Conversion of lowland tropical forests to tree cash crop plantations loses up to one-half of stored soil organic carbon

Oliver van Straaten[a], Marife D. Corre[a], Katrin Wolf[a,1], Martin Tchienkoua[b,2], Eloy Cuellar[c], Robin B. Matthews[d], and Edzo Veldkamp[a,3]

[a]Buesgen Institute, Soil Science of Tropical and Subtropical Ecosystems, Georg-August University of Goettingen, 37077 Goettingen, Germany; [b]Institut de Recherche Agricole pour le Développement, Nkolbisson, Yaoundé, Cameroon; [c]Instituto Nacional de Investigación Agraria, La Molina, Lima 12, Peru; and [d]The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH, Scotland, United Kingdom

Edited by Peter M. Vitousek, Stanford University, Stanford, CA, and approved June 26, 2015 (received for review March 6, 2015)

Tropical deforestation for the establishment of tree cash crop plantations causes significant alterations to soil organic carbon (SOC) dynamics. Despite this recognition, the current Intergovernmental Panel on Climate Change (IPCC) tier 1 method has a SOC change factor of 1 (no SOC loss) for conversion of forests to perennial tree crops, because of scarcity of SOC data. In this pantropic study, conducted in active deforestation regions of Indonesia, Cameroon, and Peru, we quantified the impact of forest conversion to oil palm (*Elaeis guineensis*), rubber (*Hevea brasiliensis*), and cacao (*Theobroma cacao*) agroforestry plantations on SOC stocks within 3-m depth in deeply weathered mineral soils. We also investigated the underlying biophysical controls regulating SOC stock changes. Using a space-for-time substitution approach, we compared SOC stocks from paired forests (n = 32) and adjacent plantations (n = 54). Our study showed that deforestation for tree plantations decreased SOC stocks by up to 50%. The key variable that predicted SOC changes across plantations was the amount of SOC present in the forest before conversion—the higher the initial SOC, the higher the loss. Decreases in SOC stocks were most pronounced in the topsoil, although older plantations showed considerable SOC losses below 1-m depth. Our results suggest that (*i*) the IPCC tier 1 method should be revised from its current SOC change factor of 1 to 0.6 ± 0.1 for oil palm and cacao agroforestry plantations and 0.8 ± 0.3 for rubber plantations in the humid tropics; and (*ii*) land use management policies should protect natural forests on carbon-rich mineral soils to minimize SOC losses.

soil carbon | land-use change | oil palm | rubber | cacao

The ever-growing demand for cash crop plantation products such as wood, agro-biofuels (particularly oil palm), rubber, and cacao has caused significant deforestation across many regions of the humid tropics. In the past two decades (1990–2010), global demand for tree cash crop products has increased dramatically. Oil palm production areas have grown by nearly 260% (to 15.9 Mha), cacao by 166% (to 9.5 Mha), and rubber by 143% (to 9.4 Mha) (1). It is also recognized that much of the expansion of these tree cash crop plantations comes at the expense of lowland tropical forests (2, 3). Although extensive emphasis is given to the impacts of oil palm plantations in tropical carbon-rich peatlands (4, 5), mineral soils, which have a far larger areal coverage across the tropics (6), are receiving comparatively less attention for this land use. Mineral soils have high spatial variability in soil organic carbon (SOC) stocks (7), where some soils can contain considerably more carbon than other soils.

Soils in the humid tropics store 30% of the global SOC in the top 3 m (692 Gt carbon) (8), which is comparable to the amount of carbon in the atmosphere (589 Gt carbon) (9). Given the highly productive nature of tropical ecosystems, and the correspondingly short mean carbon residence times (10), even small changes in site conditions such as climate or land-use change can contribute to a significant carbon flux to the atmosphere (11, 12). It is estimated that land-use conversion in the tropics was responsible for a net release of between 0.6 and 1.2 Gt C·y^{-1} (2000–2010) (13) from aboveground sources alone. However, the magnitude of belowground carbon changes and the underlying factors regulating these changes remain highly uncertain (14). The current Intergovernmental Panel on Climate Change (IPCC) Guidelines for Greenhouse Gas (GHG) Inventory (15) reports high variability of SOC data for conversion of forests to perennial tree crops, and thus the IPCC tier 1 method has a default value of 1 (no SOC loss). This is, however, in clear contrast to a growing pool of literature that shows that SOC stocks significantly decrease when tree plantations are established following deforestation (11, 16, 17).

