FACTORS CONTROLLING SOIL CARBON AND NITROGEN STORAGE IN

PUERTO RICO AND THE US VIRGIN ISLANDS

By

Elliot Vaughan

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Abstract

Tropical soils represent a large and important carbon (C) reservoir and thus play an important role in the global C cycle. The accumulation and persistence of C in soils has implications for soil fertility and climate change. The amount of C stored in a soil can be affected by changes in land cover and human land use, although the direction and magnitude of the change is not consistent across studies, especially when comparing forests to pastures. Environmental factors, including soil type, soil texture, soil pH, precipitation, and temperature all have the potential to influence soil C storage, and may be important in determining how soil C stocks respond to land-use change. The goal of this study was to further explore the factors influencing regional patterns in soil C storage, with a focus on soil order and land cover. Soils were collected from 25 sites representing 19 soil series in three soil orders, and under two land cover types, pastures and forests, in Puerto Rico and the US Virgin Islands. Soils were analyzed at three depths, 0-100 cm, 0-30 cm, and 30-100 cm, for total carbon (TC), soil organic carbon (SOC), and total nitrogen (N). Soil order was an important predictor of soil TC, SOC, and soil N stocks for all depths. Mollisols consistently had the greatest stocks of TC, SOC and N, while Oxisols had the smallest stocks. Inceptisol stocks were intermediate, and the most variable, given the diversity of parent materials. Land cover was only a marginally significant predictor of SOC for 0-30 cm depth, at which forest soils contained 24 % more SOC than pasture sites. There was no significant interaction between soil order and land cover. Soil C:N ratios were greater in forest surface soils (0-5 cm) than in pasture soils indicating a difference in litter input chemistry or decomposition. Soil pH correlated positively with SOC and TC stocks, probably due to a number of calcium carbonate-rich Mollisol sites. Clay and fine silt content was positively yet weakly correlated with SOC stocks, suggesting that differences in soil mineralogy across the sites may be more important in predicting SOC stocks than texture alone. Mean annual temperature and mean annual precipitation were not correlated with SOC stocks in this study. These findings suggest that at a regional scale, both soil properties and land cover are important predictors of SOC stocks, and that patterns depend on the depth studied. Predictions of regional C stocks should account for the wide variability of soil types present in the tropics.

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Introduction

Soils store more carbon (C) in the top 1 m globally than is found in the atmosphere and all living plants combined (Batjes 1996, Jobbágy and Jackson 2000). Tropical soils represent between 32 % and 42 % of the global soil C reservoir (Jobbágy and Jackson 2000, Carvalhais et al. 2014); hence, even small changes in the tropical soil C budget could have important implications for global climate change. In addition to its importance for climate change, soil C directly affects soil fertility and nutrient availability as a component of soil organic matter. The amount of organic C stored in soil is determined primarily by the balance between inputs of organic matter as plant detritus, root exudates and microbial products and losses through decomposition, soil erosion and in dissolved form. The balance between these processes will determine if a soil loses C and is a source to the atmosphere (losses > inputs) or sequesters C from the atmosphere (inputs > losses). Changes in one or several of the processes above due to human land-use change can affect soil organic C (SOC) stocks. As deforestation and other land-use changes continue to affect large areas of the tropics, it is important to understand how land use influences soil C storage (Laganiére et al. 2010, Li et al. 2012).

Predicting the effects of human activities on the terrestrial C cycle is challenging because SOC stocks do not respond consistently to changes in land use. Converting land from native vegetation to crop cultivation usually leads to significant losses of C from soils (Guo and Gifford 2002, Don et al. 2011, Powers et al. 2011). Similarly, if cropland is reforested, SOC stocks can increase quite rapidly (Powers et al. 2011, Li et al. 2012). However, the change in soil C storage following pasture to forest, and forest to pasture conversion is less consistent. SOC stocks can respond in different ways to the same land-use transition (Fisher et al. 1994, López-Ulloa et al. 2005, Marín-Spiotta et al. 2009, Neumann-Cosel et al. 2011, Berthrong et al. 2012, Eclesia et al. 2012). Meta-analyses also find differences in the direction and magnitude of SOC change following transitions between forests and pastures globally and in the tropics (Post and Kwon 2000, Guo and Gifford 2002, Murty et al. 2002, Laganière et al. 2010, Don et al. 2011, Powers et al. 2011, Li et al. 2012, Fujisaki et al. 2015).

There is a need to better understand why SOC has such inconsistent responses to land cover changes between forest and pasture because grazed systems cover approximately 25% of the global land surface, making it one of the most extensive land use types globally and within the tropics (Asner et al. 2004, Grace et al. 2014). In the tropics, conversion to pasture is one of the major driving forces behind deforestation (Geist and Lambin 2001). Substantial areas of former pastureland are also converting back into secondary forest throughout the tropics (Aide et al. 2012). As a result, changes in soil C in response to land use transitions between forest and pastures represent a significant but poorly understood component in the tropical C budget. A source of difficulty in determining the direction and magnitude of soil C change following conversion between pasture and forest is that other factors beyond land cover influence soil C storage.

Site-specific environmental factors, including soil properties, climate, and nitrogen availability, can affect soil C storage (Brown and Lugo 1990, Jobbágy and Jackson 2000, Li et al. 2012, Marín-Spiotta and Sharma 2013). Interactions among and between these multiple factors can influence an individual site’s response to land-use change, adding uncertainty to soil C trajectories. Compounding these mechanistic explanations for why it is difficult to draw conclusions, Powers et al. (2011) showed a geographic bias in the literature. 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 in comparison to their global coverage, while dry forests and all other soil types have been under-studied. As a result, individual studies and meta-analyses may be biased towards specific soil types or precipitation regimes and not accurately capture differences between ecosystem types. The tropics exhibit incredible biophysical diversity (e.g., soil type, climate, vegetation) and it is important to understand how soil C responds to land-use change across the range of biophysical factors.

Soil nitrogen (N) storage is also of interest for its role in fertility, and its interactions with and influence on the C cycle. SOC and soil organic N are both important components of soil organic matter (SOM), and thus soil stocks of the two elements are often tightly correlated, as measured by the C:N ratio. The C:N ratio of SOM is often used as an indicator of soil nutrient status and organic matter decomposition state, as the C:N ratio decreases as organic matter is decomposed (Baisden et al. 2002) or changes with the type of plant litter inputs. Changes in land use and land cover can influence the two stocks differently, and the C:N ratio can differ, with implications for decomposition rates, and overall SOC storage.

To address uncertainties in land use and environmental effects on soil C and N, I measured soil C and N under forest and pasture on three different soil orders, Inceptisols, Mollisols, and Oxisols, representing soils with substantially different parent materials, weathering histories, and current environmental conditions. The research aim was to determine whether soil type or current land cover type is more important in predicting soil C storage, and what other environmental factors may also influence soil C storage at the landscape level. Many studies have shown that land-use change can influence soil C storage under some circumstances but not others, and this study seeks to improve our understanding of which environmental conditions may mediate the relationship between land use and soil C storage. Given the role of land-use change in altering soil N, I also investigated whether the relationships between C and N varied under different land cover types and soil types. My research expands on previous work in Puerto Rico by contributing a wider range of soil and climate types, as well as analyzing trends in deeper soils, down to 1 m (Brown and Lugo 1990, Beinroth et al. 1996, Marín-Spiotta et al. 2009).

To this end, soils were collected across the island of Puerto Rico and the US Virgin Islands, which represent ideal locations to study these questions due to their environmental heterogeneity. Specifically, the three main research questions were:

1. How do differences in land cover and soil type affect soil C storage?
2. To what extent do mean annual temperature and precipitation predict soil C storage?
3. Do relationships between soil C and N vary with land cover type?

Hypotheses and Literature Review

1A: Forest soils and pasture soils store different amounts of C, reflecting expected changes in plant litter inputs and decomposition rates with vegetation type and land use.

Differences in vegetation cover can influence both inputs to and losses of C from soil. In one Puerto Rican study, forest soils contained twice as much SOC compared to pasture soils, hypothesized to be a result of increased productivity and incorporation of forest litter into soils (Beinroth et al. 1996). Grazing of pastures removes aboveground biomass, which may lead to reduced litter inputs (Elmore and Asner 2006, Li et al. 2012). Pasture soil conditions may also be more favorable to decomposition if soil temperature increases. Another study in Puerto Rico showed no significant difference between forest and pasture soils (Marín-Spiotta et al. 2009). Other studies in tropical regions have shown increased SOC under pasture, attributed to greater belowground productivity and root biomass of some pasture grasses (Fisher et al. 1994). However, there is evidence that any C gains in pasture soils may be limited to upper soil depths and be offset by C losses at depth as deep tree rooting systems are replaced by shallower grass roots (Eclesia et al. 2012). Pasture management (e.g., stocking rate and whether fertilizer is applied) may also play an important role in determining soil C storage in pastures (Trumbore et al. 1995, Elmore and Asner 2006).

Given variable results in the amount of SOC stored in tropical pastures and forests, the response of soil C with conversion between forest and pasture in both directions is still uncertain. Several global syntheses have found that afforestation and reforestation of pasture soils can increase soil C (Powers et al. 2011, Li et al. 2012), have no effect (Laganiére et al. 2010), or decrease soil C (Guo and Gifford 2002). Individual studies have similarly shown positive, neutral, and negative trends in soil C with conversion of pasture to forest, possibly reflecting the importance of several different factors in determining soil C responses. The same is true with both meta-analyses and individual studies showing conflicting trends with deforestation to establish pastures (Don et al. 2011, Powers et al. 2011).

Some of the uncertainty regarding the direction and magnitude of soil C response may also be due to a lagging response of soil C stocks following land use conversion. Soil organic matter (SOM) is a heterogeneous pool made up of C compounds with different residence times in the soil. Some of these pools turn over on yearly time scales while others turn over on centennial to millennial timescales (Trumbore 1993). As a result, it might take many years for changes in slow cycling SOM pools to reflect changes in land use. For example, a study of Ecuadorian pastures found young pastures contained greater soil C stocks than mature forests, while pastures older than 20 years had significantly reduced C stocks (de Koning et al. 2003). Similarly, a study in Panama found that pastures and forests 20 years old contained similar amounts of soil C, while mature forests contained significantly more C than pasture soils (Neumann-Cosel et al. 2011). These studies show the importance of land use history and duration as well as current land cover in determining soil C trends.

I hypothesized that forest soils would store more C than pasture soils as litter inputs to the surface and root inputs to deep soils will be greater in the forests due to greater overall plant biomass. In support of this, Beinroth et al. (1996) found significantly more C in forest soils compared to pasture soils in a study similar to ours. I expected any positive effects of pasture establishment on soil C to diminish at depths up to 1 m (Eclesia et al. 2012).

1B: Soil C storage will be influenced by soil properties characteristic to soil orders, and by properties that are not strictly related to soil order (e.g., texture).

Jenny (1941) proposed a framework for studying soil formation, where soil, and by extension, soil properties, are a function of five state factors: climate, organisms, relief, parent material, and time of development. Soil C storage represents a soil property, and indeed studies at multiple scales have shown the importance of those factors in determining soil C storage (e.g., Schimel et al. 1994, Beinroth et al. 1996, Jobbágy and Jackson 2000, Schmidt et al. 2011). Differences in C storage at the soil order level can often be attributed to differences in productivity or decomposition driven by one or more of the state factors. Although there is substantial variability, generally, among the three soil orders of interest to this study, Mollisols typically have relatively large soil C stocks, Inceptisols store an intermediate but variable amount, and Oxisols are also intermediate relative to other soil orders (Cleveland et al. 2003, Johnson and Kern 2002, Tan et al. 2004). Mollisols by definition have a dark, often organic matter rich surface horizon, so they are expected to store considerable amounts of C, especially in surface soils. Inceptisols are primarily defined by degree of soil development but can be very diverse in other aspects, including parent material and climate, hence their soil C stocks are variable. Oxisols, which represent highly weathered soils and form in hot, humid climates or very old substrates show both high levels of productivity and thus plant inputs to soil, but also high rates of decomposition, leading to intermediate levels of C storage in the surface soil. In contrast to the general trends discussed above, Beinroth et al. (1996) classified Mollisols, Inceptisols, and Oxisols in Puerto Rico as all storing “high” amounts of C relative to other soil orders, and found no significant difference in C stocks down to 50 cm.

Soil properties that do not strictly correspond with soil orders (e.g., texture and mineralogy) can also influence soil C storage through their effect on SOM stability. SOM stability is usually defined as the potential for SOM to be lost through respiration, erosion, or leaching (Sollins et al. 1996, Torn et al. 2009). SOM stabilization is a decrease in the potential for SOM to be lost, and thus leads to an increase or no change in soil C. SOM can be stabilized through a number of mechanisms, predominantly through mineral associations, physical protection in aggregates, and environmental conditions (Sollins et al. 1996, von Lützow et al. 2006, Torn et al. 2009, Schmidt et al. 2011, Lehmann and Kleber 2015). The factors controlling OM stabilization are complex, but both soil properties and environmental conditions contribute to the persistence of OM (Schmidt et al. 2011).

Soil texture is one factor that may play an important role in SOM stabilization. Soil texture influences soil aggregate formation, which can physically protect SOM from decomposers (Six et al. 1998, 2000). Soil texture may also influence the stabilization of SOM through formation of mineral-organic associations (MOAs). MOAs can contain up to 90% of OM in a soil and are associated with longer soil C turnover times, potentially because they protect OM from microbial decomposition by reducing reactivity and accessibility of OM (von Lützow et al. 2006, Kleber et al. 2014). Because clay particles can have a high specific surface area and high cation exchange capacity (CEC), soils with high clay contents would be expected to store more C in MOAs than soils with coarser textures. Often, the amount of clay in a soil has been shown to correlate positively with soil C accumulation (Feller and Beare 1997, Post and Kwon 2000, López-Ulloa et al. 2005). In contrast, a review by Don et al. (2011) found that the clay content of soils did not influence SOC stocks and Hassink (1997) found that clay and silt content correlated with the amount of OC in the clay and silt fraction, but not with bulk soil OC. Differences in clay mineralogy may be more important than overall clay content in determining OM stabilization (Torn et al. 1997, Six et al. 2002). Given the wide range in mineralogy among clay-sized particles, and subsequent differences in CEC and specific surface area, it is not surprising that the importance of the clay fraction in stabilization varies (Six et al. 2002)

Clay content and mechanisms of SOM stabilization can also exert control on how soil C responds to land-use change. For example, Laganiére et al. (2010) found that soils with a high clay content stored more C following afforestation than soils with coarser textures. Another study in Ecuador found that trends in soil C storage differed between Andisols and Inceptisols following land-use change, primarily due to differences in how soil C was stabilized via interactions with soil minerals (López-Ulloa et al. 2005). In addition, a study in Ohio reported that SOC in Inceptisols was more sensitive to differences in land use than SOC in Mollisols or other soil orders, although this may have been related to differences in topography and parent material between land covers more than effects of land cover per se (Tan et al. 2004).

