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Soil characteristics, carbon stores, and nutrient distribution in eight forest types along an elevation gradient, eastern Puerto Rico

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Soil properties, carbon and nutrient distribution were studied along an elevation gradient covering eight distinct forest types in eastern Puerto Rico. The dominant soil forming parent materials are granodiorite saprolite and volcanic rocks which exert a strong influence on the soil properties. Soils on middle to high elevations are very strongly acidic with low base saturation (<20%) due to a strong leaching environments. Soils formed in lowlands, dry forest and coastal wetlands are moderately to weakly acidic with higher base saturation (>40%). Generally, organic carbon (OC), nitrogen (N) and nutrients accumulated in the surface horizons and decrease with depth. Soils formed in areas influenced by landslides or alluvium were the exception to this pattern. Soil OC and N stores follow the elevation gradient: from 26.7 kg OC m^{-2} and 1.4 kg N m^{-2} in soils of the colder and wetter mountain tops to 12.3 kg OC m^{-2} and 1.0 kg N m^{-2} in soils of the lower elevation dry forests. The C:N ratio decreased from 20 to 11 as elevation decreased along the gradient. Landscape movement on uplands through landslides, slumps and fluvial/alluvial processes has a significant effect on variation of C stores which must be considered when estimating C stores by landscape units. The coastal wetlands have exceptionally high OC stores (>90 kg m^{-2}) due to their water-saturated and reducing environment. Soil OC content showed an inverse relation with soil bulk density and played a controlling role on cation exchange capacity (CEC) and nutrient distribution. Clay content has no effect on CEC. Elevation through its influence on precipitation and temperature exerts strong influence in the quantity and quality of terrestrial OC stores, and the depth-distribution pattern of C, N and other nutrients.

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The Luquillo Experimental Forest (LEF, also known as El Yunque National Forest) is located in eastern Puerto Rico and it is a the site of many biological, ecological and soils investigations because of its unique environmental conditions. Its location within the prevailing northeast trade wind zone and its proximity to the east sea situates the LEF within an enhanced topographically-affected gradient all within a short distance. The close proximity of these conditions facilitate evaluation of biogechemical processes and their effects on soils all within a relatively short distance while covering some of the major ecological communities commonly found throughout large tropic regions. Soils of the LEF are formed from parent materials of two general lithologies quartz-diorite and andesite. These lithologies are most strongly influenced by climate and topographically mediated processes (Huffaker 2002). Vegetation communities of the LEF also exert an influence on and are affected by the prevailing soil properties. Mount and Lynn (2004) conducted a general soils investigation of Puerto Rico that focused primarily on landscape relationships of soils in various geomorphic settings. They found Oxisols with low weatherable mineral content formed on geomorphologically stable Tertiary age (>10 K yr) surfaces, Ultisols with generally low nutrient content and with more organic matter (OM) limited to the upper portion of the soils formed mostly in saprolite, colluvium and alluvium of granodiorite and andesite, and weakly developed Inceptisols formed in colluvial or alluvial deposits shallow to bedrock. With soil-forming factors like climate and parent materials of their study sites being virtually equal, they attributed the occurrence and distribution of these soils mainly to geomorphic factors and duration of stable soil-forming episodes.

Soil geochemistry and mineralogy provides some additional insight into the processes by which soils of the

LEF formed. In an early study, Briggs (1960) found that in strongly weathered saprolite material that most of the soluble plant-essential cations such as calcium (Ca^{2+}) were lost through intense leaching. Saprolite-derived soils are often capped with large quantities of Saharan dust that has been transported west from Africa across the tropical North Atlantic Ocean by the trade winds and deposited in the western Atlantic islands including Puerto Rico (Muhs et al. 1990, 2007). Pett-Ridge et al. (2009) used strontium (Sr) isotopes to provide independent evidence of Saharan dust in the watershed soils of the Luquillo Mountains. They found Saharan-dust mixed into the soil profile to >1 m deep. The dust provides vital geochemical constituents to the soil, mostly notably soluble silicon (Si) and bases that contribute to the secondary (pedogenic) mineral composition and stability of OM complexes. However, the allochthanous mineral inputs are not limited to dust. Johnston (1992) also noted in the Luquillo Mountains that the concentrations and distribution of sodium (Na^+) in the coastal soils under tabonuco forest communities were inversely related to Ca^{2+} and Mg^{2+} concentrations, reflecting the strong influence of shoreward wind currents and rainfall as the primary sources of Na^+ in the soil. Reyes-Rodríguez et al. (2009) studied the geochemistry of rainwater in the cloud forests of Puerto Rico and found acidity, SO_4^{2+}, Cl^-, Mg^{2+}, K^+, and Na^+ in the cloud water and these ions are more concentrated in Africa dust than in clean air masses. Further, they measured 1.09 mg l^{-1} and 1.25 mg l^{-1} total organic carbon (TOC) in cloud waters and from airborne particulate matter, respectively. Both Asbury et al. (1994) and Gioda et al. (2006) found the cloud water chemistry dominated by Na^+ and Cl^- followed by Mg^{2+} and SO_4^{2+} with the Na^+ content measuring 400 to 455 μeq l^{-1}. Gioda et al. (2008) measured the water soluble organic carbon and nitrogen levels in cloud and rainwaters at East Peak, Puerto Rico and they found that the Africa dust produces TOC, DOC and TN 2–4 times higher during periods under influence of trade winds. They concluded that 40–80% of TOC and nearly100% TN in the cloud and rainwater of Puerto Rico originated from long-range transport of dust, ash, and/or pollution inputs. Thus in addition to the weathered parent material, the Africa dust also provides cations such as source of Na^+ and Mg^{2+} to the soils of cloud forest. However, the anion concentrations are generally lower in soils of LEF than most sites in eastern US (Weathers et al. 1988).

Pedogenic clay minerals in particular are critical for nutrient cycling. In their evaluation of Puerto Rico soils Mount and Lynn (2004) found generally less clay in Inceptisols than in Ultisols. They also noted that Oxisols do not always have the most clay, despite their relatively higher intensity of weathering. However, there is increasing dominance of kaolinite in the clay-size fraction of Oxisols as compared to Inceptisols. Jones et al. (1982) found that kaolinite is the dominant clay mineral species in the fine to very fine texture class soils, followed by goethite (FeOOH) and quartz. In sandy soils, such as the Pina series (Typic Haplorthox) in eastern Puerto Rico, quartz is by far the dominant mineral (Fox 1982). Soil mineralogy exerts controls on aggregate stability and interactions with OM as well as nutrient dynamics. Oxisols and Ultisols with high kaolinite and Fe-oxide contents are often nutrient deficient below the upper 10–25 cm of the soil (Sánchez 1976) with OM generally concentrated in the upper portion as well. Beinroth et al. (1996) found that soil organic carbon (SOC) in the oxide and kaolinitic soils of Puerto Rico was positively correlated to clay and silt content, particularly in areas with higher precipitation.

Tropical forests communities contribute to global carbon storage in two major ways (Schedlbauer and Kavanagh 2008). The most obvious contribution of these forests particularly secondary growth forest is to increase C storage in aboveground biomass. The second and more subtle C storage contribution is to increasing C in the soils of the forested regions. Lugo and Brown (1993) pointed out that SOC in managed systems can be lower, equal, or greater than mature tropical forests depending on land use history. Silver et al. (2004) studied carbon sequestration in the 61 yr following reforestation of tropical pasture. They found more SOC (10 kg C m^{-2}) in reforested land than adjacent pasture (7 kg C m^{-2}) and total soil C pools in 0–60 cm depth are more than that in the above ground C pool. In their work in a forest/pasture transition region of Costa Rica, Schedlbauer and Kavanaugh (2008) found that despite aboveground changes in C storage, total C stores remained relatively unchanged following land use shift from pasture to secondary forest due to the presence of large passive pools of mineral-stabilized C in soils. By comparing SOC data from a variety of tropical land uses, Lugo and Brown (1993) estimated tropical soils accumulating 168–553 TgC yr^{-1} and they found the greatest potential for carbon sequestration in tropical soils to be secondary forest succession. Thus land use in the tropics has great impact in carbon sequestration. It is estimated that the top three meters of soil beneath tropical evergreen forests store 474 Pg of C globally (Jobbágy and Jackson 2000). Including the additional two meters of depth, not an unusual depth for soils formed in the tropics, soil C store estimates increased by 56% over C stores in just the upper meter. Soil C stores in the upper 1–3 m depth under tropical evergreen forest measured 158 Pg with the SOC in the top 20 cm accounting for 50% of the total C storage. In digital soil mapping on Barro Colorado Island using Random Forest analysis, Grimm et al. (2008) described the main drivers of variation in the topsoil (0–10 cm) as topographic attributes and soil texture in the subsoil (i.e. silt-clay composition at 10–50 cm depth).

For the tropical regions, forest community diversity and distribution are related to varying edaphic conditions on the landscape, particularly in regions close to marine settings with drastic elevation changes. A soil-vegetation study of the tabonuco forest community in the Luquillo Mountains, found sierra palm *Prestoea montana* was associated with wet soils having high concentrations of $Ca^{2+}$and magnesium (Mg^{2+}) and higher pH values (Johnston 1992). Another canopy species *Sloanea berteriana* was associated with soils at lower slope positions with relatively higher concentration of Mg^{2+}. In a study also based in the Luquillo Mountains, Cox et al. (2002) showed that soil nitrogen (N) decreases relative to soil C as elevation and rainfall increases and mean soil temperature falls. They attributed this to reduced decomposition rates at high soil moisture level and lower temperatures. In a study of carbon distributions among 5 life zones from tropical dry to tropical mountain wet forest in Venezuela, Delaney et al. (1997) found no clear trend of ecosystem TOC with life zone changes. They found TOC in soils of different life zones averaged 22.5 kg m^{-2} (16.0–25.3 kg m^{-2}) which account for 54% (68–55%) of the total ecosystem carbon. Further, they measured 67–70% of the SOC in the upper 50 cm. Yet Wang et al. (2002) found a clear trend of increased C storage with elevation from a validation of CENTURY soil model using 69 soil samples taken from 4 forest types at different elevations in Luquillo Experiment Forest. They measured SOC in the top 30 cm and found C storage ranges from 2 kg C m^{-2} at lower elevation to 23 kg C m^{-2} at higher elevation. In general, the C storage increase with elevation, from 12.3 kg C m^{-2} in tabonuco forest, 17.6 kg C m^{-2} in colorado forest, 10.1 kg C m^{-2} in palm forest to 18.6 kg C m^{-2} in the Elfin/dwarf forest on the highest peaks. Vargas et al. (2008) estimated below ground carbon representing 50% total ecosystem in a mature dry tropical forest. Hall et al. (1992) studied carbon balance of the Luquillo Forest using a geographically-based ecosystem model and concluded that forest acted to pump carbon from the atmosphere to the ocean at a rate of about 90 kg ha^{-1} yr^{-1}.