Improving the predictability of SOC stock changes and their controls are crucial to achieving more robust carbon accounting methods. It is well recognized that the size of the SOC stock changes is controlled by numerous (often interacting) factors, including climate, vegetation, parent material, topography, and time (18), with the importance of each of these factors varying at different spatial scales and in different environments (19). Various metaanalyses and reviews have found that precipitation and clay mineralogy are the most important controlling factors of SOC stock changes at large scales across the tropics (20–24). Precipitation strongly affects plant productivity, which in turn influences soil carbon fluxes (22). Furthermore, soil moisture regimes play a vital role in regulating the microbial communities responsible for organic

Significance

Deforestation for tree cash crop plantations such as oil palm, rubber, and cacao agroforest in the tropics results in strong decreases in soil organic carbon (SOC) stocks, with much of this carbon lost through carbon dioxide (CO_2) emissions and leaching. We found that SOC stock losses in oil palm, rubber, and cacao agroforestry plantations in Indonesia, Cameroon, and Peru could be predicted by the amount of SOC in the original forests: the more SOC present initially, the more SOC lost after conversion. When natural forests were replaced by tree cash crop plantations, SOC losses of up to 50% were found. We recommend that these SOC losses be incorporated in the Intergovernmental Panel on Climate Change tier 1 method for carbon accounting.

Author contributions: O.v.S., M.D.C., R.B.M., and E.V. designed research; O.v.S., K.W., M.T., and E.C. performed research; M.T. was field coordinator in Cameroon and scientific advisor; E.C. was field coordinator in Peru; O.v.S. analyzed data; and O.v.S., M.D.C., and E.V. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

[1]Present address: Atmosfair gGmbH, 10961 Berlin, Germany.

[2]Deceased October 8, 2014.

[3]To whom correspondence should be addressed. Email: eveldka@gwdg.de.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1504628112/-/DCSupplemental.

ENVIRONMENTAL SCIENCES

matter decomposition. Stratified within precipitation classes, clay mineralogy strongly affects the physical stabilization of carbon on mineral surfaces, and accordingly its vulnerability to losses following land-use change (25).

However, serious shortcomings remain in applying these findings to carbon inventories. Powers et al. (21) highlight that, in existing literature, there is a representational mismatch between the biophysical conditions of studied locations and the actual geographic distributions of these conditions in the tropics, thereby precluding simple spatial extrapolation of quantified SOC changes to the entire tropics. They stress the need for further research in underrepresented areas, as well as improved estimates of SOC stock changes from "new" rapidly expanding land use types such as agro-biofuel production (i.e., oil palm) and commodity-based tree cash crop plantations (i.e., cacao, rubber) (21). Additionally, there is also an urgent need to investigate SOC stock changes at deeper depths (26, 27) considering that most studies only examine changes in the topsoil despite the presence of large SOC stocks in the subsoil.

Study Description

In this pantropic study, we quantified the magnitude of SOC stock changes associated with conversion of natural forests to oil palm (27 paired sites), rubber (26 paired sites), and cacao agroforestry plantations (11 paired sites) and determined the factors that influenced SOC concentrations and the respective SOC stock changes. We explicitly selected three regions across three continents, where there is active land-use conversion to tree cash crop plantations, and where biophysical conditions are representative of large regions of the humid tropics. A spatial analysis showed that the sites we investigated are representative of the biophysical conditions found in 45% of the humid tropics (based on elevation, precipitation, and soil types; *SI Methods*, *Method S1*). Beyond the broad spatial sampling distribution, we also sampled deep in the soil (down to 3 m) to determine the extent of SOC stock changes.

The three study regions, (*i*) Jambi Province, Sumatra, Indonesia, (*ii*) Ucayali Region, Peru, and (*iii*) southern Cameroon (Fig. S1), are all situated on deeply weathered soils, either Ferralsols or Acrisols (Food and Agriculture Organization of the United Nations classification) on flat to moderately sloping topography, with low soil pH, low base saturation, and moderate levels of precipitation (Table S1). All converted land uses were smallholder plantations. Clearing was done by burning after taking out useful wood products and slashing the rest of the vegetation. Cultivation was minimal, using hand tools to plant oil palm, rubber, and cacao on each planting spot, and localized weeding was done manually. Both oil palm and rubber plantations were established as monocultures, whereas cacao trees were planted in the understory of remnant trees. These were also first-generation plantations, established right after clearing the previous land use. Using a space-for-time substitution (chronosequence) approach, we measured SOC stocks together with soil biochemical and physical properties in paired natural forest sites (reference) and adjacent tree cash crop plantations (oil palm, rubber, and cacao agroforest with distances ranging from 130 m to 6 km apart).

In total, we established 86 plots. In each plot, soil samples were taken at predefined depths (0–10, 10–30, 30–50, 50–100, 100–200, and 200–300 cm). Samples in the top 50 cm were taken using a soil auger from 12 locations within the plot and composited, whereas samples below 50 cm were taken from a central soil pit. Through careful site selection that considered both the similarity of the paired site's physical characteristics (soil texture, soil color, topographic positions) and later through an independent check of the comparability of clay contents at 50–100 cm, we ensured that soil properties between the paired reference forests and plantations were similar. Accordingly, any changes observed in SOC are likely to be directly attributable to the respective land-use conversions.

