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Clay and climate are poor predictors of regional-scale soil carbon storage in the US Caribbean

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ABSTRACT

Soils of the tropics play an important role in the global carbon (C) cycle as substrates for the most productive terrestrial ecosystems and as large C reservoirs. The amount of C stored in a soil is affected by soil properties such as texture, pH, and mineralogy, as well as climate, vegetation and land management, yet, uncertainty remains regarding the relative importance of these variables at different spatial scales. The goal of this study was to explore the factors influencing regional patterns in soil C storage. Soils were collected from 36 sites under four land cover types (forests, pastures, croplands and wetlands) and on 30 soil series in seven soil orders, representing the diversity in soil forming factors and major non-urban landscapes in Puerto Rico and the US Virgin Islands. Soils were analyzed at three depths, 0–30 cm, 30–100 cm, and 0–100 cm, for total carbon (TC), soil organic carbon (SOC), and total nitrogen (N). Traditional predictors of soil C storage such as clay content and climate were not sufficient to accurately capture regional soil C trends. The combination of clay plus fine silt was positively correlated with SOC stocks but explained a relatively small amount of the variation. Site temperature and mean annual precipitation were not correlated with SOC stocks. Soil order and land cover were weak predictors of SOC for a subset of data where forests and pastures were found on three of the same soil orders, allowing for a two-way ANOVA. Soil N showed similar trends as SOC. Patterns observed depended on the soil depth studied, reflecting relative differences in the strength of top-down and bottom-up factors influencing SOC and N storage. These findings suggest that mechanisms not described by the distribution of soil particle sizes need to be considered for better predictions of SOC dynamics. In a geologically diverse region, soil properties were better predictors of SOC than climate or land cover. Tropical regions represent a diversity of soil types yet parent material and soil physical properties other than texture are not currently included in most biogeochemical models attempting to predict the response of tropical soil C pools to environmental change. Recognition of the heterogeneity of geologic substrates and weathering gradients in tropical regions and incorporation of a more mechanistic understanding can improve soil C modeling and land management decisions.

1. Introduction

Soils of the tropics contain between 30% and 40% of the global soil C reservoir (Carvalhais et al., 2014; Jobbágy and Jackson, 2000); hence, even small changes in the tropical soil C budget could have important implications for global climate change. Soil C and nitrogen (N) also directly affect nutrient availability and soil fertility as components of soil organic matter (SOM). Despite the importance of soil C and N, the factors controlling their storage at local to global scales are challenging to predict. Human land use and site-specific factors, including climate, soil properties, and N availability, can affect soil C storage (Brown and Lugo, 1990; Jobbágy and Jackson, 2000; Li et al., 2012; Marín-Spiotta and Sharma, 2013). Interactions at multiple scales are also possible among these factors, complicating efforts to estimate soil C stocks, either for accounting purposes, or to predict responses to changes in land use and climate.

Soil organic C storage is determined by the balance of organic matter inputs and losses, so it can be affected by any variable that influences these processes. At the global scale, climate is a strong predictor of soil C through its controls on plant productivity and decomposition (Jobbágy and Jackson, 2000; Wiesmeier et al., 2019). At the millimeter scale, clay particle mineralogy and aggregate formation influences the protection of organic matter from decomposition (Mikutta et al., 2006; Rasmussen et al., 2005; Six et al., 2002; Torn et al., 1997).

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At intermediate scales, topography, soil moisture and plant communities can influence soil C accumulation and loss (Davidson and Lefebvre, 1993; Jenny, 1941; Torn et al., 2009). There is a need to better understand at which scales and under which conditions each of these variables is important, especially to inform modeling purposes.

Human activities, primarily through changes in land use and land cover (hereafter land change), can also be important drivers of soil C change through their influence on input rates and on microenvironmental conditions that affect decomposition and other loss mechanisms. Despite recognition of the role of land change, the direction and magnitude of soil C change is often unpredictable, especially for transitions between pasture and forest (Berthrong et al., 2012; Fisher et al., 1994; Fujisaki et al., 2015; Li et al., 2012; López-Ulloa et al., 2005; Marín-Spiotta et al., 2009; Neumann-Cosel et al., 2011; Post and Kwon, 2000; Powers et al., 2011). Responses of soil C to land change are dependent on a variety of factors that contribute to SOM persistence. For example, soil texture can influence the accumulation and loss of C from soils via its effects on soil moisture retention and its role in the formation of aggregates (Six et al., 2000, 1998) and mineral-organic associations (MOAs). MOAs can contain up to 90% of OM in a soil and are associated with longer soil C turnover times, assumedly because they reduce accessibility to decomposers (Kleber et al., 2015; von Lützow et al., 2006). Fine particles (clay and fine silt) are characterized by high specific surface area which can contribute to high ion exchange capacity and soils with fine textures are expected to store more C in MOAs than soils with lower clay content or coarser textures. Many studies have reported positive correlations between the amount of clay or clay and fine silt in a soil and its C content (Feller and Beare, 1997; López-Ulloa et al., 2005; Post and Kwon, 2000), and many biogeochemical models include clay content as a main predictor of soil C (Coleman and Jenkinson, 1996; Parton et al., 1993). However, given the wide range in mineralogy among clay-sized particles and subsequent reactivities, clay content may be less important in determining C storage than clay mineralogy (Six et al., 2002; Torn et al., 1997) or other physicochemical properties such as concentrations of calcium, and iron- and aluminum-oxyhydroxides (Rasmussen et al., 2018).

A further challenge to predicting soil C stocks at regional to continental scales is a strong geographic bias in the literature on soil C response to land change in the tropics (Powers et al., 2011). Wet tropical regions and soils that are highly weathered or contain large amounts of highly-reactive short-range-order minerals, such as allophane, have been over-studied relative to their global coverage. As a result, individual studies and meta-analyses may be biased towards specific soil types or precipitation regimes and not accurately capture differences among ecosystem types. The tropics exhibit substantial biophysical diversity (e.g., Townsend et al., 2008) and it is important to understand how soil C responds to land change across the range of biophysical factors.

The goal of our research was to determine the relative importance of soil properties and environmental factors on soil C and N storage at regional scales. We tested for the effects of soil texture, pH, land cover and climatic variables on soil C and N stocks down to 1 m or bedrock in the Caribbean islands of Puerto Rico and the U.S. Virgin Islands, where diverse topographies, climate, and geologic histories have created a range of soil environments representative of much of the global tropics. The diverse pedologic landscape of Puerto Rico is indicated by the presence of 10 of the 12 USDA soil orders (all but Gelisols and Andisols), and climates representing 6 Holdridge life zones from dry forests to wet montane forests. Soils have formed on a variety of substrates, including igneous rocks, limestone, sandstone, and marine and fluvial sediments.

We used samples collected across this pedological diversity as part of the U.S. Rapid Carbon Assessment (RaCA) of the U.S. Department of Agriculture Natural Resources Conservation Service (NRCS). First, we compared pasture and forest soils, two dominant tropical land cover types, stratified across three soil orders: Mollisols, Inceptisols and Oxisols. Then we used the broader dataset that includes 7 soil orders and four land cover types to build predictive models of soil C and N.

We hypothesized that of the soil orders, Mollisols would contain the greatest soil C stocks, and that forested sites would contain more soil C than pastures. We predicted that soils with greater clay contents and intermediate soil pH would have the greatest soil C stocks. Finally, we predicted that the wettest and coolest sites would store more soil C. This research builds on previous work in the Caribbean (Beinroth et al., 1996; Brown and Lugo, 1990) by contributing a wider range of soil taxonomy and climate, as well as analyzing trends in deeper soils, down to 1 m. A greater understanding of the importance of different factors controlling soil C storage at a regional scale is key for informing climate modeling efforts and land management decisions.