In this study, I expected Mollisols to store more soil C than the other two soil orders, and Inceptisols to show the most variation, due to the diversity in parent materials. I hypothesized that soil order may interact with land use to affect C storage, although I expected soil texture to be more important than soil order in this regard (Laganiére et al. 2010).

2. Mean annual temperature and mean annual precipitation will both affect soil C storage as they control productivity and decomposition rates, but precipitation will be more important in this study due to its greater range among sites.

Mean annual precipitation (MAP) and mean annual temperature (MAT) are two environmental factors that affect soil C storage through their influence on inputs and losses of C from soils. MAP and MAT also influence soil formation and properties, which can affect SOC stabilization. Generally, studies show that MAT is negatively correlated with soil C storage, as increased temperature leads to increased turnover of soil C and to decreased productivity at high enough temperatures (Jobbágy and Jackson 2000, Marín-Spiotta and Sharma 2013). MAP tends to correlate positively with soil C storage (Jobbágy and Jackson 2000, Marín-Spiotta and Sharma 2013), as increased precipitation leads to increased plant productivity and may decrease C losses to decomposition as waterlogged soils become anoxic. As a result, soil C tends to accumulate most in wet, cool soils (Beinroth et al. 1996, Marín-Spiotta and Sharma 2013). However, there are interactions among temperature, precipitation, and land use that make this relationship more complicated (Guo and Gifford 2002, Don et al. 2011, Berthrong et al. 2012, Marín-

Spiotta and Sharma 2013). For example, several studies have shown that sites with high MAP lost C when they were converted to forest from grassland while sites with lower MAP gained C with afforestation (Guo and Gifford 2002, Berthrong et al. 2012). Additionally, soil moisture can be a function of soil texture and drainage in addition to MAP, leading to further complexity.

Despite the relatively small size of Puerto Rico and the U.S. Virgin Islands, there is substantial variability in climate, with six Holdridge life zones represented (Ewel and Whitmore 1973). Both precipitation and temperature vary across the islands as a factor of elevation, proximity to the ocean, and exposure to moisture bearing winds (Daly et al. 2003). MAP in particular varies substantially, from a minimum of 700 mm yr^{-1} to 4600 mm yr^{-1} and is the primary delineating factor among life zones in Puerto Rico (Ewel and Whitmore 1973, Daly et al. 2003). MAT varies from less than 20º C to over 26º C (Daly et al. 2003). The sites in this study cover much of the island's range in both temperature and precipitation. MAT ranged from 18º C to 26º C and MAP ranged from 825 mm yr^{-1} to almost 4300 mm yr^{-1} (Table 1).

As a result of these trends, I hypothesized that cooler, wetter sites would have the greatest C stocks. I expected MAP to correlate stronger with OC stocks than MAT, due to the relatively greater range in precipitation than temperature.

3. Soil C:N ratios will vary between land cover types due to differences in inputs and decomposition rates.

As with soil C, soil N stocks are a function of many different factors, including human land use. Organic N is an important component of SOM, so stocks of SOC and N are directly related to the amount of SOM, and thus usually strongly correlated. There is substantial evidence that C and N dynamics are closely coupled following land use change, regardless of the direction of the change (Knops and Tilman 2000, Murty et al. 2002, Kirschbaum et al. 2008, Li et al. 2012). The direction of the change in soil N with land change is highly variable between studies, similar to observations for soil C (Li et al. 2012). However, there is also evidence that the two stocks may behave differently under different land uses, depending on pasture management practices.

Soil C:N ratio is a common way to look at relative changes in C and N stocks. Plants and organisms maintain fairly narrow stoichiometric ratios of C to N, so soil C:N ratios can be used to infer changes in soil nutrient status, as well as changes in decomposition rates (Sterner and Elser 2002, Manzoni et al. 2010). Fresh plant material has large C:N ratios, and SOM is expected to have progressively smaller C:N ratios approaching those of microbial biomass as it is decomposed. As a result, deeper soils with fewer fresh plant inputs are expected to have a lower C:N ratio than surface soils, where much of the SOM is more recently derived from plants (Rumpel and Kögel-Knabner 2011). Soil C:N ratio may vary with land use, either through changes in inputs or losses, or changes in decomposition.

Although not universal, soil C:N ratios are often greater under forests than pastures (Murty et al. 2002, de Koning et al. 2003, Kirschbaum et al. 2008a, Berthrong et al. 2012). This may be due to increased C:N ratios of litter inputs from woody tree species (Murty et al. 2002, Kirschbaum et al. 2008a, Berthrong et al. 2012).

Decomposition rates could also increase under pasture due to changes in edaphic conditions, leading to reduced C:N ratios. Pastures planted with N-fixing forage or that are fertilized, may accumulate N in the soil, also leading to reduced C:N ratios (Trumbore et al. 1995, Li et al. 2012). However, trends in C:N ratios under different land covers may depend somewhat on environmental conditions, particularly precipitation. N is more prone to losses through leaching than C, so a reduction in plant cover and hence plant N demand, can increase N losses, and thus lead to a larger C:N ratio in areas with high precipitation (Kirschbaum et al. 2008b, Dalal et al. 2013). Forests also store more N in aboveground biomass, which could reduce soil N stocks, and thus decrease the C:N ratio under forests. Likely, several of these processes may be occurring at once, so the final balance between C and N stocks, and thus C:N ratio is site specific.

I expected the C:N ratio of forest soils to be higher than for pasture soils due to an increase in the C:N ratio of inputs, and the possibility that pasture sites were fertilized or planted with N-fixing species.

Methods

Site Selection

Soil samples were collected in the Caribbean islands of Puerto Rico and the US Virgin Islands in collaboration with the USDA Natural Resources Conservation Service (NRCS) as part of a national soil carbon mapping effort following protocols of the Rapid Carbon Assessment (RaCA). Sampling sites were selected to be representative of the diversity of soils across the island 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. In total, 30 sites were sampled. Here I report data from 19 of these sites (Fig. 1), which represent the pasture, rangeland, and forest land-use classes, and from the Oxisol, Mollisol, and Inceptisol soil orders (Table 1). Rangeland and pastures were considered to represent similar land uses and are combined into one pasture category for this study. To increase sample size for Oxisols, three additional pasture and forest sites each are 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. In total, there were four sites representing each soil order and land cover combination, except for the Inceptisol, pasture group, which had five sites.

Site precipitation and temperature data were taken from the NRCS Official Soil Series Descriptions (Soil Survey Staff 2016). In cases where there was a range in temperature or precipitation given for a series, the midpoint of the range was used.

Sample Collection

At each site, five pits were dug in a clustered design, with 30 m distance in between each pit, following standard RaCA protocols (Fig. 2A). When that arrangement was not possible, the pits were dug in a chain cluster (Figure 2B). 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, 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, except for the top A horizon. For the A horizons, a sample was taken from 0-5 cm for every pit, and then from 5 cm to the bottom of the A horizon. Samples for bulk density calculations were collected using a 10 cm x 10 cm x 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 less than 50 cm. Horizons with an upper depth of greater than 50 cm were collected with a bucket soil augur and no bulk density measurements were taken. Soils were collected in plastic sleeves and left open to air dry. Upon shipment to UW Madison, they were transferred to cloth bags and allowed to fully air dry in a ventilated room.

Soil Laboratory Processing

Once air dried, soils were sieved to 2 mm. Rocks and roots were manually removed, as was particulate organic matter larger than 2 mm. Bulk density was measured for all samples with an upper depth shallower than 50 cm. Final soil bulk density values were calculated for each horizon 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 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). The “Cayey” sites were not analyzed using laser diffraction, but the particle size distributions for 0-10 cm of depth were previously analyzed using the hydrometer method (Marín-Spiotta et al. 2009).

Soil pH was measured on all samples on a 1:2 slurry of soil in deionized water after a 30-minute equilibration period (Robertson et al. 1999). Two pH measurements were taken roughly 5 minutes apart and repeated until measurements were consistently within 0.1 unit. Values reported are averages of the measurements.

Soil C and N Analysis

A subsample of soil was ground 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 < 7.5% and aspartic acid as standards. Samples were tested for the presence of inorganic carbon following Nelson and Sommers (1996) and those that tested positive were acid fumigated for at least 12 hours as in Harris et al. (2001). A random sample of soils was re-tested for 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). For sites that did not have inorganic C, TC and OC stocks are identical.

Soil TC, OC, and N stocks were calculated using moisture-corrected C and N percentage values and bulk density values for each horizon. Stocks are reported in Mg/ha. Total pit stocks were calculated by summing the horizon stocks, and site stocks were calculated by averaging the five pit values. Soil C:N ratios were calculated using the molar mass of C and N.

Because soils were sampled by horizon, there was substantial variability in horizon presence/absence, and thickness among pits within a site, and between sites. To allow standardized comparisons among sites for certain analyses, soil profiles were divided and aggregated into a “shallow” 0-30 cm portion and a “deep” 30-100 cm portion. The profiles were also divided into 10 cm slices for more detailed visualization of trends in 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. In cases where pits did not extend all the way to 1 m deep, values were extrapolated to 1 m using the C and N values and bulk density for the lowest horizon. Bulk density did not differ significantly by land cover or soil order, so stocks were not corrected using an equivalent soil mass as some have suggested (Ellert and Bettany 1995).

Statistical Analyses

Several different models of varying complexity were used to analyze the data. Assumptions of homogeneity of variance and normality of the residuals were checked for each model, and data were transformed as needed to fit the assumptions. TC stocks were always log-transformed. C:N ratios were transformed inversely.

To test simple relationships between continuous predictor variables (pH, soil clay content, MAP, and MAT) and OC stocks, simple linear regressions were performed. To test the relationships among soil order, land cover, and C and N stocks, 2 x 3 factor ANOVAs were run, using soil order and land cover as the predictor variables for C and N stocks. Type III Sum of Squares were calculated using the *car* package in R (Fox 2016). Fisher's LSD was used to compare means following a significant effect in an ANOVA. All continuous covariates were added to this 2 x 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. The model selection was done using the *leaps* package in R (Lumley 2009).

To test within site variability, mixed models were fit with site as a random effect nested within the soil order and land cover interaction. To test for differences by depth increments, depth was treated as a split plot design, with depth as the subplot variable. Two depths were included in this model, 0 - 30 cm and 30 - 100 cm. Both of these analyses were conducted using SAS software version 9.4 (SAS Institute Inc., Cary, NC, USA).

Results

Overall patterns in OC, TN, and TC stocks to 1 m

There was substantial variability in all stocks within land covers and soil orders. Some sites also exhibited substantial variability among the 5 replicate pits (e.g., see Supplemental Information Figs. S1 and S2) although among-site variability in all stocks was much greater than within-site variability ($p<0.0001$). TC stocks (which represent inorganic and organic C) to 1 m ranged from 69 Mg C ha^{-1} to 1167 Mg C ha^{-1} with a mean of 279.1 ± 62.7 Mg C ha^{-1} across all sites (Table 2, Fig. 3). Inceptisol TC stocks averaged 179.5 ± 28.54 Mg C ha^{-1}, Mollisol TC stocks averaged 540.8 ± 161.9 Mg C ha^{-1}, and Oxisol sites averaged 129.5 ± 15.82 Mg C ha^{-1} (Fig. 4). TC stocks averaged 325.9 ± 100.21 Mg C ha^{-1} for forests and 235.9 ± 79.3 Mg C ha^{-1} for pastures (Fig. 5).

Organic C stocks to 1 m ranged from 69 Mg C ha^{-1} to 328 Mg C ha^{-1} with an overall mean of 176.9 ± 15.1 Mg C ha^{-1} (Table 2, Fig. 3). Average Inceptisol OC stocks were 178.6 ± 28.7 Mg C ha^{-1}, Mollisol stocks averaged 222.3 ± 22.43 Mg C ha^{-1}, and Oxisol sites averaged 129.5 ± 15.8 Mg C ha^{-1} (Fig. 4). Average forest OC stocks to 1 m were 197 ± 25.7 Mg C ha^{-1} and average pasture stocks were 158.4 ± 15.9 Mg C ha^{-1} (Fig. 5).

Inorganic C made up a substantial amount of TC at three Mollisol sites, where up to 86 % of TC consisted of inorganic C. Two Inceptisol sites had small amounts of inorganic C, but inorganic C was never more than 6 % of TC. Oxisols had no detectable inorganic C.

TN stocks ranged from 5 Mg N ha^{-1} to 39 Mg N ha^{-1} with an overall mean of 18.1 ± 1.6 Mg N ha^{-1} (Table 2, Fig. 3). Average Inceptisol TN stocks were 17.9 ± 2.2 Mg N ha^{-1}, Mollisol sites averaged 23.7 ± 2.7 Mg N ha^{-1}, and Oxisol sites averaged 12.63 ± 2.5 Mg N ha^{-1} (Fig. 4). Forest sites averaged 19.1 ± 1.2 Mg N ha^{-1} and pasture sites averaged 17.2 ± 2.0 Mg N ha^{-1} (Fig. 5).

In most cases there was a significant decrease in OC density with depth. When pits were analyzed as a split plot with a shallow (0 - 30 cm) and deep (30 – 100 cm) depth, there was no significant difference in mean OC stock between the two depths. This indicates that C densities in the top 30 cm were roughly twice as great given that the deep portion was over twice as thick as the shallow portion. There were no significant interactions between depth and soil order or land cover.

Organic carbon (OC) stocks by soil order and land cover

Soil order was an important factor in determining OC stocks across different depth increments (Table 3). Mean OC stock differed by soil order, at least marginally, from 0 to 100 cm ($p = 0.04$, Fig. 4), 0 to 30 cm ($p = 0.046$, Fig. 8), and 30 to 100 cm ($p = 0.087$, Fig. 9). At these three depths, Mollisols had the greatest mean OC stocks, and Oxisols had the lowest OC stocks (Figs. 4, 8, 9). There was no significant difference in OC stocks among soil orders in the 0-5 cm depth.

The effect of land cover on SOC stocks depended on the depth increment considered. Land cover was a marginally significant predictor of mean OC stocks for 0 to 30 cm ($p = 0.062$, Fig. 10). For this depth, forest soils contained more OC than pasture soils. Land cover was not a significant predictor of OC stocks at any other depth in models that contained just land cover and soil order as predictor variables (Figs. 5, 11). At no depth was there an interaction between soil order and land cover (Fig. 12).