Results

Land-Use Change Effects on SOC Stocks. Despite steeply decreasing SOC concentrations with depth (Fig. S2*A*), most of the SOC was stored in the subsoil (below 50 cm), accounting for 53 ± 2% of the total SOC in the 3-m profile in natural forest sites (52 ± 2% in Indonesia, 52 ± 3% in Peru, and 58 ± 3% in Cameroon; Fig. S2*B*). We measured significant decreases in SOC stocks at various depths in all land use types across all three countries (Fig. 1). Even though the largest SOC changes were concentrated in the topsoil (0–10 cm), the majority of these plantations were relatively young (less than 30 y) and may not have reached a steady-state condition at deeper depths. In the Cameroon sites, where older plantations (up to 100 y) were sampled, we also measured significant SOC stock decreases in the subsoil (between 1 and 2 m in rubber plantations and between 2 and 3 m in cacao agroforests; Fig. 1). This suggests that the large quantity of deeply stored SOC stocks may be vulnerable to land-use changes over extended periods. Furthermore, we measured significant decreases in soil C/N ratios (Fig. S3) and significant increases in soil bulk density (Fig. S4) and pH (Fig. S5) in all tree plantation types compared with the reference forests.

Biophysical Controls on SOC Stocks. In our study, where we sampled across a relatively narrow range of precipitation (Table S1) and all in heavily weathered soils (Acrisols and Ferralsols), it is evident that SOC concentrations in the subsoil (50–100 cm) of the forest sites were strongly dependent on clay content and soil bulk density and not by climatic variables (Table 1). The positive correlation observed with clay (which is autocorrelated with bulk density) suggests that SOC is stabilized through organo-mineral complexation. In contrast, the changes in SOC stocks from conversion of forests to tree cash crop plantations were not correlated with soil properties and were only partially explained by precipitation (for cacao agroforests) and temperature (Table 1). Across all plantations, relative changes in SOC were positively correlated with temperature, despite the small temperature range (3.8 °C; Table S1). Also, the time since deforestation partly predicted decreases in SOC stocks across plantations (Fig. S6). The fitted monoexponential decay functions with time since conversion to oil palm, cacao agroforest, and rubber plantations indicated that 20–40% (calculated as 100% − a, the equilibrium ratio shown in Fig. S6) of the original SOC had decomposed or was lost with a turnover time of 4–8 y (reciprocal of k, the decay rate shown in Fig. S6). Indeed, the best predictor for determining the magnitude of SOC loss across plantations was the amount of SOC present before deforestation (reference forest; Fig. 2*A*).

Discussion

All tree cash crop plantations in the three regions exhibited sizable losses of SOC stocks as a result of conversion from natural forests. These SOC losses reflect a change in the equilibrium of carbon inputs and losses in the present land uses. In comparison with the forests, all three plantation types had lower net primary production (NPP) excluding yield (28, 29) and aboveground biomass (Table S1). NPP estimates from a recent study in Jambi, Indonesia, found that, although oil palm plantations had high NPP, more than one-half (49–60%) of the biomass production was removed through harvest of oil palm fruit (28). Likewise, both rubber and cacao agroforestry plantations had lower NPP estimates than natural forest (28, 29), where a large proportions was also removed through harvested products [13–20% in rubber plantations (28) and 21% in cacao agroforests (29)]. All these indicate reduction in ecosystem carbon inputs in these plantations (Table S1).

Moreover, organic matter decomposition rates will also have been affected by changes in microclimate (30–32) and soil physical and biochemical properties (24, 33) in the plantations. More specifically, the removal of the forest vegetation during land-use conversion will have increased soil surface temperatures (31), increased