Because the soil characteristics particularly C dynamics in tropical soils, are influenced as much by the vegetation community as they are by other soil forming factors, we undertook this study to elucidate: 1) changes of soil properties along the elevation gradient and 2) the dynamics of soil C and N stores and critical nutrient distributions in soils associated with eight distinct forest types along an elevation gradient in eastern Puerto Rico. We hypothesize that terrestrial C stores and nutrients distribution of these soils are being controlled more by a geomorphic landscape position that controls the key soil properties including soil temperature, soil moisture, drainage, landscape stability, and landscape nutrient dynamics.

Methods

Study area

Study sites were associated with existing long-term study projects (Gould et al. 2006, González et al. 2007) in the northeastern region of Puerto Rico and located within eight mature (>60 yr old) forest types (Fig. 1). Elevation of the study area increases from just above sea level to 1010 m to include eight forest life zones (from lowest elevation to highest): lowland subtropical dry, lowland subtropical moist, subtropical wet, subtropical rain, lower montane wet, and lower montane rain forest. In this setting, mean annual air temperatures (MAAT) decreased with increasing elevation along the gradient from 27.5 to 19.5°C and mean annual precipitation (MAP) increased along the gradient (1262–3908 mm) as measured during 2001–2004 (Gould et al. 2006) (Table 1). However the actual water available to the vegetation is higher than these values because a significant portion of the water inputs to cloud forest are from cloud condensation; water in the clouds moves horizontally thus it is not measured by ground rain gauges. There are four forests types found at elevations of 380 m and above in the LEF (18°180′N, 65°500′W; from lower to higher elevation): tabonuco (*Dacryodes excelsa*, *Sloanea berteriana* and *Manilkara bidentata*), palo colorado (*Cyrilla racemiflora*), sierra palm (*Prestoa montana*) and elfin woodland (Wadsworth 1951, Weaver 1994). Sites were located on four forest types below 380 m elevation: lowland moist and dry forests, and flooded *Pterocarpus* and mangrove forests. The latter four are located on lands owned by the Puerto Rico Commonwealth Government (some are former military lands) and privately managed and unmanaged lands. All sites are on noncalcareous colluvial or alluvial material derived from volcanic bedrock (montane and lowland sites) or marine deposits (coastal mangrove and *Pterocarpus* sites). A detailed description of forest community characteristics, locations and soil macro- and micronutrients can be found at Gould et al. (2006). To assess the nature of soils associated with the forest types we selected 19 geographically separated sampling areas in representative forest patches throughout northeastern Puerto Rico. Three sites each were located in tabonuco, palo colorado, lowland moist and elfin woodland forests, four sites in sierra palm-dominated forest and one site each for the dry forest, *Pterocarpus* swamp and mixed mangrove (Table 1). The limited number of sample sites in the latter three was due to difficult sampling conditions.

Soil sampling and analysis

At each site, physiographic and environmental characteristics and soil profile descriptions were made using USDA Natural Resources Conservation Service (NRCS) Soil Survey Division field guidelines (Schoeneberger et al. 2002). Soils pits were excavated at each site down to the C horizon, usually more than one meter depth or to lithic or paralithic contact (Table 2). Morphological properties were noted and both bulk and volumetric-core samples were collected from each genetic horizon. Litter samples were collected

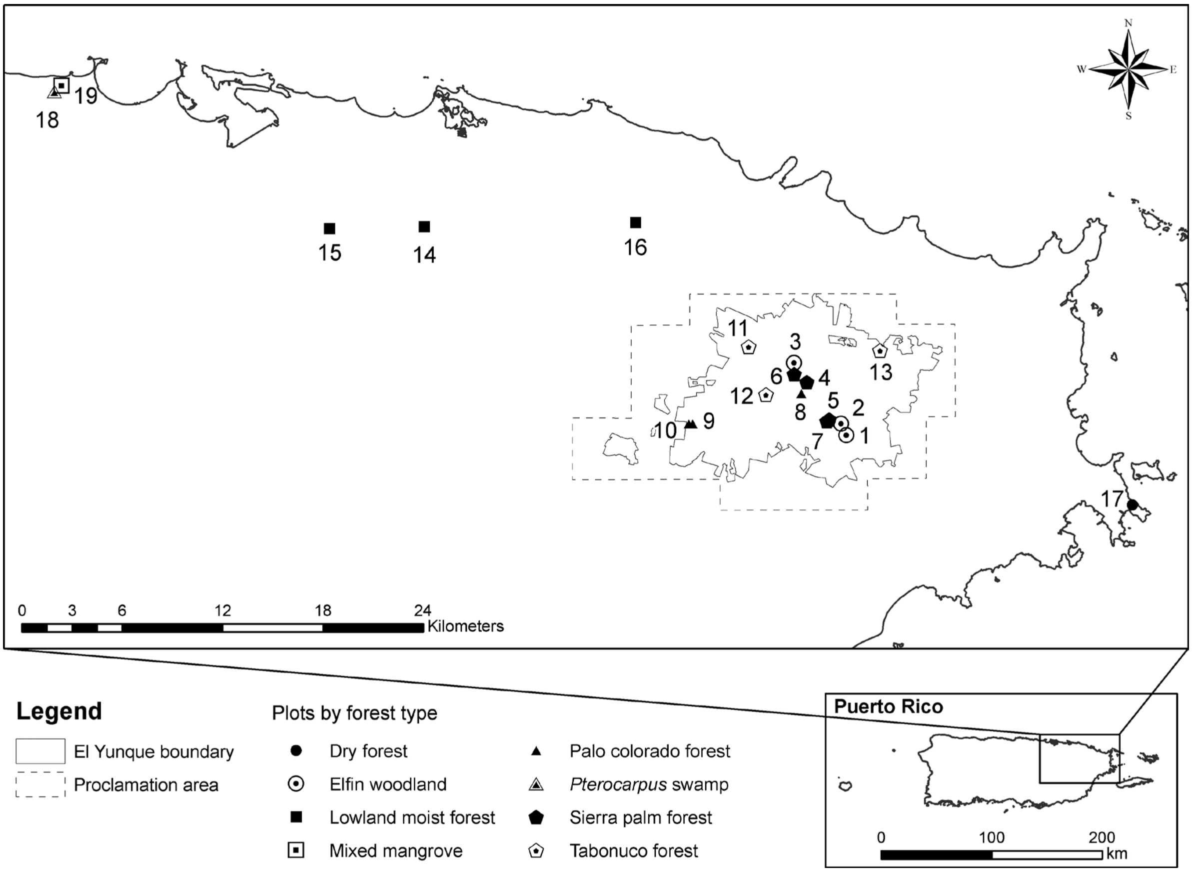

Figure 1. Locations of study sites, eastern Puerto Rico.

from the ground surface for nutrient analysis. Both soil and litter samples from 19 sites were sent to the Univ. of Alaska Palmer Research Center Laboratory and analyzed according to procedures of the USDA-NRCS Soil Survey Laboratory (Soil Survey Laboratory Staff 1996) unless otherwise noted. All mineral samples were air-dried and passed through a 2 mm sieve. Fractions >2 mm were weighed to determine gravel content. Organic horizons and litter samples were oven-dried at 65°C to a constant weight and then ground in a Wiley mill to approximately 0.425 mm (80 mesh) prior to chemical analyses. Soil bulk density was determined using a core sampler with diameter of 5 cm and sampling volume of 30 cm^3, and reported on a 105°C oven-dried weight basis. Particle size distribution was determined using the hydrometer method. Soil pH was measured in distilled water using a 1:1 ratio for mineral soils and a 1:5 ratio for organic soils. Mineral soil sub-samples were ground to approximately 0.425 mm (80 mesh) for total organic carbon (TOC) and nitrogen (TN) analysis by dry combustion using a LECO CHN-1000 analyzer. Cation exchange capacity (CEC) was determined by extracting cations with 1M NH_4OAc at pH7, washing with ethanol and steam distillation-titration determination of ammonium. Ammonium acetate extractable bases (Ca^{2+}, K^+, Mg^{2+}, and Na^+) were determined by inductively coupled plasma optical emission spectrometer (ICP-ES Optima 3000xl), and base saturation (%BS) was calculated by summation of these bases divided by CEC and multiplied by 100. Available P, Cu, and Zn were determined on a Mehlich 3 extract by ICP-ES. All above analyses except pH were reported on oven-dry basis (105°C). Pedon organic C (OC) and total N (TN) storage were calculated as the sum of soil horizon storage for each profile to depth measured, using the equation of Michaelson et al. (1996) for calculation of each horizon store:

$$\text{Horizon OC storage (kg m}^{-2}) = T \times BD \times (\%OC \text{ or } \%N) \times 10^{-1} \times (1-(PCF/100))$$

where: BD = bulk density (g cm^{-3}), T = horizon thickness (cm), and PCF=percentage coarse fragments >2 mm by volume in horizon.

Regression analysis was used to find the interrelationship among different soil properties.

Results

General morphological characteristics

Soil morphogical and selected physical properties are presented in Supplementary material Appendix 1. Representative soil profiles from each of the six upland forests and one of the lowland forests are presented in Fig. 2.

Drainage condition and soil color

Soil color reflect the kinds and degree of soil weathering (Bigham and Ciolkosz 1993) and in this setting, color is most closely related to OM accumulation and drainage conditions. Soils from the forest communities above 370 m tended to have A horizons darker then the underlying B horizons indicating accumulation of humus. Generally they have a Munsell color designation of 10 or 7.5 YR hue with value and chroma <4 and 3, respectively. In the highest elevation elfin woodland sites (sites 1–3), soils are poorly drained in the upper portion of the sola, as indicated by the gleyed color of 2.5 Y and 5 GY in the Ag and Bg horizons and the presence of iron (Fe) concentrations as pore linings around root channels (i.e. redoximorphic features). Soils in the sierra palm, palo colorado and lowland forests (sites 4–16) have drainage ranging from well to somewhat poorly. The matrix color of the Bt and Bw horizons are brown to reddish brown, with hues from 10 to 2.5 YR and values and hues from 4 to 8, indicating their highly oxidized condition. The restricted internal drainage of some sites was reflected in the abundance of redoximorphic features including Fe-concentrations and Fe-depletions as pore linings and presence of manganese concretions. In sites 1 through 4 the saprolite also has colors that are like those of redoximorphic features due to differential weathering of granodiorite. With decreasing elevation and rainfall, B horizons lost their reddish hue and the dominant color trends to yellowish brown (7.5 YR 4/6–5/8). Manganese (Mn) concentrations, which tend to be more dominantly expressed in drier soils or soils with episodic saturation, are common is these soils. In the wetlands, mainly the *Pterocarpus* and mangrove forest, the soil surface experiences long periods of inundation thus they are very poorly drained. Soil color reflects the reducing environment and is dominated by a grayish hue (2.5 Y), which also indicates the presence of iron sulfides.

