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RESEARCH REVIEW

Carbon storage in successional and plantation forest soils: a tropical analysis

Erika Marín-Spiotta[1]* & Sapna Sharma[2]

[1]*Department of Geography, University of Wisconsin-Madison, Madison, WI 53706, USA,* [2]*Department of Biology, York University, Toronto, Ontario, Canada, M3J 1P3*

*Correspondence: Erika Marín-Spiotta, Department of Geography, University of Wisconsin-Madison, 550 North Park Street, Madison, WI 53706, USA.
E-mail: marinspiotta@wisc.edu

ABSTRACT

Aim To analyse global patterns in soil carbon (C) in tropical successional and plantation forests based on climate, forest age, former land use and soil type to determine factors driving below-ground C storage.

Location Pantropical.

Methods We conducted a synthesis of 81 studies reporting soil C stocks in more than 400 reforested and tree plantation sites. We used regression models and regression tree analyses to determine the importance of multiple predictor variables on soil C stocks standardized to three common depth ranges: 0–10, 0–30 and 0–100 cm.

Results Mean annual temperature (MAT) was the most important predictor of soil C. Forest age explained little to no variability in soil C, in contrast with above-ground studies. Data on long-term trends in soil C are limited, as median time since forest growth was 15 years. Soil C stocks were similar between tropical secondary forests, tree plantations and reference forests. Differences between plantation and successional forests only appeared below 10 cm on sites with MAT < 21.3 °C. Former pastures and cultivated sites differed from each other only to depths of 30 or 100 cm. Climatic variables appeared multiple times across all layers of the regression trees, consistent with strong interactions between MAT and precipitation on soil C stocks.

Main conclusions Climate explained greater variability in soil C in successional and plantation forests than former land use or forest age, despite the tropical location of all sites. Human management factors were more important for predicting soil C stocks in cooler and drier sites, while environmental variables were more important in hotter and wetter sites. The relative importance and interactions between soil type, previous land use and forest cover type differed with soil depth, highlighting the importance of comparing C across consistent depths. Climatic controls suggest sensitivity of soil C stocks in successional and plantation forests to future climate change.

Keywords

Afforestation, plantations, reforestation, secondary forests, soil carbon, tropics.

INTRODUCTION

Tropical forestry carbon projects are being implemented in anticipation of a market that would reward increased ecosystem carbon (C) sequestration to help mitigate anthropogenic emissions (Gibbs *et al.*, 2007; Canadell & Raupach, 2008). Projects promote tree cover on lands that were formerly forested (reforestation) and on lands that have not supported forest growth in historical times (afforestation), through direct seeding and planting, through plantation forestry and through management or protection of secondary or successional forests. Successional forests and tree plantations occupy increasingly larger areas of tropical forested land (Wright, 2005). In addition to the establishment of commercial plantation forestry, many tropical

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regions are experiencing increases in forest regeneration, driven by widespread abandonment of intensive agriculture (Aide & Grau, 2004; Lambin & Meyfroidt, 2011). Understanding the role of secondary and plantation forests as C reservoirs is crucial for improving predictions of current and future effects of changes in land use and land cover on the global C cycle. Despite their geographic prevalence, these tropical forest types are understudied and their capacity for providing valuable ecosystem services in addition to C sequestration, such as watershed protection and a biodiverse habitat, remains undervalued (Brown & Lugo, 1990; Lugo, 1992; Chazdon, 2008).

Plantation forests can restore soil organic matter and nutrients to soils that were depleted under intensive cultivation (Parrotta, 1992; Paul *et al.*, 2002). In fragmented landscapes, plantation forests can provide habitat for bird biodiversity (Ranganathan *et al.*, 2008) and for secondary forest species in the understorey (Haggar *et al.*, 1997). Tree plantations may contribute to the goals of restoring forest ecosystem services and providing economic options to local communities via improved forest management practices (Lugo, 1992; Lamb *et al.*, 2005; Berthrong *et al.*, 2009).

In young successional tropical forests and plantations, soil C stocks can make up more than half the total ecosystem C pool (Eaton & Lawrence, 2009; Kauffman *et al.*, 2009). Understanding how soil C responds to increasing tree cover during forest growth and planting can inform the selection of sites to maximize C sequestration and improve our ability to restore fertility to degraded soils. Accounting models that estimate the effects of deforestation and reforestation on the global C cycle are limited by accurate assessments of C stocks in original and replacement biomass and in soils (Houghton & Goodale, 2004; Gibbs *et al.*, 2007; Ramankutty *et al.*, 2007). Identifying factors that affect the amount of C in soils under different land-cover types is furthermore important for improving predictions of feedback effects between vegetation, land-use change and climate change.

The objectives of our study were to compare soil C stocks in tropical successional forests and tree plantations and to quantitatively evaluate the importance of different environmental factors: soil type, climate, current cover type, past land use and time since forest growth, on soil C pools. We analysed 81 tropical successional and plantation forest studies comprising more than 400 chronosequence and paired-plot sites covering a diversity of soil types. Due to an explosion of research in the last decade, our study includes over three times as many data, and greater geographic representation of Africa and Asia, than previous reviews. Novel contributions of our synthesis are: (1) the comparison of soil C stocks standardized to depths of 0–10, 0–30 and 0–100 cm, to reveal biases when sampling only shallow depths; (2) the evaluation of the effect of forest age or time since abandonment on soil C stocks; and (3) the rigorous statistical analysis of a suite of environmental factors that affect soil C storage. We compare results from a multiple linear regression approach with those of a regression tree analysis, which provides a powerful determination of linear and nonlinear interactions between multiple predictor variables that include both quantitative and qualitative data.

METHODS

Data compilation

We compiled soil C data reported for 510 tropical sites (between 23°26′16″ N and 23°26′16″ S) from 81 reforestation and afforestation studies in 32 countries or territories (see Appendix S1 and S2 in Supporting Information). Sites were classified by current cover type, species type, past land use, rainfall class and soil activity class (see Table 1 for detailed descriptions of categories). Additional non-categorical data collected for each site included elevation (m a.s.l.), mean annual temperature (MAT; °C), and mean annual precipitation (MAP; mm). Data came from both chronosequence ($n = 267$) and paired-plot ($n = 229$) study sites and included associated reference or primary forests for comparison. Most site data are averages of sampling pits or cores. Averages of replicate sites were also used when individual site data were not available.