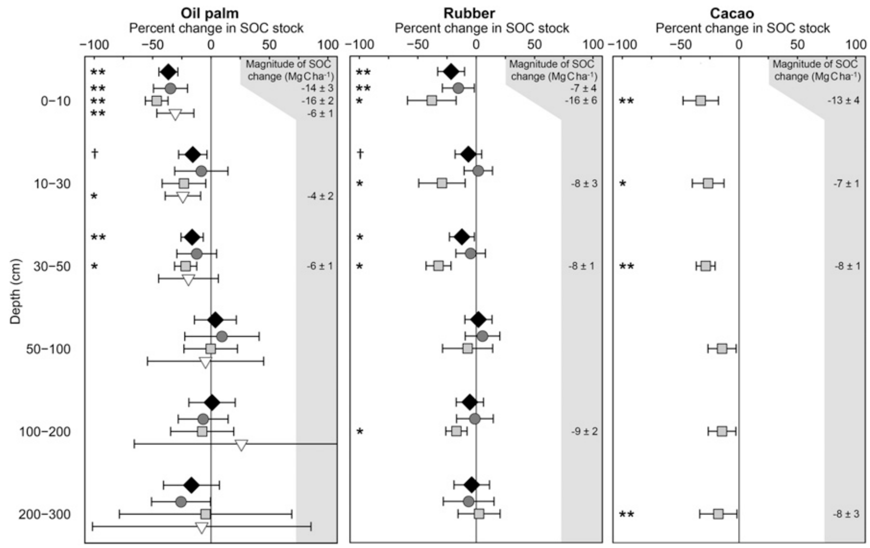

Fig. 1. Relative change [(forest – plantation)/forest × 100] in soil organic carbon (SOC) stock in the 0- to 3-m depth of the three plantation types across three regions (◆), Indonesia (●), Cameroon (□), and Peru (▽). Error bars indicate the 95% confidence intervals based on Student's *T* distribution. Statistical significance is based on LME models at $P \leq 0.10$ (†, marginally significant), $P \leq 0.05$ (*), and $P \leq 0.01$ (**). Cumulative decreases in SOC stocks (considering only the depths with significant changes) for oil palm were 14 ± 3 Mg C·ha^{-1} (n = 11) in Indonesia, 22 ± 1 Mg C·ha^{-1} (n = 5) in Cameroon, and 10 ± 2 Mg C·ha^{-1} (n = 5) in Peru. Cumulative decreases in SOC stocks for rubber were 7 ± 4 Mg C·ha^{-1} (n = 16) in Indonesia and 41 ± 3 Mg C·ha^{-1} (n = 6) in Cameroon. SOC loss for cacao agroforest was 35 ± 2 Mg C·ha^{-1} (n = 11) in Cameroon. The magnitude of SOC losses for the depths with significant changes are presented in the gray-shaded area.

erosional losses (34), and increased compaction because of trampling (i.e., evident in increased bulk density; Fig. S4), thereby affecting soil aeration, water transport, and root penetration (and accordingly root distributions) (35). The ash deposits left after burning are likely responsible for the measured increases in soil pH (Fig. S5), which, in turn, may have improved the soil biochemical properties and organic matter decomposition. Consequently, the decreases in soil C/N ratios (Fig. S3) reflected enhanced microbial processing in soils and/or improved quality of organic matter input.

The magnitude of SOC losses across plantations was, however, best predicted by the amount of SOC present before deforestation. This has not been shown by any single study before for these tree plantation types. Data points below the 1:1 line in Fig. 2*A* indicate that the input of SOC from plantations was less than the loss of SOC from the original forests due to conversion. Because the slope of the linear regression between SOC stocks (0–10 cm) in reference forests and plantations was significantly different from 1 (represented by the 1:1 line), it highlights how SOC losses were dependent on the initial SOC stocks: the higher the SOC stocks in the reference forests, the more SOC was lost in the plantations. It is evident that forests that have SOC stocks exceeding 30 Mg C·ha^{-1} in the top 10 cm (Fig. 2*A*; 30 sites out of 54) lost ∼40–50% of their SOC stocks due to the land-use conversion [losses of 44.9 ± 2.8% (n = 13) for oil palm, 39.7 ± 5.7% (n = 11) for rubber, and 49.1 ± 5.4% (n = 6) for cacao agroforestry plantations]. This implies that forests that have high SOC stocks are also at the greatest risk of losing large quantities of their stored SOC if converted. The residuals of this linear regression model showed that the deviation from the predicted line was significantly explained by clay contents (Fig. 2*B*), suggesting that soils with high clay contents are less susceptible to SOC losses. This could be due to both physicochemical protection of SOC through organo-mineral complexation (36) and

Table 1. Spearman correlation coefficients of SOC concentrations (50–100 cm) and SOC stock changes (0–10 cm) with explanatory variables

	SOC concentration, %, 50–100 cm	Percent relative change in SOC stock†, 0–10 cm			
Explanatory variables	Natural forest (n = 32)	Oil palm (n = 21)	Rubber (n = 22)	Cacao (n = 11)	All plantations combined (n = 54)
Soil variables					
Clay, %	**0.59****	−0.04	−0.15	0.13	−0.03
Bulk density, g·cm^{-3}	**−0.78****	0.07	−0.14	0.08	−0.09
Soil pH	−0.16	−0.03	0.17	−0.06	−0.03
Effective cation exchange capacity, mmol$_c$·kg^{-1}	0.24	0.26	0.29	0.06	0.15
Base saturation, %	−0.20	0.04	−0.09	0.12	−0.05
Climatic variables					
Mean annual precipitation, mm·y^{-1}	−0.25	0.18	0.23	**−0.61***	0.12
Mean annual temperature, °C	−0.21	**0.37**‡	**0.46***	0.25	**0.34***

†Percent relative change in SOC: (forest – plantation)/forest × 100.
‡Boldface numbers are marginally significant at $P \leq 0.1$, and significant at $^*P \leq 0.05$, and $^{**}P \leq 0.01$.