Soil texture and rock fragment content

Topographical location and precipitation intensity play an important role in the general nature of soil texture in the <2 mm fraction and the content of rock fragments, whether as colluvial deposits or as weathering saprolite. The upland soil characteristics are influenced by hill slope processes (e.g. landslides and overwash erosion) and the influence of bedrock is evident from the increased rock fragment content. At the highest elevations (elfin woodland), input of externally sourced eolian materials over weathered granodiorite and saprolite is common. This results in A horizons with silty textures and no rock fragments. The underlying B horizons of these soils are clay-rich (clay content >50%) (site 1–4). In the palm and palo colorado forests, most soils formed in colluvium due to slope failure or slump. As a result, most of the soils horizons have 20–70% angular granodiorite and volcanic rocks with sizes from cobblestone to boulder and the distribution in the profile has no relation to depth. Soil textures in these two vegetation communities vary widely from silt loam to clay reflecting the complex landscape processes. Soils under the tabonuco forest and lowland moist forest formed in highly weathered granodiorite or volcanic rocks and saprolite is common in the lower profile in addition to hard bed rock with the exception of site 16 which is formed in deep alluvium. Soil texture is dominantly clay. Soils in the dry forest (site 17) have a clay texture and 50% angular volcanic rock fragments in their surface horizons rather than subsurface horizons. This is apparently the result of talus activity from upper slopes. The wetland sites have dominantly muck texture due to accumulation of highly decomposed organic matter. The stratification of organic and mineral horizons in site 18 reflects the fluvial depositional process active in the swamp.

Soil structure, consistence, horizon boundary and bulk density

Bioturbation due to soil fauna and plant roots often results in granular structure, normally in the surface A horizons. This is especially true where earthworms are active. In the elfin woodland and sierra palm forest, earthworm holes are common and krotovina are common where the earthworm cast is filled with earthworm pellets or granules. The B horizons are generally dominated by subangular block structure. Owing to the clay contents, most soils exhibit different degrees of stickiness and plasticity when wet and varying degree of firmness in the moist state. The boundary between two adjacent horizons reflects the soil forming processes. Most soil horizons have a clear smooth boundary transition the horizon below under stable landscape conditions. However where there is a texture discontinuity due to depositional process such as dust fall, colluvium, or landslide, abrupt smooth or abrupt wavy boundaries appear. Bioturbation such as with tree-fall often results in wavy or broken boundaries. Bulk densities (BD) of the mineral horizons generally increased with depth (Table 2), but were lower ranging from 0.44 to 1.34 g cm^{-3} for the Ultisol and Inceptisols (sites 1–15), compared to the higher densities of the Alfisols (sites 16–17) ranging from 1.41 to 1.74 g cm^{-3}. Bulk densities of Inceptisols and Ultisols followed a good relationship with soil C and decreased exponentially with increased soil C (R^2=0.94 and 0.68, re-

Table 1. Physical environment of study sites along an elevation gradient in eastern Puerto Rico.

Site no./ name	Site name	Latitude, N/ longitude, W	Elev. m a.s.l.	Landform	Parent material	Slope %	Aspect degree	Drainage class	Soil order/ great group
Elfin woodland – *Tabebuia rigida–Eugenia borinquensis* community, MAAT 20°C, MAP 396 cm									
1. 22-1 (16)	Pico del Este Cloud	18°16.286´/ 65°45.674´	953	Backslope	Eolian (dust)/ granodiorite saprolite	36	55	Sw poor	Inceptisol/ Eipaquepts
2. 23-1 (05-2)	Pico del Oeste Cloud	18°16.653´/ 65°45.857´	954	Backslope	Eolian (dust)/ granodiorite saprolite	52	142	Poor	Ultisol/ Epiaquults
3. 24-1 (11)	Yunque Cloud	18°18.637´/ 65°47.436´	1000	Ridge	Eolian (dust)/ granodiorite saprolite	32	210	Sw poor	Inceptisol/ Epiaquepts
Palm forest – *Prestoea montana–Cecropia schreberiana* community, MAAT 20°C, MAP 396 cm									
4. 16-1 (10)	Palm (nido)	18°18.013´/ 65°47.001´	634	Slump block at the base of backslope	Colluvium over granodiorite saprolite	18	340	Mod well	Inceptisol/ Dystrudepts
5. 17-1 (17)	Pico del este Palm	18°16.797´/ 65°46.247´	836	Dissected alluvial fan	Alluvium over granodiorite saprolite	10	80	Mod well	Inceptisol/ Dystrudepts
6. 18-1 (12)	Mt. Britton	18°18.267´/ 65°47.435´	902	Slump block side slope	Mixed colluvium	28	260	Sw poor	Inceptisol/ Epiaquepts
7. S-3 (05-3)	Sierra Palm	18°16.742´/ 65°46.335´	845	Back slope	Colluvium	38	310	Sw poor	Inceptisol/ Dystrudepts
Palo colorado forest – *Cyrilla racemiflora–Micropholis garciniifolia* community, MAAT 20.4°C, MAP 327 cm									
8. 19-1 (05-1)	Pico del Este Colorado	18°17.643´/ 65°47.191´	751	Back slope	Dustfall/ granodiorite saprolite	52	250	Poor	Ultisol/ Epiaquults
9. 20-1 (13)	Toro Trail 1	18°16.668´/ 65°50.890´	811	Shoulder slope base of colluvial deposit	Diorite colluvium/ saprolite	29	220	Mod well	Ultisol/ Epiaquults
10. 21-1 (15)	Toro Trail 2	18°16.672´/ 65°51.022´	798	Summit	Granodiorite saprolite	10	190	Mod well	Ultisol/ Haplohumult
Tabonuco forest – *Dacroydes excelsa–Manilkara bidentata* community, MAAT 22.7°C, MAP 323 cm									
11. 13-1 (05-8)	El Verde	18°19.168´/ 65°48.971´	434	Backslope	Andesitic residuum	44	285	Mod well	Ultisol/ Haplohumult
12. 14-1 (14)	Rio Grande	18°17.614´/ 65°48.391´	525	Shoulder slope	Granodiorite saprolite	52	300	Mod well	Ultisol/ Haplohumult
13. 15-1 (9)	Sabana 4	18°19.027´/ 65°44.511´	265	Back slope	Colluvium/ granodiorite saprolite	72	90	Well	Inceptisol/ Dystrudept.
Lowland moist forest – *Manilkara bidentata–Ocotea leucoxylon* community, MAAT 26.2°C, MAP 166 cm									
14. 10-1 (18)	St. Just	18°23.082´/ 65°59.970´	81	Slump on lower back	Colluvium mixed with saprolite	46	180	Well	Inceptisol/ Dystrudepts
15. 11-1 (19)	Botanical Garden	18°23.022´/ 66°03.188´	100	Toeslope , base of slump	Colluvium mixed with saprolite	12	285	Well	Inceptisol/ Dystrudepts
16. 12-1 (05-4)	Ford Plant	18°23.204´/ 65°52.801´	23	Floodplain	Alluvium	2	90	Sw poor	Alfisol/ Hapludalf
Dry forest – *Bucida buceras–Guapira fragrans* community, MAAT 28.1°C, MAP 128 cm									
17. 5-1 (05-7)	Ceiba Dry 1	18°13.983´/ 65°35.986´	7	Footslope	Colluvium/ Andesitic residuum	14	290	Well	Alfisol/ Hapustalfs

Table 1. Continued.

Site no./ name	Site name	Latitude, N/ longitude, W	Elev. m a.s.l.	Landform	Parent material	Slope %	Aspect degree	Drainage class	Soil order/ great group
Pterocarpus swamp – *Pterocarpus officinalis–Acrostichum aureum* community, MAAT 25.7°C, MAP 180 cm									
18. 7-1 (05-5)	Sabana Seca	18°27.482´/ 66°12.516´	5	Coastal plain	Alluvium	–	–	V. poor	Inceptisol/ Endoaquepts
Mixed mangrove – *Avicennia germinans–Laguncularia racemosa* community, MAAT 25.7°C, MAP 180 cm									
19. 2-1 (05-6)	Sabana Seca	18°27.674´/ 66°12.277´	2	Floodplain	Alluvium			V. poor	Histosol/ Sulfosaprists

spectively) (Fig. 3D). The two Alfisols (sites 16–17) had higher BD compared to other soils due to the low C content. Clay content did not have a clear or significant affect on BD with R^2=0.19 overall (Fig. 3B).

Soil pH, exchange properties and base saturation (BS)

Soil reactions are very strongly acid to nearly-neutral with pH values ranging from 3.83 to 6.92 (Table 2). Upland soils ranged from pH 3.83 to 5.84 (sites 1–16) with the higher pH at the surface for all sites. The dry forest and wetland soils (sites 17–19) had higher pH values ranging from 4.52 to 6.92 with horizons having pH ≤5 found at depths >85 cm in buried organic layers of the swamp soil (site 19). The lowland (sites 17–19) and floodplain (site 16) soils tended to group together with respect to pH and BS having both higher pH and >40% BS (Fig. 3F). Soils of the upland (sites 1–15) also tended to group together having both generally lower pH and <40% BS except for a few surface horizons where BS was >40 but <85%. Low pH values are accompanied by very low base saturation, usually <20% along with extremely low extractable cations and low CEC. The CEC is a measure of the capacity of the soil to retain on its exchange complex the essential bases (Ca^{2+}, Mg^{2+}, K^+, and Na^+) for plant growth. The Ultisols are highly leached and thus the BS in the B-horizons are <20% whereas in the less leached Alfisols the BS is >35% (site 16, 18). Due to increased leaching of the surface horizons there was a general trend of increasing pH values with depth. However such trend is not evident or only very small in most soils studied likely due to the mixing-effects of slump, slope movement and intermittent alluvial deposition (Table 2 and Supplementary material Appendix 1). Soils at the lower elevations commonly have higher pH throughout their profiles (sites 14–19) or in the surface horizon (site 13). Soils in the dry forest (site 17) have a circum-neutral reaction with pH from 5.5 to 6.9 and BS in the B horizons of 87–100% reflecting the least influence of leaching along the elevation gradient for this site.

In the upland soils (site 1–15) the cation exchange capacity (CEC) is highest in the surface O horizons and surface litters (Table 2), followed by the A horizons and lowest in the B horizons. In the A horizons the CEC range from 8–40 cmol kg^{-1} and in the B horizons from 3 to 21 cmol kg^{-1}. Soil CEC was closely tied to C content with R^2=0.89 and 0.97 for the upland and lowland soils respectively (Fig. 3E). Soils from most sites fell into two groups with upland soils (sites 1–16) having generally lower CEC values at any given C content compared to both lowland soils and dry forest soils (sites 17–19). Soil CEC increased with C content in both groups but at a lower rate (increase in CEC per unit C) in the upland soils compared to lowland soils (sites 18–19). The general trend of CEC is decreasing with decreased C contents at depth except for the dry forest site. The CEC in the wet lowland sites (18, 19) is very high ranging from 53 to 100 cmol kg^{-1}, and is associated with the high OC contents.

Extractable cations mainly Ca^{2+}, Mg^{2+}, K^+, and Na^+ are highest in the surface organic horizons or in the litter followed by the A-horizons. In the highly leached upland soils (sites 1–12), levels of Ca^{2+} and Mg^{2+} in the B-horizons are generally <1 cmol kg^{-1} with the exception of site 6 which is influenced by slumping. In most soils, extractable cations are dominated by Ca^{2+}, followed by Mg^{2+} and the levels of K^+ and Na^+ are very low due to their higher solubility and mobility in the soils. However, such a trend is not obvious in these highly leached soils that have lost most of their bases. It is interesting to note that in the dry forest, the extractable cations are dominated by Mg^{2+} followed by Na^+, then Ca^{2+} and K^+. The higher Mg^{2+} level is most likely due to the parent andesidic rock. The high Na^+ level is likely from both marine and marine aerosol influence. A similar trend is noted in the coastal lowlands where the base saturation is the highest and the bases are high in Mg^{2+} and Na^+ due to the influence of the sea.

