matrices in a hierarchical fashion with regard to site, topography, vegetation type, and season. Each matrix represented the correlation between all possible pairs of soil characteristics at a site (pH; Al [meq/100 g]; Ca, K, Mg, Na, P, Fe, Mn [mg/g]; C, N, S, soil moisture [%]; and bulk density [g/cm^3]) based on six replicates. All variables except pH were ln–transformed (pH is already a logarithmic transformation). Letters represent sites, whereas symbols at the nodes of the dendrogram indicate significance levels from the Mantel analysis (NS, $0.10 < P$; @, $0.05 < P \leq 0.10$; *, $0.01 < P \leq 0.05$; **, $0.001 < P \leq 0.01$, ***, $P \leq 0.001$).

P, C, N, and S. Carbon, N, and S are cycled biologically and reflect the balance of forest inputs and decomposition. Bulk density is related to both C and soil moisture. Although Na can come from some bedrock, in the LEF, it is primarily derived from sea salts via rainfall (McDowell et al., 1990). Hence, differences in Na among vegetation types probably reflect increasing rainfall with elevation. In contrast, PC2, which did not account for differences among forest types (Figure 2), reflected variation in Ca, Mg, K, and Al. These are all weathered from bedrock and are abundant in the LEF.

Other evidence supports the contention that differences among vegetation types primarily are related to biological rather than geological processes. At the local scale (10–100 m among locations within a site), variablility in soil moisture, and concentrations of Mn, C, N, and S all differed significantly among forest types (Table 1). However, soil parameters related to geochemical processes (e.g., Al, Ca, Mg, and K) were not responsible for such differences. In addition, pasture, tabonuco forest, and dwarf forest share similar bedrock geology (i.e., volcanoclastics), whereas the locations where palo colorado soils were sampled are underlain by a granidorite that weathers into a sandy soil (Seiders, 1971). If geology is solely responsible for surface soil characteristics, palo colorado would be expected to have the most disparate soil parameters. However, tabonuco and palo colorado are the most similar of the forest types, with dwarf forest having the most disparate soils.

Productivity and nutrient pool size

Determining mechanisms responsible for a decrease in productivity with increasing elevation within tropical forests has been the focus of considerable effort (Bruijnzeel and Veneklaas, 1998; Tanner et al., 1998;

Waide et al., 1998). For example, in the LEF, NPP decreases from 10.5 t/ha yr in the tabonuco forest to 7.60 t/ha yr in palo colorado and 3.7 t/ha yr in the dwarf forest (Weaver and Murphy, 1990). Although data on levels of extractable soil nutrients in tropical forests are few, speculation from experimental results, and patterns of foliar and litterfall concentrations, has led to the hypothesis that, in general, P limits growth in lowland forests and N limits growth in montane forests (Sollins, 1998; Tanner et al., 1998). For example, lowland forests produce litter with much lower C to N ratios (higher concentration of N) than do temperate or boreal forests. In fact, with regard to N, tropical montane forests function more like many temperate and boreal forests than like most lowland tropical forests (Tanner et al., 1998).

When soils from lowland and montane forests in the LEF are sampled in a systematic and comparable fashion, data do not support the contention that the total amount of soil N becomes limiting with an increase in elevation. In fact, N levels are much higher in dwarf forest than at any other elevation, and no elevational pattern in P pools is evident. Thus, absolute pool sizes of these nutrients cannot be responsible for the reduction in productivity with elevation.

Relative to C, however, soil N decreases with elevation (Figure 2C) as a result of reduced decomposition rates at high levels of soil moisture and lower temperatures. This is paralleled by a decrease in leaf N (Medina et al., 1981) and litter N (Bruijnzeel and Proctor, 1993) contents. Although nutrients are abundant in montane soils, plants suffer a reduced ability to acquire these nutrients. For example, low solar energy and rates of transpiration due to cloud cover (Odum, 1970), low soil oxygen (Silver et al., 1999), and soil toxicity (Bruijnzeel and Proctor, 1995) are the major factors limiting nutrient acquisition in these environments.

Forest clearing

Most research on the effects of anthropogenic disturbances has focused on aboveground characteristics of ecosystems (e.g., changes in species composition, Willig and Walker, 1999); however, the effects of disturbances on belowground characteristics are considerable (Lugo et al., 1990; Scatena and Lugo, 1995; Silver and Vogt, 1993; Willig et al., 1996). The conversion of tabonuco forest to cattle pastures results in soil characteristics that are different from those in nearby undisturbed forest. Clearcutting in tropical forests usually leads to increased losses of nitrate and other nutrients (Vitousek, 1985), and evidence of reduced N levels is still evident in pastures, at least 60 years after clearing and 10 years after abandonment (Figure 2D). Such anthropogenic disturbances disrupt processes which elicit topographic - specific distributions of nutrients. Differences between ridges and valleys in pastures are reflected in PC1, suggesting the operation of the same biological processes and inputs of soil moisture that account for differences among forest types. Although pasture soils are significantly different from tabonuco soils when topographic units are combined, these differences most prominently reflect the effect of pasture ridges (Figures 2B,D). Despite this, C to N ratios are similar between pasture and tabonuco forest sites (Figure 2C).

Conclusions

Considerable spatial variation characterizes soils in the LEF, especially between sites within topographic positions. This variation has important implications for flora, microbiota, and ecosystem parameters. For example, failure to hierarchically replicate sites within treatments could lead to the assertion of treatment differences (e.g., vegetation type or topography) that are really site differences. Moreover, significant differences between topographic positions, especially within tabonuco and palo colorado forests, confound differences between forest types. Consideration of the high degree of spatial variability and the elimination pseudoreplication (Hurlbert, 1984) is critical to understanding the effects of landscape features on soils of the LEF in particular, and in forested systems in general.

Nevertheless, when soils are sampled in an extensive and comparable fashion, soil properties exhibit distinctive patterns at both broad and local spatial scales. The mechanisms responsible for topographic differences in tabonuco and palo colorado are different from those in dwarf forest. In addition, differences among surface soils associated with vegetation types derive from ecological and climatic processes rather than considerations of geology or geochemical processes.

Production of pasture from tabonuco forest results in dramatic differences in surface soils at both local and broad scales. At the scale of patches, conversion to pasture alters the mechanisms responsible for topographic variation in soils. At the landscape scale, conversion to pasture results in soils significantly different than adjacent tabonuco soils. Clearly, modifications of ecological processes that maintain soil characteristics represent an important, yet poorly understood component of anthropogenic disturbance.

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