Total carbon (TC) stocks by soil order and land cover

Mean TC stocks differed significantly by soil order for all depth increments considered (Table 3). For most depth increments, Mollisols had greater TC stocks than Inceptisols and Oxisols (Fig. 4, Fig. 8). The one exception was for 30 to 100 cm, where Inceptisol and Mollisol mean TC stocks were not significantly different, but both were greater than Oxisol TC stocks (Fig. 9).

Land cover was not a significant predictor of TC stocks at any depth increment when soil order and land cover were the two predictor variables in the model (Figs. 5, 10, 11). There were no interactions between soil order and land cover (Fig. 12).

Total nitrogen (TN) stocks by soil order and land cover

Mean TN stocks differed by soil order at least marginally for all of the depth increments considered (Table 3). Mollisol ($p = 0.002$) and Inceptisol ($p = 0.06$) mean TN stocks were both greater than Oxisol TN stocks from 0 to 100 cm (overall $p = 0.009$; Fig. 4). Similarly, TN stocks were greater in Mollisols and Inceptisols than in Oxisols for 0 to 30 cm ($p = 0.003$ and 0.07 respectively, overall $p = 0.009$, Fig. 8). The same pattern also held for 30-100 cm (overall $p = 0.06$, Fig. 9). For 0-5 cm, Oxisols had greater TN stocks than Mollisols ($p = 0.037$).

Land cover was not a significant predictor of TN stocks for any depth increment when soil order and land cover were the two predictor variables in the model (Figs. 5, 10, 11). There were no interactions between soil order and land cover (Fig. 12).

Effects of environmental variables on soil C and N stocks

Combined, the clay and fine silt (< 20 μm) fractions of a horizon showed a significant positive relationship with horizon OC content for the subset of the sites measured with laser diffraction ($p = 0.0007$) but explained only 12 % of the variability in OC content. At the pit level, the average clay, and average fine silt and clay fractions did not show a significant relationship with pit OC stock (Fig. 13, $p = 0.15$). Removing one pit with a particularly high OC stock and low clay content, made the fine silt + clay relationship significant ($p = 0.002$) at the pit level and increased the explained variance substantially, from 12 % to 39 %. Horizon soil pH values showed a weak positive relationship ($R^2 = 0.01$) with OC content per horizon (Fig. 14). At the site level, average pH was significantly correlated with OC and explained 21% of the variation in site OC stocks (Fig. 15, $p=0.021$). There was no significant relationship between mean annual precipitation and SOC stocks (Fig. 16) or mean annual temperature and SOC stocks (Fig. 17).

Predictive ability increased when all the environmental variables were added to models with soil order and land cover, explaining 69% of the total variance. Due to the potential for overfitting given the relatively small number of sites relative to predictor variables, model selection was performed to identify which environmental variables were most important. For OC stocks to 1 m, the model that was both most predictive and parsimonious contained soil order, land cover, percent clay and pH. This model explained 66 % of the total variance. For the 0 to 30 cm depth, the best model contained only land cover, pH, and MAP. However, one point with very high MAP was overly influential in this model. With that site removed, the final model contained land cover, pH, and percent clay. For the 30 to 100 cm depths, the final model contained just soil order.

Soil C:N ratios

Soil OC and TN stocks were strongly correlated across pits, sites, and horizons. In general soil C:N ratios decreased with depth, and became more variable with depth. This general trend was observed under both land cover classes and for all three soil orders (Figs. 18 and 19). C:N ratios did not differ significantly by land cover or soil order, except for the 0-5 cm depth. Forest soils had significantly greater C:N ratios than pasture soils in the top 5 cm ($p = 0.049$) with a mean C:N ratio in forests of 13.6 ± 0.6 compared to a mean of 12.0 ± 0.6 in pastures. There was a marginally significant difference between C:N ratio by soil order for the 0-5 cm depth, with Oxisols having a greater C:N ratio than the other two soil orders ($p = 0.079$). The mean C:N ratio in Oxisols for the 0-5 cm depth was 14.14 ± 0.7, in Inceptisols it was 12.08 ± 0.7, and in Mollisols it was 12.18 ± 0.6.

Discussion

Soil order is a more important predictor of soil C than land use at a regional scale

Overall, soil order was the most important predictor of mean OC, TC, and TN stocks across all depth increments. As predicted, mean OC stocks were greatest in

Mollisols, for all depths, and lowest for Oxisols at all depths, as has been found by others (Johnson and Kern 2002, Cleveland et al. 2003, Tan et al. 2004). Mollisols are principally defined by a thick mollic epipedon that is often rich in organic matter, hence they are predicted to have relatively large OC stocks. Most of the Mollisols in our study formed on calcareous parent material (also known as rendzinas or carbonate-humus soils, e.g., Jenny 1941) and thus developed a mollic epipedon primarily due to the calcareous parent material rather than from the large amounts of organic matter from root inputs as for temperate Mollisols developing under prairie or grasslands. However, the Mollisols in our study still had greater OC stocks than the other two soil orders studied. Average Mollisol OC stocks at our sites (145 ± 13 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 (1996) and less than the 268 Mg C ha^{-1} reported in Hawaiian Mollisols by Johnson and Kern (2002) (See Table S1). 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 was inorganic C), while only two Inceptisol had small amounts of inorganic C (less than 6 % of total C), and no Oxisol sites had any inorganic C. The large amounts of inorganic C in the Mollisols also 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) and a significant portion of the US Virgin Islands.

Oxisols had the lowest mean SOC stocks, as expected for highly-weathered soils. In contrast, an earlier analysis of Puerto Rican soils, Beinroth et al. (1996) reported no differences in OC stocks down to 50 cm between Oxisols and Mollisols. In general, the

Oxisol OC stocks reported here are lower than the averages reported in that study, and the Mollisol OC stocks reported here are higher. When analyzing to 50 cm, Oxisols in this study averaged 95.7 ± 10.0 Mg C ha^{-1} compared to 111.9 Mg C ha^{-1} as reported in Beinroth et al. (1996). The average OC stock to 1 m in our study is also lower than the 167 Mg C ha^{-1} reported for Puerto Rican Oxisols by Johnson and Kern (2003) (Table S1). Seven of our Oxisol sites came from one soil series (Los Guineos), which is not representative of the spectrum of Oxisols in Puerto Rico. For instance, a grassland Oxisol site listed in Beinroth's study had OC stocks to 50 cm of 240 Mg C ha^{-1} or more than double what we found. Our findings are closer to those reported by a study of Panamanian Oxisols on Barro Colorado Island, which reported OC stocks in the top 50 cm of 86.6 Mg C ha^{-1} (Grimm et al. 2008). Because climate is relatively similar among the sites in these and our study, additional factors such as soil mineralogy or land use and disturbance history may contribute to the wide range in SOC stocks for Oxisols.

As predicted, Inceptisols were variable in their OC stocks, 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 Inceptisol site that had the greatest OC stocks of any site in the study had an organic horizon as well as evidence of waterlogging, which was unique for these sites. Our reported OC stocks are lower than the stocks reported for Johnson and Kern (2003) but greater than the stocks reported by Beinroth et al. (1996).

The differences we observed by soil order are at least partially a function of how we extrapolated soil profiles to 1 m. We used extrapolation to standardize across pits, but it does introduce uncertainty and overestimates stocks in pits and sites with shallow soils. A number of the Inceptisols and Mollisols in this study were shallow and needed extrapolation, whereas all Oxisols extended to at least 1 m deep (Table S2). We cannot speculate as to the total soil depth or OC stock, but all Oxisols extended at least to 1 m so total C stocks are certainly greater than what is reported here. Analysis of the raw data without extrapolation to 1 m found no significant difference in OC or TN stocks to 1 m (or deepest horizon) among soil orders, although the relative order is the same (i.e., Mollisols > Inceptisols > Oxisols). For the 0-30 cm depth, which needed almost no extrapolation, Mollisols contained greater OC stocks than Oxisols in surface soils (Fig. 8). These patterns lend support to the claim that Oxisols, while potentially having a lower C density than other soil orders, can have equal or greater C stocks if the full soil profile is considered.

Land cover influences OC stocks in shallower soil depths

Unlike soil order, current land cover was not a strong predictor of soil C content at the regional scale. OC stocks differed by land cover only in the shallower soil depths, from 0 to 30 cm. 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, but a relatively small amount relative to the total variability. Additionally, this variability was probably 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.

Forest soils contained on average 24% more OC than pasture soils, similar to studies by Brown and Lugo (1990) and Beinroth et al. (1996). Other studies have reported greater OC stocks in pasture surface soils (Schipper and Sparling 2011, Eclesia et al. 2012, Fujisaki et al. 2015) and greater OC stocks in deeper soils of forests (Eclesia et al. 2012). We did not see evidence of this pattern with depth, as deeper OC stocks did not differ by land cover.

Differences in land use within a given land cover class can influence depth patterns and overall trends in soil C storage. For example, pasture management can affect SOC storage, with fertilization, active management for productive species, and grazing intensity all having the potential to influence organic matter inputs (Trumbore et al. 1995, Fearnside and Barbosa 1998, Elmore and Asner 2006). Pasture age can also have an important effect on soil C stocks, as older pastures tend to have reduced C stocks relative to reference forests, whereas younger pastures may have greater SOC stocks (Brown and Lugo 1990, de Koning et al. 2003). It is possible that the 13 pasture sites in our study were heavily grazed or old, which could explain the reduced OC stocks relative to the forest sites, but we do not have detailed land use histories for these sites.

We found the greatest effect of land cover in the shallower depths, and no effect in deeper soils, indicating the importance of sampling depth. Other studies have noted the importance of analyzing deeper soil horizons to fully capture the effects of land-use change on soil C stocks. Roots are the most significant C input to soils (Rasse et al. 2005), and rooting depth typically differs between trees and grasses (Eclesia et al. 2012). Grasses have relatively larger root biomass, but shallower roots than trees; although some forage grasses introduced from Africa to tropical America are known to have exceptionally deep roots (Fisher et al. 1994). The lack of a response to land cover in deeper soil in this study could be due to several factors. One methodological explanation is that deep soil stocks in our study could be confounded by our method of extrapolating certain sites to 1 m. Another possibility is that the forests in this study are relatively young secondary forests, and deep soil C has not responded to the surface changes in land cover yet. Alternatively, OC stabilization mechanisms likely differ by depth, and C in deep soils may be particularly stabilized through mineral-organic associations (Rumpel and Kögel-Knabner 2011) making it more resistant to changes in land cover.

Effects of additional edaphic and environmental factors on SOC stocks

Including additional soil properties into the models substantially 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 still substantial variation in OC stocks within soil orders (Mayes et al. 2014). Although there is often a strong relationship between environmental variables (e.g., precipitation or temperature) and soil orders, there can still be substantial variation within a soil order, particularly for Inceptisols, which represented the driest and wettest sites in this study. Soil texture and pH can also vary substantially within soil orders, so it makes sense that these variables explained significant variation even after accounting for soil order.

Our findings support other studies that have found a positive correlation between OC storage and the clay content of soil (Feller and Beare 1997, Post and Kwon 2000, de

Carvalho Conceicão Telles et al. 2003, Laganière et al. 2010), but the relatively weak association indicates that other variables are more important. On its own, soil clay content was not a strong predictor of SOC storage. The combined fine silt (<20 μm) and clay fraction was a better predictor, but the exclusion of the "Cayey" sites from the silt and clay analysis likely strengthened the relationship we observed due to the high clay but low OC contents of these sites in the Los Guineos soil series. Soil texture, as percent clay, was included in the best model for OC stocks to 1 m, and had a positive slope, which indicates that especially after controlling for other factors, it did show a positive relationship with OC. However, clay mineralogy has been shown to be more important than soil texture for OC stabilization (Torn et al. 1997, Feller and Beare 1997, Six et al. 2002, López-Ulloa et al. 2005). Indeed, kaolinitic soils in our study tended to have lower OC stocks for a given clay content than other clay mineralogy types (Fig. 15), 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 a high OC stocks was considered to be "active" due to its relatively high CEC (Soil Survey Staff 2014). Further mineralogical analyses could reveal stronger relationships with OC contents.

Soil pH can influence OM stabilization through effects on soil fauna, and organic matter chemistry and reactivity (van Noordwijk et al. 1997, Kleber et al. 2014, Catoni et al. 2016, Kaiser et al. 2016). Soil pH varies systematically by soil order, and can also be influenced by land use, although we saw no evidence of that in this study. We observed a significant and positive correlation between pH and OC stocks. Other studies have reported conflicting relationships between pH and soil OC, although decomposition rates are often lowest in acidic and alkaline soils (Motavalli et al. 1995, van Noordwijk et al. 1997). One potential explanation for the positive correlation between pH and soil OC stocks is that calcium cations, abundant in calcareous soils with high pH, can stabilize soil OM through several mechanisms. 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 in soil also promotes aggregation of soil mineral particles, potentially leading to increased physical protection of OM (Six et al. 2004). A number of the sites with alkaline soils in this study contained free calcium carbonates, suggesting elevated calcium content. In particular, three of the Mollisols featured strong effervescence and limestone parent material indicative of free carbonates. We did not measure mechanisms of OM stabilization directly, but our findings corroborate the pattern of increased OC stocks in alkaline soils (Oades 1988, van Noordwijk et al. 1997).

Contrary to expectations, neither MAP and MAT were significant predictors in any of the models despite numerous studies that have shown an influence of both temperature and precipitation on soil C stocks at global and regional scales (e.g., Beinroth et al. 1996, Jobbágy and Jackson 2000, Marín-Spiotta and Sharma 2013). The temperature range represented in this study was not very large (8 degrees C), and all sites are relatively warm year-round so it is likely that temperature does not limit decomposition or productivity in this range.

Mean precipitation amounts varied much more substantially across the study region, from 825 to 4300 mm year^{-1} MAP. The effect of precipitation on soil C may have been confounded by soil order effects, as the soils with the greatest soil C content, Mollisols were found in drier sites where carbonates persist, 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 precipitation, which was overly influential in models containing MAP. That particular site, a forest on an Inceptisol located in the El Yunque National Forest, had an organic horizon and showed signs of low redox deeper in the profile, suggesting both high primary productivity and decreased decomposition rates. As site-level climatic data becomes available, stronger relationship between OC and these environmental factors may emerge.

