## Geographic bias of field observations of soil carbon stocks with tropical land-use changes precludes spatial extrapolation

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Accurately quantifying changes in soil carbon (C) stocks with landuse change is important for estimating the anthropogenic fluxes of greenhouse gases to the atmosphere and for implementing policies such as REDD (Reducing Emissions from Deforestation and Degradation) that provide financial incentives to reduce carbon dioxide fluxes from deforestation and land degradation. Despite hundreds of field studies and at least a dozen literature reviews, there is still considerable disagreement on the direction and magnitude of changes in soil C stocks with land-use change. We conducted a meta-analysis of studies that quantified changes in soil C stocks with land use in the tropics. Conversion from one land use to another caused significant increases or decreases in soil C stocks for 8 of the 14 transitions examined. For the three land-use transitions with sufficient observations, both the direction and magnitude of the change in soil C pools depended strongly on biophysical factors of mean annual precipitation and dominant soil clay mineralogy. When we compared the distribution of biophysical conditions of the field observations to the area-weighted distribution of those factors in the tropics as a whole or the tropical lands that have undergone conversion, we found that field observations are highly unrepresentative of most tropical landscapes. Because of this geographic bias we strongly caution against extrapolating average values of land-cover change effects on soil C stocks, such as those generated through meta-analysis and literature reviews, to regions that differ in biophysical conditions.

Organic carbon stored in the world's soils is the largest ter-restrial pool of carbon, and is at least three times larger than the pool of atmospheric carbon dioxide  $(1-3)$ . It has long been recognized that land-cover change and management can alter the amount of organic carbon stored in the soil (4, 5), and this in turn affects both soil fertility and atmospheric carbon dioxide  $(CO_2)$  concentrations. Although the contributions of land-cover change to anthropogenic  $CO<sub>2</sub>$  atmospheric emissions have recently been revised downward (6), the estimated current annual contribution of 1.2 Pg, or about 12 to 15% of total anthropogenic fluxes, is still significant. The terrestrial  $CO<sub>2</sub>$  flux includes emissions from both biomass and soils (7, 8). Continued improvements in remote sensing allow for ever-better estimates of both the areal extent of different land uses and above-ground biomass stocks (9). In contrast, remote sensing is currently not a reliable option for measuring stocks of soil C. Despite hundreds of field studies and dozens of literature reviews, there is still considerable disagreement on the direction and magnitude of changes in soil C stocks with land-use change. Indeed, the Intergovernmental Panel on Climate Change 2006 Guidelines for National Greenhouse Gas Inventories states, "the current knowledge remains inconclusive on both the magnitude and direction of C stock changes in mineral forest soils associated with forest type, management and other disturbances, and cannot support broad generalizations" (10).

We conducted a meta-analysis of field studies of land-use change effects on total soil organic carbon stocks to determine whether general patterns exist and if including biophysical factors reduces unexplained variation in observed responses. We focused on the tropics, as these latitudes account for the bulk of the current  $CO<sub>2</sub>$  emissions from land-cover change (11). We considered precipitation and clay mineralogy as the most important biophysical drivers, as precipitation strongly influences soil C stocks and residence time (1) and, within a precipitation regime, clay mineralogy is often the most important factor explaining differences in soil C stocks in tropical regions (12, 13). Here we show that mean annual precipitation (MAP) and clay mineralogy affect the direction and magnitude of changes in soil C stocks with different land-cover changes. However, the distribution of field observations does not match the distribution of biophysical factors on an areal basis, and is highly skewed toward high-precipitation regions with allophanic clay mineralogy. Historically, land-conversion activities in the tropics have focused on high-activity clay soils in lower precipitation regions. Thus, we strongly caution against extrapolating average values of landcover change effects on soil C stocks, such as those generated through meta-analysis and literature reviews, to regions that differ in biophysical conditions.

## Results

Patterns of Land-Cover Change Effects. Our search of the literature yielded 837 observations from 80 studies that met our criteria for inclusion in the database [\(Dataset S1](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1016774108/-/DCSupplemental/sd01.xlsx)). Across all sampling depths, precipitation classes, and clay mineralogy classes, 8 of 14 land-use changes had significant effects on soil C stocks (Fig. 1). The conversion of forests to shifting cultivation or permanent crops reduced soil C stocks by an average of 15.4 or 18.5%, respectively. Interestingly, both the conversions of forests to pastures and pastures to secondary forests, which were the two bestrepresented land-cover transitions in the database, increased soil C stocks (Fig. 1). The establishment of perennial tree plantations on lands that were previously grazed or cropped increased soil C stocks, but the conversion of unmanaged forests, grasslands, or savannas to plantations had no effect.