Distribution of carbon, nitrogen and other nutrients

Carbon contents of soil A-horizons from the higher elevation elfin forest and the sierra palm forest sites range from 8 to 18%, while at the middle elevation palo colorado and tabonuco sites range from 5 to 9%, and at the lowland moist

Table 2. Selected chemical properties of study sites along the elevation gradient in eastern Puerto Rico.

Site no.	Hori-zon	Depth cm	pH 1:1	TOC	TN	Mehlich 3 extractable P	Cu	Zn	CEC	Extractable cations K	Ca	Mg	Na	BS %	Bulk density g cm^{-3}
				%		mg kg^{-1}			cmol kg^{-1}						
Elfin forest															
1	Ag	0–22	4.54	12.6	0.68	<1	4.7	0.7	23.2	0.13	0.73	0.90	0.13	4.3	0.54
	Bg	22–28	5.00	2.1	0.09	<1	24.1	0.3	7.3	0.01	0.05	0.13	0.01	2.7	0.97
	BCr	28–45	4.81	1.1	0.06	<1	6.3	0.2	5.2	0.01	0.05	0.08	0.01	2.8	1.10
2	Oi	0–1	4.69	40.6	1.34	14.0	7.0	13.6	85.1	3.23	17.3	11.5	1.81	0.1	0.01
	Ag1	1–10	4.55	15.1	0.74	<1	3.9	0.9	31.2	0.14	1.36	1.13	0.32	9.4	0.55
	Ag2	10–23	4.66	13.2	0.65	<1	6.4	0.9	25.3	0.08	0.35	0.55	0.21	4.7	0.55
	B/A	23–31	4.53	4.8	0.25	<1	7.6	0.5	13.1	0.03	0.02	0.33	0.12	3.8	0.72
	Bt1	31–49	4.51	1. 7	0.10	<1	4.1	0.5	8.0	0.01	0.01	0.20	0.12	4.2	0.90
	Bt2	49–74	4.60	1.1	0.07	<1	4.2	0.1	7.9	0.01	0.01	0.19	0.13	4.3	0.87
	CrT	74–105	4.87	0.2	0.04	<1	2.4	0.1	7.5	0.02	0.01	0.17	0.14	4.5	1.08
3	Ag1	0–21	4.22	18.4	0.82	<1	1.2	1.5	38.6	0.15	1.24	0.81	0.38	6.7	0.44
	Ag2	21–28	4.44	11.1	0.46	<1	1.9	1.2	24.8	0.04	0.42	0.38	0.13	3.9	0.62
	A/B	28–44	4.43	5.7	0.24	<1	1.2	1.3	15.8	0.02	0.12	0.13	0.14	2.6	0.84
	Bw1	44–72	4.47	1.1	0.05	<1	1.2	2.4	11.2	0.01	0.11	0.12	0.20	3.9	0.94
	Bw2	72–96	4.47	0.6	0.02	<1	2.7	5.0	11.0	0.01	0.13	0.18	0.27	5.3	1.04
	BCr	96–110	4.52	0.5	0.02	<1	4.3	7.6	10.9	0.01	0.14	0.16	0.25	5.1	1.02
Palm forest															
4	A	0–34	4.50	7.6	0.47	<1	11.8	0.8	17.2	0.08	0.76	0.48	0.07	8.1	0.67
	Bt1	34–54	4.78	1.2	0.07	<1	8.9	0.6	9.5	0.02	1.09	0.98	0.08	22.8	1.12
	Bt2	54–83	4.89	0.5	0.01	<1	4.9	0.5	8.9	0.04	0.68	0.91	0.07	19.1	1.05
	BC	83–105	4.83	0.5	0.02	<1	5.0	0.4	9.5	0.03	0.49	0.64	0.07	13.0	0.98
5	A1	0–10	4.45	3.2	0.22	<1	5.3	0.6	7.3	0.05	1.40	0.77	0.03	30.8	0.92
	A2	10–19	4.69	1.8	0.11	<1	4.0	0.3	4.5	0.02	0.78	0.58	0.01	31.0	1.00
	Bg	19–30	4.71	1.4	0.11	<1	2.8	0.3	3.8	0.02	0.54	0.48	<.01	27.3	1.15
	Bw1	30–43	4.76	1.0	0.07	<1	1.7	0.1	3.9	0.01	0.32	0.39	<.01	18.7	1.21
	Bw2	43–64	4.79	0.3	0.02	<1	3.0	0.1	5.4	0.02	0.19	0.32	0.04	10.5	1.17
	Bw3	64–81	4.78	0.2	0.01	<1	2.5	0.1	6.8	0.02	0.09	0.27	0.05	6.3	1.19
	Ab	81–109	4.37	0.2	0.02	<1	2.0	0.1	4.5	0.02	0.07	0.16	0.04	6.4	1.11
	Bwb	109+	4.74	0.2	<.01	<1	2.2	0.1	5.1	0.04	0.07	0.13	0.02	5.1	1.12
6	A	0–9	4.95	18.2	0.95	<1	15.5	6.2	40.2	0.77	18.2	3.29	0.41	56.2	0.50
	Bw	9–21	4.81	7.7	0.48	<1	12.9	2.4	24.3	0.10	6.17	1.21	0.13	31.3	0.50
	Ab1	21–40	4.77	10.9	0.59	<1	7.1	2.9	30.7	0.24	6.67	0.92	0.12	25.9	0.63
	Ab2	40–60	4.75	11.4	0.60	<1	6.2	1.8	31.5	0.16	6.17	0.95	0.08	23.4	0.48
	Ab3	60–98	4.65	13.6	0.58	<1	3.1	0.9	39.7	0.09	6.49	1.87	0.15	21.7	0.54
	Ab4	98–128	4.53	9.3	0.36	<1	5.8	1.3	31.1	0.06	5.48	1.52	0.18	23.3	0.58
7	Oi/ Oa	0–10	5.08	32.1	2.01	24.0	13.5	13.6	66.8	1.08	24.2	8.83	1.09	52.7	0.15
	Bw	10–32	5.12	10.7	0.66	2.0	3.8	0.4	26.7	0.09	0.30	0.31	0.20	3.4	0.50

Table 2. Continued.

Site no.	Horizon	Depth cm	pH 1:1	TOC	TN	Mehlich 3 extractable P	Cu	Zn	CEC	Extractable cations K	Ca	Mg	Na	BS %	Bulk density g cm^{-3}
				%		mg kg^{-1}			cmol kg^{-1}						
	Ab	32–53	5.05	11.6	0.70	3.0	3.2	0.3	27.1	0.07	0.22	0.26	0.17	2.6	0.64
	Bgb	53–85	5.17	5.0	0.24	7.0	3.3	0.5	16.2	0.02	0.07	0.07	0.10	1.6	0.79
	BCb	85–101	5.18	4.0	0.18	8.0	3.8	0.7	13.6	0.02	0.07	0.04	0.08	1.5	0.81
	C	101–130	5.21	3.5	0.16	16.0	8.7	1.0	14.0	0.02	0.17	0.08	0.10	2.6	0.92
Palo colorado forest															
8	Oi	0–2	3.9	36.5	1.13	4.0	3.4	6.8	95.1	1.46	6.67	8.05	1.92	nd	0.02
	A1	0–21	4.40	6.2	0.31	<1	0.5	0.5	14.4	0.10	0.72	0.41	0.18	9.8	0.91
	A2	21–34	4.49	4.0	0.19	<1	0.2	0.1	6.3	0.03	0.06	0.08	0.07	3.8	0.91
	Btg	34–44	4.34	1.9	0.11	<1	0.1	0.1	3.7	0.01	0.01	0.03	0.04	2.4	1.07
	Bt1	44–72	4.30	1.2	0.12	<1	0.1	0.1	3.2	0.01	0.01	0.02	0.02	1.8	0.98
	Bt2	72–99	4.51	0.5	0.04	<1	0.1	0.1	4.1	0.02	0.01	0.03	0.03	2.2	1.34
	BC	99–122	4.72	0.4	0.03	<1	0.1	0.1	3.7	0.02	0.01	0.02	0.05	2.7	1.34
9	Oi	0–1	5.29	41.3	1.47	42	6.0	34.4	73.7	1.29	36.4	16.2	0.65	74.0	0.15
	A	1–5	4.14	8.5	0.58	<1	2.4	1.8	28.6	0.22	2.74	2.77	0.26	20.9	0.68
	BA	5–24	4.31	4.0	0.32	<1	2.5	0.5	14.9	0.07	0.32	1.29	0.13	12.1	0.84
	Bw1	24–51	4.35	3.2	0.25	<1	2.7	0.5	12.6	0.06	0.22	0.73	0.08	8.6	0.93
	Bw2	51–67	4.25	1.5	0.12	<1	2.7	0.3	11.6	0.03	0.11	0.59	0.13	7.4	0.96
	BC	67–10	4.23	0.9	0.06	<1	2.7	0.5	13.4	0.02	0.10	0.62	0.13	6.5	0.92
10	Oi	0–1	4.30	37.0	0.92	4	2.3	6.0	64.5	0.72	22.5	8.10	0.63	49.5	0.16
	A	1–15	4.00	8.5	0.47	<1	0.2	0.7	26.7	0.12	2.13	1.09	0.17	12.8	0.61
	BA	15–26	3.97	3.4	0.22	<1	0.9	0.3	13.6	0.05	0.30	0.30	0.05	5.1	0.91
	Bw1	26–47	3.87	1.9	0.15	<1	0.9	0.2	9.4	0.03	0.09	0.23	<.01	3.8	0.94
	Bw2	47–73	4.05	1.1	0.06	<1	1.3	0.1	12.2	0.01	0.02	0.23	0.02	2.3	0.89
	Bw3	73–95	3.91	1.0	0.06	<1	1.4	<.1	12.7	0.01	0.01	0.24	<.01	2.1	0.81
	BC	95–115	3.83	0.5	0.03	<1	1.4	<.1	25.1	0.01	0.01	0.23	0.02	1.1	1.11
Tabonuco forest															
11	A	0–13	4.53	9.5	0.55	<1	2.7	1.8	28.6	0.26	1.57	1.81	0.60	14.8	0.74
	Bw1	13–28	4.75	3.5	0.23	<1	1.6	0.4	15.2	0.06	0.09	0.50	0.26	6.0	1.11
	Bw2	28–47	4.80	2.5	0.17	<1	1.2	0.2	13.2	0.04	0.05	0.59	0.28	7.3	1.15
	Bw3	47–62	4.89	1.9	0.13	<1	1.3	0.2	12.6	0.03	0.05	0.51	0.23	6.5	1.11
	BC	62–86	5.14	0.9	0.09	<1	0.9	0.1	9.9	0.01	0.02	0.54	0.31	8.9	0.97
	C	86–130	5.19	0.7	0.05	<1	0.8	0.1	6.7	0.01	0.02	0.46	0.35	12.5	0.94
12	A1	0–16	4.29	7.3	0.53	<1	2.7	1.9	23.9	0.18	2.84	2.46	0.15	23.5	0.58
	A2	16–26	4.37	4.0	0.30	<1	1.9	0.7	17.9	0.07	1.04	1.62	0.13	16.0	0.83
	BA	26–39	4.53	2.2	0.16	<1	1.6	0.4	12.2	0.03	0.41	0.88	0.08	11.5	0.95
	Bw1	39–70	4.43	1.8	0.14	<1	1.5	0.2	11.7	0.02	0.12	0.69	0.06	7.6	0.99
	Bw2	70–91	4.49	0.9	0.07	<1	1.7	0.1	11.1	0.01	0.04	0.54	0.04	5.7	0.94
	BCr	91–110	4.61	0.5	0.04	<1	0.7	0.1	11.5	0.01	0.02	0.41	0.05	4.3	1.05

Table 2. Continued.