2. Methods

2.1. Site selection

Soil samples were collected in the Caribbean islands of Puerto Rico and the US Virgin Islands in collaboration with the USDA NRCS as part of a national soil carbon mapping effort following protocols of the Rapid Carbon Assessment (RaCA) (Soil Survey Staff and Loecke, 2016). Sampling sites were selected to be representative of the diversity of soils across the islands under five main land covers: forest, pasture, cropland, wetland, and rangeland. For each soil order and land use combination, a number of regionally important soil series were selected proportionate to the geographic extent of that soil order and land use. Sampling sites within each soil series were chosen randomly from a subset of accessible locations for a total of 30 sites (Fig. 1, Table 1). Rangeland and pastures were considered similar land uses and were combined into one pasture category for our analyses. To increase the sample size for Oxisols, which were underrepresented in the RaCA sampling, three additional pasture and forest sites each were included from an earlier study on a Puerto Rican pasture and forest chronosequence (Marín-Spiotta et al., 2009). These six sites will be referred to as the "Cayey" sites for certain analyses and interpretations and bring the full dataset to 36 sites (Fig. 1, Table 1).

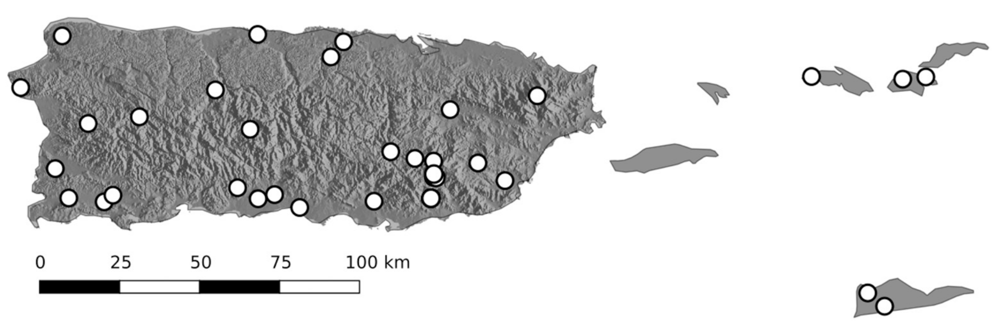

Fig. 1. Location of study sites in Puerto Rico and the US Virgin Islands.

Table 1
Site description and soil characteristics of 36 field sites used to identify regional predictors of soil carbon stocks across a diversity of parent materials in Puerto Rico and the U.S. Virgin Islands as part of the U.S. Natural Resources Conservation Service Rapid Carbon Assessment survey. The first set of field sites were included in the land cover (LC) × soil analyses, and the remaining sites were also included in the Full dataset for analyses of site environment (including mean annual precipitation (MAP), mean minimum temperature (Mean Min. Temp.) and mean maximum temperature (Mean Max. Temp.), soil texture and pH. Sites indicated with † were located in St. Croix, those with § were located in St. John, those with # were located in St. Thomas, and the rest were located in Puerto Rico. Soil series with an * were originally classified as "Rangeland" by the NRCS, but have been reclassified as pasture for our analyses.

Dataset	Site #	Soil Series	Soil Order	Soil Subgroup	Parent Material	Lat.	Long.	MAP (mm)	Mean Min. Temp. (C)	Mean Max. Temp. (C)
					LC × soil dataset					
Forest	1	Guayabota	Inceptisol	Typic Humaquepts	volcanic bedrock	18.30	−65.78	4064	18.0	24.6
	2	Pandura	Inceptisol	Dystric Eutrudepts	plutonic rocks	18.12	−65.95	2385	18.7	28.7
	3	Pellejas	Inceptisol	Typic Dystrudepts	plutonic rocks	18.21	−66.59	1814	16.3	27.3
	4	Southgate §	Inceptisol	Lithic Haplustepts	igneous bedrock	18.36	−64.69	1187	20.6	29.3
	5	Cintrona	Mollisol	Typic Calciaquolls	calcareous sediment	18.02	−66.57	887	21.0	31.3
	6	Soller	Mollisol	Typic Haprendolls	limestone	18.32	−66.69	2026	17.8	29.6
	7	Susannaberg §	Mollisol	Typic Haplustolls	basic volcanic rock	18.35	−64.76	1115	20.6	29.3
	8	Fredricksdal #	Mollisol	Lithic Haplustolls	igneous bedrock	18.36	−65.01	999	24.2	30.9
	9	Los Guineos	Oxisol	Humic Hapludox	sandstone	18.12	−66.08	2042	17.0	26.4
	10	Los Guineos	Oxisol	Humic Hapludox	sandstone	18.02	−66.08	1775	18.1	27.6
	11	Los Guineos	Oxisol	Humic Hapludox	sandstone	18.08	−66.07	1717	17.5	27.2
	12	Los Guineos	Oxisol	Humic Hapludox	sandstone	18.09	−66.08	1965	16.8	26.0
Pasture	13	Coloso	Inceptisol	Vertic Dystrudepts	alluvial sediments	18.27	−66.03	1597	18.8	30.1
	14	Malaya	Inceptisol	Typic Eutrudepts	calcareous tuffaceous rock	18.33	−67.24	1652	20.4	30.7
	15	Mucara	Inceptisol	Dystric Eutrudepts	basalt lava and breccia	18.15	−66.20	1395	18.2	28.6
	16	Victory †	Inceptisol	Typic Haplustepts	volcanic rock	17.75	−64.86	1216	24.1	30.3
	17	Callabo *	Inceptisol	Typic Dystrustepts	basic volcanic rock	18.05	−66.63	1324	19.9	30.5
	18	Bajura	Mollisol	Vertic Endoaquolls	mixed origin	18.10	−67.14	1379	18.4	32.1
	19	Toa	Mollisol	Fluventic Hapludolls	floodplain, mixed origin	18.13	−66.13	1417	18.0	28.0
	20	Sion †	Mollisol	Typic Calciustolls	alkaline marine deposits	17.71	−64.81	982	24.1	30.3
	21	Descalabrado *	Mollisol	Typic Haplustolls	mixed basic volcanic rock	18.01	−66.24	1046	20.8	30.6
	22	Coto	Oxisol	Typic Eutrustox	limestone	18.47	−67.12	1418	20.9	29.5
	23	Los Guineos	Oxisol	Humic Hapludox	sandstone	18.08	−66.08	1802	17.0	26.5
	24	Los Guineos	Oxisol	Humic Hapludox	sandstone	18.02	−66.08	1775	18.1	27.6
	25	Los Guineos	Oxisol	Humic Hapludox	sandstone	18.02	−66.08	1775	18.1	27.6
Full dataset										
Forest	26	Humatas	Ultisol	Typic Haplohumults	basic igneous	18.23	−67.05	2163	17.9	29.5
Pasture	27	Guanica	Vertisol	Typic Calciaquerts	alluvial sediments	18.03	−66.98	767	19.7	31.7
Crop	28	Talante	Entisol	Aeric Fluvaquents	floodplain, granitic regolith	18.07	−65.88	2025	21.4	30.1
	29	Caguabo	Inceptisol	Typic Eutrudepts	basalt	18.25	−66.90	1888	18.4	31.2
	30	Constancia	Mollisol	Aeric Calciaquolls	limestone and volcanic	17.99	−66.45	765	21.0	31.3
	31	Espinosa	Ultisol	Typic Kandiudults	mixed origin	18.41	−66.36	1703	20.3	30.2
	32	Fraternidad	Vertisol	Typic Haplusterts	volcanic rock and limestone	18.03	−66.52	924	21.0	31.2
Wetland	33	Jareales	Entisol	Thapto-Histic Fluvaquents	organic, mixed	18.48	−66.57	1375	20.4	30.8
	34	Vigia	Histosol	Terric Haplosaprists	organic	18.46	−66.33	1643	20.9	30.4
	35	Aguirre	Vertisol	Sodic Haplusterts	marine deposits/limestone	18.01	−67.01	768	20.0	31.7
	36	Teresa	Vertisol	Sodic Haplusterts	marine sediments	18.02	−67.10	1126	19.2	31.5