**Effects of Biophysical Drivers.** Even though many of the patterns of land-cover change effects are statistically significant, there is still unexplained variance that may be reduced by including additional variables in the analyses (14). We reanalyzed the data by pooling all observations across land-use transitions and stratifying the data into potential drivers that could be readily extracted

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Fig. 1. Average percentage change in total soil C stocks for different landuse changes in the tropical region with bootstrapped 95% confidence intervals. Land-use transitions appear beside means, and are arranged by decreasing number of observations. The number of observations for each mean is in parentheses, followed by the number of studies from which the observations were drawn.

from the literature, including mean annual temperature, years since conversion, species (for transitions to plantations), MAP, and clay mineral composition [\(Fig. S1](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1016774108/-/DCSupplemental/pnas.201016774SI.pdf?targetid=nameddest=SF1)). These analyses identified two of the major soil-forming factors of MAP (a key facet of climate) and clay mineral composition (in part inherited from parent material) as the most important variables that separated observations into statistically significant groups [\(Fig. S1](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1016774108/-/DCSupplemental/pnas.201016774SI.pdf?targetid=nameddest=SF1)). Thus, subsequent analyses focused on these biophysical drivers. Observations were grouped into four precipitation regimes based on MAP (500–1,500 mm, 1,501–2,500 mm, 2,501–3,500 mm, and >3,501 mm). We chose 500 mm as a minimum cutoff because there were very few studies in regions with MAP < 500. Although precipitation does vary continuously, dividing the data into more classes unduly reduces the number of observations per class and these divisions correspond roughly to life-zone classification schemes. We further classified observations into three classes of clay minerals based on reported soil types or characteristics: allophanic soils dominated by noncrystalline clay minerals that may stabilize soil C, highly weathered soils dominated by lowactivity clay with low surface area and cation exchange capacity (CEC), and young to moderately weathered soils dominated by high-activity clay with high surface area and CEC. Three additional meta-analyses were conducted for observations from depths including 0 to 30 cm for the land-cover change transitions with sufficient data to examine whether soil C dynamics depended on biophysical variables: the conversions of forest to pasture, pasture to secondary forest, and forest to crop (Table 1). These analyses show that the effects of land-use change on soil C stocks depend upon both precipitation regime and soil clay mineralogy, and that the interactions between these two drivers are significant (Table 1). For example, on allophanic soils, conversion of forest to pasture reduced soil C stocks, but only in high precipitation (MAP  $> 3,501$  mm) regions. In contrast, forest-topasture conversion increased soil C stocks on soils with lowactivity clay receiving from 1,501 to 2,500 mm of precipitation annually, but had no effect in regions receiving  $> 2,500$  mm. Secondary forest regeneration on abandoned pastures increased soil C stocks from 19.0 to 32.6% on soils with low-activity clay, but had smaller or no effects on other soil types, although we view the results for pasture-to-forest conversion with extreme caution because of the limited number of studies (Table 1). Finally, conversion of forest to crops caused large losses of soil C stocks under diverse precipitation conditions on soils with allophane and high-activity clay, but no effect on soils with low-activity clay receiving from 1,501 to 2,500 mm annual precipitation. Regardless of the exact magnitude of increase or decrease in soil C stock under each combination of clay mineralogy class and precipitation regime, the most salient result from this analysis is that the effects of land-use change on soil C stocks may vary as a function of biophysical drivers. Although we approach conclusions drawn from such limited data with caution, what these data suggest is that extrapolating average stock-change factors (e.g., Fig. 1) to unmeasured sites across the tropics would be

Table 1. Mean values of land-cover change effects on soil carbon contents (including 0- to 30-cm sampling depths), grouped by clay mineralogy and annual precipitation classes