Soil C:N ratios differ by land cover and soil order

We found differences in soil C:N ratios by land cover types and soil orders, but only in the top 5 cm. Our findings support other studies reporting greater C:N ratios in forest soils than pasture soils (Murty et al. 2002, Kirschbaum et al. 2008a, Berthrong et al. 2012). Greater C:N ratios in forest soils could indicate a difference in the C:N ratio of plant inputs, as tree litter and woody plant debris generally have a greater C:N ratio than grass inputs (Kirschbaum et al. 2008b, Berthrong et al. 2012). Effects of litter inputs would be most noticeable at the surface so our findings generally support this explanation. Differences in soil C:N ratios may also indicate differences in stage of decomposition, as organic matter C:N ratios predictably decrease with degradation of plant material and incorporation of microbial biomass and products, which have a much smaller C:N ratio (Baisden et al. 2002). Changes in the soil environment through land cover change could stimulate decomposition in pastures, through raising the soil temperature or changing soil moisture, for example (Reiners et al. 1994, Fearnside and Barbosa 1998). Decomposition rates could also be affected by differences in litter chemistry under different land cover, as tree litter often contains more lignin and tannins than grass litter (Marín-Spiotta et al. 2008) and is slower to decompose.

In addition to being indicative of processes influencing the C cycle, changes in the soil C:N ratio can have implications for overall soil C storage. Organic C in soil is bound to organic N in organic matter, and the stoichiometric ratio of organic matter influences the total amount of C that can be stored in organic matter. Modeling studies have suggested that changes in the C:N ratio or N stocks are one of the primary controls on site level soil OC (Kirschbaum et al. 2008b, 2008a). Our study shows an increase in OC stocks under forests, but no significant change in soil N stocks, which contributed the observed increase in C:N ratio.

Conclusion

This study shows the importance of considering site-level environmental and edaphic factors when considering soil C storage at regional scales. Soil properties were important predictors of soil organic carbon, soil total nitrogen, and soil total carbon. There were significant differences in OC, TN, and TC stocks by soil order, with Mollisols containing the most OC at all depths. Inceptisols had intermediate stocks, and Oxisols had the lowest stocks. Soil pH was strongly and positively related to SOC stocks. Soil texture, as clay content, showed a weakly positive relationship overall, but was an important variable in several models predicting OC stocks. Land cover was most important in predicting OC stocks for the 0-30 cm depth, but it also explained significant variability in models predicting OC to 1 m when the additional covariates percent clay and soil pH were included. These findings illustrate the importance of extending beyond surface soils and considering different sampling depths to determine the effects of land use and land cover on OC stocks. Although there is much interest in predicting the changes to soil C following land-use change, this study also shows remarkable variability in soil C across a variety of soils and environmental conditions, highlighting the importance of understanding the role of soil properties in determining soil C stocks. An effort should be made to increase study of the broad range of soil types and environments present in the tropics, to better predict soil C stocks at regional scales.

Tables

Table 1. Site characteristics. Data come from USDA NRCS official soil series descriptions. pH and percent clay values are from the A horizon.

Site	Soil series	Land cover	Soil order	Suborder	MAP	MAT	Mineralogy	Parent Material
CPR03F02	Guayabota	Forest	Inceptisol	Aquepts	4293	18	Mixed, subactive	volcanic bedrock
CPR02F35	Pandura	Forest	Inceptisol	Udepts	2032	26	Mixed, active	plutonic rocks
CPR01F16	Pellejas	Forest	Inceptisol	Udepts	2032	25	Mixed, subactive	plutonic rocks
CPR11F03	Southgate	Forest	Inceptisol	Ustepts	1016	27	Mixed, active	igneous bedrock
CPR03P06	Coloso	Pasture	Inceptisol	Udepts	2032	26	Mixed, active	alluvial sediments
CPR02P03	Malaya	Pasture	Inceptisol	Udepts	1295	24	Mixed, superactive	calcareous tuffaceous rock
CPR01P71	Mucara	Pasture	Inceptisol	Udepts	1473	25	Vermiculitic	basalt lava and breccia
CPR11P07	Victory	Pasture	Inceptisol	Ustepts	1016	26	Mixed, superactive	volcanic rock
CPR01R03	Callabo	Rangeland	Inceptisol	Ustepts	1016	25	Mixed, superactive	basic volcanic rock
CPR04F01	Cintrona	Forest	Mollisol	Aquolls	826	26	Mixed, superactive	calcareous sediment and volcanic
CPR02F10	Soller	Forest	Mollisol	Rendolls	2159	25	Mixed, active	limestone
CPR11F04	Susannaberg	Forest	Mollisol	Ustolls	1016	26	Vermiculitic	basic volcanic rock
CPR01F100	Fredricksdal	Forest	Mollisol	Ustolls	1016	26	Vermiculitic	igneous bedrock
CPR04P03	Bajura	Pasture	Mollisol	Aquolls	1461	25	Mixed, superactive	mixed origin
CPR01P85	Toa	Pasture	Mollisol	Udolls	1803	26	Mixed, active	floodplain, mixed origin
CPR10P03	Sion	Pasture	Mollisol	Ustolls	1016	26	Carbonatic	alkaline marine deposits
CPR02R06	Descalabrado	Rangeland	Mollisol	Ustolls	889	25	Mixed, superactive	mixed basic volcanic rock
CPR01F130	Los Guineos	Forest	Oxisol	Udox	3048	20	Kaolinitic	sandstone
Cayey-28	Los Guineos	Forest	Oxisol	Udox	2000	22	Kaolinitic	sandstone
Cayey-38	Los Guineos	Forest	Oxisol	Udox	2000	22	Kaolinitic	sandstone
Cayey-68	Los Guineos	Forest	Oxisol	Udox	2000	22	Kaolinitic	sandstone
CPR01P27	Coto	Pasture	Oxisol	Ustox	1740	25	Kaolinitic	limestone
Cayey-100	Los Guineos	Pasture	Oxisol	Udox	2000	22	Kaolinitic	sandstone
Cayey-101	Los Guineos	Pasture	Oxisol	Udox	2000	22	Kaolinitic	sandstone
Cayey-99	Los Guineos	Pasture	Oxisol	Udox	2000	22	Kaolinitic	sandstone

Table 2. Average site characteristics for 0-100 cm. Pits that did not extend to 1 m were extrapolated using the values of the lowest horizon. C:N ratio, mean pH, and mean clay content were calculated as the averages of the horizons for each pit. The standard error of the mean is in parentheses.

Site	Soil series	Land cover	Soil order	TC Stock (Mg C / ha)	OC Stock (Mg C / ha)	TN Stock (Mg N / ha)	C:N Ratio	Mean pH	Mean clay content (%)
CPR01F16	Pellejas	Forest	Inceptisol	108 (10.3)	108 (10.3)	10.8 (1.4)	8.75 (0.3)	5.78 (0.1)	4
CPR02F35	Pandura	Forest	Inceptisol	124 (18.9)	124 (18.9)	13.6 (1.5)	7.74 (0.3)	5.27 (0.1)	9
CPR03F02	Guayabota	Forest	Inceptisol	318 (68.3)	318 (68.3)	20.3 (3.8)	13.29 (0.8)	5.00 (0.1)	16
CPR11F03	Southgate	Forest	Inceptisol	328 (27.7)	328 (27.7)	33.3 (2.6)	8.46 (0.2)	6.97 (0.3)	12
CPR01P71	Mucara	Pasture	Inceptisol	175 (13.3)	175 (13.3)	20.6 (1.8)	7.33 (0.2)	7.31 (0.1)	18
CPR01R03	Callabo	Pasture	Inceptisol	181 (23.9)	181 (23.9)	19.2 (2.3)	8.06 (0.2)	7.03 (0.1)	23
CPR02P03	Malaya	Pasture	Inceptisol	129 (36.0)	122 (26.6)	14.4 (3.3)	7.29 (0.2)	7.67 (0.2)	9
CPR03P06	Coloso	Pasture	Inceptisol	145 (4.7)	145 (4.7)	15.8 (0.6)	7.88 (0.1)	6.22 (0.2)	24
CPR11P07	Victory	Pasture	Inceptisol	105 (12.3)	105 (12.3)	13.3 (1.8)	6.83 (0.1)	6.83 (0.1)	16
CPR01F100	Fredricksdal	Forest	Mollisol	158 (14.3)	158 (14.3)	18.2 (2.2)	7.57 (0.4)	7.41 (0.2)	25
CPR02F10	Soller	Forest	Mollisol	1148 (171.5)	286 (50.8)	39.1 (7.4)	6.35 (0.1)	8.05 (0.1)	41
CPR04F01	Cintrona	Forest	Mollisol	934 (12.9)	248 (6.2)	21.7 (0.6)	9.81 (0.1)	8.62 (0)	31
CPR11F04	Susannaberg	Forest	Mollisol	278 (40.2)	278 (40.2)	25.2 (2.3)	9.32 (0.5)	7.43 (0.1)	23
CPR01P85	Toa	Pasture	Mollisol	144 (8.5)	144 (8.5)	15.7 (1.3)	7.93 (0.3)	6.03 (0.1)	17
CPR02R06	Descalabrado	Pasture	Mollisol	194 (22.1)	194 (22.1)	18.7 (1.5)	8.82 (0.4)	7.01 (0.1)	24
CPR04P03	Bajura	Pasture	Mollisol	302 (14.4)	302 (14.4)	29.7 (1.9)	8.74 (0.1)	6.72 (0.1)	35
CPR10P03	Sion	Pasture	Mollisol	1168 (131.5)	169 (9.0)	21.9 (0.8)	6.60 (0.3)	8.42 (0)	19
Cayey-28	Los Guineos	Forest	Oxisol	108 (4.2)	108 (4.2)	8.6 (0.3)	10.8 (0.7)	4.49 (0)	28
Cayey-38	Los Guineos	Forest	Oxisol	88 (8.8)	88 (8.8)	7.8 (1.1)	9.81 (0.8)	4.33 (0)	29
Cayey-68	Los Guineos	Forest	Oxisol	137 (8.5)	137 (8.5)	11.9 (0.5)	9.82 (0.4)	4.44 (0)	37
CPR01F130	Los Guineos	Forest	Oxisol	181 (13.2)	181 (13.2)	18.4 (1.8)	8.53 (0.3)	5.00 (0)	43
Cayey-100	Los Guineos	Pasture	Oxisol	70 (18.4)	70 (18.4)	5.7 (1.5)	10.59 (0.2)	4.24 (0)	34
Cayey-101	Los Guineos	Pasture	Oxisol	135 (20.6)	135 (20.6)	10.2 (1.5)	11.35 (0.3)	4.63 (0)	41
Cayey-99	Los Guineos	Pasture	Oxisol	115 (9.7)	115 (9.7)	10.7 (0.7)	9.20 (0.3)	5.02 (0)	28
CPR01P27	Coto	Pasture	Oxisol	203 (9.5)	203 (9.5)	27.8 (0.7)	6.27 (0.3)	5.91 (0.2)	34

Table 3. ANOVA output for models including soil order, land cover and the interaction between soil order and land cover for three depths. All models for TC stock were natural log transformed to meet assumptions of normality and equal variance. P-values in bold indicate significant effects at the α=.05 level and those in italics indicate significant effects at the α=.10 level

		Depth					
		0-100 cm		0-30 cm		30-100 cm	
		F	P-value	F	P-value	F	P-value
Model:	**OC stock = Soilorder + Landcover + Soilorder:Landcover**	2.023	*0.097*	2.899	**0.041**	1.72	0.18
Variable	Soilorder	3.826	**0.047**	3.63	**0.046**	2.79	**0.087**
	Landcover	1.914	0.183	3.94	*0.062*	0.778	0.389
	Soilorder:Landcover	0.677	0.520	1.69	0.21	1.09	0.357
Model:	**TN stock = Soilorder + Landcover + Soilorder:Landcover**	2.555	*0.063*	3.57	**0.019**	1.49	0.239
Variable	Soilorder	4.49	**0.025**	6.1	**0.009**	3.166	*0.065*
	Landcover	0.369	0.551	0.768	0.392	0.199	0.661
	Soilorder:Landcover	0.405	0.673	2.49	0.11	0.434	0.654
Model:	**ln(TC stock)= Soilorder+Landcover+Soilorder:Landcover**	3.13	**0.03**	3.32	**0.026**	2.94	**0.04**
Variable	Soilorder	5.56	**0.005**	6.29	**0.008**	6.78	**0.006**
	Landcover	0.34	0.363	1.9	0.184	0.5	0.388
	Soilorder:Landcover	0.15	0.825	1.06	0.366	0.211	0.811

Figures

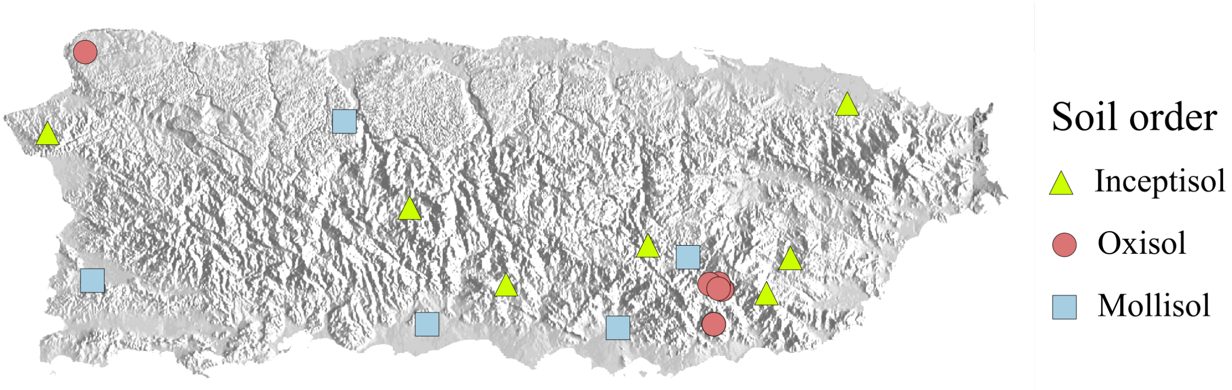

Figure 1. Map of Puerto Rico showing location of 20 study sites. The symbols represent the three soil orders sampled: Inceptisols (green triangles), Oxisols (red circles) and Mollisols (blue squares). The sites in the US Virgin Islands are not shown here. The “Cayey” sites are overlapped in the Oxisol cluster in the southeastern part of the island.

