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Global pattern of soil carbon losses due to the conversion of forests to agricultural land

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Several reviews have analyzed the factors that affect the change in soil organic C (SOC) when forest is converted to agricultural land; however, the effects of forest type and cultivation stage on these changes have generally been overlooked. We collated observations from 453 paired or chronosequential sites where forests have been converted to agricultural land and then assessed the effects of forest type, cultivation stage, climate factors, and soil properties on the change in the SOC stock and the SOC turnover rate constant (*k*). The percent decrease in SOC stocks and the turnover rate constants both varied significantly according to forest type and cultivation stage. The largest decrease in SOC stocks was observed in temperate regions (52% decrease), followed by tropical regions (41% decrease) and boreal regions (31% decrease). Climate and soil factors affected the decrease in SOC stocks. The SOC turnover rate constant after the conversion of forests to agricultural land increased with the mean annual precipitation and temperature. To our knowledge, this is the first time that original forest type was considered when evaluating changes in SOC after being converted to agricultural land. The differences between forest types should be considered when calculating global changes in SOC stocks.

More than 40% of the total organic C in terrestrial ecosystems is stored in forest soil¹. Converting natural forests to agricultural land results in the mineralization of soil organic C (SOC), thus reducing SOC stocks and increasing atmospheric CO₂ concentrations^{2,3}. The decreases in SOC following a land-use change are difficult to predict due to variations in the factors that drive SOC mineralization, e.g., forest type, climate, and soil properties¹. Understanding the effects of these factors is important for assessing the C flux between the soil and the atmosphere and for understanding the feedbacks within the global C cycle^{4,5}.

The conversion of forest to agricultural land destroys the soil's aggregate structure, which enhances organic matter mineralization and CO₂ emissions. Generally, SOC stocks decrease rapidly and then stabilize after a land-use change^{2,6}. However, previous reviews have largely ignored the effects of forest type and cultivation stage on SOC changes^{2,6–8}, which is especially true in temperate and boreal regions. The SOC turnover rate constant is often unreported following a land-use change even though it is essential for predicting SOC changes and understanding the feedbacks between C cycling and the climate system.

The objectives of this study were to learn more about how global SOC stocks change in response to the conversion of forests to agricultural land and to understand how the changes depend on climate and soil properties. We collated observations from 119 peer-reviewed publications to create a global dataset of 453 paired or chronosequential sites where forests have been converted to agricultural land (Fig. 1). We then assessed the effects of forest type, cultivation stage, climate, and soil properties on SOC stocks and the SOC turnover rate constant (*k*).

Results

1. Changes in SOC stocks. The SOC stocks decreased at 98% of the sites following the conversion of forests to agricultural land; the mean decrease in SOC stocks was $44.5 \pm 1.0\%$ (Fig. 2). The SOC stocks increased after the land-use change at the other 2% of the sites. The mean increase at these sites was $23.6 \pm 8.9\%$. Regardless, the SOC stocks decreased by an average of $43.1 \pm 1.1\%$ for all sites. Moreover, the mean rate of decrease was $1.31 \pm 0.10 \text{ mg ha}^{-1} \text{ yr}^{-1}$, and the mean turnover rate constant was $0.016 \pm 0.002 \text{ yr}^{-1}$ (corresponding to a mean turnover time of 62 years).

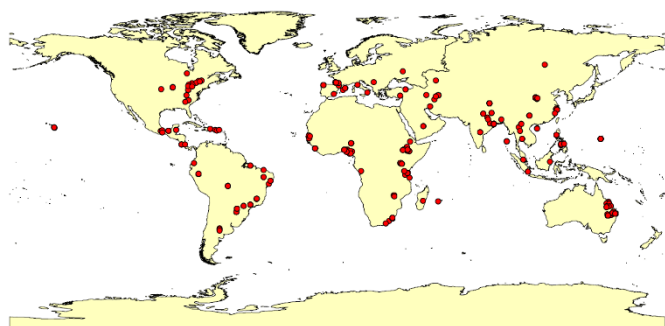


Figure 1 | Distribution of the study sites in which forests have been converted to agricultural land (created in ArcGis 10.0).