Clay mineralogy class	Annual precipitation class (mm)	Mean percent change (lower and upper 95% bootstrapped confidence intervals)	Number of observations	Number of studies
Forest to pasture conversion				
Allophane	2,501-3,500	$-2.7$ ( $-16.1$ , 15.0)		4
	>3,501	$-15.8$ ( $-24.5$ , $-7.5$ )		5
High activity	$<$ 1,500	$16.4 (-1.8, 39.3)$		3
	1,501-2,500	$-10.2$ ( $-21.7, -0.8$ )		3
Low activity	1,501-2,500	26.4 (20.5, 31.9)	79	16
	2,501-3,500	$1.1 (-13.9, 18.7)$	9	5
	>3,501	$14.1 (-1.0, 29.7)$	12	6
Pasture to secondary forest conversion				
Allophane	2,501-3,500	$4.0$ (-5.0, 19.5)	9	
High activity	$<$ 1,500	16.5(6.3, 24.1)		
	1,501-2,500	$10.8 (-0.7, 21.9)$	15	
	2,501-3,500	$-5.0$ ( $-18.6$ , 6.8)	8	
Low activity	1,501-2,500	19.0 (0.8, 34.7)	11	
	2,501-3,500	23.6 (4.8, 44.1)	6	
	>3,501	32.6 (25.9, 39.2)	4	2
Forest to crop conversion				
Allophane	$<$ 1,500	$-36.9$ ( $-46.2$ , $-24.7$ )	5.	
	2,501-3,500	$-41.8$ ( $-50.7$ , $-33.6$ )		з
High activity	1,501-2,500	$30.8$ (-40.2, -22.8)	16	3
Low activity	1,501-2,500	$-10.4$ ( $-23.3$ , 7.4)	12	5

Significant transitions, inferred as approximate 95% bootstrapped confidence intervals that do not contain 0, are in bold. Only data from clay mineralogy and precipitation classes that had at least four observations were included in the analyses.

warranted only if the distribution of field observations corresponds to the biophysical conditions in the landscape.

Geographic Bias in the Field Observation Dataset. There is strong evidence that the distribution of field observations is not representative of the distribution of biophysical variables in tropical regions that affect the magnitude and direction of change in soil C stocks following land-cover change (Fig. 2A and B) ( $\chi^2 = 11,789$ ,  $df = 11, P < 0.0001$ ). Although the global areal distribution of biophysical factors in the tropics is skewed toward lower precipitation areas (500–1,500 mm MAP) with high-activity clay soils (Fig. 2B), the distribution of field observations is skewed toward regions with higher precipitation and allophanic clay mineralogy (Fig. 2A). It is possible that land-conversion activities are biased toward regions with certain combinations of biophysical factors, and therefore field studies merely reflect the nonrandom nature of land conversion. However, when we compared the distribution of field observations to the distribution of biophysical factors in tropical lands that have experienced > 50% conversion over the past century or longer, the patterns are even more striking (Fig. 2C). Historically, over 75% of tropical land-use activities have occurred primarily in drier regions (500–1,500 mm MAP) with high-activity clay soils, allowing us to reject the hypothesis that the distribution of biophysical factors represented in the field obser-



Fig. 2. Numbers of observations or grid cells grouped into 12 biophysical classes defined by annual precipitation and soil clay mineralogy. (A) Field observations of soil C changes. (B) Pan-tropical distribution of 1° x 1° grid cells. (C) Tropical grid cells that have experienced >50% conversion to other land uses. Gray bars are low activity clay, open bars are high-activity clay, and black bars are allophanic clays.

vations reflects the typical conditions on managed lands in the tropics ( $\chi^2 = 12,262$ , df = 11,  $P < 0.0001$ ).

## **Discussion**

Biophysical Drivers of Land Use-Related Soil C Changes. There is growing recognition that unless biophysical drivers are explicitly considered, we will not be able to estimate the consequences of land-use changes on soil C stocks (15) or predict the effects of management decisions, such as biochar amendment, to increase carbon sequestration (16). Precipitation strongly influences plant production, fluxes of soil C pools, and ultimately total soil C stocks and residence time (1). The control of clay mineralogy on total soil C stocks, residence time, and susceptibility of the soil C pool to land-use change (17, 18) is through mechanisms such as differential chemical complexation, aggregation, or physical protection (19). Large-scale quantifications of soil C stocks in tropical regions show that within a precipitation regime, clay mineralogy is often the single largest factor explaining differences in soil C stocks within the landscape or with land-use change (12, 13). These findings are not unique and date back to the work of Jenny (1941) (20). What is unique is that we are able to illustrate these effects (and their interactions) in this pan-tropical database (in contrast to local- and regional-based studies) of the relationship between land-use change and soil C stocks.