2.2. Sample collection

At each site, five pits were dug in a clustered or chain design, with 30 m distance in between each pit, following standard RaCA protocols (Soil Survey Staff and Loecke, 2016). Each pit was dug down to 1 m, or to bedrock, whichever came first. The central pit was described in detail, with field measurements of soil pH, texture by hand, presence of carbonates, and soil structure. Deviations from the central pit were noted for the four additional pits. One soil sample was collected per horizon per pit down to 100 cm depth, except for the top A horizon. For the A horizons, one sample was taken from 0 to 5 cm and from 5 cm to the bottom of the A horizon. Samples for bulk density calculations were collected using a 10 cm × 10 cm × 5 cm scoop from the top 0–5 cm of every soil profile. A 7-cm diameter core was used for all other horizons with an upper depth of < 50 cm. Horizons with an upper depth of > 50 cm were collected using a bucket soil auger. Samples were air dried in the NRCS office in Mayagüez and shipped to the University of Wisconsin – Madison for processing and analysis.

2.3. Soil properties

Air-dried soils were sieved to 2 mm. Bulk density was measured for all samples with an upper depth shallower than 50 cm. Soil bulk density values were calculated after subtracting the mass and volume of rocks and roots from the total sample mass and volume. Mineral soil horizons that were not measured for bulk density were assumed to have the same bulk density as the horizon immediately above it. Particle size was analyzed for every horizon of one pit per site, using laser diffraction on a Malvern Mastersizer 2000. Approximately 0.5 mg of sieved soils were lightly ground by hand using a mortar and pestle and aggregates were dispersed using 10 mL of 50 g/L sodium hexametaphosphate and sonication until particle size readings stabilized. In a few cases, the particle size fractions did not stabilize, and the reading with the largest clay fraction was used, as it was assumed that very small clay particles were being missed by the laser (sensu Mason et al., 2011). Soil pH was measured on all samples on a 1:2 slurry of soil in deionized water after a 30-min equilibration period (Robertson et al., 1999). Two pH measurements were taken roughly 5 min apart and repeated until measurements were consistently within 0.1 unit. Values reported are analytical averages.

Soil parent material was determined using the NRCS official soil series descriptions and categorized to enable statistical analysis (Table S1). The categories were defined as "igneous" (any parent material containing "volcanic", "igneous", "basalt" etc.), "sedimentary" (any parent material containing "sandstone", "sediment", etc. but omitting "limestone"), "calcareous" (any parent material containing "calcareous" or "limestone"), and "organic" (any parent material containing "organic"). Similarly, we used categories to characterize clay mineralogy based on the NRCS description of clay activity. Given the many categories used and unequal representation in our dataset, we attempted to simplify the analysis by reducing the number of categories to "high" or "low" activity (Table S2). Soils that were classified by the NRCS as "active", "carbonatic", "euic", "smectitic", "superactive", or "vermiculitic" were categorized by us as high activity soils. Soils that were classified by the NRCS as "kaolinitic", "mixed", "parasesquic", or "subactive" were categorized by us as low activity soils.

2.4. Soil C and N analysis

A subsample of soil from each sample was pulverized in a SpexMill 8000D for analysis of total C (TC) and total N (TN) concentrations on a Flash 2000 Elemental Analyzer. All samples were run in duplicate with replicate error of < 10% and aspartic acid as a standard and both aspartic acid and soil reference material as a check standard. Samples that tested positive for the presence of inorganic carbon (Nelson and Sommers, 1996) were acid fumigated for at least 12 h (Harris et al., 2001). A random sample of soils was re-tested for the presence of carbonates following fumigation to verify complete carbonate removal. The fumigated samples were run on the elemental analyzer and the remaining C is taken to represent organic C (OC). Soil TC, OC, and N stocks (Mg/ha) were calculated using moisture-corrected C and N concentrations and bulk density values for each horizon.

Because soils were sampled by horizon, there was substantial variability in horizon presence/absence and thickness among pits. To allow for comparisons of stocks at standardized depths, soil profiles were divided and aggregated into a "shallow" 0–30 cm portion and a "deep" 30–100 cm portion. Soil pits that were shallower than 100 cm were aggregated as above, but to their actual depth. Pits that were shallower than 30 cm were aggregated to their actual depth. The profiles were also divided into 10 cm slices for more detailed visualization of trends C, N, and C:N ratios with depth. Division of the soil horizons into depth portions was accomplished using the "slice" and "slab" functions in the *aqp* package in R (Baudette and Roudier, 2015; R Core Team, 2016). Each horizon was first divided into identical 1 cm slices, and then aggregated using the 1 cm slices into the various depths. Soil properties for these aggregated depths were weighted by the relative contributions of each horizon within that depth. Soil bulk density by horizon did not differ by land cover or soil order, so stocks were not corrected using an equivalent soil mass (Ellert and Bettany, 1995).

2.5. Site environmental conditions

Site mean annual precipitation (MAP) and temperature data were extracted from the dataset in Daly et al. (2003) for each site across the island of Puerto Rico. Both average minimum January temperature and average maximum July temperature were used in analyses instead of mean annual temperature because they were available at a finer spatial scale (15″ or approximately 450 m grid size). Climate data for the US Virgin Islands came from the nearest available weather station (US National Oceanic and Atmospheric Administration).

2.6. Statistical analyses

Statistical analyses were conducted using two nested datasets in order to deal with the uneven sampling scheme. The full dataset of 30 NRCS RaCA sites and the 6 Cayey sites (hereafter the "full dataset") were analyzed for relationships between SOC and measured soil properties and climate. We used several models of varying complexity to test the relationship between SOC and predictor variables. To test simple relationships between continuous predictor variables (pH, soil clay content, soil clay + fine silt content, MAP, and mean minimum and maximum temperature) and SOC stocks, we performed simple linear regressions using the full dataset. We tested for relationships between environmental factors that affected the whole site (e.g., temperature and precipitation) and site-level average stocks to 100 cm. For soil properties that varied by horizon (e.g., soil texture and pH) we tested for relationships between the individual horizon OC density (g C cm^{-3}) and the variable of interest. This was done to control for differences in depth and the thickness of horizons.

Due to the uneven sampling design across soil orders and land covers, we focused analyses incorporating land cover and soil order to 25 of these sites (hereafter the "LC x soil subset"; Table. 1), which represent the pasture (and rangeland), and forest land-use classes, and from the Oxisol, Mollisol, and Inceptisol soil orders (Table 1). In total, there were four sites representing each soil order and land cover combination, except for the Inceptisol pasture group, which had five sites.