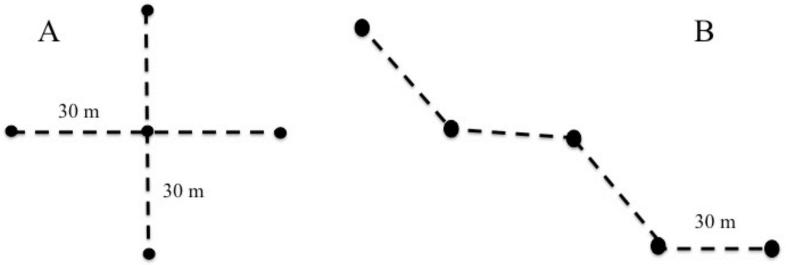

Figure 2. Soil collection design at each site. If possible, the clustered design in A was used. If that design was not possible for a given site, a version of the chain transect in B was used, to keep the pits on the same soil type and land cover at each site.

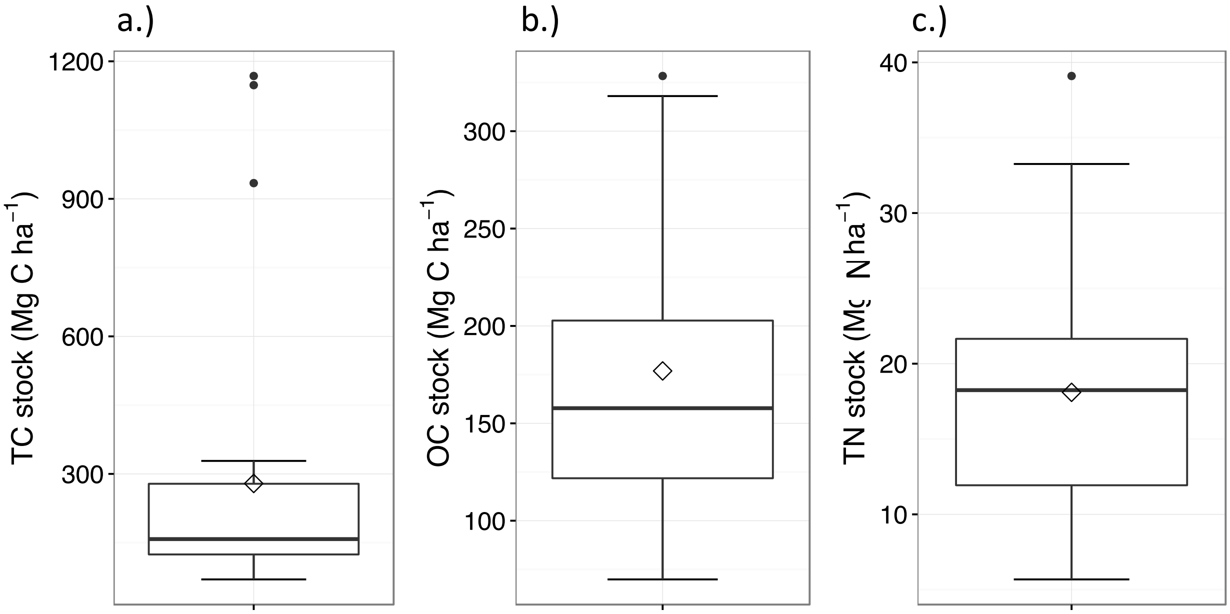

Figure 3. Distribution of average site stocks for all sites to 1 m. The median is denoted by the solid horizontal line. The mean is denoted by the diamond. The box covers the first through third quartiles and the whiskers extend to the last points within a distance of 1.5 times the interquartile range. Points outside 1.5 times the interquartile range (IQR) are marked by dots. Note the different scale of the y axes.

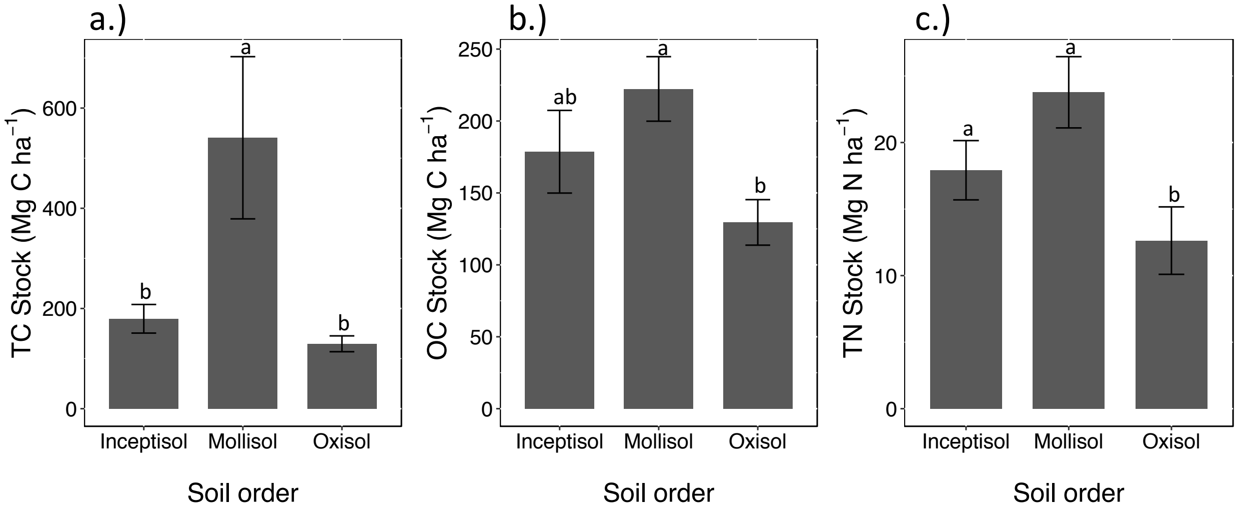

Figure 4. Total C (a), organic C (b), and total N (c) stocks from 0 to 100 cm by soil order in sites from Puerto Rico and US Virgin Islands. Error bars represent ±1 SE. Note the different scales on the y axes. Different letters within each panel represent significant differences at the $\alpha = .05$ level by Fisher's LSD.

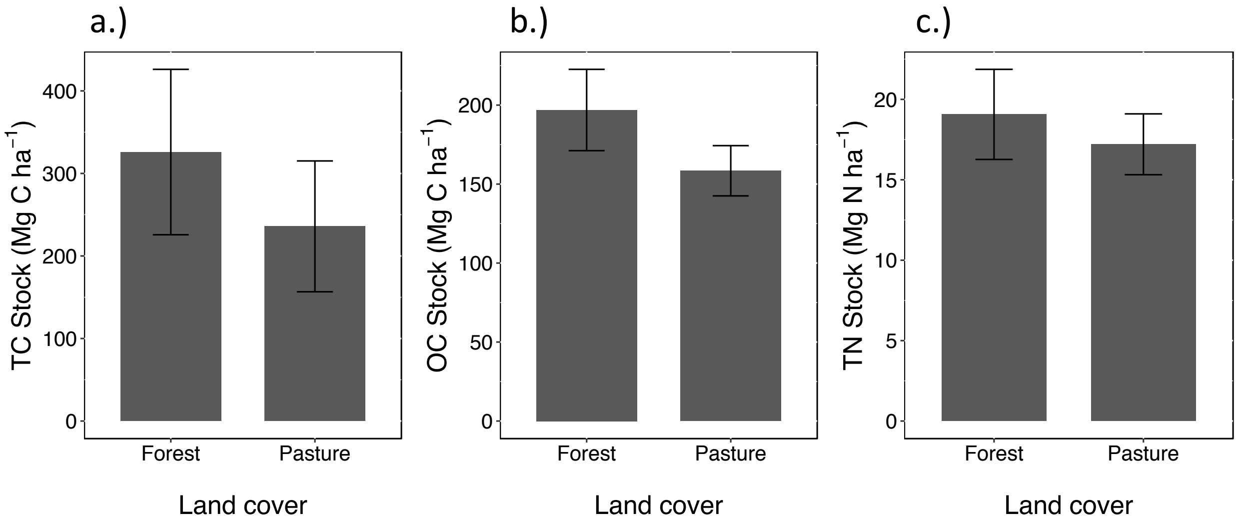

Figure 5. Total C (a), organic C (b), and total N (c) stocks from 0 to 100 cm by land cover in sites from Puerto Rico and US Virgin Islands. Error bars represent ±1 SE. Note the different scales on the y axes.

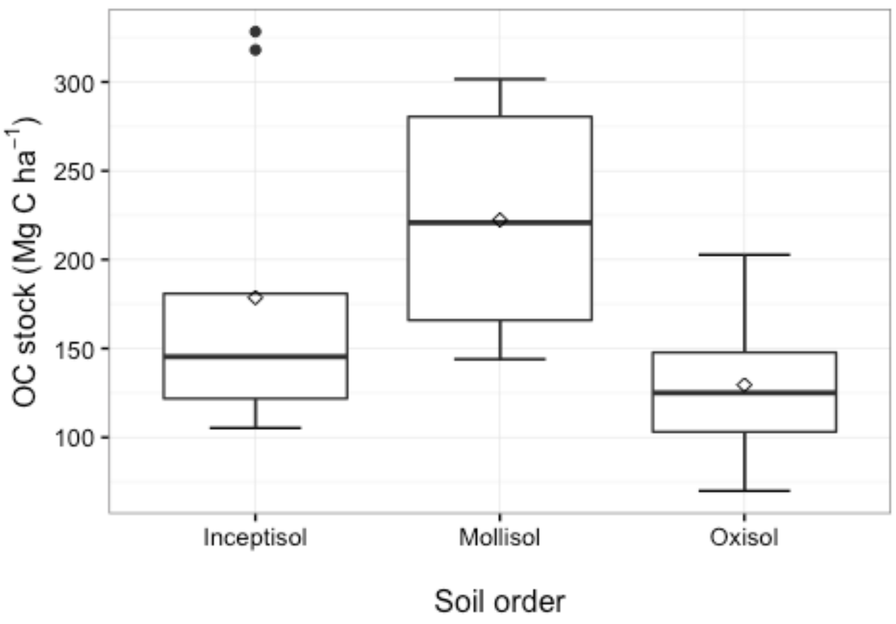

Figure 6. Distribution of average site organic C stocks to 1 m by soil order. The median is denoted by the solid horizontal line. The mean is denoted by the diamond. The box covers the first through third quartiles and the whiskers extend to the last points within a distance of 1.5 times the interquartile range. Points outside 1.5 times the interquartile range (IQR) are marked by dots.

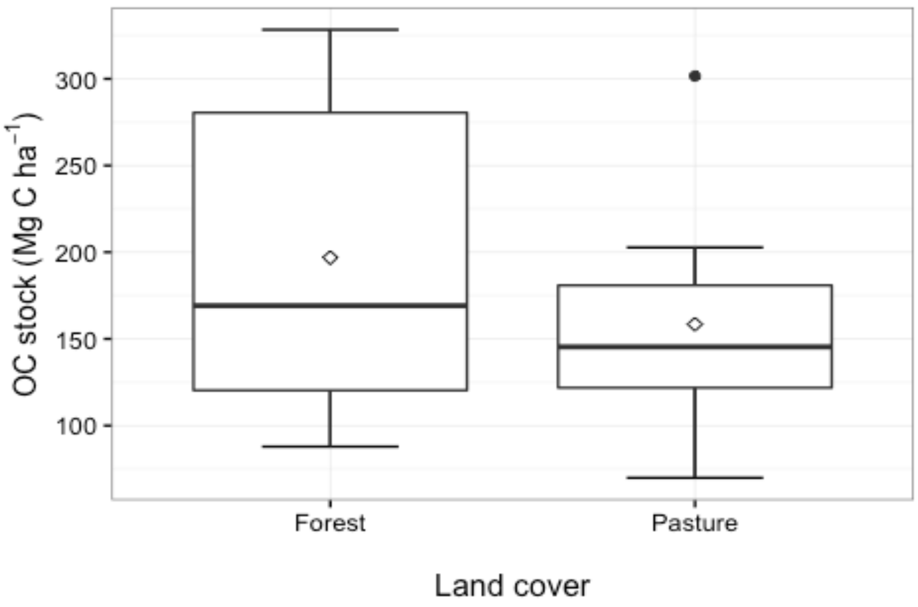

Figure 7. Distribution of average site organic C stocks to 1 m by land cover. The median is denoted by the solid horizontal line and the mean by the diamond. The box covers the first through third quartiles and the whiskers extend to the last points within a distance of

1.5 times the interquartile range. Points outside 1.5 times the interquartile range (IQR) are marked by dots.

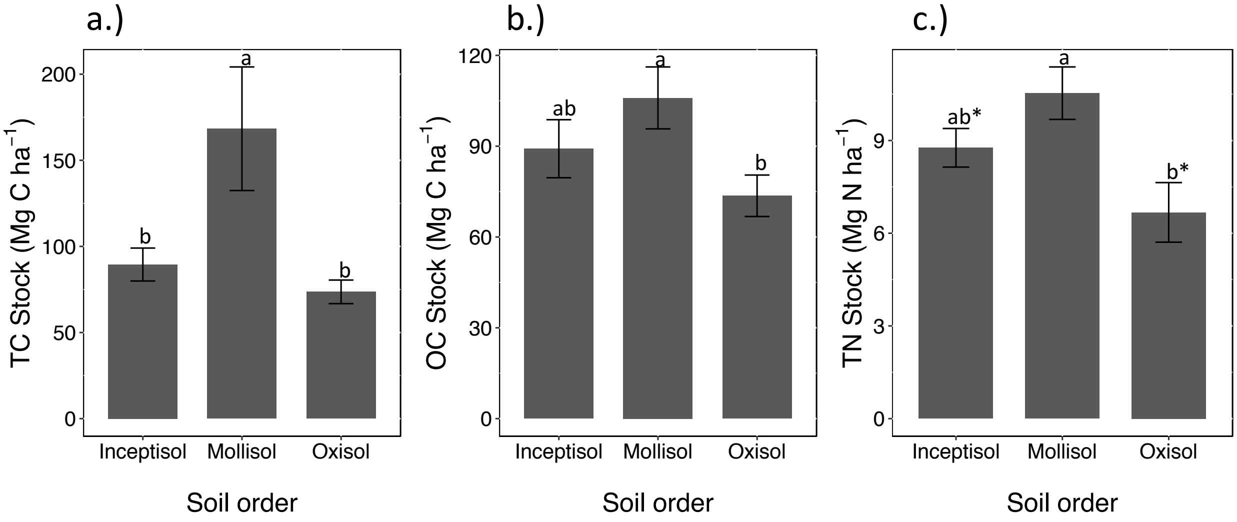

Figure 8. Total C (a), organic C (b), and total N (c) stocks from 0 to 30 cm by soil order in sites from Puerto Rico and US Virgin Islands. Error bars represent ±1 SE. Note the different scales on the y axes. Different letters within each panel represent significant differences at the $\alpha = .05$ level by Fisher's LSD. An asterisk next to a shared letter indicates a significant difference at the $\alpha = .10$ level.