Standardization of soil C to common depths

We conducted our analyses on soil C content (Mg C ha^{-1}). Where only C concentrations were reported, we used reported bulk density values to calculate C content using equation 1:

$$\text{Mg C ha}^{-1} = (\%\ \text{C}/100) \times D_b \times \text{soil depth} \times 100 \quad (1)$$

where D_b is bulk density (g cm^{-3}) and soil depth is in cm. For the 13 (out of 81) studies that did not report bulk density, we used equation 2 to estimate D_b (Post & Kwon, 2000):

$$D_b = 100/(\%\text{OM}/0.244) + [(100 - \%\text{OM})/MD_b] \quad (2)$$

where OM is organic matter and MD_b is mineral bulk density, and then calculated the C content using equation 1. We used a value of 1.64 for MD_b (Post & Kwon, 2000) and the recommended conversion value of 0.5 to calculate C concentrations from OM values (Nelson & Sommers, 1996).

There is no standard depth for reporting soil C. The mean and median values of soil depth reported in our studies were 47.7 ± 1.9 and 30 cm, respectively. The most common depths were 0–30 ($n = 217$), 0–10 ($n = 210$), and 0–20 and 0–50 cm (both at $n = 174$). The next most common depth was 0–100 cm ($n = 136$). The maximum soil depth reported was 800 cm ($n = 2$). Soil C typically decreases exponentially with depth. To avoid confounding errors when comparing soil C contents across different depths, we standardized C contents per site to three common depths (0–10, 0–30 and 0–100 cm) using the following approach adapted from Silver *et al.* (2000).

We calculated regression equations between log cumulative soil C and log soil depth for sites from different rainfall classes (Table 2), as patterns of soil C with depth may differ with climate (Jobbágy & Jackson, 2000). For the very few sites with no rainfall data, we used a non-specific equation generated from all of the data (Table 2). The mathematical relationships were used to calculate ratios between soil C predicted by a regression equa-

Table 1 Description and classification of sites used in our analysis of soil C stocks in tropical successional forests and tree plantations.

Categorical variable	*n*	Description
Cover type		
Secondary forests	297	Secondary forests included both unassisted and assisted forest regeneration, agricultural fallows with tree cover, and diverse agroforestry systems
Plantations	88	Tree plantations included monocultures and planted forests actively managed for timber or other products
Reference forests	86	Reference, or primary, uncut or undisturbed, forests from the same studies as the secondary forests and tree plantations for comparison
Unknown	39	Original study did not specify which of these sites were plantation or secondary forests
Tree plantation species type		
N-fixers	12	Including *Acacia*, *Albizia*, *Leucocephala* species
Conifers	17	*Pinus* or *Cupressus* species
Eucalypts	14	A variety of *Eucalyptus* species
Casuarina	4	*Casuarina* species
Broadleaf	30	A variety of species including teak (*Tectona grandis*) and mahogany (*Swietenia* spp.)
Mixed	11	A mixture of tree species with no clear dominance.
Past land use		
Cleared	34	Cleared and abandoned without any cultivation
Cultivated	154	Former agricultural crops
Pasture	203	Grazing lands and managed grasslands
Unknown	33	Uncertain or unreported former land use
Rainfall class		
Dry	79	Mean annual precipitation < 1000 mm yr^{-1}
Moist	223	Mean annual precipitation 1000–2500 mm yr^{-1}
Wet	205	Mean annual precipitation > 2500 mm yr^{-1}
Soil activity		Based on reported soil mineralogy and/or soil classification converted to USDA* taxonomy
Low	324	Low-activity clay or highly weathered soils, e.g. Entisols, Oxisols, Ultisols
Medium	108	Young to moderately weathered soils with high surface area and high cation exchange capacity, e.g. Inceptisols, Alfisols, Mollisols, Vertisols, Histosols
High	56	Soils dominated by allophane or other non-crystalline minerals, i.e. Andisols

*United States Department of Agriculture soil order taxonomy.

Table 2 Best fit regression equations for soil carbon (Mg C ha^{-1}) with soil depth used to normalize soil C stocks to standardized depths for all sites, and for sites classified by rainfall class. See Methods for details.

Variable	*n*	Equation	r^2	*P*-value
All data	1355	log (Mg C ha^{-1}) = 0.59 (log depth) + 2.18	0.45	< 0.0001
Rainfall class				
Dry forests	83	log (Mg C ha^{-1}) = 0.53 (log depth) + 2.25	0.23	< 0.0001
Moist forests	678	log (Mg C ha^{-1}) = 0.61 (log depth) + 1.96	0.47	< 0.0001
Wet forests	588	log (Mg C ha^{-1}) = 0.64 (log depth) + 2.20	0.59	< 0.0001

tion for the standardized depth and soil C predicted for the reported depth. These ratios were used as multipliers to adjust soil C stocks for the reported depth closest to 10, 30 or 100 cm, for each site. For example, for a study reporting soil C values to 0–5, 5–10, 10–15 and 15–25 cm, we would select the cumulative total soil C value for 0–25 cm (72 Mg C ha^{-1}) for standardization to 30 cm. The specific regression equation for this particular site (a wet forest) yielded a multiplier of 1.125 (ratio of predicted soil C value at 30 cm over the predicted soil C value at 25 cm). The adjusted soil C value at the desired depth of 30 cm was recalculated to be 81 Mg C ha^{-1}. Following this example, the multiplier value for soil C stocks reported at the desired depths would be 1. In our final statistical analyses, each site was represented by one soil C stock at each of 0–10, 0–30 and 0–100 cm depths, regardless of how many depth intervals were reported in the original manuscript.

One limitation of this approach is the error associated with adjusting depths far from the standardized depths; hence we adjusted cumulative reported soil C stocks for the depth closest to 10, 30 or 100 cm as appropriate. These depth intervals were selected because they represent three of those most commonly reported, thus reducing uncertainties propagated by underrepresentation in the calculated regressions, and for comparison with other global syntheses.

Statistical analyses

First, we tested for differences in soil C stocks standardized to depths of 10, 30 and 100 cm between broad site categories.