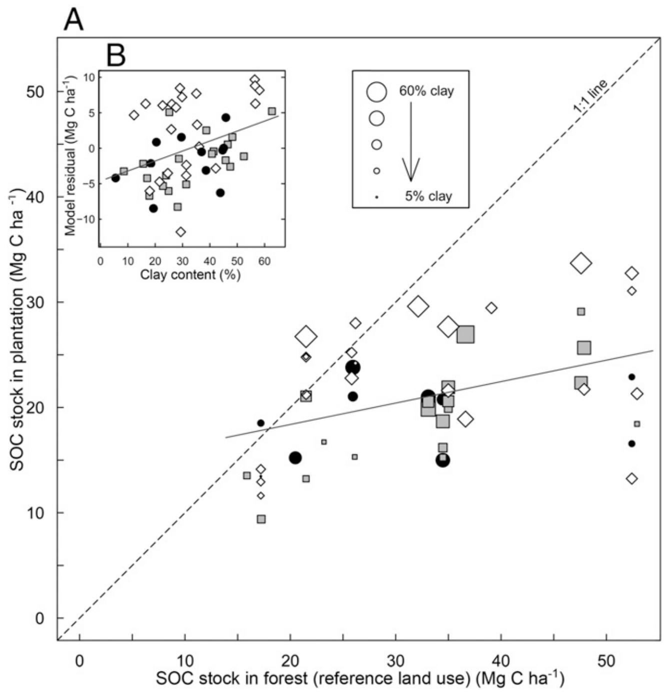

Fig. 2. (*A*) The higher the initial soil organic carbon (SOC) stock, the larger the SOC losses, evident from the slope (slope = 0.21, which is significantly different from the 1; $P \leq 0.01$) of the regression model ($R^2 = 0.18$; $P \leq 0.01$; $n = 54$) of SOC stocks within 0- to 10-cm depth between paired reference forests and oil palm (□), rubber (◇), and cacao agroforestry (●) plantations. The size of the data points is proportional to the soil clay percentage measured in the plantation plots. (*B*) The residuals of the regression model explained by clay contents of the soils ($R^2 = 0.14$; $P = 0.01$; $n = 54$).

sufficient organic matter input because clayey soils have large nutrient ion exchange capacity and NPP (37).

These findings highlight that changes in the SOC stocks associated with deforestation for tree cash crop plantations are predictable by the initial SOC in the forests and clay content. Furthermore, the large SOC losses reinforce the need for the IPCC to update their default values in the Climate Change Guidelines for GHG Inventory to recognize the impact of these land-use conversions on global carbon emissions. Considering that our study sites were representative of 45% of the humid tropics, we suggest that the IPCC tier 1 method should be revised from its current SOC change factor of 1 (no SOC loss) to 0.6 ± 0.1 (SOC remaining after forest conversion) for oil palm and cacao agroforestry plantations and 0.8 ± 0.3 for rubber plantations (i.e., the *a* values or the equilibrium ratios, shown in Fig. S6). The conversion factor for rubber plantations is similar to what de Blécourt et al. (16) reported. Last, land use management policies aiming to mitigate GHG emissions need to protect forests on carbon-rich mineral soils to effectively curtail carbon losses.

Methods

Experimental Design. In each of the three study regions (see *SI Methods, Method S2*, for further detailed information), we used a space-for-time substitution approach to measure changes in SOC stocks. A total of 24 clustered sites (13 clusters in Indonesia, 6 clusters in Cameroon, and 5 clusters in Peru) were selected in converted plantations around a central reference forest plot. In total, 21 plots were established in oil palm plantations (ranging in age between 10 and 25 y), 22 plots in rubber plantations (10–55 y), 11 plots in cacao agroforestry plantations (20–100 y), and 32 plots in natural forests. Careful site selection was exercised such that the reference forests were representative of the original land cover. The implicit assumption of this approach is that soil and environmental characteristics and SOC stocks between the reference forests and converted sites to plantations were initially the same within a cluster such that measured changes in SOC can be attributed solely to land-use change. Accordingly, we chose clustered sites that had similar soil texture, soil color, and climatic conditions, and were located on similar landscape positions. A posteriori soil texture analysis of the sites was used to exclude plantation sites where the subsoil (50–100 cm, presumably less affected by land cover change) had a greater than 20% difference in clay contents from the respective reference forests. In total, 10 of the original 96 plots were removed from the analysis. We also chose converted sites that (*i*) were close to the reference forests, (*ii*) were well established (>10 y old), and (*iii*) had clear prior land use (i.e., forest). The only exception was the oil palm plantations in Peru, which were previously pastures converted from forests; such land use history was, however, representative of the study region because conversion to oil palm plantation was driven by decreases in beef prices. To evaluate whether SOC in pastures and oil palm plantations have changed, we compared their δ^{13}C-SOC signatures and found that the δ^{13}C-SOC signatures changed from −24.4‰ in pastures to −23.4‰ in oil palm plantations. Thus, we recognized that the change in SOC under the present oil palm plantations included the SOC loss during the intermediary pasture land use.