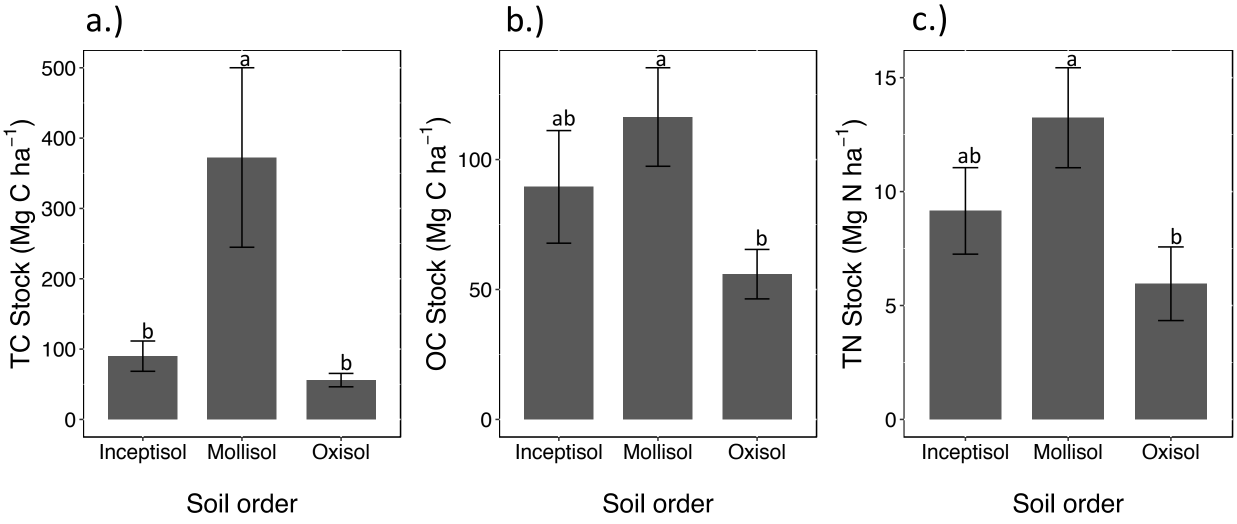

Figure 9. Total C (a), organic C (b), and total N (c) stocks from 30 to 100 cm by soil order in sites from Puerto Rico and US Virgin Islands. Error bars represent ±1 SE. Note the different scales on the y axes. Different letters within each panel represent significant differences at the $\alpha = .05$ level by Fisher's LSD.

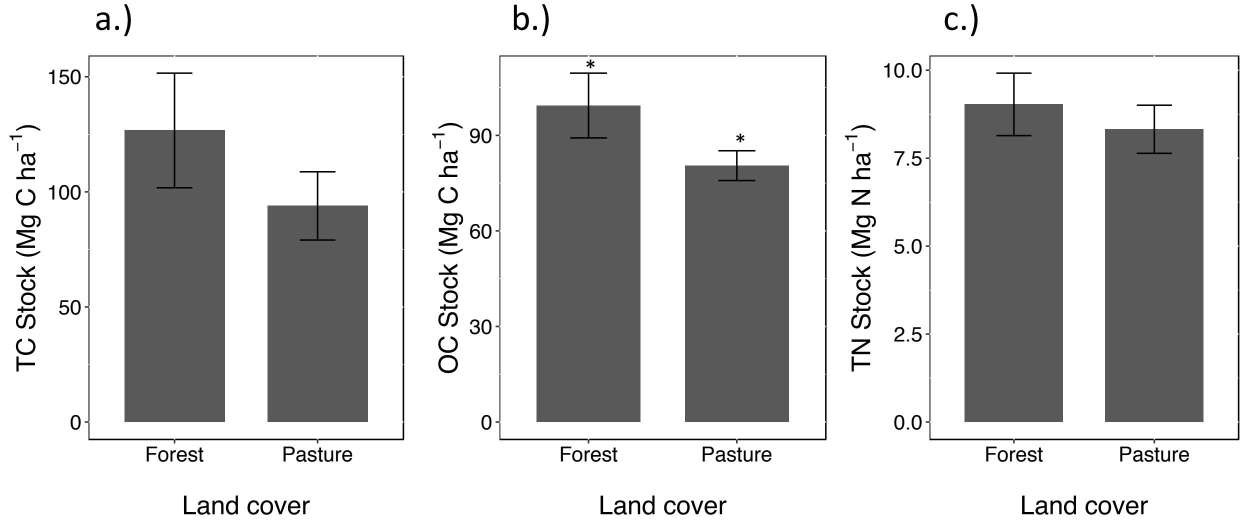

Figure 10. Total C (a), organic C (b), and total N (c) stocks from 0 to 30 cm by land cover in sites from Puerto Rico and US Virgin Islands. Error bars represent ±1 SE. Note the different scales on the y axes. Bars with asterisks represent significant differences at the α = .10 level by Fisher's LSD.

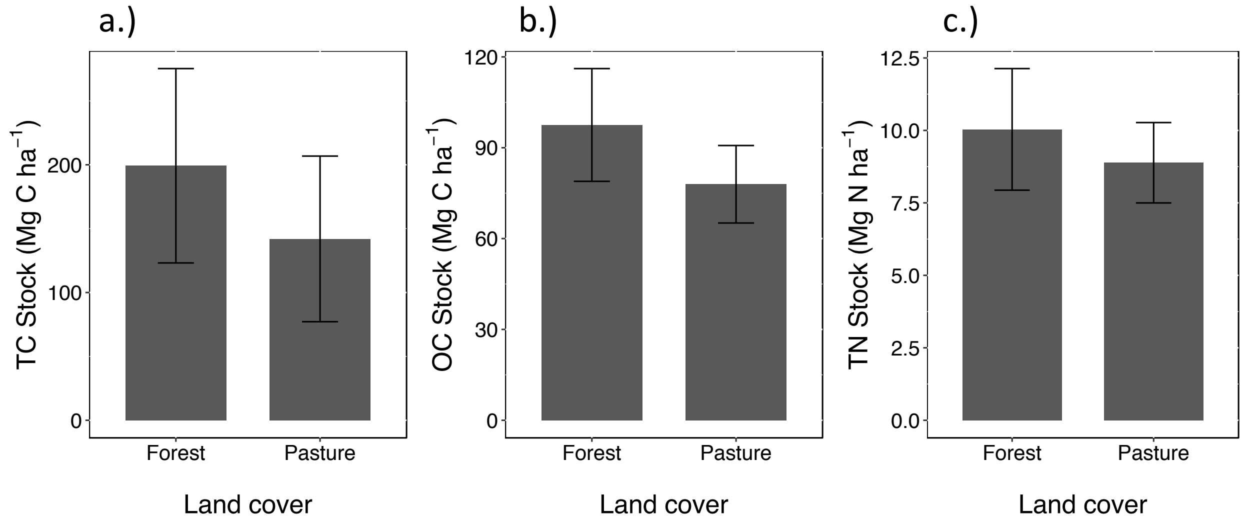

Figure 11. Total C (a), organic C (b), and total N (c) stocks from 30 to 100 cm by land cover in sites from Puerto Rico and US Virgin Islands. Error bars represent ±1 SE. Note the different scales on the y axes.

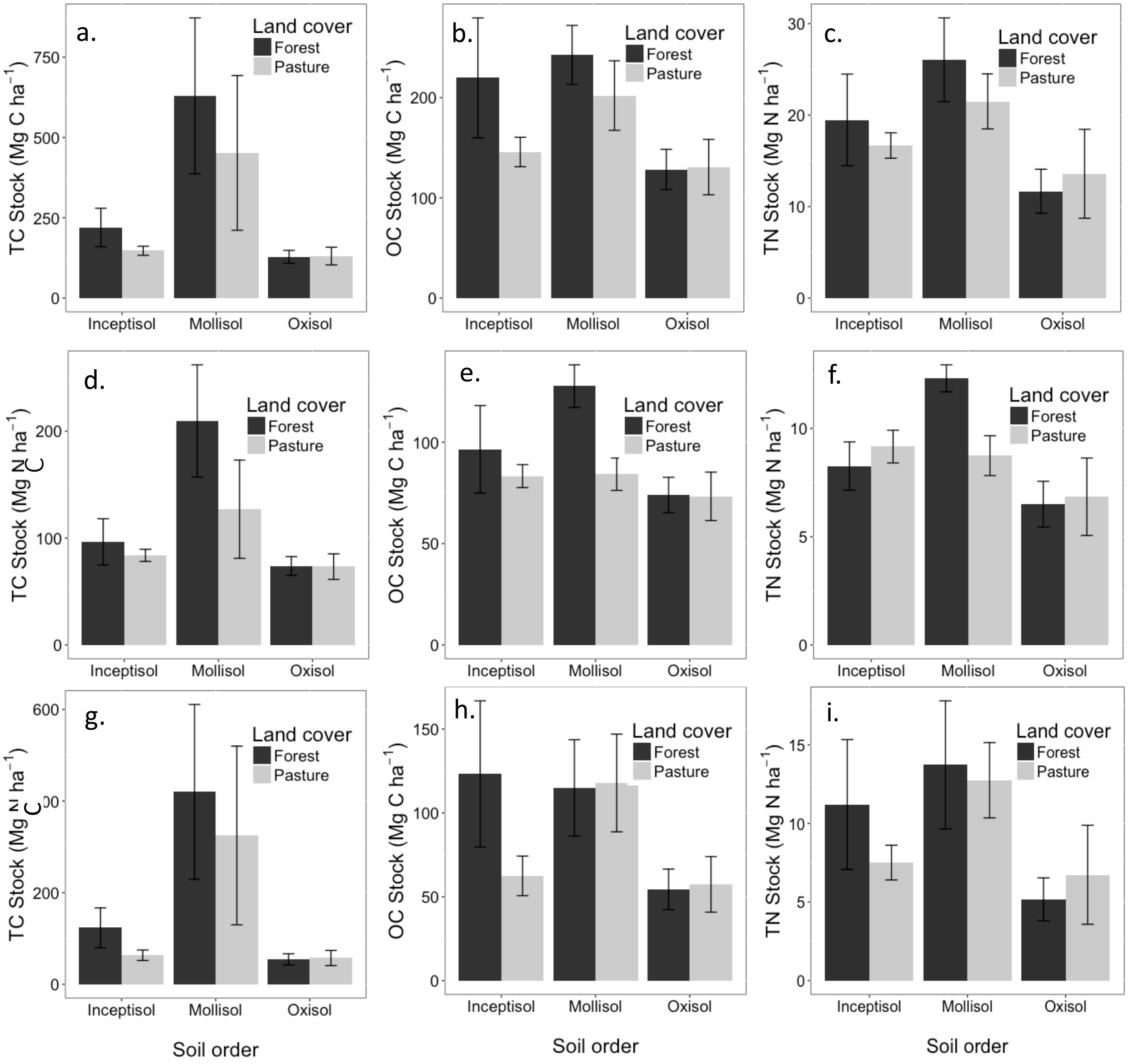

Figure 12. Total C (left column), organic C (middle column), and total N (right column) stocks by soil order and land cover in sites from Puerto Rico and US Virgin Islands. 0 to 100 cm is shown in the top row (a, b, and c), 0-30 cm is shown in the middle row (d, e, and f), and 30 to 100 cm is in the bottom row (g, h, and i). Error bars represent ±1 SE. Note the different scales on the y axes. There were no significant differences by land cover within a soil order.

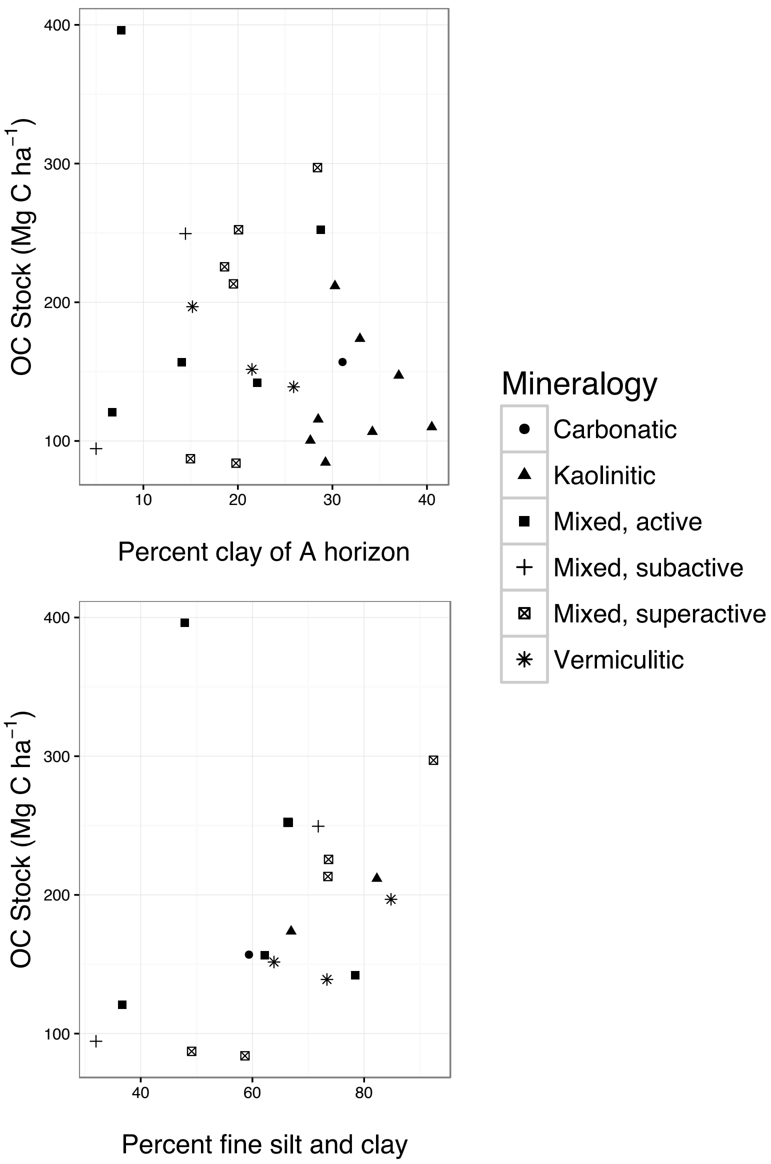

Figure 13. Relationship between soil texture and OC stocks. The top figure has the percent clay of the A horizon for all 25 sites on the x axis and the relationship is not statistically significant. The bottom figure has the average combined fine silt (<20 um) and clay fraction for the pit for the 19 sites that were measured using laser diffraction. Sites are color-coded based on the clay mineralogy from the NRCS soil series description. The regression in the bottom panel is not significant (p= 0.15), but removing the outlier point in the upper left hand corner makes the relationship significant (R^2 = 0.48, p = 0.002).