Datasets that were not normally distributed were log-transformed before means were compared using one-way ANOVA, followed by all pairs Tukey honest significance difference tests. All statistics, with the exception of multiple regression and regression tree analysis, were run on JMP IN version 9 software (SAS Institute). Values reported are means ± 1 standard error.

To test for the effect of forest age on soil C stocks, we ran linear regressions by rainfall class, past land use and cover type. We use forest age and time since abandonment of previous land use interchangeably. To fulfil assumptions of normality, we used the natural log of soil C and of site age. Reference forests were excluded, as we were interested in the effects of time since abandonment of previous land use.

Multiple regression analyses were performed separately for the three depths (0–10, 0–30 and 0–100 cm) on secondary forest and plantation data only, using soil C as the response variable and MAP, MAT, soil activity class, former land use, forest age and current cover type as predictor variables. We did not include plantation species type because data were typically not available for secondary forests, and our sample sizes would have been too small. Categorical predictor variables were transformed into dummy variables and used as covariates in the multiple regression analysis. A modified forward selection procedure was used to select significant environmental variables, which were subsequently used in multiple regression analyses (Blanchet *et al.*, 2008). Per cent variation explained by each predictor variable on soil C was calculated by dividing the regression sum of squares for each variable by the total sum of squares. Multiple regressions were performed in R (R Development Core Team, 2011).

Regression tree analyses were performed on the same variables as the multiple regressions. Regression trees iteratively divide data into two homogeneous groups along the values of one of the explanatory variables, in such a way that they have mutually exclusive memberships. Regression trees can be constructed using continuous and/or categorical predictor variables and provide graphical interpretation of complex ecological interactions (De'ath & Fabricius, 2000). Regression trees perform well on complex, untransformed ecological data that consist of high-order interactions and multicollinear and nonlinear relationships between predictor variables (De'ath & Fabricius, 2000; De'ath, 2002). We pruned regression trees to the level where the complexity parameter minimized the cross-validation error. The per cent variation (R^2) explained by the regression tree using the predictor variables was calculated using $R^2 = 1 -$ relative error. The relative error is the absolute error (difference between the exact and the approximate values) divided by the exact value. All regression trees were developed using the rpart package in R (R Development Core Team, 2011).

RESULTS

The majority of sites were located in the moist rainfall class, followed by the wet rainfall class and dry forests (Table 2). Mean (and median) MAT, MAP, elevation and site age were: 25.3 ± 0.2 (25.4) °C, 2294 ± 53 (2000) mm, 501 ± 36 (200) m a.s.l., and 19 ± 0.8 (15) years (Fig. 1). There were over three times as many data reported for secondary forests as for plantations (Table 2). The most common prior land use was pasture, followed by crop agriculture. All USDA soil orders except for vertisol, aridisol and gelisol were represented in the database. The most common soil activity class was low activity (66% of all sites), followed by medium activity (22%) and high activity (11%). Geographically, 71% of the sites were located in the Americas and Caribbean, with lower representation by tropical Africa (19%), and Asia and the tropical Pacific combined (10%).

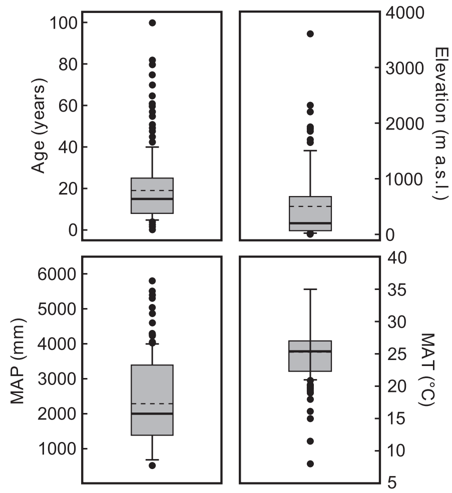

Figure 1 Distribution of site ages (years), elevation (m a.s.l.), mean annual precipitation (MAP) (mm) and mean annual temperature (MAT) (°C) for plantations, secondary forest and reference (unconverted) forest sites in the database. The lower limit of the box represents the 25th percentile, the upper limit represents the 75th percentile, the solid line and dotted line within the box mark the median and mean values, and the whiskers (error bars) below and above the box indicate the 10th and 90th percentiles. The dots represent outlier values.

General patterns in soil C stocks

Mean (and median) soil C stocks (Mg C ha^{-1}) for depths of 0–10, 0–30 and 0–100 cm were: 38.2 ± 0.9 (34.3), 78.1 ± 1.8 (70) and 164 ± 4.0 (142). Soil C stocks from secondary forests and plantations did not differ from each other, or from reference forest sites at any of the three depth intervals (Table 3). Significant differences arose when taking into account interactions between multiple environmental variables. There were no significant differences in soil C content by tree plantation species types. Sites on former pasturelands and former cultivated sites did not differ from each other, but all sites on former agricultural land (except for pastures in the 0–10 cm) had greater soil C than sites that were cleared and immediately abandoned before forest regrowth or planting. Dry forests had significantly lower soil C stocks (65.7 ± 4.3 Mg C ha^{-1} compared with 78.1 ± 3.3 Mg C ha^{-1} and 80.8 ± 2.2 Mg C ha^{-1} for moist and wet, respectively) when measured to 30 cm (Fig. 2). Wet forests

Table 3 Mean ± standard error and range (min–max) soil C (Mg C ha^{-1}) estimated for three standardized depths and grouped by current cover type, plantation species type, past land use or soil activity class.