Soil Sampling. At each site, we established a 20×20-m plot, keeping at least 10 m away from the land use perimeter to avoid edge effects. At the plot center, we dug a soil pit 2 m in depth and $\sim 1 \times 1$ m in width and length. Soil samples for biochemical and physical property analysis were taken at predefined depth intervals of 0–10, 10–30, 30–50, 50–100, and 100–200 cm. Using a soil auger, we took a final sample at the bottom of the soil pit to 3-m depth (200–300 cm). Additionally, samples were taken from 12 fixed sampling points in the plot at three depth intervals (0–10, 10–30, and 30–50 cm) and were pooled into one composite sample for each depth and plot. We used the composite sample for SOC analysis for the top 50-cm depth, as its sampling had spatially represented the plot, and used the soil pit samples for depths below 50 cm. Soil bulk density (Fig. S4) was measured at seven depths in the soil profile (10, 20, 40, 75, 100, 150, and 200 cm) using the soil core method. Because the soil profiles were heavily weathered and rarely contained any stones or rock fragments, we did not correct for gravel content. Additional information on site history, land use management, site location, climatic conditions, and ecosystem biomass are provided in *SI Methods, Method S2*.

Soil Sample Analyses. To ensure comparability across the study areas, the soil samples from all three countries were analyzed at the same laboratory at the Georg-August University of Goettingen, Germany, using the same instruments and methods (*SI Methods, Method S3*). SOC stock was calculated for each respective sampling depth based on the soil carbon concentrations, the soil layer's bulk density, and the layer thickness. The SOC stock for the 2- to 3-m depth interval was calculated using the bulk density measured at 200-cm depth because the subsoil structure was relatively homogeneous and there were no significant differences in bulk densities between 150- and 200-cm depths. The bulk density of the reference plots was used for calculating the SOC stocks of the converted land uses in the same cluster (38). We used this conservative approach to avoid overestimating the SOC stock due to increases in soil bulk densities with land-use conversion (Fig. S4). We used the relative SOC change, expressed in percentage and calculated as $(\text{forest}_{SOC} - \text{plantation}_{SOC})/(\text{forest}_{SOC} \times 100)$, as the metric for changes in SOC stock to account for the differences in initial SOC stocks of the reference forests (21).

Statistical Analysis. A paired *t* test was used to evaluate the comparability of plot pairs (reference forest vs. converted plantation), based on the subsoil soil clay content in the 50- to 100-cm depth, which should not be or only minimally influenced by land-use change. Once we ascertained that paired plots had statistically comparable subsoil texture, we tested the differences in SOC stocks between the reference forests and converted plantations using linear mixed effects (LME) models. In the LME analysis, SOC stock is the response variable, and land use types were considered fixed effects and the plot clusters (spatial replications) as random effects. Differences were considered significant if $P \leq 0.05$ and marginally significant if $P \leq 0.1$.The input SOC data as well as the output model residuals were tested for normality using Shapiro–Wilk test. To gain an insight into the underlying factors regulating SOC concentrations and relative changes in SOC stocks, we used Spearman's rank correlation analyses of SOC variables with soil properties (clay content, bulk density, soil pH, effective cation exchange capacity, base saturation), aboveground biomass carbon and with climatic variables (mean annual precipitation, mean annual temperature, length of the dry season). The trend between relative SOC stock changes in plantations with time since forest conversion was examined using a monoexponential decay function, based on the assumption that SOC stocks will reach a new equilibrium with time (39).

The goodness of fit of the model was assessed using Pearson correlation analyses between model-predicted values and measured values. We used a linear regression model to fit the relationship of SOC stocks in the reference forests with those in the paired plantation sites. The slope of the regression model was tested using a one-sample *t* test to determine whether it is significantly different from 1. Finally, the residuals of this regression model were then related to soil parameters that best explained the variance unaccounted by the initial SOC stocks of the reference forests. All statistical analyses were carried out using R, version 2.14.2 (40).