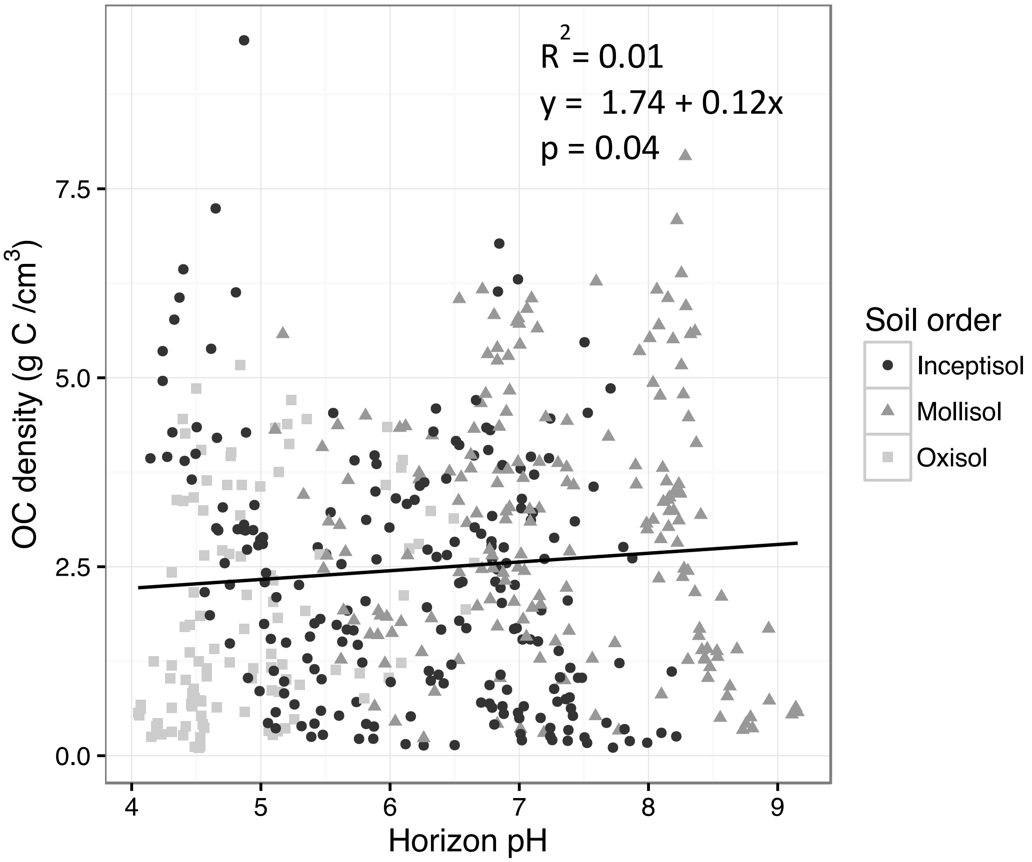

Figure 14. Relationship between soil horizon pH and OC density across 20 sites distributed across three soil orders representing pasture and forest cover in Puerto Rico and the U.S. Virgin Islands.

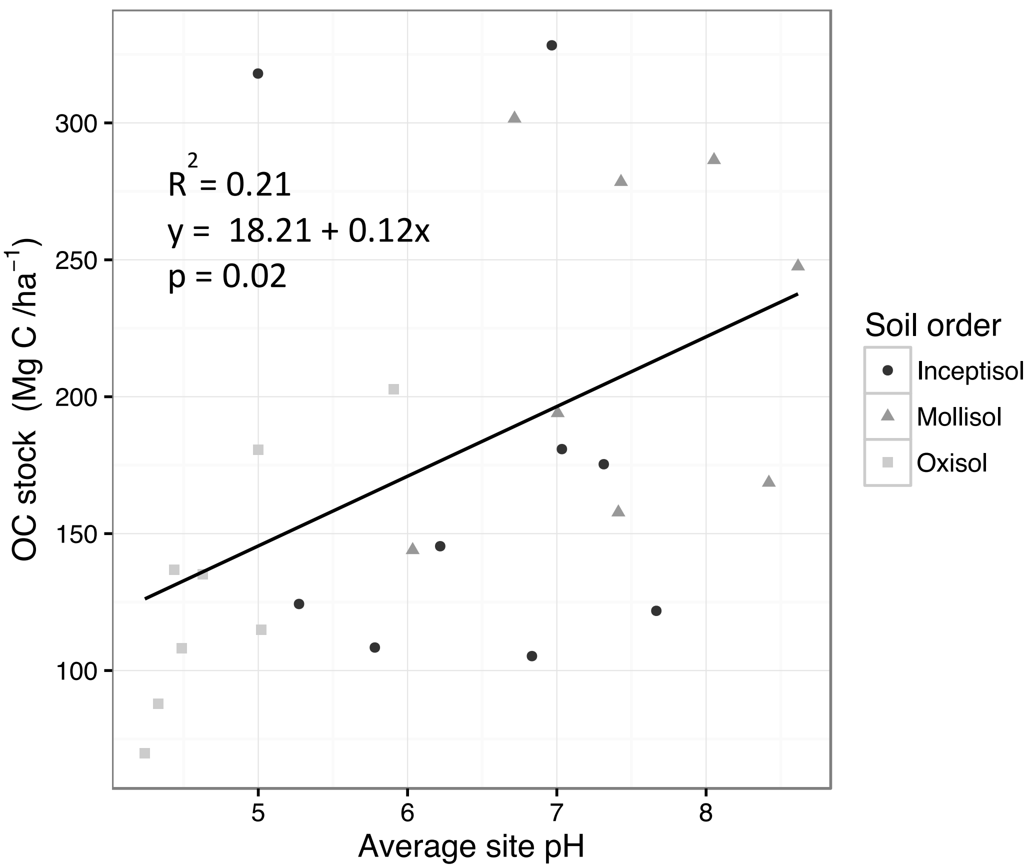

Figure 15. Relationship between average site pH and mean site OC stock.

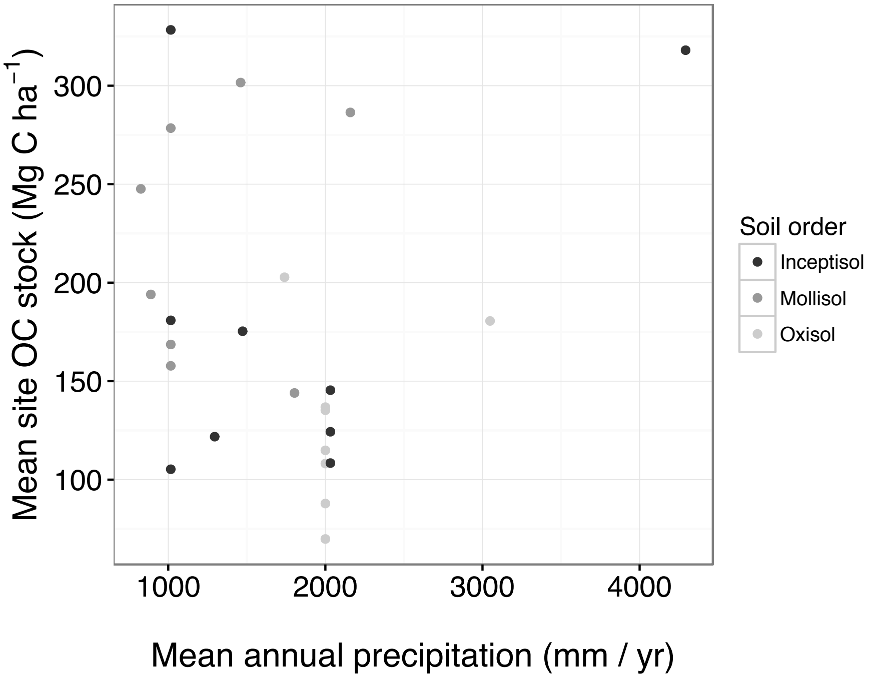

Figure 16. Relationship between mean site OC stock to 1 m and mean annual precipitation (MAP). There is no significant relationship between the two variables for these sites.

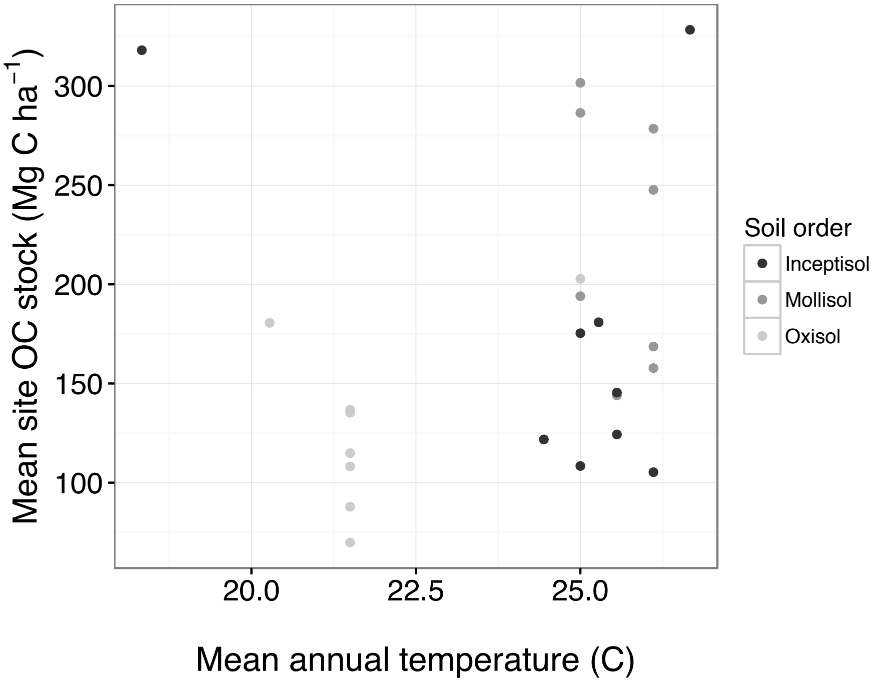

Figure 17. Relationship between mean site OC stock to 1 m and mean annual temperature (MAT). There is no significant relationship between the two variables for these sites.

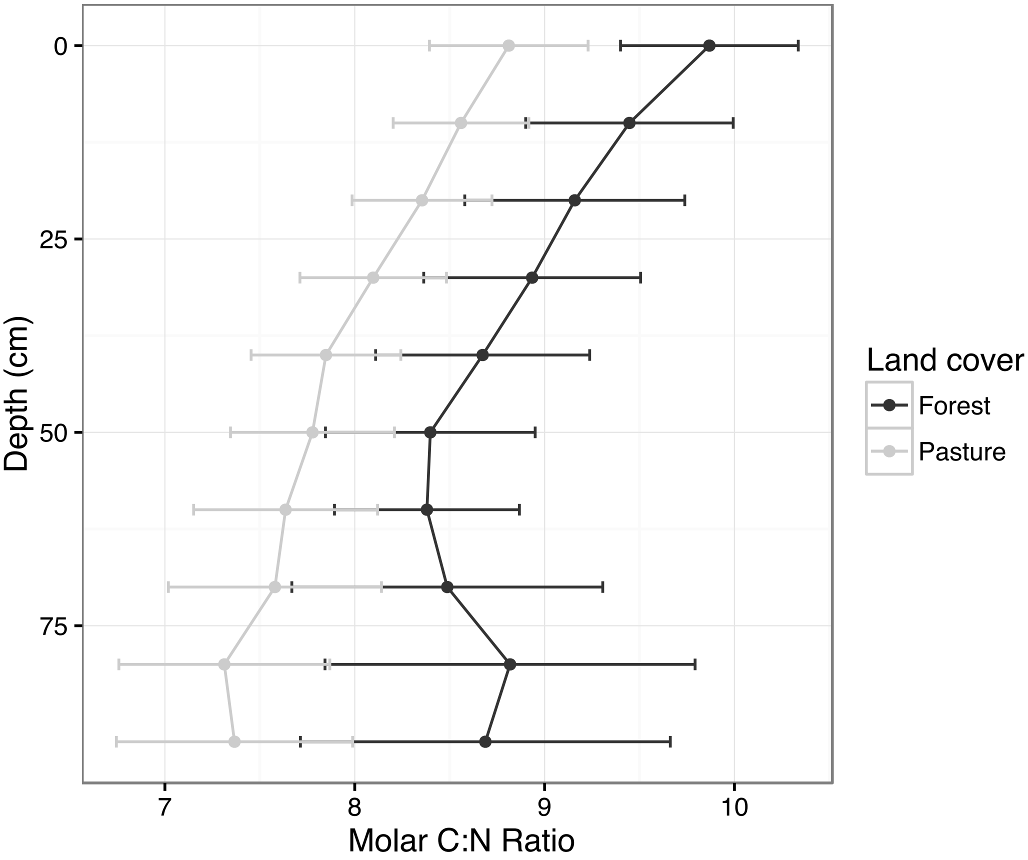

Figure 18. Change in mean soil C:N ratio with depth by land cover. The horizontal error bars represent one standard error.