Variable	n	Soil C content for depth: 0–10 cm	0–30 cm	0–100 cm
Cover type				
Plantations	88	38.8 ± 2.07	79.2 ± 4.0	169.8 ± 9.5
Reference forests	86	40.7 ± 2.8	79.9 ± 5.7	162.0 ± 12.2
Secondary forests	297	37.3 ± 1.2	77.6 ± 2.3	162.8 ± 5.2
Unknown*	39	38.2 ± 1.6	76.3 ± 3.4	164.5 ± 7.1
Plantation species type				
N-fixers	12	45.9 ± 8.3	94.2 ± 15.8	194.1 ± 32.4
Conifers	17	40.9 ± 4.4	82.8 ± 8.6	166.7 ± 19.8
Eucalypts	14	40.3 ± 5.6	78.2 ± 11.0	182.2 ± 24.9
Casuarina	4	39.0 ± 14.7	80.0 ± 27.4	166.0 ± 57.1
Broadleaf	30	34.3 ± 2.8	71.6 ± 5.5	153.6 ± 15.5
Mixed	11	38.1 ± 4.4	79.2 ± 9.6	177.7 ± 23.3
Past land use				
Cleared	34	31.7 ± 3.5 A	64.7 ± 7.8 A	131.8 ± 16.4 A
Cultivated	154	43.0 ± 1.9 B	85.1 ± 3.6 B	177.9 ± 7.8 B
Pasture	203	35.2 ± 0.9 AB	75.8 ± 2.0 B	159.2 ± 4.7 B
Unknown*	33	35.2 ± 4.0 B	69.5 ± 7.5 AB	166.9 ± 20.5 AB
Soil activity				
Low	324	35.6 ± 1.03 A	71.7 ± 2.0 A	147.8 ± 4.5 A
Medium	108	43.6 ± 2.3 B	90.8 ± 4.3 B	195.6 ± 9.0 B
High	56	46.7 ± 2.8 B	96.7 ± 6.3 B	208.7 ± 14.9 B

*Unknown sites are plantation or secondary forests with uncertain or unreported former land uses. Different capital letters represent significant within-group differences by columns.

stored more soil C (176.3 ± 5.3 Mg C ha^{-1}) to a 1 m depth. Low-activity clay soils had the lowest soil C stocks.

Effect of time since forest growth on soil C stocks

There were no strong patterns between forest age and soil C stocks (Fig. 3, Table 4), suggesting that factors other than time since forest growth are important in explaining variability in below-ground C storage. The strongest relationship between forest age and soil C was for sites with no intermediate land use after initial clearing ($r^2 = 0.41$–0.44) (Table 4), which also had the lowest sample size. Forests growing on former pastures showed very weak relationships with age ($r^2 \leq 0.06$) in the top two depths and none at 0–100 cm depth. Sites on previously cultivated land showed no significant relationships at any depth. Of the three rainfall categories, only moist forest soil C showed a weak trend with forest age.

Multiple predictors of soil C

At all soil depths, multiple regression analyses revealed a combination of factors driving soil C stocks (Table 5). Climatic factors explained on average 65% of the total variation in soil C, followed by age, former land use and cover type. The regression tree models explained twice as much variation in the soil C data (53.7%) as the multiple regression models (25.3%) on average for all depths. The regression trees illustrated that the most important variable explaining soil C stocks at all depths was MAT (Figs 4–6), followed by interactions between different factors. Former land use was the next most significant factor for soil C in the top 10 cm, followed by soil activity class and rainfall for sites with MAT < 26.1 °C (Fig. 4). Forests growing on cleared sites distinguished themselves from other former land uses. Site age did not appear until the fifth level of the regression tree for soil depths of 0–10 cm, isolating sites in the first decade of growth. Climatic factors appeared in seven of the top 10 interaction nodes in the regression tree describing soil C stocks in the top 10 cm. Current cover type did not appear as a significant variable. Highest soil C stocks were found on formerly cleared and abandoned sites with cooler temperatures (< 26.1 °C) and intermediate amounts of precipitation (MAP 2215–2455 mm) (Fig. 4). Lowest soil C stocks were found in forests aged < 9.5 years on low- and medium-activity soils that had been formerly cultivated or grazed in cooler and drier climates.

At depths of 0–30 cm, secondary forests on cooler sites had higher mean soil C stocks than plantations, but at sites with MAT ≥ 21.3 °C, there was no significant difference between forest cover types (Fig. 5). Secondary forests on former pastures had lower soil C stocks than those on former cultivated or cleared and abandoned sites. Soil type was a significant factor explaining variability in soil C stocks at this depth under plantation forests. The greatest soil C stocks to 30 cm were found under secondary forests growing on former cultivated sites with MAT < 21.3 °C. At warmer sites, only temperature and rainfall were significant predictors of soil C.

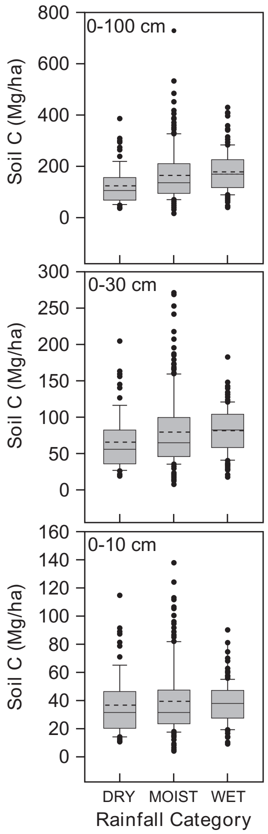

Figure 2 Distribution of soil C (Mg ha^{-1}) for three standardized soil depths for plantations, secondary forests and reference (unconverted) forest sites in the database grouped by rainfall category. The lower limit of the box represents the 25th percentile, the upper limit represents the 75th percentile, the solid line and dotted line within the box mark the median and mean values, and the whiskers (error bars) below and above the box indicate the 10th and 90th percentiles. The dots represent outlier values. Different letters at the base of each box-plot represent significant differences within each soil depth class.

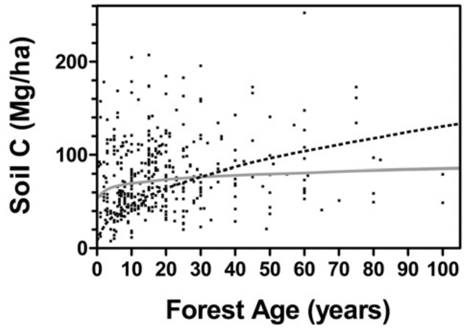

Figure 3 Trends in soil C (Mg ha^{-1}) (0–30 cm) with site age in secondary forests and plantation forests. The black dotted line represents sites that were previously cleared and abandoned with no agricultural use before reforestation or plantation establishment and the solid grey line represents forests on former pastures. Equations for the regression lines are given in Table 3.

At depths of 0–100 cm, MAT was the most important variable predicting soil C, followed by MAP, cover type and land use (Fig. 6). Here, factors other than climate were found to be significant at both cooler and warmer sites. The greatest soil C stocks were found in warm sites with MAP between 2370 and 2455 mm and in secondary forests growing after cultivation or after clearing and abandonment in cooler climates.