Using this knowledge in predicting land-use change effects on soil C stocks is both promising and challenging. It is promising that stratification along biophysical drivers indeed reduces variance in the dataset (Table 1) and that methods exist for employing efficient sampling and monitoring schemes (21, 22). The patterns in the data suggest that extrapolating average stock-change factors (e.g., Fig. 1) to unmeasured sites across the tropics would result in large errors of unknown direction and magnitude. Stratification would strongly reduce this error. The challenge is, however, that the present database is insufficient for this approach. Even with our simple stratification of 12 biophysical strata (four annual precipitation classes by three clay mineralogy classes) only three land-cover change transitions can be included.

Caveats of Datasets. The database of our meta-analysis was selected using rigorous criteria. This process prevented errors related to bulk density estimates instead of measurements (23, 24) and errors related to unclear reference land uses (25). Although the database is one of the largest used for meta-analysis or reviews for the tropics, we acknowledge the many limitations of our datasets. First, the paucity of field observations did not allow us to evaluate temporal trends in soil C dynamics with land-use change within biophysical categories. Thus, our analysis assumes that soil C stocks have reached equilibrium values under current land uses. Undoubtedly, other factors not incorporated in our analyses also affect the direction and magnitude of changes in soil C stocks, including site preparation, fertilization and improved management (26), species effects (27), and legacy effects of multiple landuse transitions. However, we did not stratify according to these factors, as their effect is less studied and no georeferenced databases of these factors exist that might be used to improve predictions of soil C stock changes following land-use change.

Second, even for the three land-cover change transitions, for which data enabled us to examine whether soil C dynamics depended interactively on biophysical variables, many of the categories did not have enough observations, whereas one category (i.e., forest-to-pasture conversion on soils with low-activity clay in the 1,501- to 2,500-mm annual precipitation class) (Table 1) was overrepresented. This finding illustrates that no systematic effort has been made to sample underrepresented land-use changes or regions. On the contrary, the nonrandom character of our database strongly suggests sampling and geographic bias (see below).

Third, the majority of field observations are sampled at inconsistent depths that are typically only above 30 cm. Thus, we cannot draw reliable conclusions about land-use effects deeper in the soil profile.

Fourth, the coarse spatial resolution of the global maps of precipitation, soil type, and land cover likely masks important spatial heterogeneity (28). For example, because of their high native fertility, we would expect that agricultural activities would be preferentially located on allophanic soils. However, the global soil map only considers the dominant soil types. Consequently, soils dominated by allophanes (Andosols) appear in very few of the  $1^{\circ}$  by  $1^{\circ}$  grid cells we sampled (and none in the  $>3,500$ -mm precipitation category), even though Andosols cover about 98 million hectares worldwide, or an estimated 1.0% of the total tropical area (28). This mismatch in spatial scales helps in part to reconcile our finding that 9% of field observations were located on high precipitation, allophanic soils, but the global map contained no grid cells with this combination of precipitation and clay mineralogy composition. Nevertheless, we believe that our main conclusions are robust to these limitations.

Causes and Consequences of Geographic and Sampling Bias. One of the strongest conclusions from our analyses is the existence of geographic bias in the field observations of land-use change effects relative to biophysical drivers (Fig. 2). What this means is that we have concentrated our scientific research on regions that are highly unrepresentative of the tropics as a whole, and are particularly unrepresentative of the tropical lands that have undergone conversion to other land covers. A likely cause of this bias is that published scientific research in tropical countries is disproportionately conducted in countries and locations of large, internationally funded field stations (e.g., Costa Rica and Panama) (29). Not only are certain combinations of biophysical variables undersampled as our data show (e.g., regions with precipitation <1,500 mm and high-activity clays), but also the intellectual and scientific infrastructure for conducting research in certain geographical regions (e.g., Africa) remains underdeveloped, which should be a cause for global concern (29).