Both forest type and cultivation stage exhibited significant effects on the percent decrease in SOC; however, their interaction did not. Averaged across all forest types, the SOC stocks decreased by an average of $34.7 \pm 1.6\%$ at sites in the early stage (≤ 10 yr) of cultivation, $45.3 \pm 1.4\%$ at sites in the middle stage (11–50 yr) of cultivation, and $53.2 \pm 3.4\%$ at sites in the late stage (> 50 yr) of cultivation ($P < 0.05$, Fig. 3A). Averaged across cultivation stages, the SOC stocks decreased by $31.1 \pm 5.3\%$ in boreal regions, $40.8 \pm 1.3\%$ in tropical regions, and $52.3 \pm 2.0\%$ in temperate regions ($P < 0.05$, Fig. 3A). The effect of cultivation stage varied with forest type (Fig. 3A). Specifically, in boreal regions, SOC decreased more at sites in the middle cultivation stage than at sites in the late stage. Moreover, in the temperate and tropical regions, more SOC was lost as the cultivation time increased.

Cultivation stage and forest type also had significant effects on the SOC turnover rate constant. Averaged across all cultivation stages, the turnover rate constants were $0.020 \pm 0.003 \text{ yr}^{-1}$ in tropical regions, $0.020 \pm 0.003 \text{ yr}^{-1}$ in temperate regions, and $0.006 \pm 0.003 \text{ yr}^{-1}$ in boreal regions ($P < 0.05$, Fig. 3B). Averaged across all forest types, the turnover rate constants were $0.090 \pm 0.018 \text{ yr}^{-1}$ at sites in the early stage, $0.023 \pm 0.003 \text{ yr}^{-1}$ at sites in the middle stage, and $0.010 \pm 0.001 \text{ yr}^{-1}$ at sites in the late stage of cultivation ($P < 0.05$, Fig. 3B). For each cultivation stage, the turnover rate constants were higher in both temperate and tropical regions than in boreal regions (Fig. 3B).

2. Effects of soil properties and climate. The percent decrease in SOC stocks after the land-use change was significantly and positively correlated with the initial SOC concentration and with the initial total soil N concentration; however, a negative correlation was found with the soil clay content and the bulk density (Fig. 4). The turnover rate constants were significantly and positively correlated with the mean annual precipitation and mean annual temperature (Fig. 5). There were no significant interactive effects between the mean annual precipitation and the mean annual temperature or among soil properties (Table S1) in this study. Additionally, the effects of climate and soil properties on the percent decrease in SOC stocks varied with cultivation age and forest type (Tables S2–3).

During the early stage of cultivation, the percent decrease in SOC stocks was significantly affected by the mean annual precipitation, mean annual temperature, soil clay content, initial SOC concentration, and initial total N concentration (Table S2). Moreover, the percent decrease in SOC stocks was significantly affected by the soil bulk density, initial SOC concentration, and initial total N concentration during the middle stage of cultivation (Table S2). During the late stage of cultivation, the percent decrease in SOC stocks was significantly affected by the soil bulk density, initial SOC concentration, and initial total N concentration (Table S2).

In boreal regions, the percent decrease in SOC stocks was significantly affected by the soil bulk density, initial SOC concentration, and the initial total N concentration. Furthermore, the decrease in

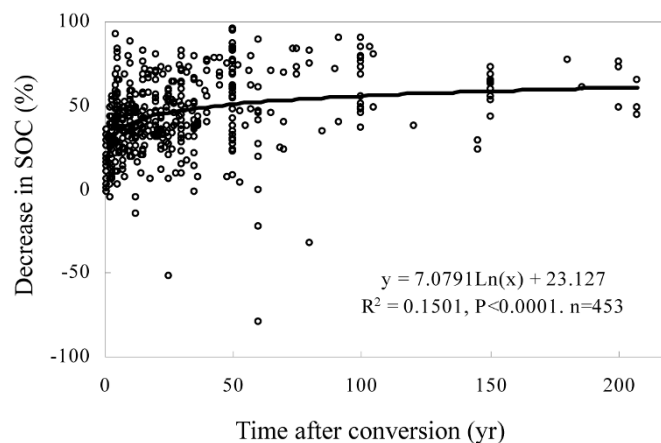


Figure 2 | Percent decrease in SOC after the conversion of forests to agricultural land. Negative values indicate that SOC stocks increased after the land-use change.