DISCUSSION

Climatic variables control soil C stocks in regenerating and plantation forests

At the global scale, climate determines ecosystem productivity, litter decomposition rates and C accumulation in biomass and in soils (Post *et al.*, 1982; Torn *et al.*, 1997; Malhi *et al.*, 1999; Jobbágy & Jackson, 2000; Liski *et al.*, 2003; Anderson *et al.*, 2006; Cusack *et al.*, 2009). Our finding that climatic variables explained the greatest variability in soil C stocks is consistent with these studies; what is surprising is that former land use and forest age had such little influence on soil C in tropical regenerating and plantation forests.

MAT was the most important variable for soil C stocks at all depths analysed. Temperature appeared multiple times in the regression trees along with MAP, suggesting strong interactions between these two climatic variables and other factors. At all depths, variables other than climate (land use, current forest cover type and soil type) were more significant at the lower temperature range. When deeper soil profiles were accounted for, interactions between climate and other environmental and historical conditions became important across the entire temperature gradient.

In general, sites with higher MAT had lower soil C stocks, except under high rainfall, which is consistent with other global and continental-scale syntheses (Jobbágy & Jackson, 2000; Wynn *et al.*, 2006). Lower soil C storage at high temperatures can be explained by several factors, including decreased primary productivity (Clark *et al.*, 2003) and increased rates of C loss. Globally, the residence time of organic C in soils is shortest at lower latitudes, where MAT is highest (Bird *et al.*, 1996). Many of the effects of temperature on soil organic matter decomposition and primary production are influenced by overall moisture availability (Torn *et al.*, 1997; Liski *et al.*, 2003), which can explain the multiple interactions between MAT and MAP in our analyses.

Soil C differences between rainfall classes became even greater when deeper soil profiles were integrated, as rainfall can affect the vertical distribution of roots and the stabilization of C in deep mineral horizons (Torn *et al.*, 1997; Jobbágy & Jackson, 2000). Our results suggest that there is an optimal climatic range for maximum soil C stocks. Wetter and cooler sites generally stored more soil C than drier and hotter sites. In tropical forests under high rainfall, fluctuations in O_2 can shift microbial metabolism to less efficient pathways (Schuur, 2001; Teh *et al.*, 2005), resulting in lower microbial decomposition rates and

Table 4 Best fit regression equations for soil carbon (Mg C ha^{-1}) with time following tropical re/afforestation. Equations were calculated for all data and for sites by life zone, past land use and cover type, for the three standardized depths.

		0–10 cm		0–30 cm		0–100 cm	
Variable	n	Equation	r^2	Equation	r^2	Equation	r^2
All data	412	log C = 0.11(log age) + 3.23	0.03†	log C = 0.11(log age) + 3.95	0.03†	log C = 0.09(log age) + 4.72	0.02**
Life zone							
Dry forests	52	n.s.	n.s.	n.s.	n.s.	ns	
Moist forests	178	log C = 0.19(log age) + 2.97	0.09†	log C = 0.20(log age) + 3.66	0.10†	log C = 0.18(log age) + 4.44	0.08†
Wet forests	180	n.s.	n.s.	n.s.	n.s.	ns	
Past land use							
Cultivated	154	n.s.	n.s.	n.s.	n.s.	n.s.	
Pasture	203	log C = 0.12(log age) + 3.19	0.06***	log C = 0.09(log age) + 4.031	0.04**	n.s.	
Cleared	34	log C = 0.43(log age) + 2.16	0.41†	log C = 0.45(log age) + 2.81	0.44†	log C = 0.43(log age) + 3.55	0.42†
Cover type							
Plantations	88	log C = 0.24(log age) + 2.86	0.09**	log C = 0.23(log age) + 3.61	0.08**	log C = 0.20(log age) + 4.43	0.06*
Secondary forests	297	log C = 0.08(log age) + 3.28	0.02**	log C = 0.08(log age) + 4.00	0.03**	log C = 0.07(log age) + 4.76	0.02*

n.s., not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; †$P < 0.0001$.

Table 5 Variation (%) and relative variation of the total (%) variation in soil C stocks for the three common depths explained by predictor variables in multiple linear regression models. Predictor variables are mean annual temperature (MAT), mean annual precipitation (MAP), former land use (cleared, cultivation or pasture), site age, and current cover type (plantation or secondary forest).

	0–10 cm		0–30 cm		0–100 cm	
Variable	Explained variation (%)	Relative explained variation (%)	Explained variation (%)	Relative explained variation (%)	Explained variation (%)	Relative explained variation (%)
Model predicting soil C	Soil C = 4.1 + 0.004 age + 0.6 land use (cultivation) + 0.2 land use (pasture) – 0.06 land use (unknown) + 0.00005 MAP – 0.05 MAT		Soil C = 4.8 + 0.004 age + 0.06 land use (cultivation) + 0.3 land use (pasture) – 0.08 land use (unknown) + 0.00008 MAP – 0.05 MAT		Soil C = 5.5 + 0.6 land use (cultivation) + 0.3 land use (pasture) + 0.05 land use (unknown) + 0.0001 MAP – 0.05 MAT	
MAT	12.5	45.8	9.4	32.8	10.5	36.4
MAP	4.6	16.9	6.7	23.4	11.1	38.6
Land use	9.8	35.8			4.1	14.2
Age	4.2	15.3	2.8	9.8		
Cover type			5.9	20.5		
Total Adjusted Explained Variation (R^2_{adj}%)	24.8	100	26.7	100	25.6	100

*All models were significant at $P < 0.00001$.

greater soil C storage. Previous syntheses of tropical soil C data all consistently showed greater C stocks to 1 m in the wetter tropical forests (Table 6).

Forest age is not a good predictor of soil C

Above-ground biomass typically increases with stand age (Johnson *et al.*, 2000; Anderson *et al.*, 2006), but we found below-ground C pools to show little to no relationship with time since forest regrowth or planting. Secondary forest and plantation age were poor predictors of soil C across a suite of environmental variables. The weak effect of age on soil C is not surprising given that growing tropical forests can attain structural characteristics of mature stands quite rapidly (Guariguata & Ostertag, 2001; Marín-Spiotta *et al.*, 2007). Our sites ranged widely in age (0.94–100 years) but the predictive power of forest age did not improve for the first two decades (0–20 years only) and became insignificant for sites aged 0–10 years.