Site no.	Horizon	Depth cm	pH 1:1	TOC	TN	Mehlich 3 extractable P	Cu	Zn	CEC	Extractable cations K	Ca	Mg	Na	BS %	Bulk density g cm^{-3}
				%		mg kg^{-1}			cmol kg^{-1}						
13	A	0–10	5.33	5.4	0.33	<1	13.2	6.6	25.8	0.29	13.0	6.87	0.33	79.6	0.76
	BA	10–31	4.85	0.9	0.08	<1	6.5	3.9	16.0	0.06	1.04	4.36	0.25	35.7	0.94
	Bw1	31–64	4.78	0.2	<0.01	<1	8.4	1.7	9.9	0.04	0.25	2.05	0.25	26.2	1.05
	Bw2	64–87	4.87	0.9	0.05	<1	6.3	1.7	9.5	0.03	0.04	1.84	0.23	22.5	0.90
	BC	87–100	4.74	0.7	0.03	<1	5.6	1.2	10.9	0.02	0.02	1.31	0.30	15.1	1.06
Lowland moist forest															
14	Oe/Oi	0–4	5.12	25.8	1.39	28	4.5	18.8	59.8	1.53	38.9	8.83	0.27	82.8	0.24
	A	4–36	4.29	1.9	0.16	<1	4.0	1.1	8.4	0.05	1.20	0.54	0.01	21.4	0.92
	Bw	36–73	4.35	0.6	0.04	<1	3.7	0.5	5.0	0.02	0.82	0.74	<0.01	31.8	0.75
	BC	73–100	4.34	0.4	0.05	<1	3.4	0.2	4.7	0.02	0.39	1.02	0.03	31.1	0.87
15	Oi	0–1	5.55	32.4	1.77	53	6.4	20.4	68.1	1.62	54.80	12.7	0.27	100	0.14
	A	1–20	5.18	3.4	0.33	1	5.4	6.3	16.1	0.25	7.26	2.48	0.03	62.2	0.90
	AB	20–31	4.43	0.7	0.09	<1	3.4	1.5	8.0	0.09	2.58	1.38	<0.01	25.7	1.05
	Bw1	31–52	4.40	0.2	0.04	<1	2.7	0.4	10.2	0.06	1.67	1.14	<0.01	18.4	1.10
	Bw2	52–90	4.28	0.2	0.02	<1	2.6	0.1	11.1	0.05	1.40	1.07	0.02	22.9	1.10
Lowland moist forest															
16	A1	0–5	5.84	5.2	0.42	2.0	7.3	3.2	23.9	0.17	15.8	3.85	0.31	84.2	1.41
	A2	5–18	5.20	1.8	0.18	<1	6.1	1.1	15.0	0.05	5.87	2.60	0.26	58.5	1.41
	Bt1	18–42	4.55	0.8	0.10	<1	4.4	0.8	18.1	0.07	5.05	3.25	0.41	48.5	1.42
	Bt2	42–56	4.42	0.5	0.06	<1	4.2	1.1	19.9	0.09	4.86	3.25	0.55	44.0	1.44
	Btg1	56–94	4.45	0.5	0.07	<1	3.9	1.4	20.6	0.08	4.97	3.17	0.63	43.0	1.41
	Btg2	94–105	4.35	0.3	0.03	<1	3.9	3.4	23.4	0.13	9.75	3.62	1.07	62.3	nd
Dry forest															
17	A	0–19	6.74	3.37	0.26	<1	6.8	1.1	33.9	0.25	15.5	12.51	1.26	87.1	1.53
	AB	19–35	5.50	1.02	0.11	<1	4.8	0.4	35.6	0.23	4.85	18.00	5.88	81.3	1.74
	Bt1	35–57	6.12	0.58	0.06	<1	2.8	0.3	39.3	0.27	5.39	21.20	11.8	98.4	1.62
	Bt2	57–73	5.95	0.50	0.05	<1	2.9	0.4	35.5	0.25	4.43	18.82	11.6	98.8	1.73
	Bt3	73–98	6.59	0.34	0.01	<1	3.2	0.3	50.3	0.29	7.0	23.80	20.0	100	1.50
	BC	98–111	6.88	0.61	0.06	<1	5.6	0.4	52.1	0.24	7.5	24.28	18.9	100	1.54
	Crt	111–125	6.92	0.23	0.01	<1	2.5	0.2	56.0	0.23	7.5	23.09	22.7	94.6	1.54
Pterocarpus swamp															
	Oi	0–7	5.75	45.8	2.68	10.0	1.8	12.4	147	0.40	110	18.23	5.22	90.0	0.02
18	Oa	7–22	6.03	26.1	1.83	7.0	7.9	7.9	100	1.09	68.0	14.11	4.38	87.5	0.22
	Bg1	22–45	5.68	16.3	1.07	5.0	11.5	2.7	69.1	0.98	32.4	16.73	9.93	86.8	0.41
	Bg2	45–65	5.71	9.4	0.51	8.0	22.9	3.5	53.0	1.22	19.6	18.01	19.9	100	0.62
	Bwb	65–85	5.56	16.1	0.74	8.0	12.5	3.8	64.4	1.22	26.2	24.05	28.0	100	0.41
	Oa1	85–105	4.52	19.2	0.58	<1	<1	11.1	71.0	1.20	27.9	23.69	35.4	100	0.35

Table 2. Continued.

Site no.	Hori- zon	Depth cm	pH 1:1	TOC	TN	Mehlich 3 extractable P	Cu	Zn	CEC	Extractable cations K	Ca	Mg	Na	BS %	Bulk density g cm^{-3}
				%		mg kg^{-1}			cmol kg^{-1}						
	Oa2	105–130	4.78	17.4	0.59	<1	0.1	9.9	64.0	1.35	28.3	22.64	36.6	100	0.39
	Oa3	130–160	5.15	12.3	0.33	1.0	0.2	3.2	55.9	1.63	25.5	22.80	33.8	100	0.31
Mangrove															
	Oa1	0–50	6.64	13.7	0.69	10.0	14.4	5.0	66.5	2.23	24.1	30.46	36.8	100	0.40
19	Oa2	50–76	6.05	13.1	0.49	9.0	16.8	5.2	56.7	2.17	19.2	30.55	60.1	100	0.40
	Oa3	76–100	5.21	21.6	0.54	1.0	0.7	5.1	78.4	2.98	30.4	49.74	108	100	0.40
	Oa4	100–125	5.67	16.9	0.58	2.0	9.6	4.6	66.1	3.37	29.0	51.59	119	100	0.40
	Oa5	125–155	4.24	26.4	0.74	5.0	4.4	8.6	74.0	1.20	32.8	12.46	28.0	100	0.50

forest carbon contents were only 2–3% (Table 2). Generally there is a sharp decrease of C and N with depth except for variations found in the sites associated with slump activity. Sites 6, 7, 8, and 12 had higher spikes in C content at depth due to slump or colluvial action while sites 5, 16, and 18 exhibit similar spikes due to alluvium deposition (Fig. 4). On an area basis, soil profiles at high elevation sites in elfin and sierra palm forests, stored the highest average amount of carbon at 26 kg C m^{-2}, followed by 16 kg C m^{-2} in the mid elevation sites under palo colorado and tabonuco forests and then 12 kg C m^{-2} in the lowland moist forest and dry forest. These carbon store values are comparable to that of Delaney et al. (1997), Post et al. (1982) and to that of Wang et al. (2002) at lower elevations. The discrepancy here is likely due to sampling depth. Our study followed the whole pedon sampling protocol to more than one meter depth where the roots reach, signaling a zone a maximum depth of biological influence of soil genesis whereas Wang et al. (2002) only sampled to 30 cm. They reasoned that most of the SCO stored in the upper part because the carbon stores decrease drastically with depth. By comparison with our data, the omitting of the depth beyond 30 cm can result in 15–20% underestimation of the total soil carbon. In addition, in sites like the sierra palm, there is considerable amount of soil carbon stored in depth below 30 cm due to landscape dynamics such as land slide and slumps. Carbon stores are exceptionally high (>90 kg C m^{-2}) in the swamp and mangrove sites due to the deep accumulation of organic matter which was largely preserved due to and the reducing conditions cause by high water table. Nitrogen content of soils closely followed C content and overall sites (R^2=0.88, $p<0.01$) with an overall average C:N ratio of 18 (Fig. 4, Table 2). The C:N ratio drops to 16 in soils with <10% C, mostly from deeper B-horizons and well developed A-horizons (R^2=0.93, $p<0.01$). Most variable are soils with C contents above 10% where overall C:N ratio increases to 19 (R^2=0.01). Upland sites N-storage ranged from 0.4 to 2.5 kg N m^{-2} and the coastal wetlands stored the highest at >4 kg N m^{-2}.

Generally, the C:N ratio decreases with depth, reflecting the more humified SOM incorporated into the subsoils whereas the less humified mostly particulate SOM remains on the soil surface. Such a trend is observed in most of the soils along the study gradient except those formed in colluvium or landslide materials (site 3–9). Using the whole pedon C and N stores, the C:N ratio for Ultisols averaged 15.6 (range 13.3–18.8), Inceptisols averaged 16.0 (range 9.3–23.0), Alfisols averaged 10.6 (9.2–11.9), and the poorly drained soils (Histosols and Aquic Inceptisols) averaged 23.7 (22.0–25.5). The C:N ratio in the litter layer showed a good relationship with elevation ranging from 44.2 in the highest site (site 1) to 23.6 in the lowland site (site 18) and representing 4 different vegetation communities on uplands (Table 3).

Available P levels were generally highest in surface O-horizons (4–53 mg kg^{-1}) and <1 mg kg^{-1} in underlying horizons of profile. The exceptions to this were site 7 that had a higher pH throughout the profile and the coastal wet sites 18 and 19, with the highest carbon and available P contents throughout the profiles (Table 2). Available Zn also tended to be highest in the surface O and A horizons and decrease with depth (Table 2) and overall samples were significantly correlated to soil C (R^2=0.59, $p<0.01$) indicating importance of bioaccumulation. Available Cu however was not significantly related to soil C (R^2=0.04).