To test for effects of soil order and land cover on soil C and N stocks (0–100 cm) averaged by site, we conducted 2 × 3 factor ANOVAs for the "LC x soil" subset including the soil order and land cover interaction term. Type III Sum of Squares were calculated using the *car* package in R (Fox, 2016). Tukey's HSD tests were used to compare means following a significant effect in an ANOVA. Continuous covariates (pH, soil clay + fine silt content, MAP, and temperature variables) were added to this 2 × 3 factor ANOVA, and then models were selected using an exhaustive search to find the models that maximized parsimony and explanatory power using adjusted R^2 and Bayesian Information Criterion (BIC) as the metric. For model selection, clay + fine silt was used instead of percent clay because it was shown to have more predictive power in individual regressions. The model selection was done using the *leaps* package in R (Lumley, 2009). To test for within site variability on the land cover subset, mixed models were fit with site as a random effect nested within the soil order and land cover interaction. This analysis was conducted using SAS software version 9.4 (SAS Institute Inc., Cary, NC, USA).

Assumptions of homogeneity of variance and normality of the residuals were checked visually using plots for each model and data were transformed as needed. TC stocks were always log-transformed. Statistical significance was determined at $p < 0.05$ although relationships are described as marginally significant for $p < 0.10$.

3. Results

3.1. Effects of soil order and land cover on soil C and N

We first present results for the "LC x soil" subset of sites. Stocks of soil C and N varied substantially within soil orders and land cover types (Tables 2 and 3). Some sites also exhibited large variability among the five pits, although among-site variability was much greater than within-site variability ($p < 0.0001$).

SOC stocks down to 1 m did not differ among Mollisols (173.0 ± 24.8 Mg C ha^{-1}), Inceptisols (138.5 ± 19.9 Mg C ha^{-1}) or Oxisols (129.5 ± 15.8 Mg C ha^{-1}) (Fig. 2). Mollisols had marginally more SOC than Oxisols in the top 30 cm ($p = 0.07$, Fig. 1). Mollisols contained more TC than Inceptisols or Oxisols for both 0 to 100 cm and 0 to 30 cm (Fig. 2). Soil N stocks differed by soil order only for 0 to 30 cm ($p = 0.01$), with greater stocks in Mollisols (10.3 ± 0.7 Mg N ha^{-1}) than in Oxisols (6.7 ± 1.0 Mg N ha^{-1}) (Fig. 2).

All Oxisols were sampled to 100 cm, whereas overall mean depth to bedrock for Mollisols was 73 cm and 80 cm for Inceptisols. At some non-Oxisol sites, mean depth to bedrock was only 30 cm. As a result, Mollisols and Inceptisols had greater OC densities than Oxisols, as there was little difference in stocks, despite having shallower profiles on average.

Land cover had a marginal effect on OC stocks for 0 to 30 cm ($p = 0.09$, Fig. 3), with forest soils containing 97.7 ± 10.1 Mg C ha^{-1} and pastures 80.4 ± 4.7 Mg C ha^{-1}. Land cover was not a significant

Table 2
Summary of average (and standard error) stocks of total carbon (TC), organic carbon (OC) and total nitrogen (TN) in soils down to 100 cm depth or bedrock by soil order and land cover across 36 sites (full dataset) in Puerto Rico and the U.S. Virgin Islands.

Data set	n	Total Carbon (Mg C ha^{-1})	Organic Carbon (Mg C ha^{-1})	Total Nitrogen (Mg N ha^{-1})
All	36	237.3 (61.3)	176.4 (27.3)	16.3 (1.6)
Soil order				
Entisol	2	566.4 (502.9)	566.4 (502.9)	34.4 (27.4)
Histosol	1	245.0	245.0	21.0
Inceptisol	10	131.2 (19.4)	130.7 (19.5)	13.2 (1.2)
Mollisol	9	390.2 (122.8)	174.2 (21.9)	18.0 (1.9)
Oxisol	8	129.5 (15.8)	129.5 (15.8)	12.6 (2.5)
Ultisol	2	191.4 (19.4)	191.4 (19.4)	18.6 (3.5)
Vertisol	4	230.3 (41.1)	169.6 (12.5)	16.5 (0.2)
Land cover				
Crop	5	144.8 (38.1)	131.4 (30.6)	14.0 (2.9)
Forest	13	225.2 (62.7)	153.0 (16.2)	14.2 (1.1)
Pasture	14	218.8 (70.5)	145.8 (16.0)	15.6 (1.9)
Wetland	4	456.7 (206.0)	415.9 (218.5)	28.9 (11.0)

Table 3
Individual site stocks (and standard error) of organic carbon (OC), total carbon (TC) and total nitrogen (TN) to 100 cm. Site stocks were averaged across five soil pits. Soil series with an * were originally classified as "Rangeland" by the NRCS, but have been reclassified as pasture for our analyses. Site numbers correspond with the sites in Table 1.

Data set	Site #	Soil order	OC stock (Mg C ha^{-1})	TC stock (Mg C ha^{-1})	TN stock (Mg N ha^{-1}
			LC × soil dataset		
Forest	1	Inceptisol	283.1 (52.8)	283.1 (52.8)	18.1 (2.9)
	2	Inceptisol	124.3 (18.9)	124.3 (18.9)	13.6 (1.5)
	3	Inceptisol	108.4 (10.3)	108.4 (10.3)	10.8 (1.4)
	4	Inceptisol	109.1 (15.2)	109.1 (15.2)	11.0 (1.5)
	5	Mollisol	247.6 (6.2)	247.6 (6.2)	21.7 (0.6)
	6	Mollisol	105.1 (17.2)	105.1 (17.2)	13.3 (2.2)
	7	Mollisol	176.0 (26.7)	176.0 (26.7)	16.7 (2.2)
	8	Mollisol	150.1 (15.1)	150.1 (15.1)	17.5 (2.3)
	9	Oxisol	180.6 (13.2)	180.6 (13.2)	18.4 (1.8)
	10	Oxisol	108.2 (4.2)	108.2 (4.2)	8.6 (0.3)
	11	Oxisol	87.9 (8.8)	87.9 (8.8)	7.8 (1.1)
	12	Oxisol	136.8 (8.5)	136.8 (8.5)	11.9 (0.5)
Pasture	13	Inceptisol	145.4 (4.7)	145.4 (4.7)	15.8 (0.6)
	14	Inceptisol	99.9 (17.8)	99.9 (17.8)	11.5 (2.0)
	15	Inceptisol	175.5 (13.3)	175.5 (13.3)	20.6 (1.8)
	16	Inceptisol	105.3 (12.3)	105.3 (12.3)	13.3 (1.8)
	17 *	Inceptisol	95.6 (17.6)	95.6 (17.6)	10.0 (1.9)
	18	Mollisol	301.6 (14.4)	301.6 (14.4)	29.7 (1.9)
	19	Mollisol	144.0 (8.5)	144.0 (8.5)	15.7 (1.3)
	20	Mollisol	165.9 (10.2)	165.9 (10.2)	21.4 (0.8)
	21 *	Mollisol	94.1 (6.2)	94.1 (6.2)	9.0 (0.6)
	22	Oxisol	202.8 (9.5)	202.8 (9.5)	27.8 (0.7)
	23	Oxisol	69.9 (18.4)	69.9 (18.4)	5.7 (1.5)
	24	Oxisol	135.2 (20.6)	135.2 (20.6)	10.2 (1.5)
	25	Oxisol	114.9 (9.7)	114.9 (9.7)	10.7 (0.7)
Full (RaCA) dataset					
Forest	26	Ultisol	172.0 (36.0)	172.0 (36.0)	15.1 (2.6)
Pasture	27 *	Vertisol	190.6 (17.1)	190.6 (17.1)	16.8 (1.2)
Crop	28	Entisol	63.5 (7.2)	63.5 (7.2)	6.9 (0.7)
	29	Inceptisol	60.6 (9.6)	60.6 (9.6)	7.6 (1.5)
	30	Mollisol	183.4 (4.7)	183.4 (4.7)	17.1 (0.9)
	31	Ultisol	210.8 (5.7)	210.8 (5.7)	22.0 (0.4)
	32	Vertisol	138.6 (9.6)	138.6 (9.6)	16.2 (0.9)
Wetland	33	Entisol	1069.3 (171.2)	1069.3 (171.2)	61.8 (9.4)
	34	Histosol	245.0 (19.4)	245.0 (19.4)	21.0 (1.0)
	35	Vertisol	160.0 (9.0)	160.0 (9.0)	16.9 (1.5)
	36	Vertisol	189.3 (13.6)	189.3 (13.6)	16.1 (1.1)

