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Authors

Durrer, Ademir
Margenot, Andrew J
Silva, Lucas CR
[et al.](#)

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Beyond total carbon: conversion of amazon forest to pasture alters indicators of soil C cycling

Ademir Durrer · Andrew J. Margenot · Lucas C. R. Silva · Brendan J. M. Bohannan · Klaus Nusslein · Joost van Haren · Fernando D. Andreote · Sanjai J. Parikh · Jorge L. Mazza Rodrigues

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Abstract It is well established that land use change (LUC) can impact soil organic carbon (SOC) in tropical regions, but the long-term effects of LUC on soil quality and C cycling remain unclear. Here, we evaluated how LUC affects soil C cycling in the Amazon region using a 100-year observational chronosequence spanning primary forest-to-pasture conversion and subsequent secondary forest succession. We found a surprising increase in topsoil SOC concentrations 60 years following conversion, despite

major losses (> 85%) of forest-derived SOC within the first 25 years. Shifts in molecular composition of SOC, identified with diffuse reflectance infrared Fourier transform (DRIFT) spectroscopy, occurred in tandem with a significant decline in permanganate-oxidizable C (POXC) and β -glucosidase activity (per unit SOC), interpreted as a deceleration of soil C cycling after pasture grasses became the dominant source of C inputs to soil. Secondary forest succession caused rapid reversal to conditions observed under primary forest for β -glucosidase activity but not for SOC molecular composition (DRIFT spectroscopy), reflecting a long-lasting effect of LUC on soil C cycling. Our results show that rapid changes in the origin of SOC occur following deforestation with legacy effects on some indicators of C cycling (e.g. enzyme activity) but not others (e.g. molecular composition). This approach offers mechanistic

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Ademir Durrer and Andrew J. Margenot have contributed equally to this work.

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A. Durrer · S. J. Parikh · J. L. Mazza Rodrigues
Department of Land, Air and Water Resources, University of California Davis, California, CA 95616, USA

A. Durrer · F. D. Andreote
Department of Soil Science, University of São Paulo, Piracicaba 13418-900, Brazil

A. J. Margenot
Department of Crop Sciences, University of Illinois Urbana-Champaign, Urbana, IL 61801, USA

L. C. R. Silva (✉)
Environmental Studies Program, Department of Geography, Institute of Ecology and Evolution, University of Oregon, Eugene, OR 97403, USA
e-mail: lsilva7@uoregon.edu

B. J. M. Bohannan
Department of Biology, Institute of Ecology and Evolution, University of Oregon, Eugene, OR 97403, USA

K. Nusslein
Department of Microbiology, University of Massachusetts, Amherst, MA, USA

understanding of LUC in the Amazon basin and can be used to help explain conflicting reports on how deforestation impacts SOC in the region.

Keywords Soil organic carbon · Amazon · β -glucosidase · Secondary forest · Permanganateoxidizable Carbon (POXC)

Introduction

Land use change (LUC) is a key driver of biogeochemical alterations across the planet (Houghton 1994; Klein Goldewijk et al. 2011; Sanderman et al. 2017). In the 21st century, primary forests in the tropics have been converted to agricultural use at unprecedented rates, with significant losses incurred for C stored in soils as soil organic C (SOC) (Berenguer et al. 2014; Sheil et al. 2016). An iconic example is Amazonia, the largest evergreen forest in the world with an estimated extent of 6.2 million km² (Malhi et al. 2008). The Amazon forest is often regarded as the largest remaining agricultural frontier in the world, within which LUC is expected to drive further anthropogenic C emissions (Galford et al. 2010). As of 2013, an estimated 750,000 km² of Amazon forest had been converted to agriculture, entailing a loss of 11.2 Gt C (Nogueira et al. 2015). The majority of these emissions (66–78%) are caused by conversion of forest to pasture (Elizabeth et al. 2010; Stahl et al. 2016). Moreover, the removal of forest cover causes rapid deterioration of soil quality, leading to declines in pasture productivity and subsequent abandonment of nearly half of pastures within 5–15 years following forest-to-pasture conversion (Aguiar et al. 2016) and the emergence of secondary forests. Increasing rates of deforestation, therefore,