Discussion

Soil characteristics and morphology

Soils under litter layers along this elevation transect generally lack an organic horizon but where present they are

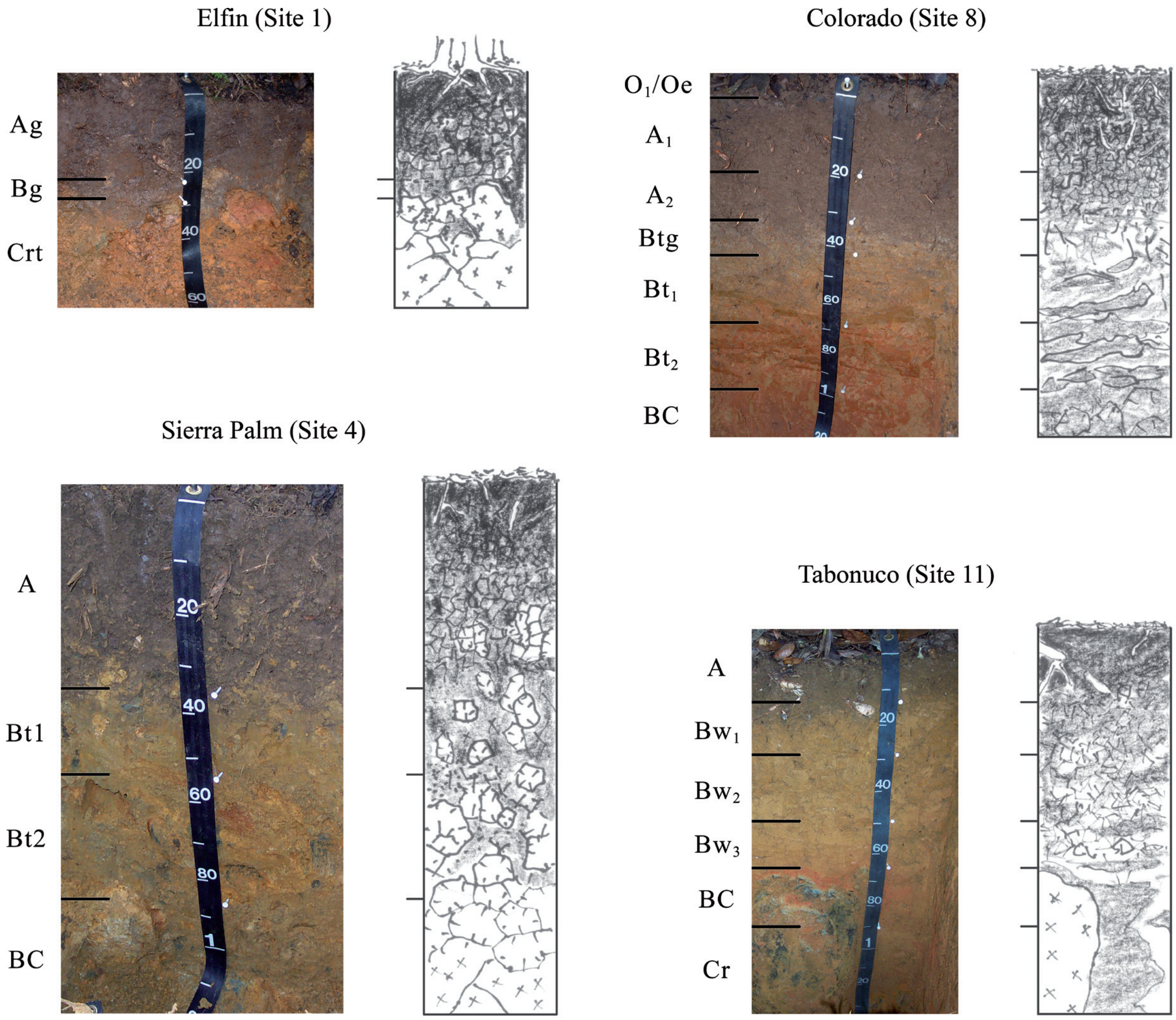

Figure 2. Photos and illustrations of soil profiles of study sites.

thin ranging from 1 to 10 cm (sites 2, 7, 8, 9, 10, 14 and 15). Wet lowland swamp and mangrove community sites had thicker organic horizons ranging from 22 to 150 cm (Table 2). Most upland sites however have well developed A-horizons which are characterized by a dark color suggesting the accumulation of humus associated with the mineral soil matrix as opposed to the accumulation of organic layers found commonly in cooler or more temperate climates (Fig. 2). Organic matter accumulation in these mineral A-horizons of the upland soils depends heavily on influx of litter-layer decomposition products and in situ accumulation of root decomposition products. Clay rich or Bt horizons are commonly found below the A-horizons in most Ultisols and Alfisols. But for Inceptisols only weakly altered Bw-horizons are developing at depth instead of Bt horizons. Site 19 is a Histosol in which the soil material is dominated by sapric organic matter. Soils in the elfin forest are poorly drained due to excess moisture even at slopes >30%, thus these soils have gleyed surface horizons designated as Ag and Bg-horizons. Such wetness in the upper part of the soils in the elfin forest appears to be caused by a moisture infiltration barrier at the interface between the A and the underlying Bt-horizons. The porous A-horizons hold more water than the underlying denser Bt-horizons (Supplementary material Appendix 1). The low bulk densities of the A-horizons are consistent with their being influenced by dust deposition as reported by Muhs et al. (1990, 2007) and Pett-Ridge et al. (2009). However, our study indicated that organic matter plays a stronger role in lowering the bulk density. Such horizons are also noted for other high elevation sites including the sierra palm forest and palo colorado forest (sites 4–10). Most soils in tabonuco, lowland moist and dry forests are well drained due to their landscape position, lower precipitation and lack

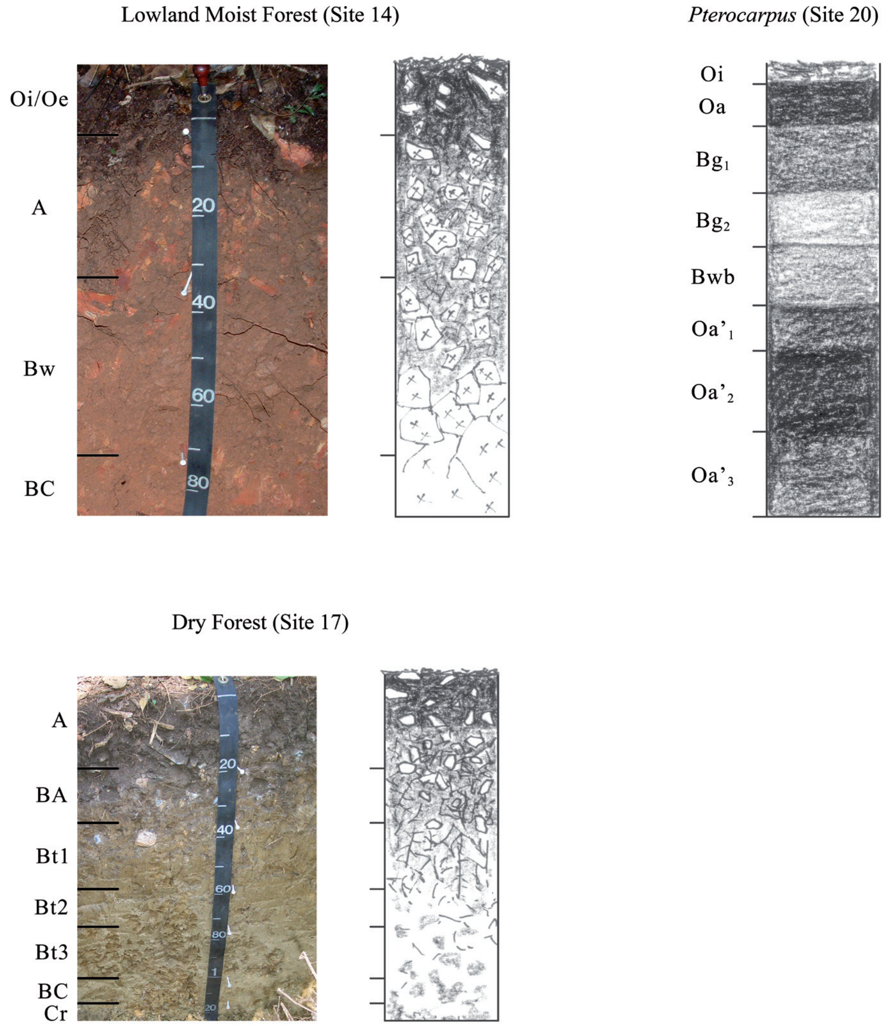

Figure 2. Continued.

of the restricting layer. Soils in the *Pterocarpus* swamp and mixed mangrove are very poorly drained due to the influence of continual or periodic inundation and flooding.

The effect of slope stability is reflected in the presence or absence of various soil horizons. On stable slopes, soils formed from the surface with the influence of biota and weathering strongest at the surface and resulted in soil horizon sequences of A, Bw or Bt, BC and C as reflected at most sites (Supplementary material Appendix 1 and Fig. 2). However, the effects of slump or slope failure is evident in most soils of the palm forest (sites 6, 7) as indicated by the buried horizons (a lower case 'b' following the master horizons, such as Ab, BwB, Btb, etc.), and spikes in carbon distribution at depth (Supplementary material Appendix 1, Table 2, Fig. 4). Across the elevation gradient there are several factors that are important to increased C storage. The formation of an A-horizon is important throughout the area. Also the burial preservation of C and N stores as a result of both slope movement and alluvial deposition is important on slopes and in floodplain positions, respectively. Formation of O-horizons is important to increased soil C and N stores mainly in the wet lowlands. As Wilcke et al. (2003) noted that the most obvious change in soil properties caused by landslides was the partial or complete removal of the organic layer and resulting in poor fertility in the slide area. Based on soils examined in this study, the deposition area of the slide certainly gained and affected preservation of organic matter and nutrients from slides.

Soil depth is controlled by bedrock. Along the mountain slopes the fine earth portion of most soils was limited to 130 cm before encountering weathered bedrock or saprolite, for a few sites the weathered bedrock is within 50 cm (site 1).