SOC stocks was significantly affected by the soil clay content, soil pH, and initial total N concentration in temperate regions (Table S3). The mean annual temperature and precipitation exhibited no significant effects on the decrease in SOC stocks in either boreal or temperate regions (Tables S3). In tropical regions, the decrease in SOC stocks was significantly affected by the mean annual precipitation, soil clay content, bulk density, initial SOC concentration, and initial total N concentration (Table S3).

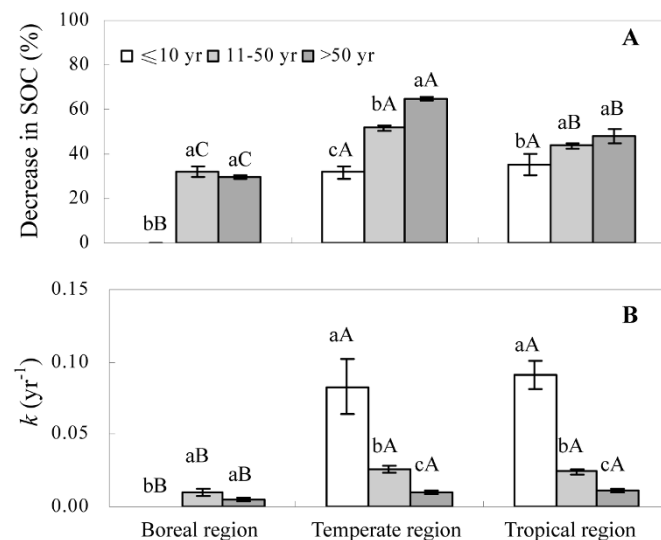


Figure 3 | The effects of cultivation age and forest type on the percent decrease in SOC stocks (A) and turnover rate constants (k) (B) after the conversion of forests to agricultural land. Negative values indicate that SOC stocks increased after the land-use change. The error bars represent the standard errors for each group. The boreal region had 0, 12, and 10 sites in the early (≤ 10 yr), middle (11–50 yr), and late (> 50 yr) stages of cultivation, respectively. The temperate region had 19, 58, and 34 sites in the early, middle, and late stages of cultivation, respectively. The tropical region had 128, 162, and 30 sites in the early, middle, and late stages of cultivation, respectively. Values with different lowercase letters are different at a significance level of $P < 0.05$ for each cultivation stage. Values with different uppercase letters are different at a significance level of $P < 0.05$ for each forest type. The interaction between forest type and cultivation stage had no significant effect on the turnover rate constant ($P = 0.3073$) or the percent decrease in SOC ($P = 0.0793$).