A consequence of unrepresentative sampling is that it precludes us from extrapolating field observations to the continental or global scales that are relevant for global biogeochemistry and policy. For example, in our analyses we obtained the curious result that both forest-to-pasture and pasture-to-secondary forest conversions increased soil C contents (Fig. 1). One biological explanation for this is that productive pastures are unlikely to be abandoned, which biases the pasture-to-secondary forest conversion field studies toward low-productivity pastures that likely lost soil C when they initially were converted from forest. A second explanation is unequal sampling across the biophysical driving variables. Of the data that estimate the mean effect of forest-to-pasture conversion, 62% came from low-activity clay soils with precipitation between 1,501 and 2,500 mm, which was the only combination of biophysical factors that yielded increases in soil C stocks for this land-use conversion (Table 1). In contrast, soil C stocks increased when secondary forests grew on abandoned pastures in four of seven classes of biophysical variables. In summary, the mean estimated stock-change factors are highly dependent on the number of observations from each class of biophysical variables, and the data we have do not allow us to discriminate between the biological and the sampling bias explanation for this result.

Recommendations. We believe that a relatively simple set of criteria could significantly improve estimates of average soil C stock-change factors following land-use conversion. First, we recommend that clear reference land-use and -change trajectories should be sampled under comparable biophysical conditions, and sampling should be based on defined depths with measured soil bulk density and not based on soil horizons. These have been recurring recommendations from the literature in the past few decades, but are still commonly neglected, given the number of studies that we had to exclude from our database because of this missing critical information. Second, field studies should focus on areas that are underrepresented in the present database [i.e., drier part of the tropics (500–1,500 mm annual precipitation) on soils dominated by high-activity clay] to amend the present geographic bias. Third, the present dataset does not include current, important land-cover changes (i.e., conversion of tropical peatland and savanna to agro-biofuel production) (30, 31), and detailed quantification of soil C stock changes is missing for these areas. Finally, we should abandon the idea that we can extrapolate average values of land-cover change effects on soil C stocks unless the distribution of field observations corresponds to the distribution of biophysical conditions in the tropics.

## Methods

Literature Review and Meta-Analysis. Published studies located between 28° 35′ N and 28°15′ S latitude were identified from previous meta-analyses and reviews (14, 27, 32–34) or from searching online scientific databases. The majority of the studies were conducted between 23° N and 23° S latitudes and only a few are considered subtropical. Most of the studies quantified land-cover change effects by comparing plots on different land uses, assuming that soil C stocks were identical before land-cover change (i.e., chronosequence and space-for-time substitution designs). The final database consisted of studies that: (i) reported soil C stocks or information that allowed us to calculate it (carbon percentages, measured bulk density, and sampling depth) and excluded studies lacking bulk density or that estimated it from soil function formulas; (ii) included clear, logical reference sites that represented the immediate, previous land cover; (iii) included data on cli-mate and soils; and (iv) had not been published elsewhere [\(Dataset S1\)](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1016774108/-/DCSupplemental/sd01.xlsx). Although it is desirable to compare changes in soil C stocks between land uses based on common soil mass rather than volume because of compaction (23, 24), it was not possible for us to correct data for all these studies, as not all studies we surveyed reported both bulk densities and C concentrations. Thus, we did not adjust reported data to a common mass, but we used masscorrected soil C stock changes when authors expressed them.

Most studies reported data for more than one pair of sites or more than one soil depth, and the decision of what constitutes an independent observation from each study can affect the results of meta-analyses (35). Our approach was to be conservative in what we called "independent observations." In the few longitudinal studies we found where the same plots were sampled repeatedly, we included the data from only the first and most recent sampling period. In studies that sampled many replicate plots over a landscape, plots with the same age, edaphic conditions, and land use were pooled together, and compared with the mean value from the reference sites representing the previous land use. We considered data from different sampling depths as independent observations in the overall analysis testing for land-use change effects and comparisons to global distributions of biophysical variables, but restricted the three additional meta-analyses that explored effects of biophysical variables on specific land-use transitions to surface samples up to 30-cm profile depth so as not to confound any biophysical effects with depth effects. Observations were assigned to one of the following land-cover transitions: forest to pasture, forest to plantation (i.e., perennial trees), forest to crop, pasture to secondary forest, pasture to plantation, crop to plantation, crop to secondary forest, crop to pasture, savanna to crop, savanna to pasture, or savanna to plantation. We also included two types of shifting-cultivation studies: those that compared shifting cultivation to primary forest (forest to shifting cultivation), and those that compared cropped fields to fallow forest (crop to forest fallow). Observations were assigned one of three clay mineralogy classes (lowactivity clay, high-activity clay, and allophanic mineralogy) that we inferred from reported soil classification, CEC, geological substrate, or a combination of these criteria. In general, soils dominated by low activity clay have a CEC of <24 cmol<sub>c</sub>·kg<sup>-1</sup> clay or <4 cmol<sub>c</sub>·kg<sup>-1</sup> soil (e.g., Acrisols, Ferralsols, and Nitisols); soils dominated by high activity clay have a CEC of >24 cmol<sub>c</sub>·kg<sup>-1</sup> clay (e.g., Alisols, Cambisols, Fluvisols, and Luvisols); soils dominated by allophane are typically developed on volcanic ash (e.g., Andosols) (36).