entail increasing rates of secondary forest succession. For example, between 1978 and 2002, the extent of secondary forest increased by more than five-fold to approximately 161,000 km² (Neeff et al. 2006). Despite the growing importance of deforestation and secondary forests in the tropics (FAO 2016), the impact of this type of LUC on soil C cycling is poorly understood (Aragão et al. 2014; Cook et al. 2014).

Impacts of LUC on SOC are ultimately mediated by shifts in drivers of soil C cycling, which could help explain conflicting consequences of LUC outcomes for SOC. In the Amazon basin, forest-to-pasture conversion has been variously reported to result in SOC losses (Fearnside 1980; Buschbacher 1984; Veldkamp 1994), increases (Trumbore et al. 1995; de Moraes et al. 1996; Neill et al. 1997) or no changes (Rittl et al. 2017). Crucially, those studies have not examined the effect of secondary forest development on soil C cycling, which would be necessary to assess the anticipated legacy of pasture expansion effects on SOC. Moreover, disparate site-specific changes in SOC may be explained by shifts in SOC cycling triggered by abrupt changes in the primary source and lability of soil C cycling following deforestation (Figueira et al. 2016; Navarrete et al. 2016).

To address this critical knowledge gap, we rely on a spatially-explicit design that takes advantage of a well documented and long-term forest-to-pasture and pasture-to secondary forest conversion observational chronosequence to characterize soil C cycling by integrating $\delta^{13}\text{C}$ measurements with lability, molecular composition, and C-mineralizing enzyme activities. This integrative approach reveals changes in C cycling following LUC that would otherwise be masked by measures of total SOC. Here, we tested the hypothesis that LUC of primary forest conversion to pasture eventually achieves a SOC concentration equilibrium in which a relic fraction of forest-derived SOC persists despite shifts in lability (POXC) and composition (organic functional groups), and biochemical drivers of SOC mineralization (β -glucosidase activity). For the conversion of abandoned pasture to secondary forest, we tested the hypothesis that secondary forest SOC composition and lability revert to those found in primary forests as a result of natural succession. While observational, this well-studied chronosequence of LUC nonetheless offers unique insights to soil C cycling by virtue of its duration. To integrate all LUC effects, we developed a

J. van Haren
Biosphere 2, University of Arizona, Tucson,
AZ 85721, USA

J. van Haren
Honors College, University of Arizona, Tucson,
AZ 85721, USA

J. L. Mazza Rodrigues
Environmental Genomics and Systems Biology Division,
Lawrence Berkeley National Laboratory, Berkeley,
CA 94720, USA

mixed model to predict SOC turnover under different land uses, which will be useful for estimating the impact of LUC across the Amazon region.