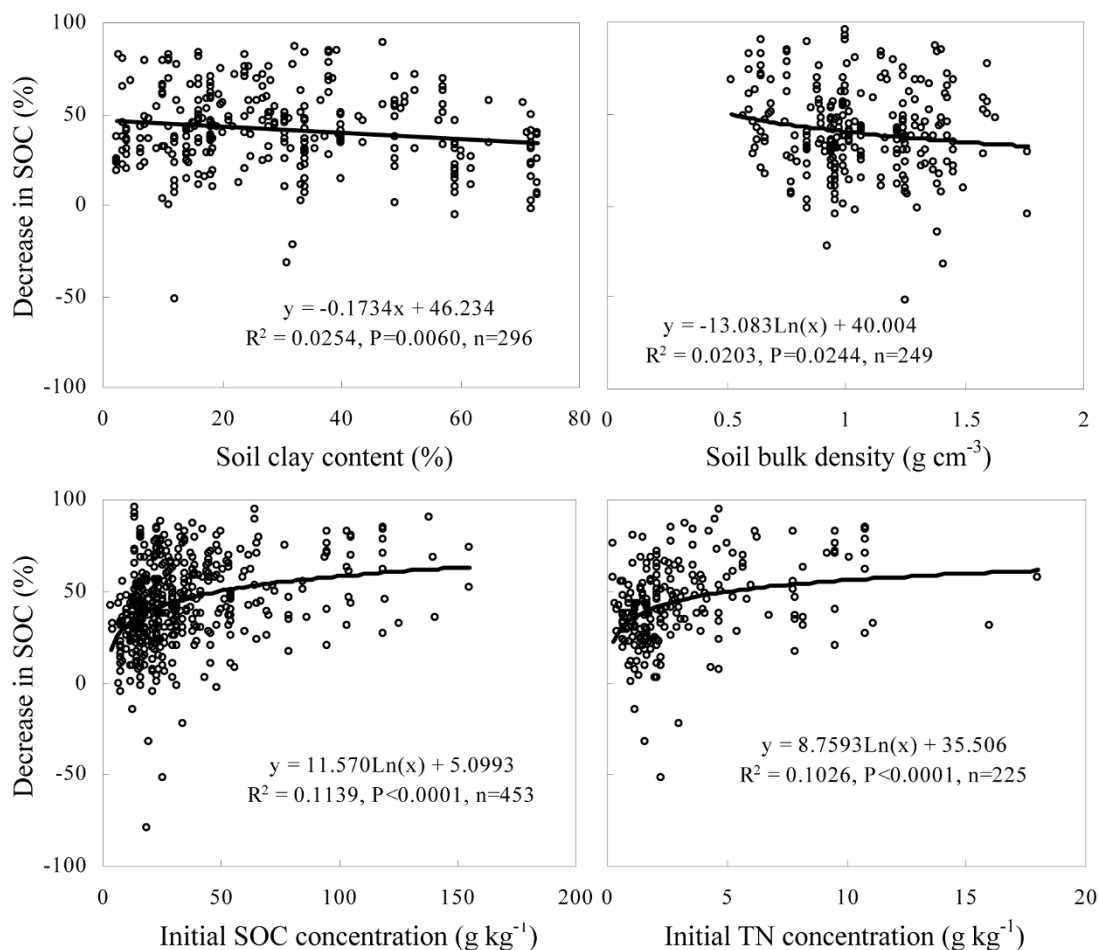


Figure 4 | The effects of initial soil clay content, bulk density, initial SOC concentration, and initial N concentration on the percent decrease in SOC stock after the conversion of forests to agricultural land. Negative values indicate that SOC stocks increased after the land-use change.

Discussion

The conversion of forests to agricultural land caused a rapid initial decrease in SOC stocks, followed by a slow decline. This description is consistent with reports that most SOC losses occur within the first few years after the cultivation of previously untilled soils^{6,9,10}. For example, Davidson and Ackerman (1993) observed that 20% of SOC was lost within the first 5 yr of cultivation and that an additional 5% of SOC was lost within the next 15 yr⁶.

Across all of the cultivation stages in our study, the SOC stocks decreased by $43.1 \pm 1.1\%$. This decline was much higher than the 30% decrease reported by Davidson and Ackerman (1993)⁶ and Murty et al. (2002)⁸ but similar to the 42% decrease observed by Guo and Gifford (2002)⁷. Cultivation stage should be considered when comparing datasets. For example, 58% of the sites in the review by Murty et al. (2002)⁸ were in the early stage of cultivation. However, in our study, 68% of the sites were in the middle or late stages of

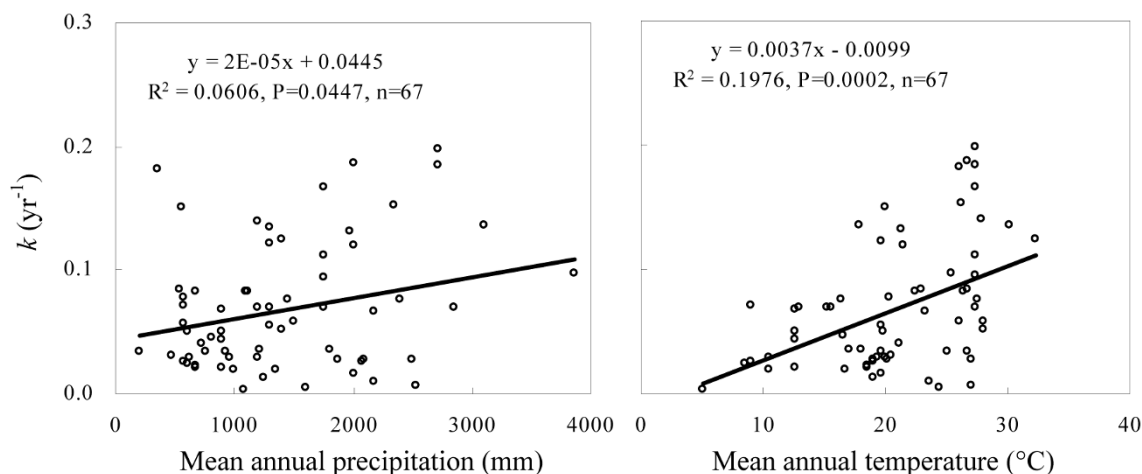


Figure 5 | The effects of mean annual precipitation and mean annual temperature on the SOC turnover rate constant (k) after the conversion of forests to agricultural land.