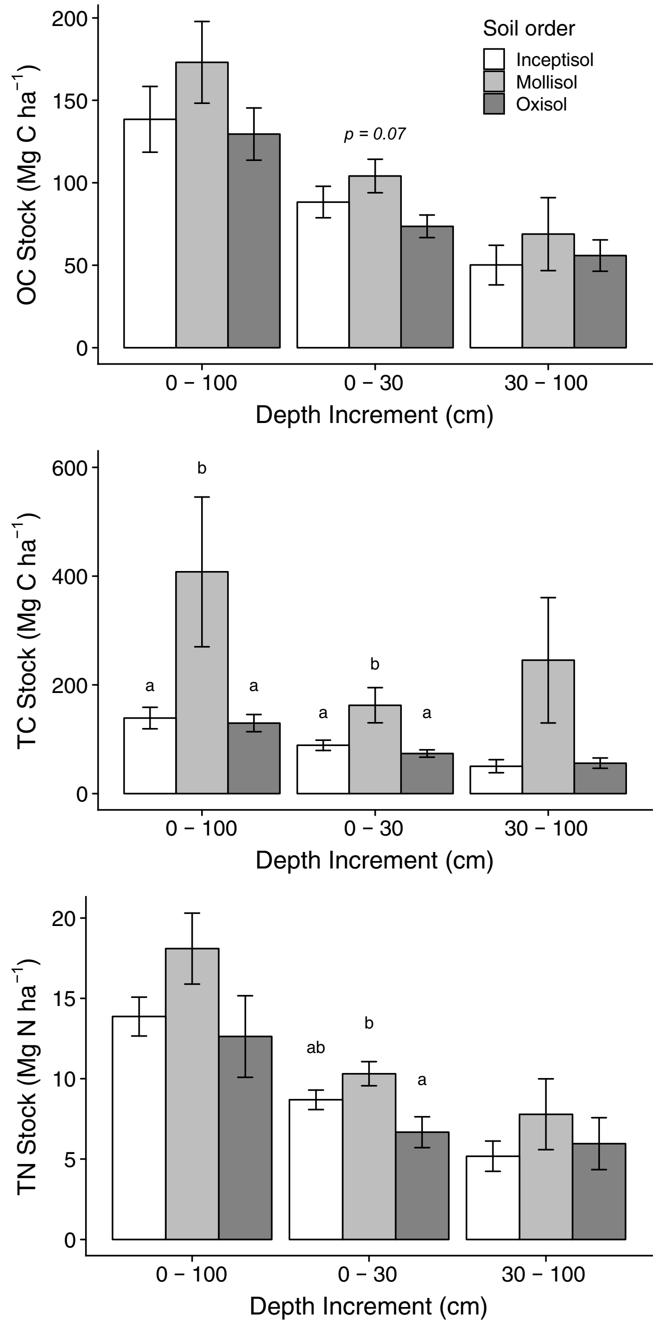

Fig. 2. Average and standard error stocks (Mg ha^{-1}) of soil organic carbon (OC) (top), total carbon (TC) (middle), and total nitrogen (TN) by soil order for three depth increments (0–10, 0–30, 30–100 cm) for the land cover (LC) x soil dataset. Lower case letters denote a significant difference within a depth increment at the $p = 0.05$ level. Marginally significant ANOVA p-values are noted.

predictor of OC stocks at any other depth when models contained just land cover and soil order. At no depth was there an interaction between soil order and land cover. Land cover was not a significant predictor of TN or TC stocks at any depth increment (Fig. 3).

3.2. Effects of environmental variables on soil C and N for full data set

We next present results for the full dataset of 36 sites representing 7 soil orders and 4 land cover classes. Within the full dataset, there were

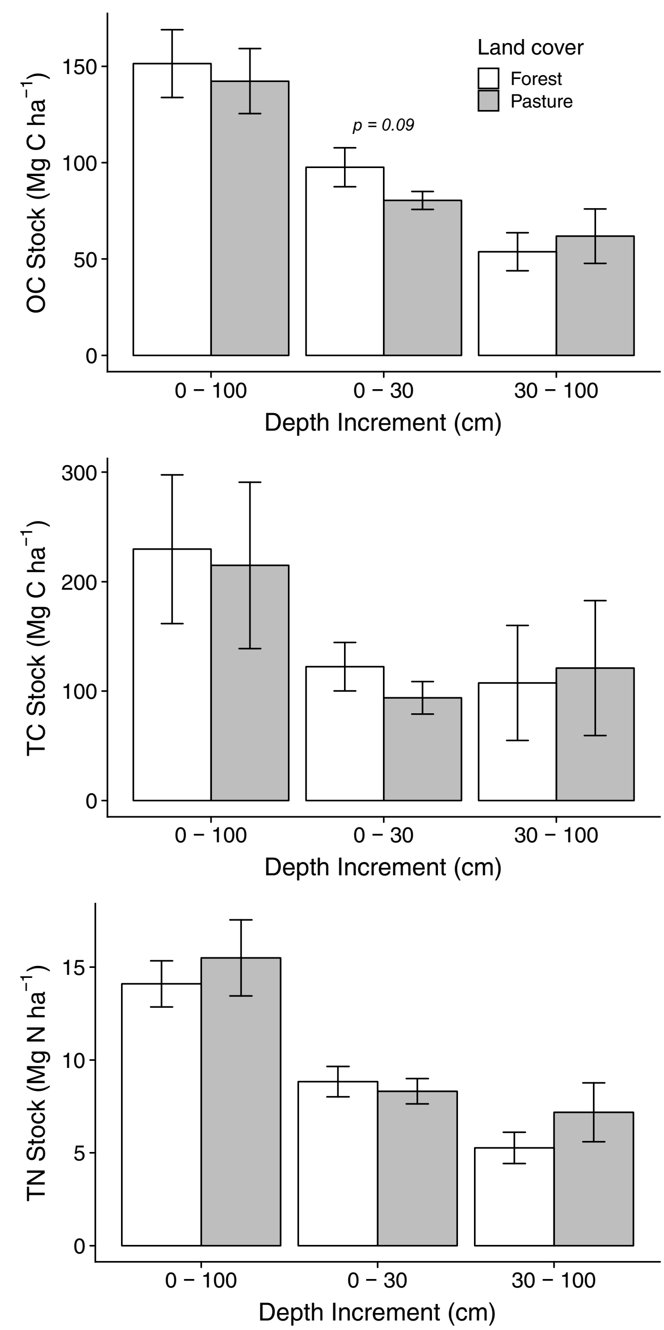

Fig. 3. Average and standard error stocks (Mg ha^{-1}) of soil organic carbon (OC) (top), total carbon (TC) (middle), and total nitrogen (TN) for pasture and forest sites for three depth increments (0–10, 0–30, 30–100 cm) for the land cover (LC) x soil dataset. Only the difference in OC between pastures and forests at 0–30 cm was marginally significant at $p = 0.09$.

no significant relationships between MAP or mean minimum or maximum annual temperatures and site-level OC stocks to 1 m (Fig. 4). This held even when removing the high-OC outlier site. At the horizon level, there was no relationship between pH and OC density (g C/cm^3) (Fig. 5). TN showed similar trends with all environmental factors as OC. TC correlated positively with site temperature and soil pH (data not shown). There were no effects of parent material category or clay activity, as a proxy for clay mineralogy, on OC stocks, but soils with high activity clays did have greater stocks of TN ($p = 0.004$) and TC ($p = 0.04$) (Tables S1 and S2).