Materials and methods

Site description

The study was conducted at the Amazon Rainforest Microbial Observatory (ARMO), Fazenda Nova Vida ranch (10°10'5''S and 62°49'27''W), in the State of Rondônia, Brazil. This region experiences the highest forest loss in the Amazon basin and the site represents one of the longest studied chronosequences in the Amazon region (Neil et al. 1997; Cerri et al. 2004). The local climate is tropical humid with a mean annual temperature of 25.5 °C and a historical mean annual precipitation of 2200 mm distributed over a well-defined wet season from September to May (Bastos and Diniz 1982). The primary forest at the site is classified as upland humid evergreen ombrophilous (Pires and Prance 1985) supported by soils classified as Kandiodults (USDA Soil Taxonomy) or red-yellow podzolic Latosols (World Reference Base for Soil Resources), with sandy loam texture (Feigl et al. 2006). The sampling site has a 30 year-history as a model for forest-to-pasture conversion due to varying times of primary forest conversion to pasture across the last century, which provides the basis for characterizing long-term changes in soil C cycling. Pastures were developed by slash and burn practices, in which trees are harvested for timber, the remaining biomass is burned and seeded with *Brachiaria brizantha* (Cerri et al. 2004). Pastures at and near the study sites are typically grazed with a stocking density of one cow per hectare. Pastures were burned every 4–10 years for weed control, did not receive fertilizer or other inputs, and were not subject to mechanical disturbances such as tillage. At and near the study sites, secondary forests were established when 7–10 year old pastures were abandoned due to insufficient grass regeneration and increasing weed invasion (Paula et al. 2014), which is thought to reflect soil degradation (Cerri et al. 2005). The secondary forests at our study sites are comprised of ~ 63% herbaceous species (including pasture grasses), 15–18% woody tree species, and ~ 12% palm species (Feigl et al. 2006). As with any chronosequence study, we

assumed that sites differed only in age and that, regardless of the spatial location, they began with similar soil properties, including SOC concentration in the sampled 0–10 cm depth (De Palma et al. 2018; Miyanishi and Johnson 2007).

Soil sampling

For this study, soils were sampled at the end of the austral summer (i.e., rainy season) in 2011 under different land use types. Soils were collected from two primary forests (FII and FIII) and four pastures representing an observational chronosequence of forest-to-pasture conversion from initial deforestation in 1911 (P11), 1972 (P72I and P72III), 1987 (P87I and P87II) and 2004 (P04); and two secondary forests developed after pasture abandonment in 1993 (SF93) and in 1998 (SF98) (Supporting Fig. 1) corresponding to previous studies of LUC impacts on total SOC (de Moraes et al. 1996; Neill et al. 1997; Cerri et al. 2004; Paula et al. 2014). All the SF sites were under at least 10 years of pasture production before their respective year of abandonment. For each site, soils were sampled at 1, 10, and 100 m from an origin (plot center) along north and east coordinates (Supporting Fig. 2 and Supporting Table 1). After the removal of the surface litter layer, we sampled soils to 0–10 cm depth with a 5 cm diameter sterile PVC tube for a total of seven samples for each site (Rodrigues et al. 2013; Paula et al. 2014).

Soil analyses

Prior to analyses, all soils were air-dried at 25 °C and sieved to pass < 2 mm diameter. Elemental concentrations and soil physico-chemical parameters were analyzed at the Laboratory of Soil Analysis at the “Luiz de Queiroz” College of Agriculture, University of São Paulo, Piracicaba, Brazil (Supporting Table 1).

Total and labile C

We measured total SOC concentrations using a LECO CN elemental analyzer (St. Joseph, MI, USA), and labile C as permanganate-oxidizable C (POXC) in soils (Culman et al. 2012). Briefly, we subjected 2.50 g of soil in triplicate to horizontal shaking at 240 rpm in 20 mL of 0.02 mol L⁻¹ KMnO₄ for 2 min followed by 10 min incubation. We quantified

permanganate remaining in the supernatant by colorimetry (550 nm) and calculated POXC (mg kg⁻¹ soil) using Eq. 1 (Culman et al. 2012):

$$\begin{aligned} \text{mg POXC kg}^{-1} \text{soil} = & [0.02 \text{ mol L}^{-1} - (a + b \times \text{abs})] \\ & \times (9000 \text{ mg C mol}^{-1}) \\ & \times \left(\frac{0.02 \text{ L}}{\text{kg soil}} \right) \end{aligned} \quad (1)$$

where 0.02 mol L⁻¹ is the initial concentration of permanganate (Mn⁷⁺), *a* is the intercept of the standard curve, *b* is the slope of the standard curve, *abs* is the sample absorbance, 9000 mg C mol⁻¹ is the assumed stoichiometry of C oxidation and reduction of Mn⁷⁺ to Mn²⁺ (Gruver 2015), 0.02 L is the volume of 0.2 mol L⁻¹ KMnO₄ solution, and kg soil is the mass of air-dried soil.