ACKNOWLEDGMENTS. We thank Lou Verchot and Kristell Hergoualc'h at Center for International Forestry Research and Meine van Noordwijk at World Agroforestry Centre for logistical support in Indonesia. This study was completed within the framework of the "Reducing Emissions from Deforestation and Degradation from Alternative Land Uses in Rainforests of the Tropics" project funded by the European Community's Seventh Framework Programme (FP7/2007–2013) under Grant Agreement 226310. Parts of this study were also funded by Deutsche Forschungsgemeinschaft in Project A05 (SFB 990/1) of the Collaborative Research Center 990: Ecological and Socioeconomic Function of Tropical Lowland Rainforest Transformation Systems.

1. Food and Agriculture Organization of the United Nations (2013) Food and Agriculture Organization of the United Nations Statistical Database (28/09/2009). Available at faostat.fao.org. Accessed March 3, 2015.
2. Laumonier Y, et al. (2010) Eco-floristic sectors and deforestation threats in Sumatra: Identifying new conservation area network priorities for ecosystem-based land use planning. *Biodivers Conserv* 19(4):1153–1174.
3. Warren-Thomas E, Dolman PM, Edwards DP (2015) Increasing demand for natural rubber necessitates a robust sustainability initiative to mitigate impacts on tropical biodiversity. *Conserv Lett*. Available at doi.wiley.com/10.1111/conl.12170. Accessed June 1, 2015.
4. Hergoualc'h K, Verchot LV (2011) Stocks and fluxes of carbon associated with land use change in Southeast Asian tropical peatlands: A review. *Global Biogeochem Cycles* 25(2):1–13.
5. Murdiyarso D, Hergoualc'h K, Verchot LV (2010) Opportunities for reducing greenhouse gas emissions in tropical peatlands. *Proc Natl Acad Sci USA* 107(46):19655–19660.
6. FAO/IIASA/ISRIC/ISSCAS/JRC (2012) Harmonized World Soil Database (version 1.2) (FAO, IIASA 2012). Available at webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/. Accessed August 3, 2014.
7. Scharlemann JP, Tanner EV, Hiederer R, Kapos V (2014) Global soil carbon: Understanding and managing the largest terrestrial carbon pool. *Carbon Manag* 5(1): 81–91.
8. Jobbágy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl* 10(2):423–436.
9. Ciais P, et al. (2013) Carbon and other biogeochemical cycles. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Stocker TF, et al. (Cambridge Univ Press, Cambridge, UK). Available at https://www.ipcc.ch/pdf/assessment-report/ar5/wg1/WG1AR5_Chapter06_FINAL.pdf. Accessed July 10, 2015.
10. Amundson R (2001) The carbon budget in soils. *Annu Rev Earth Planet Sci* 29:535–562.
11. Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: A meta analysis. *Glob Change Biol* 8(4):345–360.
12. Post WM, Kwon KC (2000) Soil carbon sequestration and land-use change: Processes and potential. *Glob Change Biol* 6(3):317–327.
13. Achard F, et al. (2014) Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Glob Change Biol* 20(8):2540–2554.
14. Grace J, Mitchard E, Gloor E (2014) Perturbations in the carbon budget of the tropics. *Glob Change Biol* 20(10):3238–3255.
15. Lasco RD, et al. (2006) Cropland. *2006 IPCC Guidelines for National Greenhouse Gas Inventories, Volume 4, Agriculture, Forestry and Other Land Use* (Institute for Global Environmental Strategies, Hayama, Japan), pp 5.1–5.66.
16. de Blécourt M, Brumme R, Xu J, Corre MD, Veldkamp E (2013) Soil carbon stocks decrease following conversion of secondary forests to rubber (*Hevea brasiliensis*) plantations. *PLoS One* 8(7):e69357.
17. Chiti T, Grieco E, Perugini L, Rey A, Valentini R (2014) Effect of the replacement of tropical forests with tree plantations on soil organic carbon levels in the Jomoro District, Ghana. *Plant Soil* 375(1-2):47–59.
18. Trumbore SE (1997) Potential responses of soil organic carbon to global environmental change. *Proc Natl Acad Sci USA* 94(16):8284–8291.
19. Powers JS, Schlesinger WH (2002) Relationships among soil carbon distributions and biophysical factors at nested spatial scales in rain forests of northeastern Costa Rica. *Geoderma* 109(3-4):165–190.
20. Don A, Schumacher J, Freibauer A (2011) Impact of tropical land-use change on soil organic carbon stocks—a meta-analysis. *Glob Change Biol* 17(4):1658–1670.