Soil OC density per horizon (g C/cm^3) increased with the combined clay and fine silt (< 20 μm) fractions as measured by laser diffraction for all mineral horizons ($p < 0.0001$, Fig. 5). Clay and fine silt combined explained 7% of the variation in OC density for A horizons, 5% of the variation for B horizons, and 30% of the variation for C horizons. Percent clay alone explained less of the variability in percent OC and OC density (< 1% for A horizon, 2% for B horizon, and 10% for C horizon), and was not a significant effect in models ($p = 0.24$).

3.3. *Effects of environmental variables for land cover × soil subset*

Trends for most variables were similar to the full dataset. However, for the "LC x soil" subset, there was a significant quadratic relationship between horizon pH and OC density (p < 0.0001), with greater OC stocks at low and high pH values (data not shown).

Including all the environmental variables (MAP, temperature, percent fine silt + clay, pH) in models with soil order and land cover increased the variability explained, from 13% to 54% of the total variance. Model selection included different explanatory variables for the different depth increments (Table 4). Percent fine silt + clay was included in all models with the lowest Bayesian information criterion (BIC) except for the 30–100 cm depth. MAP was also included in the best models for all depths, but one site with very high MAP was overly influential in these models. With that site excluded, MAP no longer remained in the best models for 0–100 cm and 0–30 cm. For OC stocks to 1 m, the model that both explained the most variability (43%) and was most parsimonious contained percent fine silt + clay and pH. For the 0 to 30 cm depth, the best model contained land cover, pH, and percent fine silt + clay. No models using these variables explained a significant amount of variation for the 30–100 cm depth.

4. Discussion

4.1. *Clay alone was a poor predictor of soil C*

Despite the fact that clay is a common predictor variable of soil C in biogeochemical models, our results show that on its own, soil clay content was not a significant predictor of SOC storage across a diversity of soils in Puerto Rico and the U.S. Virgin Islands. Consistent with other findings of the importance of fine texture (Feller and Beare, 1997; Laganiére et al., 2010; Post and Kwon, 2000; Telles et al., 2003), the combined fine silt (< 20 μm) and clay fraction was a better predictor, explaining between 5 and 30% of variation in soil horizon C densities. This large variability was influenced by the genetic horizon of interest. Fine soil texture (fraction < 20 μm) correlated more strongly with OC stocks for C soil horizons, supporting an increased role for mineral-organic associations in SOM stabilization with depth (Eusterhues et al., 2003; Rumpel and Kögel-Knabner, 2011; Spielvogel et al., 2008). The poor role of clay alone in predicting SOC stocks in our study could be explained by the potential underestimation of the clay fraction via the laser diffraction method relative to other methods of particle size analysis (Centeri et al., 2015; Di Stefano et al., 2010). However, the diversity of geologic substrates represented in our dataset (Table 1 and Table S1) and recent research highlighting the role of soil properties other than clay content in determining soil C storage across a range of biomes (Rasmussen et al., 2018; Rowley et al., 2018) suggest this finding has a mechanistic explanation.

Clay mineralogy has been shown often to be more important than clay content for SOC stabilization (Feller and Beare, 1997; López-Ulloa et al., 2005; Powers and Veldkamp, 2005; Rasmussen et al., 2005; Six et al., 2002; Torn et al., 1997). Our dataset represents a diversity of parent materials and resulting mineralogy, allowing some opportunity to explore the relationship with C storage. For example, kaolinitic soils in our study tended to have lower OC stocks for a given clay content than other clay mineralogy types as expected given the low surface area and cation-exchange capacity (CEC) of kaolinite (Six et al., 2002; von Lützow et al., 2006). The one outlier site that had low clay content but large OC stocks is considered to have "active" mineralogy according to

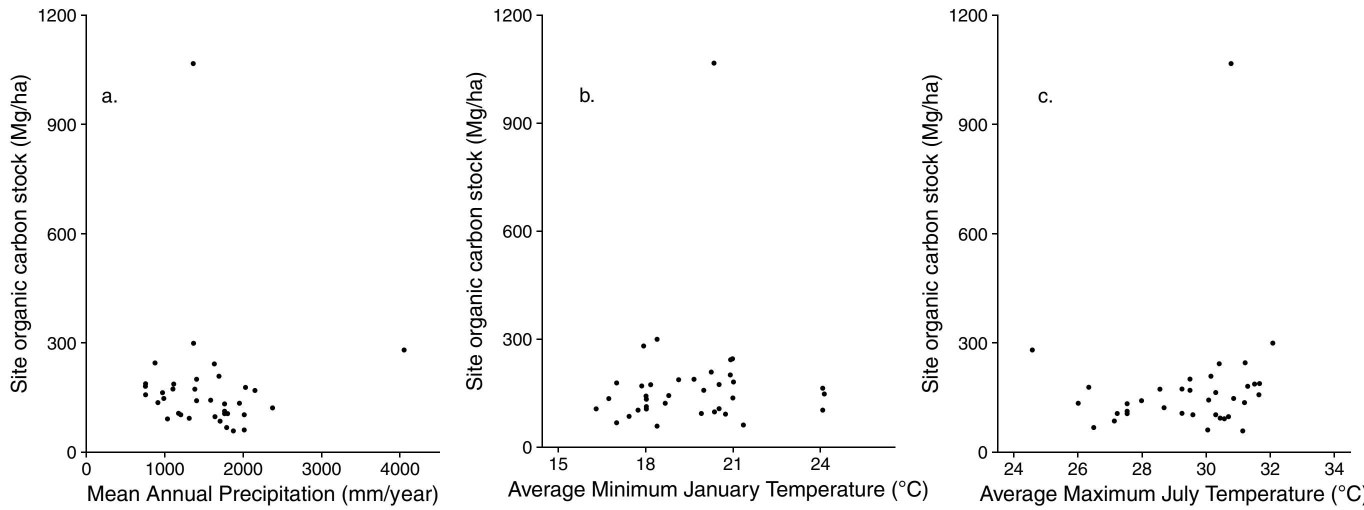

Fig. 4. Full dataset mean site organic carbon stocks to 100 cm (Mg C/ha) as a function of (left to right) (a) site mean annual precipitation, (b) site average minimum January temperature and (c) site average maximum July temperature. None of these relationships were statistically significant both with and without the high-SOC outlier site.