cultivation. This difference is important because the percent decrease in SOC stocks increases with time. Therefore, decreases in SOC stocks will be underestimated in recently converted land. Soil depth is another important consideration in estimating SOC stocks. Our dataset focused on changes in stocks within the topsoil (0–30 cm) because that is where the largest changes in SOC occur. Therefore, the percent decrease in SOC stocks was expected to be higher than in studies that considered a depth of 0–100 cm.

The decrease in SOC following the land-use change was largest in temperate regions, which was followed by tropical regions and then boreal regions. The turnover rate constants followed a slightly different order, i.e., higher in tropical and temperate regions than in boreal regions. This finding was expected because the higher mean annual temperatures in temperate and tropical regions accelerate organic matter mineralization compared with boreal regions^{11–14}. Moreover, SOC should decrease more after a forest is converted to agricultural land in tropical regions compared to temperate regions due to the higher mean annual temperatures; however, we observed greater changes in temperate regions. One explanation for this discrepancy is that the sites in temperate regions have generally been cultivated longer than the sites in tropical areas (i.e., 83% of the temperate sites have been cultivated for more than 10 yr, whereas only 60% of the tropical sites have been cultivated for more than 10 yr).

The percent decrease in SOC during the early stage of cultivation was significantly affected by both climate (i.e., mean annual precipitation and mean annual temperature) and soil properties (i.e., soil clay content, pH and initial SOC and total N concentrations). Rapid decreases in SOC during the early stage of cultivation are likely caused by the destruction of soil aggregates by tillage¹⁵. Rainfall during this period can accelerate the destruction of aggregates. Moreover, high temperatures and the greater availability of SOC and N can increase the SOC mineralization rates^{14,16–18}. During the middle and late stages of cultivation, the percent decrease in SOC was significantly affected by soil properties (i.e., soil bulk density, initial SOC concentration, and initial total N concentration) and not by climate.

Comparisons within forest types indicated that the decreases in SOC after conversion to agricultural land were determined by the mean annual precipitation in tropical regions. The SOC loss was expected to depend on climate conditions in tropical regions because the moisture and higher temperatures enhance soil organic matter decomposition and thus the loss of SOC^{13,14}. However, climatic factors in neither boreal nor temperate areas significantly affected the percent decrease in SOC. One explanation for this finding is that the dataset contained fewer observations from boreal (22 sites) and temperate regions (111 sites) than from tropical regions (320 sites). The analysis may have been affected by the narrow gradients in the mean annual precipitation and mean annual temperature at the temperate and boreal sites. The effects of forest cultivation on SOC losses and the dependence of the losses on climate conditions should be studied further, especially in boreal regions.

Regardless of the cultivation stage or forest type, the largest decreases in SOC stocks occurred for high initial SOC or total N concentrations. The smallest decreases in SOC stocks were observed for high soil clay content or bulk density. Our results agree with previous findings that mineralization rates generally increase as the concentrations of either SOC or total N increase^{16–18} and as soil clay content decreases¹⁹. Previous studies have indicated linear relationships between SOC loss and initial SOC and N concentrations⁸. This indicates that the SOC loss would continue to increase as the initial SOC and N concentration increased. In contrast, our results exhibited nonlinear relationships between SOC loss and initial SOC and N concentrations. The nonlinear relationship in which SOC losses eventually stop increasing with continually increasing initial SOC and N concentrations is more realistic. Accordingly, the SOC stocks

should decrease more rapidly in soils with high sand or initial SOC levels than in soils with low sand or initial SOC levels. Moreover, atmospheric N deposition and the application of nitrogenous fertilizers could also result in greater decreases in SOC stocks. All of these factors should be considered when predicting the SOC response to the conversion of forests to agricultural land.