21. Powers JS, Corre MD, Twine TE, Veldkamp E (2011) Geographic bias of field observations of soil carbon stocks with tropical land-use changes precludes spatial extrapolation. *Proc Natl Acad Sci USA* 108(15):6318–6322.
22. Marín-Spiotta E, Sharma S (2013) Carbon storage in successional and plantation forest soils: A tropical analysis. *Glob Ecol Biogeogr* 22(1):105–117.
23. De Koning GHJ, Veldkamp E, Lopez-Ulloa M (2003) Quantification of carbon sequestration in soils following pasture to forest conversion in northwestern Ecuador. *Global Biogeochem Cycles* 17(4):1–12.
24. Van Noordwijk M, et al. (1997) Soil carbon dynamics in the humid tropical forest zone. *Geoderma* 79(1-4):187–225.
25. Verchot LV, Dutaur L, Shepherd KD, Albrecht A (2011) Organic matter stabilization in soil aggregates: Understanding the biogeochemical mechanisms that determine the fate of carbon inputs in soils. *Geoderma* 161(3-4):182–193.
26. Harper RJ, Tibbett M (2013) The hidden organic carbon in deep mineral soils. *Plant Soil* 368(1-2):641–648.
27. Rumpel C, Kögel-Knabner I (2010) Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. *Plant Soil* 338(1-2):143–158.
28. Kotowska MM, Leuschner C, Triadiati T, Meriem S, Hertel D (May 16, 2015) Quantifying above- and belowground biomass carbon loss with forest conversion in tropical lowlands of Sumatra (Indonesia). *Glob Chang Biol*, 10.1111/gcb.12979.
29. Leuschner C, et al. (2013) Conversion of tropical moist forest into cacao agroforest: Consequences for carbon pools and annual C sequestration. *Agrofor Syst* 87(5): 1173–1187.
30. Luskin MS, Potts MD (2011) Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic Appl Ecol* 12(6):540–551.
31. Yonekura Y, et al. (2010) Changes in soil carbon stock after deforestation and subsequent establishment of "Imperata" grassland in the Asian humid tropics. *Plant Soil* 329(1-2):495–507.
32. Bellamy PH, Loveland PJ, Bradley RI, Lark RM, Kirk GJD (2005) Carbon losses from all soils across England and Wales 1978–2003. *Nature* 437(7056):245–248.
33. Certini G (2005) Effects of fire on properties of forest soils: A review. *Oecologia* 143(1):1–10.
34. Guillaume T, Muhammad D, Kuzyakov Y (April 15, 2015) Losses of soil carbon by converting tropical forest to plantations: Erosion and decomposition estimated by δ13C. *Glob Chang Biol*, 10.1111/gcb.12907.
35. Lipiec J, Hatano R (2003) Quantification of compaction effects on soil physical properties and crop growth. *Geoderma* 116(1-2):107–136.
36. Sollins P, Homann P, Caldwell BA (1996) Stabilization and destabilization of soil organic matter: Mechanisms and controls. *Geoderma* 74(1-2):65–105.
37. Uehara G (1995) Management of isoelectric soils of the humid tropics. *Soil Management and the Greenhouse Effect, Advances in Soil Science*, eds Lal R, Kimble JM, Levine E, Stewart B (CRC, Boca Raton, FL), pp 247–278.
38. Veldkamp E (1994) Organic-carbon turnover in three tropical soils under pasture after deforestation. *Soil Sci Soc Am J* 58(1):175–180.
39. Lobe I, Amelung W, Du Preez CC (2001) Losses of carbon and nitrogen with prolonged arable cropping from sandy soils of the South African Highveld. *Eur J Soil Sci* 52(1): 93–101.
40. R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. Available at www.r-project.org. Accessed June 24, 2012.
41. Food and Agriculture Organization of the United Nations (2001) *FRA 2000: Global Ecological Zoning for the Global Forest Resources Assessment 2000, Final Report (Rome, 2001)*. Available at www.fao.org/docrep/006/ad652e/ad652e00.htm. Accessed October 29, 2014.
42. Jarvis AHI, Reuter A, Nelson EG (2008) Hole-Filled SRTM 90m for the Globe, Version 4 Database. Available at srtm.csi.cgiar.org. Accessed October 29, 2014.
43. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25(15):1965–1978.
44. Duguma B, Gockowski J, Bakala J (2001) Smallholder cacao (*Theobroma cacao* Linn.) cultivation in agroforestry systems of West and Central Africa: Challenges and opportunities. *Agrofor Syst* 51(3):177–188.
45. Walker W, et al. (2011) *Field Guide for Forest Biomass and Carbon Estimation* (Woods Hole Research Center, Falmouth, MA). Available at www.whrc.org/resources/fieldguides/carbon/pdf/FieldGuideSmall.pdf. Accessed June 5, 2014.