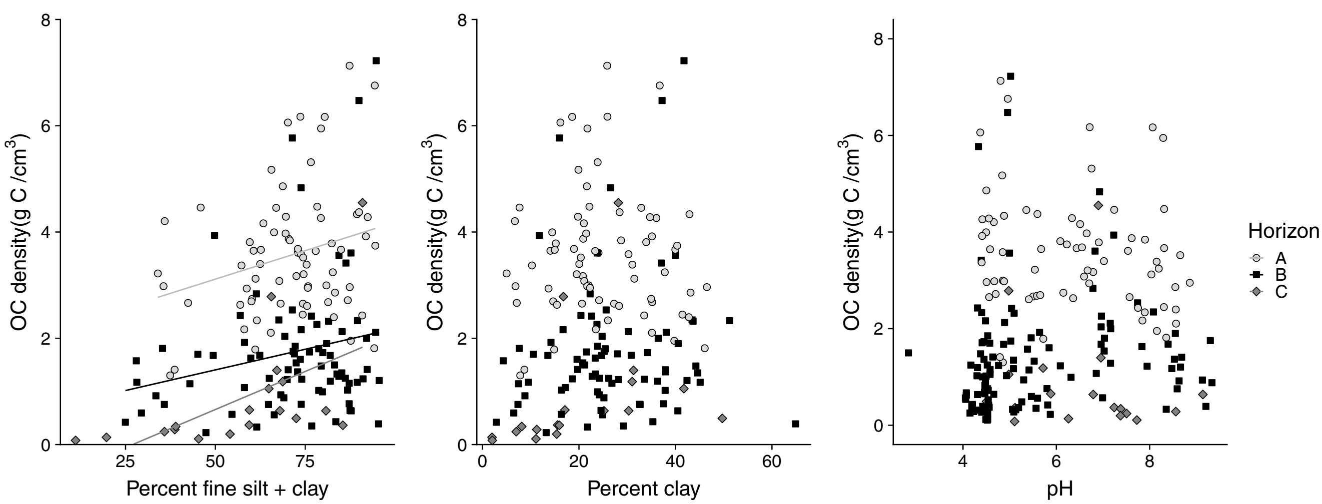

Fig. 5. Full dataset soil horizon organic carbon (OC) density (g C / cm^3) as a function of different soil variables (left to right): (a) percent fine silt and clay (fraction < 20 μm), (b) percent clay (fraction < 2 μm), and (c) soil horizon pH. OC density differed by horizon for all three analyses ($p < 0.001$). Of the soil properties, only percent fine silt and clay showed a significant relationship with OC density (A horizon: $r^2 = 0.07$; B horizon: $r^2 = 0.05$, C horizon: $r^2 = 0.30$; $p < 0.001$).

the NRCS soil series description due to the relatively high CEC of the clay minerals (Soil Survey, 2014). Our findings corroborate those of a recent synthesis that show that clay alone is a poor predictor of C stocks across a wide range of biomes whereas iron and aluminum (oxy)hydroxides may play a more important role in stabilizing SOC (Rasmussen et al., 2018). Although we did not detect differences in SOC content

Table 4
Results from model selection for 25 sites with equal land cover and soil order distribution (LC x soil dataset). The table shows all variables that were included in the full model. One site was overly influential with respect to MAP (Site # 1 from Table 1) so it was removed from additional analyses. Model selection for analyses with and without the outlier site are shown below. Cells with a value indicate that the variable was retained in the model with the lowest BIC for that depth. Values are the *p*-value for the effect of that variable from ANOVA analysis of the final selected model. Values in bold indicate significance at the $p < 0.05$ level, and values in italics represent significance at the $p < 0.10$ level.

Model	Depth (cm)	Land cover	Soil order	Land cover × soil order	% clay + fine silt	Soil pH	MAP	Mean minimum January Temp.	Mean maximum July Temp.	Overall model p -value	R^2
OC stock with outlier	0–100				**0.01**	**0.01**	**0.01**			**0.007**	0.43
	0–30	**0.03**			**0.003**	**< 0.001**	**0.003**			**0.001**	0.67
	30–100		0.32				**0.05**		0.21	0.29	0.21
OC stock without outlier	0–100				**0.02**	**0.02**				*0.06*	0.22
	0–30	**0.01**			**0.003**	**< 0.001**				**< 0.001**	0.71
	30–100	0.235						*0.09*	**0.05**	0.18	0.27

between clay activity classes, stocks of TN and TC were greater in high activity clays. The lack of differences in SOC are likely due to the simplification of categorizing clay activity into two classes. Greater TC content in high activity clays could be explained by the inclusion of carbonatic clays (i.e., soils with high concentrations of carbonates).

4.2. Climate was a poor predictor of SOC and TN stocks

Contrary to expectations, precipitation and temperature were not significant predictors of soil C across a diversity of soils in Puerto Rico and the U.S. Virgin Islands. Climatic variables are known to influence net primary production and rates of decomposition and numerous studies have shown an influence of both temperature and precipitation on soil C stocks at global and continental scales (Beinroth et al., 1996; Jobbágy and Jackson, 2000; Marín-Spiotta and Sharma, 2013). The temperature range represented in our study area corresponded to differences in altitude but was modest (8 °C), and all sites are relatively warm year-round, so it is likely that temperature does not limit productivity or decomposition in this range.

Rainfall also did not predict SOC at our study sites, despite other studies reporting differences in soil C with life zone in the tropics (Beinroth et al., 1996; Jobbágy and Jackson, 2000). Mean rainfall amounts varied more substantially than temperature across the study region, from 825 to 4300 mm $year^{-1}$. The expected effect of precipitation on soil C may have been confounded by soil order effects. The soils with the greatest soil C content, Mollisols were found in drier sites, and Oxisols were found in wetter sites. There was some evidence that precipitation related positively to OC stocks after controlling for soil order, but much of this was due to the one site with the greatest rainfall, which was overly influential in models containing MAP. That particular site, a forest on an Inceptisol located in the El Yunque National Forest, had a well-developed organic horizon and showed gleying, a sign of low redox potential deeper in the profile (data not shown). These properties suggest both high primary productivity and decreased decomposition rates due to prolonged elevated soil moisture, which would lead to greater SOC stocks.

This study investigated relationships between SOC and environmental and soil properties at the regional scale, which may help explain the lack of predictive power of some variables that have been important in other research. Climate is an important control on soil C at global scales and land cover, pH, and texture can influence site-level soil C dynamics. Interactions among these variables across different scales are complex and differ by region (Doetterl et al., 2015; Rasmussen et al., 2018). For example, in addition to its effect on primary production at the latitudinal scale, climate also influences local soil properties (e.g., clay weathering and mineralogy, pH, etc.) that affect the accumulation and stabilization of SOC. Our work highlights the need to explicitly consider environmental heterogeneity at different spatial scales.

At our sites geologic substrate diversity appears to be more important in influencing soil properties than climate, perhaps due to the wide range of parent materials present in the sample set. This study included soils formed from volcanic and sedimentary rocks as well as alluvial and marine sediments. Although we did not find a relationship between parent material and SOC stocks in this study (Table S1), this was likely due to the coarse classification of parent material required to conduct analysis on this unbalanced data set. Whether parent material is a more important control than climate throughout the tropics, and if so, over which scales it may be true requires additional study.

4.3. Land cover influenced OC stocks in shallower soil depths

The effect of land cover on soil C content was more visible for shallow soils than the soil profile down to 1 m depths at the regional scale in our study. From 0 to 30 cm, forest soils contained on average 24% more OC than pasture soils, similar to studies by Brown and Lugo (1990) and Beinroth et al. (1996). In contrast, other studies have reported greater OC stocks in pasture surface soils (Eclesia et al., 2012; Fujisaki et al., 2015; Schipper and Sparling, 2011) and greater OC stocks in deeper soils of forests (Eclesia et al., 2012). Variable trends in soil C under tropical forests and pastures are often attributed to C inputs depths under tropical forage grasses (Fisher et al., 1994) and potential soil nutrient depletion under intensive pasture management (Elmore and Asner, 2006).

Land cover did become more important in models predicting OC to 1 m as additional covariates were added, suggesting that it was explaining some variability in OC stocks. However, this probably was mostly explaining patterns in the surface soils, as land cover was not a significant predictor for the deep soils regardless of what other variables were included in the model. Although land cover is considered an important global driver of soil C dynamics, this study corroborates other studies that show complex relationships between land cover and soil C, especially for forests and pastures (Li et al., 2012; Post and Kwon, 2000; Powers et al., 2011).