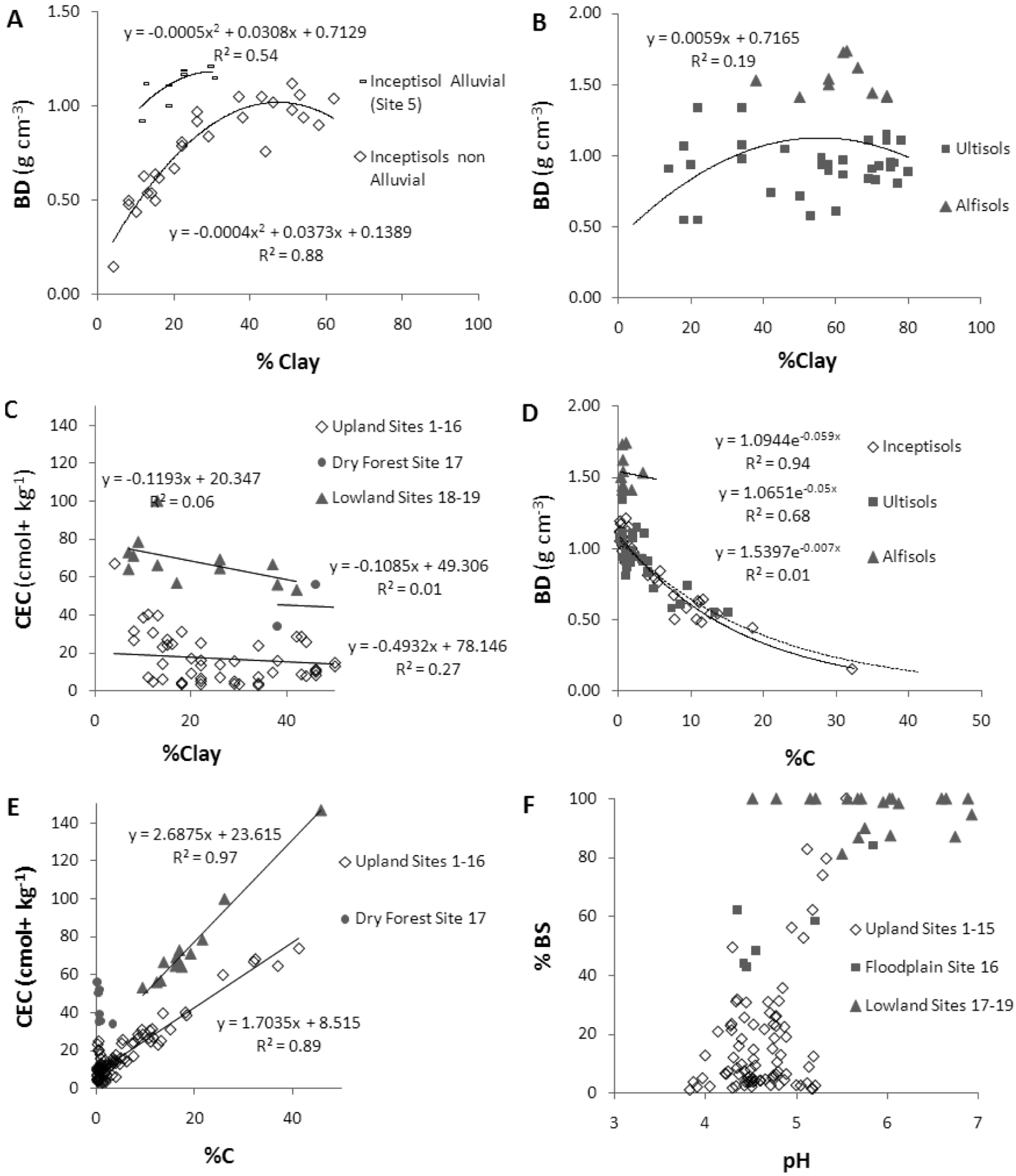

Figure 3. The relationships between (A, B) bulk density and clay, (C) CEC and clay, (D) bulk density and carbon, (E) CEC and carbon, and (F) base saturation and pH.

Patterns of carbon and nutrient distribution

As in many other tropical soils most carbon and nitrogen is stored in the surface or upper horizons (Delaney et al. 1997, Jobbágy and Jackson 2000, Mount and Lynn 2004). In this study carbon and nutrient distribution follow the general pattern of decrease with depth (Table 2). But there are three distinct variations on this main pat-

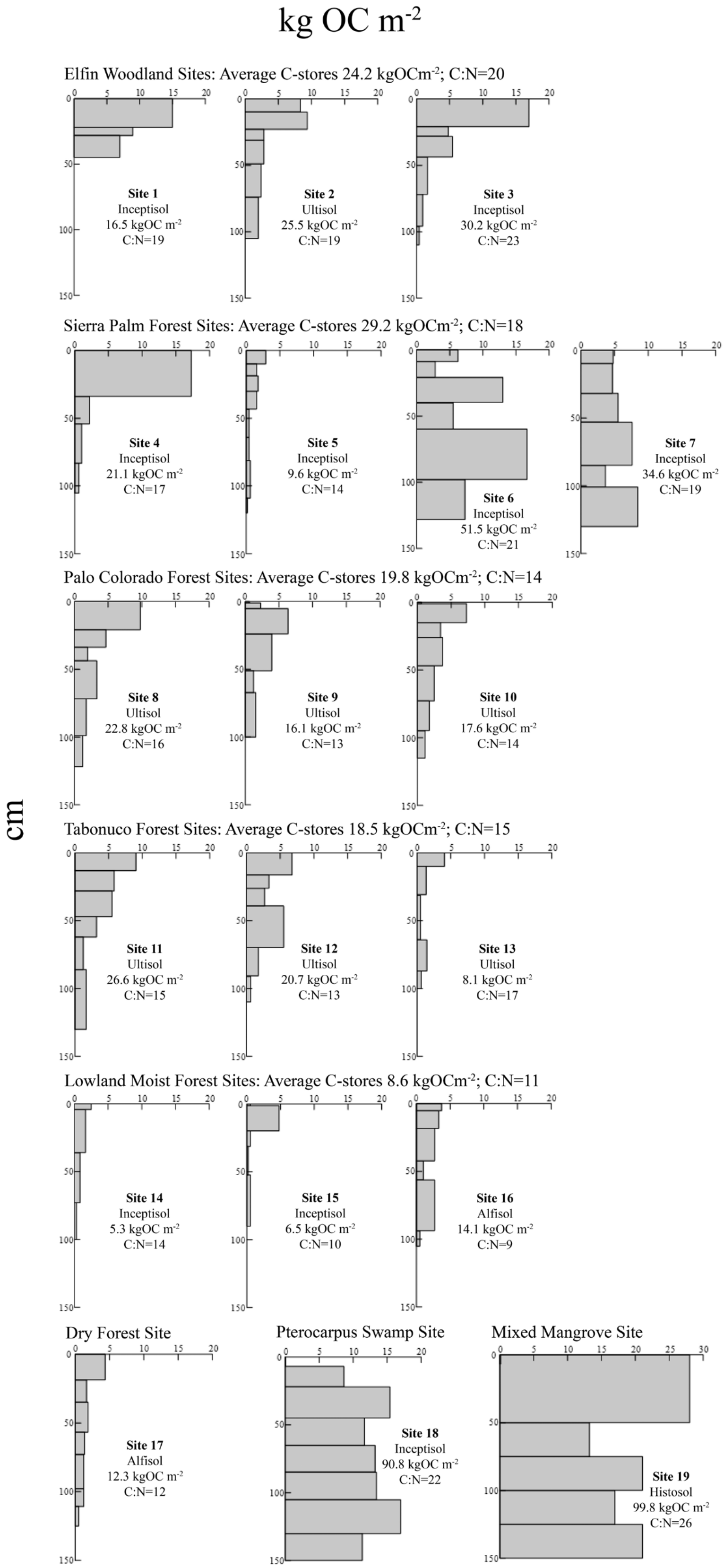

Figure 4. Bar diagram showing soil carbon stores, C:N ratio and carbon distribution in soils along an elevation gradient in eastern Puerto Rico.

Table 3. Nutrient contents of litters from selected sites in eastern Puerto Rico.

Site no.	pH	TOC	TN	C/N	Mehlich 3 extractable								
					P	K	Ca	Mg	Na	Cu	Zn	Mn	Fe
		%			mg kg^{-1}								
1	3.51	47.7	1.08	44.2	107	700	2800	1220	347	9	15	107	1120
11	3.85	44.7	1.15	38.7	135	743	4460	1250	444	8	15	466	384
16	5.71	26.0	0.97	26.8	131	461	10020	1434	171	8	9	405	1267
17	5.98	26.2	1.11	23.6	222	1212	7950	3021	519	9	11	479	1230

tern. In high elevations carbon contents are high in surface horizons, mainly the eolian A horizons formed from Saharan dust deposits, and then decrease drastically with depth in the underlying B horizons. In the middle elevations where the soils formed in uniform parent material, the carbon decreases with depth more gradually, an effect of the physical mixing of surface OC with deeper horizons due to slope processes. In the sierra palm sites (sites 6 and 7) and lowland wetland sites (sites 18 and 19) carbon contents are high throughout the profile but vary with depth due to the episodic nature of depositional processes. The distribution of total nitrogen and extractable cations basically follow the same trend and is apparently tied closely to the presence of organic matter (level of C present). Rainfall correlated well along the elevation gradient (R^2=0.84). However, only about 34 and 35% of the variation or increases in C stores can be explained by changes in rainfall and elevation, respectively. This points to the importance of landscape processes such as landslides, slumps and alluvial/fluvial activity in contributing to the variation in C stores across the uplands. The most striking example of this in the upland site 6 a slump block on a sideslope, with the highest C stores (52 kg C m^{-2}) much of which is in buried A-horizons at depth (Table 1 and Fig. 4). However keeping the variation in mind, the average carbon and nitrogen stores do follow an elevation gradient, decreasing from elfin woodland to dry forest demonstrating the effects of elevation driven-climate (rainfall and temperature) on C and N accumulation (Fig. 4). In most upland soils, the upper 50 cm holds >60% of the TOC with the exception of sites 6 and 7, sites that were heavily impacted by landslide or slump in that the surface organic carbon-rich layers were repeatedly buried (Fig. 4). The extremely low C stores of site 5 (palm forest) is likely due to the fact that the soil was formed in an old landslide scar in which the original carbon-rich surface horizons were stripped off and deposited below the site.

The carbon to nitrogen ratio (C:N) is commonly used as an indicator of organic matter quality. Delaney et al. (1997) found that the quality of carbon is highest in high mountain wet forest followed by lower mountain moist forest and dry forest. The quality of SOC is indicated by C:N ratio. The less decomposed or humified organic matter has a higher C:N ratio (15–20) and thus a more labile or more potential for decomposition. More highly humified SOM has a ratio between 10 and 12 and thus lower potential for further or rapid decomposition (Fig. 4). Aitkenhead and McDowell (2000) found that C:N ratio can be used to predict soil solution DOC concentration and riverine DOC flux. According to their study that there was very little or no DOC export once the C:N ratio reached below 12. Thus, in the soils along this elevation gradient, both Ultisols and Inceptisols with the exception of site 15, have the potential to export significant amounts of DOC to the rivers. The SOM in the Alfisols are highly humified and stabilized by divalent cations, mainly Ca^{2+} and Mg^{2+}, thus less likely to release DOC into the stream. The higher C:N ratio in the 2 wetland sites (18 and 19) indicated the incomplete decomposition of SOM due to the saturated and anaerobic conditions. It is also interesting to note the very high C:N ratio of the litter layers in the upland sites which are two to three times higher than that of the surface A horizons. This could be interpreted as an indicator of their potential for rapid SOC turnover.