Previously, Pregitzer & Euskirchen (2004) reported that above-ground biomass C and soil C stocks showed positive trends with site age in boreal, temperate and tropical forests. Soil C stocks in their tropical sites increased sharply between their first (0–30 years) and second (31–70 years) age classes, with values levelling afterwards. In contrast, their above-ground

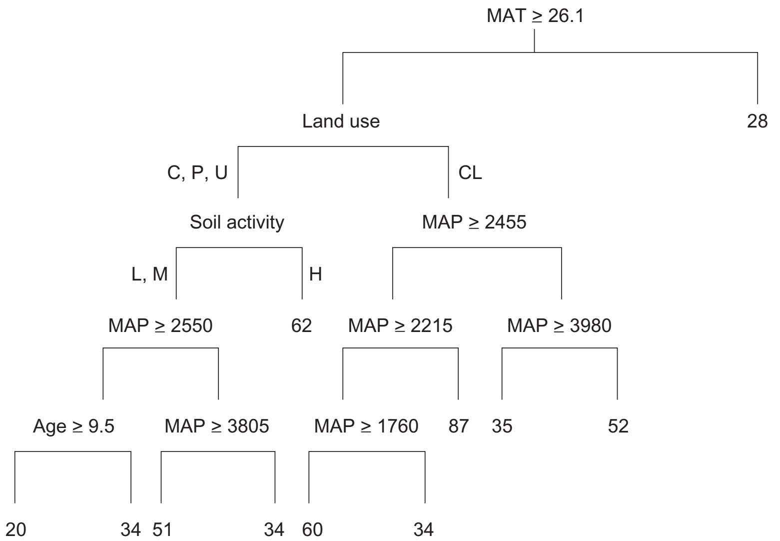

Figure 4 Regression tree for soil depth 0–10 cm illustrating the important environmental variables, their interactions and nonlinear responses to predicting soil C (mean values Mg ha^{-1}, in bold): MAT = mean annual temperature (°C); MAP = mean annual precipitation (mm); land use, C = cultivated, P = pasture, U = unknown, CL = cleared; soil activity, L = low, M = medium, H = high; age (years).

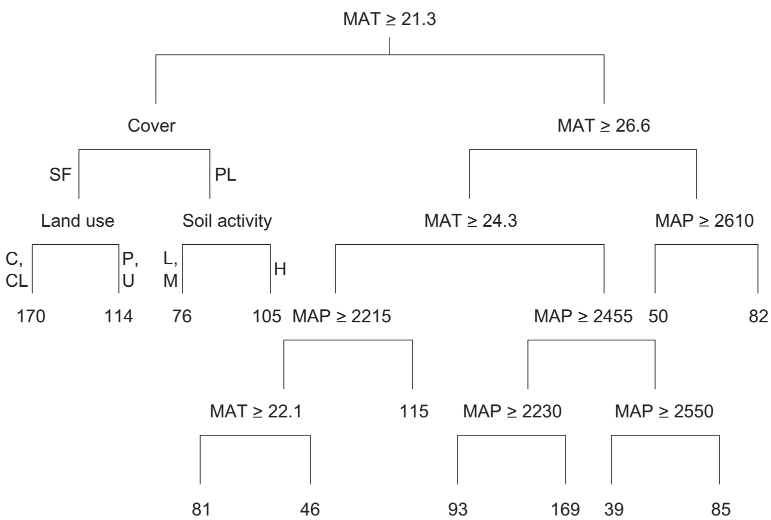

Figure 5 Regression tree for soil depth 0–30 cm illustrating the important environmental variables, their interactions and nonlinear responses to predicting soil C (mean values Mg ha^{-1}, in bold): MAT = mean annual temperature (°C); MAP = mean annual precipitation (mm); land use, C = cultivated, P = pasture, U = unknown, CL = cleared; soil activity, L = low, M = medium, H = high; cover, SF = secondary forest, PL = plantation.

biomass data showed a gradual increase in the first 120 years post-disturbance. They reported age as categories, rather than as continuous variables, and did not standardize their soil C dataset to a common depth, so it is difficult to directly compare their results with ours. In one of the earliest syntheses of changes in soil C stocks with land-use change in the tropics (Detwiler, 1986), soil C stocks in forest fallows after abandonment of agricultural land were modelled to increase steadily to full recovery of primary forest levels in the first 35 years. Recent tropical meta-analyses do not consider the effect of forest age on soil C stocks (Don *et al*., 2011; Powers *et al*., 2011).

Results from individual studies at the site level are mixed. In a seasonally dry region of Mexico, soil C stocks in the top 10 cm did not differ between reference forests, early (10–15 years), mid (20–30 years) or late successional (60 years) forests growing on former maize fields (Saynes *et al*., 2005). Forest age was found to be a significant predictor of above-ground biomass but not of soil C in a replicated chronosequence of forest fallows after multiple cycles of shifting cultivation (Eaton & Lawrence, 2009). In contrast, time since agricultural abandonment was more important than soil type in the accumulation of soil C in temperate mixed-hardwood successional forests (Foote & Grogan, 2010).

Trends in soil C may also not follow a unidirectional relationship with time since abandonment of the former land use. Tree plantations may experience losses of soil C in the first decade, with accumulation occurring in sites with 30-year rotations (Paul *et al*., 2002; Laganière *et al*., 2010). In the southern Yucatán Peninsula, soil C stocks were highest in the youngest and oldest successional forests and lowest in sites of intermediate age (Eaton & Lawrence, 2009).