4.4. Soil C differed more by soil order than by land cover

Overall, soil properties and soil order were more important predictors of mean OC stocks than land cover or climate in our regional study. Organic C stocks were greatest in Mollisols and lowest in Oxisols, as reported by others (Cleveland et al., 2003; Johnson and Kern, 2002; Tan et al., 2004). These differences only held for the top 30 cm across our sites; as Oxisols were also the deepest soils (extending much deeper than 1 m), they are expected to contain greater OC stocks than Mollisols over the entire soil profile. Consideration of deep soils will improve accuracy of soil C inventories at the regional scale, taking into account differences in depth to bedrock of soils across the landscape, especially in dynamic mountainous regions where landslides and other disturbances can expose soils below 1 m to the surface.

Including texture and pH into our statistical models improved the amount of variation explained in soil C and N content beyond that explained by soil order alone. Soil orders are broad classifications, and because this study looked across different series within orders, it is not surprising that there was substantial variation in OC stocks within soil orders (Mayes et al., 2014). Although there is often a strong relationship between edaphic and environmental variables (e.g., texture, pH, precipitation, or temperature) and soil orders, there can still be substantial variation within a soil order.

Soil pH is another factor that can influence biogeochemical processes, including OC storage through effects on soil biota and organo-mineral reactions (Catoni et al., 2016; Kaiser et al., 2016; Kleber et al., 2015; Rasmussen et al., 2018; van Noordwijk et al., 1997). We observed a significant and positive correlation between pH and OC stocks for the land cover subset of sites, but no significant relationship when the full 36 sites were considered. This discrepancy may be explained due to the high representation of karst-derived Mollisols in the smaller subset of sites. Calcium cations, abundant in calcareous soils with high pH, can protect soil OM from decomposition through several mechanisms (Rasmussen et al., 2018; Rowley et al., 2018). Calcium and other base cations can form cation bridges between clay particles and OM, leading to stabilization in mineral-organic associations (Oades, 1988; von Lützow et al., 2006). Calcium also promotes formation of soil aggregates, potentially leading to increased physical protection of OM from decomposers (Six et al., 2004). Several sites with alkaline soils in this study contained free calcium carbonates, as evidenced by strong effervescence under acid in the field and in the lab. We did not measure mechanisms of OM stabilization directly, but our findings agree with reported patterns of OC accumulation in alkaline soils (Oades, 1988; van Noordwijk et al., 1997). The strength of this effect appears to have been reduced when samples for all 36 sites where analyzed, likely due to the presence of sites with low pH soils and large OC stocks, such as wetlands. Indeed, we observed increasing SOC stocks at sites with the lowest and highest pH values, and reduced SOC stocks at intermediate values, but there was substantial variability.

SOC stocks in our study generally fall within the range of observations of C stocks by soil order in the tropics. Average Mollisol OC stocks at our sites (134 ± 14 Mg C ha^{-1} in the top 50 cm) were greater than the OC stocks (107.4 Mg C ha^{-1} to 50 cm) in Puerto Rican Mollisols reported by Beinroth et al. (1996) and less than the 268 Mg C ha^{-1} reported in Hawaiian Mollisols by Johnson and Kern (2002). Mollisols also had the greatest TC stocks, reflecting both greater OC and inorganic C stocks. In particular, three Mollisol sites had substantial stocks of inorganic C (over 70% of total C). The large amounts of inorganic C in the Mollisols come from the weathered carbonate-rich parent material, typical of tropical karst regions, which make up about 28% of Puerto Rico's landscape (Lugo et al., 2001). Limestone parent material also constitutes a significant portion of the US Virgin Islands (Rankin, 2002).

The Oxisol SOC stocks we report are within the range of other studies on Oxisols, although on the lower end of estimates for Puerto Rico (Beinroth et al., 1996; Grimm et al., 2008; Johnson and Kern, 2002). Seven of our Oxisol sites came from one soil series (Los Guineos), which is not representative of the full spectrum of Oxisols in Puerto Rico. Those sites were on mountainous slopes and may contain lower OC stocks than other lowland Oxisols. They are also relatively drier than many other Oxisol sites both within Puerto Rico and elsewhere in the tropics. Finally, all our Los Guineos sites, including the forested sites, have undergone past anthropogenic disturbance and deforestation, which may reduce current surface SOC stocks compared to other less disturbed Oxisol sites.

As predicted, Inceptisol OC stocks were highly variable, reflecting the wide range of parent materials, climate, and vegetation possible for Inceptisols. For example, Inceptisols in this study were formed from alluvial deposits, volcanic rock, and calcareous parent materials. Inceptisols also represented the driest and the wettest sites in the study.

The soils included in this analysis focus mostly on the soils of greatest spatial extent in Puerto Rico and the US Virgin Islands. Of the ten soil orders currently recognized in Puerto Rico, Inceptisols cover 29%, Ultisols 20%, Mollisols 15%, Oxisols 7.5%, Alfisols 5%, Vertisols 4%, Entisols 2%, Aridisols 1.5%, Histosols 0.5%, and Spodosols 0.2% of the total land area. Of the 5 soil orders currently recognized in US Virgin Islands, Inceptisols cover 24.9%, Mollisols 63.6%, Alfisols 4.7%, Vertisols 3.1% and Entisols 3.7% of the total land area (González et al. in review).

This study helps to address some of the geographic bias in tropical soils literature which has historically been heavily weighted towards highly weathered and allophanic soils in very wet climates (Powers et al., 2011). We show a number of sites from drier locations, and with a diversity of parent materials and weathering histories that is representative of much of the tropics. Given the large variability in C and N stocks within soil orders as well as between soil orders, we continue to show the need for improved representation across the range of soils of the tropics. Further studies should continue to address these under-studied regions to better understand the relationships between soil mineralogy, texture, and land cover across a wider range of soil types and predict C storage dynamics across the tropics.

5. Conclusions

Our study of regional scale predictors of soil C and N storage shows the relative importance of soil properties, land cover, and climate variables in predicting soil C storage across a diverse range of soils of the tropics. We found that soil order and soil properties, such as pH and silt + clay, were more important than land cover or climatic variables in predicting soil OC stocks across a diversity of geologic substrates in the Caribbean islands of Puerto Rico and the U.S. Virgin Islands. In particular, soils with finer texture (greater percentage of fine silt and clay) contained more OC than soils with coarser texture. Clay alone was not a good predictor of soil C stocks. Mollisols derived from limestone contained greater organic C stocks than Oxisols and Inceptisols but only for surface soils; the effect of soil order disappeared when deeper profiles were considered. Forest soils contained marginally more soil C than pasture soils in the top 30 cm. Temperature and precipitation were not significant predictors of soil C. Patterns of TN storage were similar to those for TC, although land cover was not an important predictor of TN.

Our findings have several implications for regional estimates of SOC and for improving predictions of the response of tropical soil C to environmental change. Many biogeochemical models (e.g., CENTURY and RothC) incorporate climate, land cover, and clay, as important variables, yet, there is growing recognition that additional parameters such as mineralogy may be needed to improve predictions of SOC across a range of spatial and temporal scales (Schmidt et al., 2011; Torn et al., 1997; Wiesmeier et al., 2019). This study also shows substantial variability in SOC stocks across a diversity of soils of the tropics, illustrating the need to account for under-represented soil orders and different SOC dynamics as differences in stabilization mechanisms can influence responses of SOC stocks to disturbance and future environmental change.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2019.06.044.

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