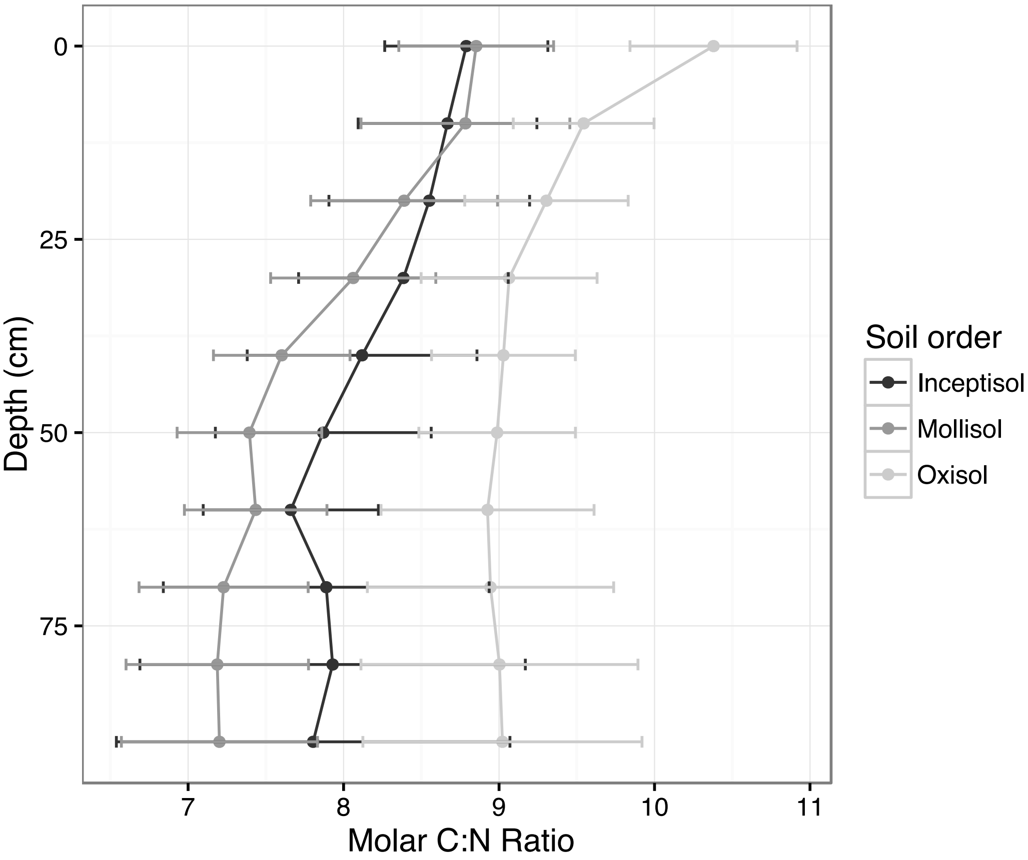

Figure 19. Change in mean soil C:N ratio with depth by soil order. The horizontal error bars represent one standard error.

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Supplementary Information

Table S1. SOC stocks for Inceptisol, Oxisol, and Mollisol sites from other studies in the tropics. This table is not exhaustive, but provides a few examples for comparison.

Location	**Soil Order**	**Land cover**	**Depth Interval (cm)**	**OC Density (% C)**	**OC Stock (Mg C ha^{-1})**	**Reference**
Puerto Rico	Inceptisol	Multiple	0-50	n.d.	107	Beinroth et al. 1996
Puerto Rico	Mollisol	Multiple	0-50	n.d.	101	Beinroth et al. 1996
Puerto Rico	Oxisol	Multiple	0-50	n.d.	120	Beinroth et al. 1996
Puerto Rico	Inceptisol	Multiple	0-20	n.d.	61	Beinroth et al. 1996
Puerto Rico	Mollisol	Multiple	0-20	n.d.	70	Beinroth et al. 1996
Puerto Rico	Oxisol	Multiple	0-20	n.d.	72	Beinroth et al. 1996
Panama	Oxisol	Forest	0-30	2.75	65	Grimm et al. 2008
Panama	Inceptisol	Forest	0-30	2.95	67	Grimm et al. 2008
Panama	Oxisol	Forest	0-50	n.d.	87	Grimm et al. 2008
Panama	Inceptisol	Forest	0-50	n.d.	88	Grimm et al. 2008
Hawaii	Inceptisol	Multiple	0-100	3	344	Johnson and Kern 2002
Hawaii	Mollisol	Multiple	0-100	2.2	268	Johnson and Kern 2002
Hawaii	Oxisol	Multiple	0-100	1	131	Johnson and Kern 2002
Puerto Rico	Inceptisol	Multiple	0-100	1.3	206	Johnson and Kern 2002
Puerto Rico	Oxisol	Multiple	0-100	1	167	Johnson and Kern 2002
Brazil	Oxisol	Forest	0-100	n.d.	102	Trumbore et al. 1995
Brazil	Oxisol	Managed Pasture	0-100	n.d.	108	Trumbore et al. 1995
Brazil	Oxisol	Degraded Pasture	0-100	n.d.	100	Trumbore et al. 1995
Costa Rica	Oxisol	Forest	0-10	6.5	34	Cleveland et al. 2003
Costa Rica	Oxisol	Pasture	0-10	5	37	Cleveland et al. 2003
Costa Rica	Mollisol	Forest	0-10	6.8	45	Cleveland et al. 2003
Costa Rica	Mollisol	Pasture	0-10	5.6	55	Cleveland et al. 2003

Table S2. Mean site C and N stocks as sampled, without extrapolation. Average pit depth refers to the average depth of the five pits at that site. The standard error of the mean stocks is in parentheses.

Site	Soil series	Land cover	Soil order	Average pit depth (cm)	TC Stock (Mg C / ha)	OC Stock (Mg C / ha)	TN Stock (Mg N / ha)
CPR01F16	Pellejas	Forest	Inceptisol	100	108 (10.3)	108 (10.3)	11 (1.4)
CPR02F35	Pandura	Forest	Inceptisol	100	124 (18.9)	124 (18.9)	14 (1.5)
CPR03F02	Guayabota	Forest	Inceptisol	88	283 (52.8)	283 (52.8)	18 (2.9)
CPR11F03	Southgate	Forest	Inceptisol	32	109 (15.2)	109 (15.2)	11 (1.5)
CPR01P71	Mucara	Pasture	Inceptisol	100	175 (13.3)	175 (13.3)	21 (1.8)
CPR01R03	Callabo	Pasture	Inceptisol	39	96 (17.6)	96 (17.6)	10 (1.9)
CPR02P03	Malaya	Pasture	Inceptisol	60	104 (22.2)	100 (17.8)	12 (2 .0)
CPR03P06	Coloso	Pasture	Inceptisol	100	145 (4.7)	145 (4.7)	16 (0.6)
CPR11P07	Victory	Pasture	Inceptisol	100	105 (12.3)	105 (12.3)	13 (1.8)
CPR01F100	Fredricksdal	Forest	Mollisol	75	151 (14.7)	151 (14.7)	17 (2.3)
CPR02F10	Soller	Forest	Mollisol	30	353 (99.1)	105 (17.2)	13 (2.2)
CPR04F01	Cintrona	Forest	Mollisol	100	934 (12.9)	248 (6.2)	22 (0.6)
CPR11F04	Susannaberg	Forest	Mollisol	50	180 (26.4)	180 (26.4)	17 (2.2)
CPR01P85	Toa	Pasture	Mollisol	100	144 (8.5)	144 (8.5)	16 (1.3)
CPR02R06	Descalabrado	Pasture	Mollisol	38	94 (6.2)	94 (6.2)	9 (0.6)
CPR04P03	Bajura	Pasture	Mollisol	100	302 (14.4)	302 (14.4)	30 (1.9)
CPR10P03	Sion	Pasture	Mollisol	97	1105 (78.9)	166 (10.2)	21 (0.8)
Cayey-28	Los Guineos	Forest	Oxisol	100	108 (4.2)	108 (4.2)	9 (0.3)
Cayey-38	Los Guineos	Forest	Oxisol	100	88 (8.8)	88 (8.8)	8 (1.1)
Cayey-68	Los Guineos	Forest	Oxisol	100	137 (8.5)	137 (8.5)	12 (0.5)
CPR01F130	Los Guineos	Forest	Oxisol	100	181 (13.2)	181 (13.2)	18 (1.8)
Cayey-100	Los Guineos	Pasture	Oxisol	100	70 (18.4)	70 (18.4)	6 (1.5)
Cayey-101	Los Guineos	Pasture	Oxisol	100	135 (20.6)	135 (20.6)	10 (1.5)
Cayey-99	Los Guineos	Pasture	Oxisol	100	115 (9.7)	115 (9.7)	11 (0.7)
CPR01P27	Coto	Pasture	Oxisol	100	203 (9.5)	203 (9.5)	28 (0.7)

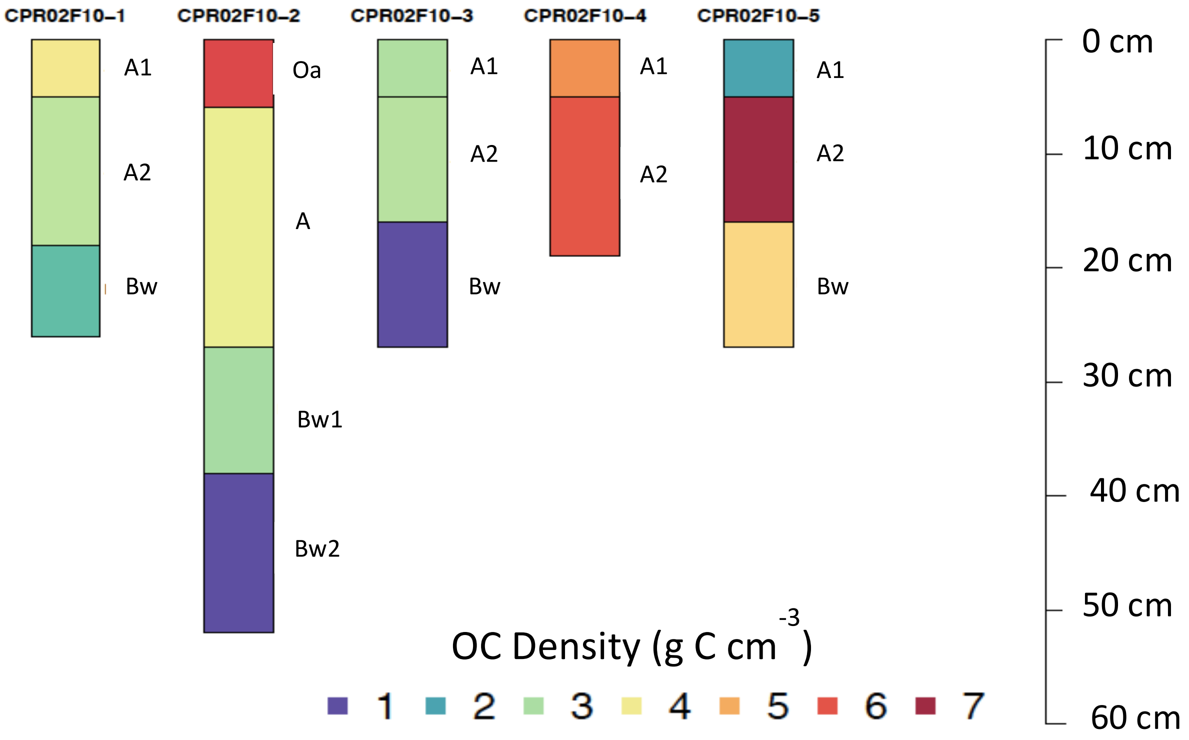

Figure S1. An example site profile. The five soil profiles represent the replicate pits per site, divided into the sampled horizons. The profile depth is located on the right-hand axis. The horizons are color coded based on the OC density (g C cm^{-3}) of that horizon. This figure illustrates a forested Mollisol site with great variability among pits.

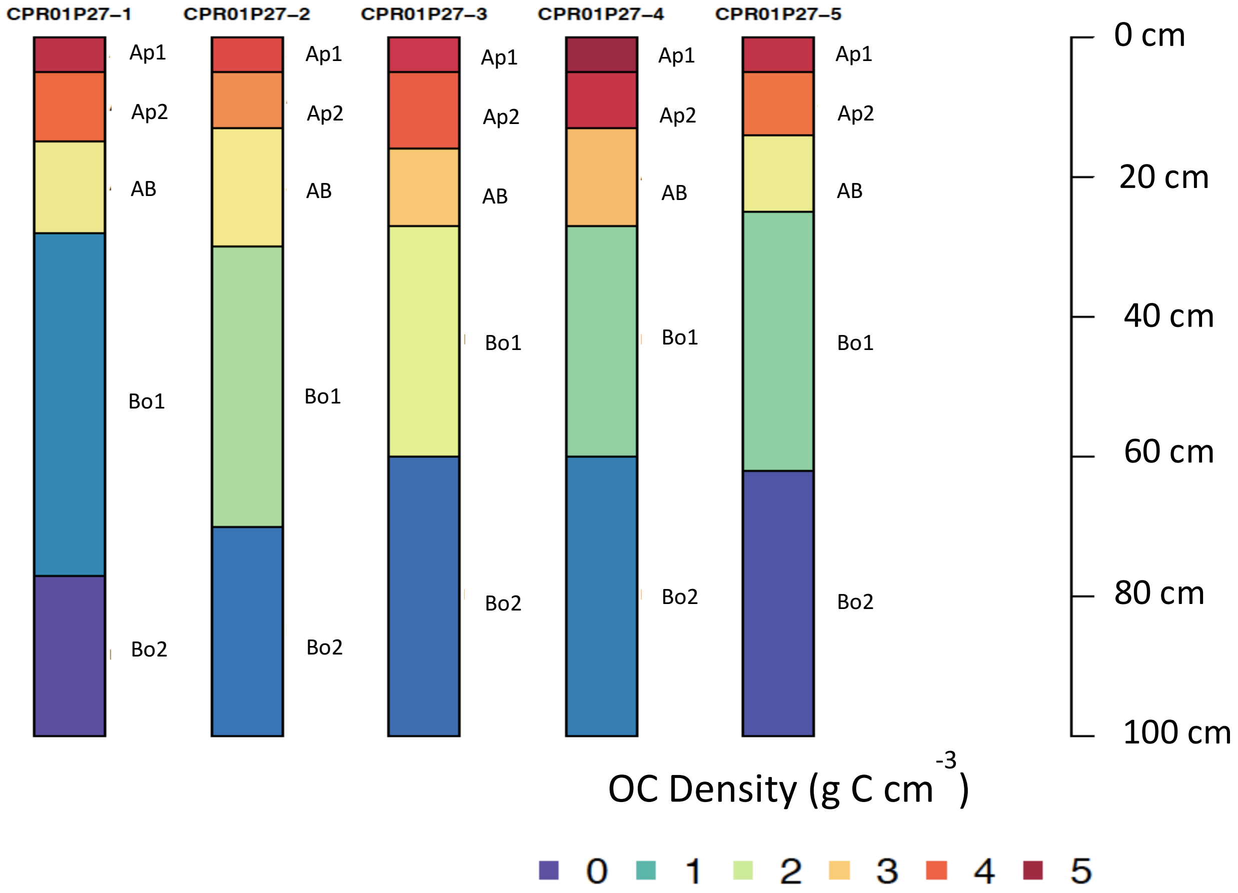

Figure S2. An example site profile. The five soil profiles represent the replicate pits per site, divided into the sampled horizons. The profile depth is located on the right-hand axis. The horizons are color coded based on the OC density (g C cm^{-3}) of that horizon. This figure illustrates a pasture Oxisol site with low variability among pits.