Earthworms are an indicator of soil quality and soil biological activity. González et al. (2007) studied the earthworm communities along an elevation gradient in NE Puerto Rico, and they recorded the fresh weight of worms in study plots located near the plots of this study. The earthworm biomass measured 181, 28, 47, 49, 34, 1, 168 g m^{-2} and trace under elfin woodland, sierra palm, palo colorado, tabonuco, lowland moist, dry forests, *Pterocarpus* swamp and mangrove, respectively. There is a marked difference between the upland and the lowland but there is no apparent relationship with elevation in upland sites. Apparently site conditions and soil properties play the controlling roles. As they found that earthworm biomass is negatively correlated with pH and Ca^{2+}, but positively correlated with bulk density, water content and organic horizon thickness. Based on their study, the earthworm biomass is more closely related to soil moisture which in turn exerts control on soil pH and extractable Ca^{2+}. It is interesting to note the marked difference in earthworm biomass between the elfin forest (site 1–3) and the coastal wetlands (site 18). Besides the pH and Ca^{2+} content differences, the wetness in the elfin forest is caused by episaturation in which the water is from precipitation and soil saturation is perched on top of the denser subsoils. Excess soil water apparently, is moving along this interface following the slope gradient. Thus it is reasonable to assume that the saturated surface soil horizons are not totally depleted of oxygen as they could be in the lower swamp site. Silver et al. (1999) studied soil O_2 availability in soils of LEF and found it decreased significantly with increased rainfall, but among elfin woodland sites the O_2 availability was much higher on ridges than in the valleys. However in the coastal lowlands, the O_2 availability is very low due to prolonged saturation which resulted in a reducing environment. The low earthworm biomass in the palm forest is consistent with the instability of the landscape and burial of organic matter. The fertility of tropical forest is limited based on the extremely low available P in the mineral soils but some P maybe released and made available through the reduction of Fe (III) (Chacon et al. 2006). Detectable P is highest in the surface litter (Table 2) and organic horizon but generally not detectable in the underlying mineral soils. This indicates a rapid biocycling of P in the soil surface. Another explanation of this extremely low available P in the mineral soils is the high P fixing capacity of these highly weathered soils that have high iron oxide and hydroxide content (Jones et al. 1982) with high affinity for P (Chacon et al. 2006). The only upland soil with detectable P levels to depth was the palm site 7 where organic matter levels are elevated to depth as a result of slope burial indicating that slope movement can play an important role in P storage and availability as it does for C storage. This effect was however not evident at site 6 soils where soils were strongly acidic. In the lowland wet and swamp sites 18 and 19, the P levels were relatively high throughout the profiles as were the C levels, which is consistent with the importance of biocycling to P availability at these sites. The effects of biocycling are also demonstrated by the concentration of C, N, Zn and extractable cations in the A horizons.

Bulk density (BD)

Soil bulk density decreased with increases in soil organic matter as indicated by increased C content (Fig. 3D). The Alfisols (sites 16 and 17) have higher BD compared to the other soils due to their low OC content. For the Inceptisols of a non-alluvial origin, clay content increases in the range of about 0–30% corresponded to increased soil BD (Fig. 3A). The soils classified as Ultisol and Alfisol were similar and grouped with little correlation of BD to clay content (R^2=0.19). This wide range in soil BD at various clay contents further supports the role of OC controlling the BD.

Cation exchange capacity (CEC) and exchangable cations

It is apparent from the data that soil organic matter in the form of humus is primarily responsible for soil cation exchange capacity (CEC) across all these soils (Fig. 3E). However differences in the relative contribution of organic matter are evident from the distinct relationships of CEC as a function of %C obtained for upland versus lowland soils. Not only do the lowland soils have higher CEC than the upland soils but there also seems to be larger increase in CEC with increasing C contents. Although C contents were low for the dry forest site it seemed to fit better with the Upland soils than with those of the lowland. The higher CEC per unit C for the lowland soils is consistent with a more humified organic matter (lower C:N ratio) present in the lowland soils compared to the uplands. Organic matter inputs from different vegetation communities under different environments for decomposition with different nutrients available could also have a strong influence on the differing qualities of soil organic matter present. Clay content should also add to soil CEC but for these soils its influence is minimal relative to that from organic matter (Fig. 3C) as there was no significant relationship between CEC and clay content because the clay minerals are dominated by the low-activity (low exchange capacity) kaolinite. However, it is interesting to note that there is a discrepancy between the field texture and the particle size distribution analysis by the hydrometer method in the laboratory. The lab methods measured considerable less clay especially in most surface horizons (Supplementary material Appendix 1). The highly weathered tropical soils contain appreciable amounts of iron hydroxides (Jones et al. 1982, Mount and Lynn 2004) and these compounds experience irreversible dispersion upon drying at 60°C as required by the hydrometer method. Ping et al. (1989) found similar results in highly weathered volcanic-ash derived soils in southeast Alaska. These soils contain large amount of short range clay minerals and iron hydroxides and the field texture tested mostly silt loam but the hydrometer method only measured loamy sand or sand due to the irreversible drying of these minerals. Such a discrepancy warrants the development of different protocols in soil sampling and laboratory procedures for these highly weathered soils. Better methodology for the dispersion of clays could reveal a stronger relationship for clay with CEC especially among the Bw and Bt horizons but overall organic matter (indicated by C content) seems dominant. Therefore, organic matter very likely provided most of the exchange sites, increased soil porosity and lowered bulk density. Among the soils studied, the highly weathered Ultisols had the lowest CEC, generally <15 cmol kg^{-1} in the Bt horizons even though their clay contents are >50%. This is characteristics of Ultisols and some of the Inceptisols (sites 1–5 and 8–16) in which the clay minerals are dominated by kaolinite that has low exchange capacity (Jones et al. 1982, Mount and

Lynn 2004). Thus in these soils clay content can be expected to have little effect on CEC as seen in Fig. 3C. The CEC in the subsurface horizons in sites 6 and 7 have CEC >20 but <35 cmol kg^{-1} due to soil mixing from landslides and slump. Site 16 is an Alfisol because it base saturation is >35% even though its CEC is very low (<20%) and with its high clay content (70–74%). In site 17 the CEC of the B horizons averaged >40 cmol kg^{-1} due to its andesitic parent material which has mixed mineralogy and is rich in bases, thus it is also an Alfisol. In the very poorly drained lowland sites (18 and 19) the high CEC is likely caused by high organic carbon contents (Fig. 3E).

Exchangeable cations (Ca^{2+}, Mg^{2+}, K^+, and Na^+) were highest in the surface O and A horizons an indication of the biocycling in these horizons with higher organic matter and CEC. The concentrations of these cations decreased sharply with depth and with carbon distribution. In all upland soils, the exchange complexes of the Ultisols, Inceptisols and Alfisols were dominated by Ca^{2+} and Mg^{2+}, although there were different patterns. In most of the upland sites with parent material derived from granodiorite, the ratio of Ca:Mg ranged from 2:1 to 1:1 in upper mineral horizons and <1:1 in lower mineral horizons. In the sites formed in slump (site 6, 7) and alluvium (site 16), the ratio of Ca:Mg in the mineral horizons raised to 5:1 then falls to nearly 1:1 at depth suggesting the effect of soil mixing that fresher parent material exposed. In the dry forest site (17), the Ca:Mg ratio 1:3 indicates of excess Mg^{2+}. This soil also has high exchangeable Na^+, likely due to the andesitic parent material and additions from the sea spray and precipitation. The ratio of Ca:Mg in the very poorly drained sites (18 and 19) varied widely, likely due to depositional processes and the influence of sea water. The Na^+ content of the *Pterocarpus* swamp (site 18) was lower than that of the mixed mangrove (site 19) especially in the upper soil profile. This is consistent with the findings of Medina et al. (2007) who found that *Pterocarpus* occupied less saline coastal sites compared to mangrove communities. Both K^+ and Na^+ are easily leached from the soil in areas with high rainfall, such as that found in the Luquillo Mountains. Sodium ion is usually more mobile than K^+, but Na^+ concentrations were always higher than K^+ in most of the upland soil samples. This can be explained by the effect of high Na^+ concentrations in precipitation derived from sea salt aerosols (Johnston 1992, Asbury et al. 1994, Gioda et al. 2006, Reyes-Rodríguez et al. 2009).

pH and base saturation

The relationship between pH and base saturation (BS) is shown in Fig. 3F. Upland soils (sites 1–15) that include both Inceptisols and some Ultisols having BS ranged from 1 to 100%. The less leached Inceptisols were able to retain >50% of its exchangeable cations as bases and had a pH of about 5.2. The upland floodplain soil (Alfisol: site 16) had intermediate BS ranging from 43 to 84% along with an intermediate pH ranging from 4.4 to 5.8. Lowland soils (sites 17–19) included an Alfisol, Inceptisol and Histosol, had high BS ranging from 81 to 100% but with wide ranging pH values from 4.5 to 6.8. The low pH-high %BS soils were due to the influence of organic acids in the buried O-horizons of the Inceptisol (site 18). The general pattern for this elevation gradient is that both pH and BS increase from the upland soils to the lowland soils. This is consistent with the uplands releasing organic acids that result from organic matter decomposition, these acids promote weathering release of bases from primary minerals but these bases under higher rainfall are subject to loss resulting in low base saturation in soils. The released and leached base cations move downslope and accumulate in the lowlands increasing base saturation of these soils.

Conclusions

Despite the strong indications of biocycling in determining soil characteristics along the elevation gradient in eastern Puerto Rico, soils differed greatly with the variation of rainfall and parent materials. In higher elevations, the soil had lower bulk density and a silty texture in the surface horizon that overlies more dense subsoil with higher clay contents. We attribute such textural discontinuity to reported eolian deposit of Sahara dust, which changes the composition and characteristics of the mineral fraction in the surface horizon relative to those below it. The textural discontinuity retards water infiltration across the interface due to decreased conductivity in the clayey subsoil, restricting internal soil drainage. Adiabatic cooling associated with increasing elevation results in greater precipitation, which with cooler temperature, enhance accumulation of humus (total carbon) in the surface horizons of the upper forest types. However landscape processes in the uplands such as landslides, slumping and fluvial/alluvial activity contributed significant variation in this relationship and must be considered when estimating C and nutrient stores over the landscape. Keeping the variation in mind the C stores of this area of Puerto Rico fit well with the averages for similar life-zones reported by others. There is strong evidence of leaching of cations especially in the uplands with depletion of cations in the mineral horizons and movement and deposition of cations in the lowlands. The result is that soil acidity increases with increasing elevation where soil pH is usually <4.8. In soils with high clay contents such as the Ultisols, clay has little influence on soil's ability to retain nutrients because of the predominance of kaolinite in the clay fraction (Jones et al. 1982). Thus it was not surprising that soil carbon played an overriding role in affecting soil properties such as CEC and bulk density. Because of the geographic location, soils in the Luquillo Mountains area receive Na^+ addition from both marine sources via precipitation and Saharan dust. The freshwater swamp and the mangrove sites favor accumulation of organic matter and soluble salts due to their landscape position. These lowland wetlands in the subtropical region serve as important carbon sinks while slope movement serves to enhance carbon stores on upland slopes.

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Supplementary material (Appendix EB54_10 at <www.oikosoffice.lu.se/appendix>). Appendix 1.