Most of the available soil C data are from the first two decades of forest growth, hindering our ability to make predictions about the long-term behaviour of soil C during reforestation and afforestation. Sites were separated within the first 10 years, confirming both the weak effect of forest age on long-term soil C stocks and the bias towards younger forests in the literature. The scarcity of older forest data may be due to short rotations of

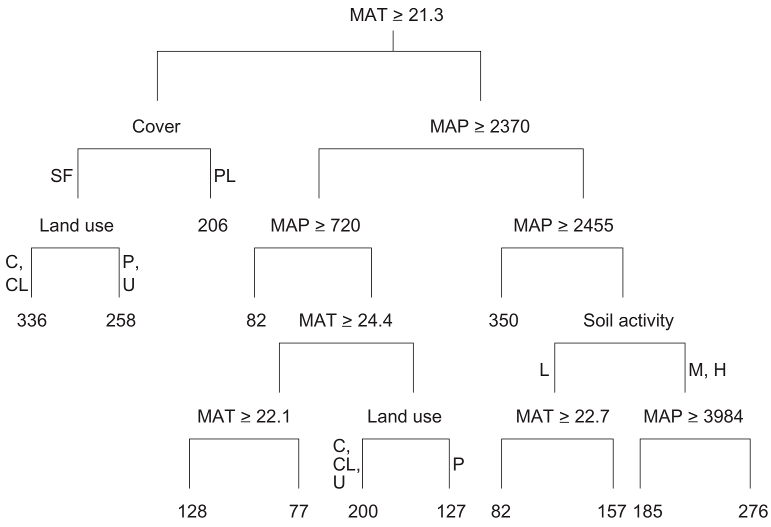

Figure 6 Regression tree for soil depth 0–100 cm illustrating the important environmental variables, their interactions and nonlinear responses to predicting soil C (mean values Mg ha^{-1}, in bold): MAT = mean annual temperature (°C); MAP = mean annual precipitation (mm); land use, C = cultivated, P = pasture, U = unknown, CL = cleared; soil activity, L = low, M = medium, H = high; cover, SF = secondary forest, PL = plantation.

plantation forests and to uncertainties in estimating forest age in sites where historical records may not be available and tree rings are not reliable measures of annual growth. Furthermore, many tropical secondary forests are in temporary stages of agricultural fallow (Etter *et al*., 2005; Eaton & Lawrence, 2009) or currently threatened by urbanization, so that many successional sites are converted again before they reach old age.

Soil carbon stocks with reforestation and afforestation

At the global scale, our analysis reveals that tropical successional forests, tree plantations and reference forests store similar amounts of soil C. Our mean soil C values are comparable with other global syntheses (Table 6), which mostly represent undisturbed forests. Our data for dry and moist forests are very similar to those reported for tropical lowland and higher-elevation secondary forests by Brown & Lugo (1990). Their high-elevation tropical wet secondary forests have significantly greater C stocks than our data, which include a wider range of elevations.

The lack of strong differences among our forest cover types is consistent with an earlier meta-analysis, which reported little effect of forest management on soil C stocks across a range of biomes (Johnson & Curtis, 2001). At our tropical sites, forest cover type became important for soil C stocks down to 30 and 100 cm in sites with MAT < 21.3°C. In those cases, plantations had less soil C than secondary forests, which could be explained by the selection of tree species with greater allocation to above-ground biomass in commercial plantations. Our plantation sites were located on average on significantly cooler sites (MAT = 22.4 ± 0.4 °C) than secondary forests (MAT = 25.9 ± 0.2 °C). Laganière *et al*. (2010) noted that plantation species most associated with losses or lowest gains of soil C also tended to occur in cooler climates. These results suggest multidirectional interactions between forest cover type and climatic variables. Establishment of tree plantations can significantly decrease soil water retention, with implications for reduced C storage below ground (Farley, 2007). Plantations may also tend to be established on lands where soil C and nutrient stocks have already been depleted through agricultural or other human activities (Lugo & Brown, 1993).

Reduced sample sizes for different plantation tree species types and inconsistent compositional data for successional forests precluded the use of this additional variable in our regression analyses. A simple test of differences between plantations by tree cover types did not reveal significant differences in soil C. While our analyses focused on quantifying stocks and not changes in soil C with reforestation and afforestation, other studies have found that the composition of the new forest cover can affect the fate of soil C. Larger gains have been measured under hardwoods or nitrogen fixers (Paul *et al*., 2002; Resh *et al*., 2002). Pine plantations commonly result in soil C losses, compared with *Eucalyptus* or broad-leaf species (Guo & Gifford, 2002; Paul *et al*., 2002; Berthrong *et al*., 2009).

Previous land use was less important than MAT in explaining variation in soil C with tropical reforestation and afforestation. At depths down to 30 and 100 cm, forest sites on formerly cultivated lands had higher mean soil C stocks than those that had been converted to pasture. Many studies have reported greater gains of soil C with forest establishment on former croplands than on former pasturelands (Laganière *et al*., 2010; Don *et al*., 2011; Powers *et al*., 2011). This is probably due to the reduction of soil C stocks that typically accompanies soil disturbance during cultivation and the harvest of above-ground biomass.

Effect of soil type on soil C storage

Soil type, represented by the three soil activity classes, was a significant predictor variable in all regression tree analyses by depth but not in the multiple linear regression models. This difference may be due to the heavy bias towards sites on low-activity clays in our dataset, which also had the lowest soil C stocks, and which reflects data availability in the literature overall (Powers *et al*., 2011). In our analysis, sites on soils

Table 6 Estimates of mean ± 1 standard error tropical soil C stocks in different forest types or by soil activity class for two common depths. Units are Mg C ha^{-1} unless otherwise specified.

			Soil C content	
Data source	Category	N*	0–30 cm	0–100 cm
This study	Pantropical successional forests, reference forests and tree plantations	510	78.1 ± 1.8	164 ± 4.0
	Dry	79		124 ± 4.0
	Moist	223		164 ± 7.0
	Wet	205		176 ± 5.3
	Low-activity soil	324	71.7 ± 2.0	147.8 ± 4.5
	Medium-activity soil	108	90.8 ± 4.3	195.6 ± 9.0
	High-activity soil	56	96.7 ± 6.3	208.7 ± 14.9
Dixon *et al.* (1994)	Low-latitude forests			120–139
Post *et al.* (1982)	Very dry			61
	Dry			99
	Moist			114
	Wet			191
Detwiler (1986)	Dry	184		104
	Moist	163		114
	Wet	23		150
Batjes (1996)†	Tropical 23.5° N–23.5° S		201–213 Pg C	384–403 Pg C
	Low-activity soil	160	67	96
	Medium-activity soil	1064	88	184
	High-activity soil	1906	114	254
Jobbágy & Jackson (2000)	Tropical deciduous forest	29		158 ± 9.2
	Tropical evergreen forest	36		186 ± 10.4
Eswaran *et al.* (1993)†	Tropical forest soils			
	Low-activity soil			24.7 ± 12.4 Pg C
	Medium-activity soil			35.3 ± 32.3 Pg C
	High-activity soil			25 Pg C
Brown & Lugo (1990)	Tropical lowland forest			
	Dry			142 ± 24
	Moist			170 ± 12
	Wet and rain forest			230 ± 64
	Subtropical lowland and higher elevation plus tropical premontane and other high-elevation forests			
	Dry			78 ± 21
	Moist			196 ± 32
	Wet and rain forest			350 ± 60