The percent-difference in C stock between plots representing managed and initial conditions, expressed relative to the initial soil C stock [i.e., (Xc −  $Xr$ /Xr  $\times$  100], was used as the metric of change in soil C (with Xc representing soil C stock in the current land use, and  $Xr$  the reference land use). Following other authors (14, 27), we used nonparametric resampling methods to generate bias-corrected bootstrapped approximate 95% confidence intervals (CI) from 10,000 randomizations in META-WIN (37), and response effects were not weighted by sample size. Observed effect sizes were considered statistically different from zero if the 95% CI did not include zero, and land-cover transitions or other categorical grouping factors were considered different from one another if their 95% CI did not overlap. For the three most studied land-use transitions (forest to pasture, pasture to secondary forest, and forest to crop), we assessed how precipitation class and clay-activity class interactively affected the responses of soil C pools to land-use change using identical statistical methods, for depths including 0 to 30 cm in the profile (average sampling depth was 14.6 cm).

Geographic Analysis. We tabulated the distribution of average precipitation conditions and soil clay mineralogy from global databases as follows. A global map of the 1961 to 1990 annual mean precipitation was derived from the Climate Research Unit dataset at 1.0° by 1.0° resolution (38) and classified into four categories: 500 to 1,500 mm, 1,501 to 2,500 mm, 2,501 to 3,500 mm, and >3,501 mm annual precipitation. All oceans, extratropical land (defining tropical lands as those occurring between 24° N and 24° S latitude), and tropical lands with mean annual precipitation <499 mm (e.g., the Sahara Desert) were omitted from the analysis. We used the 1.0° by 1.0° resolution Food and Agriculture Organization global soil map to generate a map of soil clay mineralogy ([http://data.giss.nasa.gov/landuse/soilunit.](http://data.giss.nasa.gov/landuse/soilunit.html) [html\)](http://data.giss.nasa.gov/landuse/soilunit.html). To accomplish this, we reclassified the map units into the same three clay-activity classes used for the literature studies: low-activity clay, highactivity clay, and allophanic mineralogy. This gridded, classified map was overlaid onto the precipitation map, and the numbers of grid cells in each combination of precipitation and clay mineralogy (12 classes total) were tabulated ( $n = 2,857$  grid cells).

The distribution of field observations that included information on both precipitation and soil order ( $n = 837$ ) was compared with the actual areaweighted distribution of annual precipitation and soil clay mineralogical conditions in the tropics using a  $\chi^2$  test. At the coarse-scale resolution of

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global datasets, there are no tropical grid cells in the category of allophanic mineralogy and annual precipitation >3,501 mm, even though 9.0% of the field observations come from lands with these conditions. To accommodate the fact that this precipitation/clay mineralogy class had an expectation of 0, we assigned it a pseudoexpectation of one and decreased the expected number of field observations in the 500- to 1,500-mm precipitation/highactivity clay class from 276 to 275.  $\chi^2$  tests are considered robust only when all of the expected counts are >5, which was not the case for 3 of the 12 precipitation/clay mineralogy categories we analyzed. Nevertheless, the extremely large  $\chi^2$  statistic of 11,789 (df = 11) was highly significant (P < 0.0001) and gives us assurance that the distributions of field observations and actual precipitation and clay mineralogy conditions are indeed distinct.

To control for the possibility that the distribution of field observations reflects the conditions of lands that have undergone conversion, we used a time series of global maps of grazing lands and croplands (the Global Cropland and Pasture Data from 1700 to 2007) (39) to create a map of all grid cells in the tropics that have undergone at least 50% conversion in the last century (including all lands in pasture or cropland before 1900). We used this land-conversion map as a mask and retabulated the distribution of annual precipitation/clay mineralogy classes for the 981 grid cells that had undergone >50% conversion (roughly 34% of all tropical lands with annual precipitation >500 mm). We compared the distributions of field observations to converted conditions using the  $\chi^2$  test described above.

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