In our study, the turnover rates increased (turnover times decreased) significantly as the mean annual temperature increased. This observation is consistent with previous findings that SOC decomposition rates increased with mean annual temperature at both regional and global scales^{13,14,20}. In contrast, Giardina and Ryan (2000)²¹ observed that the SOC decomposition rates in undisturbed forest soils were remarkably similar across a wide range of mean annual temperatures. This result, suggests that the mechanism behind SOC losses after the conversion of forests to agricultural land is different from the mechanism causing SOC mineralization in undisturbed soil with natural vegetation.

The dependence of SOC turnover on the mean annual temperature indicates not only that future temperature increases will result in greater SOC losses but also that there is a positive feedback between SOC mineralization and global warming. Most SOC in undisturbed land is occluded within aggregates and thereby physically protected from microbial decomposition^{22,23}. Converting forests to agricultural land damages the aggregate structure, making SOC more available for microbial attacks. Plants and soil microorganisms may acclimate to changes in temperature, minimizing the feedback between CO₂ release and global warming^{24–27}. However, the disruption of aggregates by tillage is not affected by temperature or moisture. Conversion of forests to agricultural land could thus enhance the feedback between CO₂ emission and global warming and should be carefully managed.

Most previous studies have emphasized the loss of SOC in tropical areas^{2,3}. However, 35% of the global decrease in forest cover has occurred in boreal regions²⁸. There is more organic C in boreal forest soil than in either temperate or tropical forest soils^{29,30}. Furthermore, some models predict that the largest increases in temperature due to global warming will occur in boreal regions¹. Therefore, the SOC loss following the conversion of boreal forests to agricultural land deserves more attention in future scenarios of global warming. If the loss of SOC due to the conversion of grassland to agricultural land depends on temperature, then any conversion from natural vegetation to agriculture would accelerate the positive feedback between the C cycle and the climatic system.

Methods

Data acquisition. The data were obtained from 119 peer-reviewed publications that described 453 sites in 36 countries (Table S4). To be included in this dataset, the data had to satisfy the following criteria: (1) the cultivated plots must have been converted from primary forest, (2) the cultivated and forest plots must be adjacent to ensure similar pedological conditions, and (3) the time of forest conversion must be known or derivable. Only studies with paired plots or chronosequences were included. The variables that were obtained included the following: forest type (i.e., tropical, temperate, and boreal forests), cultivation stage, SOC concentration or stock, total N concentration or stock, soil texture (i.e., percent sand and clay), bulk density, pH, sampling depth, and the mean annual precipitation and temperature. We classified the data into three stages based on the time since the conversion of forests to agricultural land: early (≤ 10 yr), middle (11–50 yr), and late (> 50 yr). The analytical methods for measuring SOC varied among the studies. However, these differences should not have affected our analysis because we compared either k or the relative change in SOC within a specific study.

The SOC stocks were calculated based on the SOC concentration, soil depth, and bulk density at each site. The bulk density of forest soil often changes after land-use change; therefore, many researchers have emphasized that corrections for changes in bulk density should be made before comparing SOC stocks in forest and cultivated soils^{2,8,31–33}.

The corrected SOC stocks were calculated in this study as^{31,33}

$$SOC_{corr}(C) \text{ Stock} = SOC(C) \text{ Stock} \times \frac{BD_F}{BD_C} = BD_F \times D \times SOC(C) \text{ Concentration},$$

where $SOC_{corr}(C) \text{ Stock}$ is the corrected SOC stock based on the equivalent soil mass in the cultivated soils, $SOC(C) \text{ Stock}$ is the uncorrected SOC stock in cultivated soils, BD_F



and BD_C are the bulk densities of forest and cultivated soils, respectively, D is the sampling depth, and $SOC(C)$ Concentration is the SOC concentration in cultivated soils.

In this study, we only considered SOC in the upper 0–30 cm because the largest changes in SOC occur there and because more data are available compared to subsoil depths. Among the 453 sites, 20 characterized the soil depth as the surface layer. We assumed a soil depth of 20 cm for these sites because we could not verify the exact soil depth. To simplify the comparisons, we reported the SOC stocks per 10 cm depth of soil at each site. The organic horizon was excluded from this study.

When the data presented in the original publications were presented as concentrations, we calculated the SOC stock by accounting for the bulk density at each depth. However, a few studies did not report bulk densities. In these cases, the bulk density was estimated using a relationship between the bulk density and the SOC concentration that was derived from the overall dataset. For forest soil, the relationship was

$$\ln(BD_F) = 0.1926 - 0.0048 \times SOC(F) \text{ Concentration}, R^2 = 0.324, n = 291, P < 0.0001,$$

where $\ln(BD_F)$ is the natural logarithm of the forest soil bulk density and $SOC(F)$ Concentration is the SOC concentration in the forest soil.