*Number of sites or soil profiles.
†We calculated averages of Batjes' (1996) FAO soil order means and Eswaran *et al.*'s (1993) USDA soil order means categorized into our low-, medium- and high-activity class, excluding those orders that were absent from our dataset, to ensure maximum comparability with our results.

classified as high activity, which represented volcanic soils dominated by non-crystalline minerals, had the greatest soil C stocks in the top 10 and 30 cm, consistent with other global syntheses (Table 6; Batjes, 1996; Batjes & Sombroek, 1997).

Soil mineralogy affects how much C is stored in soils (Post *et al.*, 1982; Torn *et al.*, 1997) as well as a site's sensitivity to land-use change, although results may appear contradictory. Hughes *et al.* (1999) found no differences in soil C between active pastures and successional forests growing on former pastures, and attributed this to the high stability of C pools in their allophanic Andisols. On the other hand, López-Ulloa *et al.* (2005) reported greater sensitivity of soil C pools to land-use change in Andisols than in Inceptisols. In a meta-analysis, Laganière *et al.* (2010) reported greater changes in soil C during plantation establishment on soils with a high proportion of clay (33% clay). Soils with a low clay content, which in their case would include both coarse-textured soils and volcanic soils dominated by non-crystalline minerals, appeared to be less sensitive to change. These results highlight the importance of not only identifying a site's soil type but also of understanding the relative importance of specific mechanisms affecting soil C stabilization.

Limitations of the dataset

Our dataset encompassed wide ranges in MAT and MAP and represented nine of the 12 USDA soil orders. However, sites were not distributed equally along these environmental gradients. The most common were secondary forests on highly weathered, low-activity clay soils (Oxisols and Ultisols made up 52% of all sites) in the moist (44%) and wet (40%) rainfall classes. Powers *et al.* (2011) highlighted geographic biases in tropical soil C studies and cautioned against global generalizations. Likewise, Don *et al.* (2011) brought attention to the underrepresentation of African and Southeast Asian sites. Our dataset includes sites from 32 different countries and territories, of which only 30% are outside Latin America and the Caribbean. Despite the growing availability of data outside tropical America, the limitations in our geographic understanding of tropical soil C is important as human management practices and drivers of land-use and land-cover change differ locally and regionally (Brown & Lugo, 1990).

Our findings that climatic factors matter most in predicting soil C reinforce the importance of awareness of the geographic distribution of available data. Forest sites with MAP < 1000 mm are grossly underrepresented. Tropical and subtropical dry forests have already experienced greater rates of conversion to agricultural use (Quesada *et al.*, 2009; Powers *et al.*, 2011), which may explain the scarcity of data. Other factors can affect a site's successional trajectory: intensity and duration of former land use (de Koning *et al.*, 2003) and soil nutrient status (Davidson *et al.*, 2004). The duration of former pasture use was found to explain differences in forest soil C stocks in Ecuador (de Koning *et al.*, 2003). Historical site information is not always available, rendering the analysis of these variables across studies difficult.

Methodological differences in sampling and the lack of standardized depth measurements can also affect the possible generalizations by global syntheses. A meta-analysis of soil C before and after tree plantation rotations found that exclusion of the topmost organic soil horizon could underestimate C inventories significantly (Laganière *et al.*, 2010). The magnitude of this source of error will vary by forest type and climate. Differences in the strength of the relationship between soil C and depth by rainfall class suggest substantial variations in C distribution by depth (Jobbágy & Jackson, 2000), which may contribute to weakened relationships between environmental variables and soil C stocks standardized to fixed depths. The lack of soil mass correction for potential changes in bulk density provides another source of uncertainty (Don *et al.*, 2011). We included those few studies for which we had to use standard equations to estimate bulk density in order to ensure a large sample size to better examine the effects of environmental factors on soil C stocks with reforestation and afforestation.

CONCLUSIONS

Our analyses revealed that MAT was the most significant predictor of soil C stocks in tropical successional and plantation forests. The relative importance and interactions between other factors, such as MAP, current cover type, soil type and previous land use, differed by soil depth, highlighting the need for sampling beyond the top 10 cm and for comparison across standard depths. At the pantropical scale, soil C stocks were similar between tropical secondary forests, tree plantations and reference forests. Our analyses suggest that environmental variables (rainfall, temperature, soil type) are more important for sites on the high end of MAT and MAP, while human management factors, such as current cover type and prior land use, are more important on the lower gradients of climate. Forest age was generally a poor predictor of soil C stocks, suggesting that information about individual site conditions, rather than time since abandonment and forest growth, are important when estimating below-ground C stocks under different forest types. The weak effect of time on soil C stocks suggests that the below-ground pool recovers quickly as most meta-analyses report losses of soil C with tropical deforestation (Don *et al.*, 2011; Powers *et al.*, 2011). Understanding which environmental factors affect soil C stocks under different land-cover types can improve modelling estimates of the effect of changes in tropical vegetation on the global C cycle and guide our selection of appropriate sites for C sequestration projects. The great effect of climate on soil C stocks across a diversity of forest cover types, soil types and former land-use histories suggests that future climatic changes may exert an important control on below-ground C storage in tropical forests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of sites used in the analyses.
Appendix S2 References for Appendix S1.

BIOSKETCHES

Erika Marín-Spiotta is an assistant professor of geography at the University of Wisconsin-Madison. Her research interests include the effects of land-use change on biodiversity and biogeochemistry.

Sapna Sharma is an assistant professor of biology at York University. Her research interests include predicting the impacts of environmental stressors, such as climate change, biological invasions and alterations in habitat, on aquatic and terrestrial ecosystems.

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