For agricultural land, the relationship was

$$\ln(BD_C) = 0.4346 - 0.0098 \times SOC(C) \text{ Concentration}, R^2 = 0.430, n = 188, P < 0.0001,$$

where $\ln(BD_C)$ is the natural logarithm of the bulk density in the agricultural soil and $SOC(C)$ Concentration is the SOC concentration in the agricultural soil.

Data analysis. The relative decrease in SOC (ΔSOC , %) after forest cultivation was calculated as

$$\Delta SOC = \frac{SOC(F) \text{ Stock} - SOC_{corr}(C) \text{ Stock}}{SOC(F) \text{ Stock}} \times 100,$$

where $SOC(F)$ Stock is the SOC stock in forest soil.

A first-order model was used to assess the turnover of SOC after the conversion from forest to agricultural land as suggested by Six and Jastrow (2002)³⁴:

$$\frac{\partial S}{\partial t} = I - kS,$$

where k is the turnover rate constant (yr^{-1}), t is the time since the land-use change (yr), S is the SOC stock at time t ($SOC_{corr}(C)$ in this study), and I is the input rate. This formulation represents a mono-exponential decay model and has been commonly used to describe the turnover of SOC. This model assumes a constant zero-order input and a first-order SOC loss rate. The solution to the model is³⁵

$$S = S_e + (S_0 - S_e) \times e^{-kt},$$

where S_0 is the SOC stock before conversion ($SOC(F)$ in this study), and S_e is the equilibrium SOC stock. This method has been used to estimate the turnover of SOC following land-use changes^{23,34,36}. In this study, the model was fitted to the entire dataset to obtain a general turnover rate constant and then fitted to each forest type across and within stages and to each cultivation stage across and within forest types to obtain turnover rate constants for each forest type and cultivation stage. We also calculated the turnover rate constant for all of the sites that were sampled at least 3 times since conversion in the same study (including pre-conversion forest as year 0). In total, turnover rate constants were determined for 67 sites. These 67 turnover rate constants were used to establish the relationships with climate and soil properties.

A two-way analysis of variance was performed to test the primary and interactive effects of the forest type and cultivation stage on the percent decrease in SOC. A one-way variance analysis was conducted to test the effects of forest type within each cultivation stage and to test the effects of cultivation stage within each forest type.

We used a 95% confidence interval (CI) to assess the statistical differences in the turnover rate constants within forest types or cultivation stages. The 95% CI was calculated as

$$95\% CI = 1.96 \times SE,$$

where SE is the standard error of the turnover rate constant and was obtained from the model fitting. The differences between groups (forest types and cultivation stages) were identified as significant when the 95% CIs did not overlap.

General linear models were used to test the primary and interactive effects of climate factors (i.e., mean annual precipitation and mean annual temperature) and the primary and interactive effects of soil characteristics (i.e., of soil clay content, soil pH, soil bulk density, and initial SOC or N concentrations) on the percent decrease in SOC and the turnover rate constant. Nitrogenous fertilizers are often applied to cultivated soil. Therefore, we did not analyze the changes in soil N after forest cultivation. Generally, the decrease in SOC is a function of both climate and soil physicochemical properties. Therefore, we used linear and nonlinear regressions to test relationships across and within forest types and cultivation stages between the percent decrease in SOC and the mean annual precipitation, mean annual temperature, soil clay content, soil pH, bulk density, or initial SOC and N concentrations.

We also used linear and nonlinear regressions to test whether the turnover rate constant was related to the mean annual precipitation, mean annual temperature, soil clay content, soil pH, bulk density, or initial SOC and N concentrations for all forest types and cultivation stages. We did not analyze the effects of climate and soil

properties on the turnover rate constant for each forest type or cultivation stage due to the limited sample sizes for each group. Data analysis was performed using JMP 10 software (SAS Institute, Cary, NC, USA).

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Author contributions

X.W., M.S. designed the study, X.W. conducted the study, X.W., W.G. wrote the paper, X.W., W.G., L.L. revised the paper.

Additional information

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