β-Glucosidase activity

Given that SOC turnover and lability is strongly influenced by and reflected in activities of soil C-cycling enzymes such as glucosidases (Stege et al. 2010), assays of enzyme activities can help explain changes in SOC cycling across LUC such as primary forest to pasture conversion of neotropical forests (Vallejo et al. 2010) or temperate forests (Scotti et al. 2015). *β*-Glucosidase catalyzes the hydrolysis of oligosaccharides to glucose in the final step of cellulose degradation (Turner et al. 2002) and is therefore considered a key step in the degradation of this major and plant-derived above-ground input to soil (Alef and Nannipieri 1995). We quantified the potential activity of *β*-glucosidase (Enzyme Commission 3.2.1.21) based on the method of Tabatabai (2003) modified to reduce artifacts of assay termination (Margenot et al. 2018). Briefly, we incubated 1 g soil for 1 h at 37 °C in 5 mL of Modified Universal Buffer (pH 6.0) with a final substrate concentration of 0.010 mol L⁻¹ *para*-nitrophenyl-*β*-D-glucopyranoside. As negative control, we included triplicate soil-free assays with substrate. Assays were terminated by adding 4 mL of 0.1 mol L⁻¹ Tris (pH 12.0) and 1 mL of 2.0 mol L⁻¹ CaCl₂, and centrifuged to remove sediment. *para*-Nitrophenol (*p*NP) in the clear supernatant was quantified colorimetrically using absorbance at 410 nm. We calculated *β*-glucosidase activity on a soil mass basis (μmol substrate

g⁻¹ soil h⁻¹) and normalized to SOC content (μmol substrate g⁻¹ SOC h⁻¹). The activity of this C-mineralizing enzyme normalized to total SOC concentration has been found to be sensitive to changes in SOC accrual and loss (Stott et al. 2013).

δ¹³C ratios and calculation of soil C source

We assessed the δ¹³C signature of soils at the University of California—Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Values of δ¹³C were expressed relative to Vienna-Pee Dee Belemnite (V-PDB) and used to identify contributions of primary forest to SOC across the deforestation and reforestation observational chronosequences. The amount of SOC derived from pasture was determined by using a two-end-member mixing model (i.e., δ¹³C signature of primary forest vegetation and isotopic signatures of grass) (Eq. 2) (Silva et al. 2015). We estimated δ¹³C values of both end members using values for tree-derived litter in this region of the Brazilian Amazon (− 28.5 ± 1.6 ‰) and for the C4 pasture grass *B. brizantha* (− 14.3 ± 0.6 ‰). These values were derived from values for soil and plant ¹³C signatures at our study site (Moraes et al. 1995; de Moraes et al. 1996; Cerri et al. 2004). The contribution of C3 species (described in Sect. 2.1), which dominate primary productivity in forests, but not in pastures, was then calculated as the percent of total SOC using Eqs. 2 and 3:

$$C_p = C_t \frac{(\delta_s - \delta_f)}{(\delta_p - \delta_f)} \quad (2)$$

$$C(\%) \text{ derived from forest} = \frac{C_p}{C_t} \times 100 \quad (3)$$

where *C_p* is the amount of soil C derived from pasture (mg g⁻¹), *C_t* is total SOC, δ_s is the δ¹³C signature of sampled soils, δ_f is the δ¹³C signature of primary forest, and δ_p is the δ¹³C signature of the seeded pasture grass *B. brizantha*.

Diffuse reflectance infrared Fourier transform spectroscopy

We used diffuse reflectance infrared Fourier transform (DRIFT) spectroscopy to characterize organic

functional groups (e.g., aliphatic C–H, aromatic C=C, carbonyl C=O, amide C=O) that compose soil organic matter (SOM) (Essington 2004) and influence its decomposability (Calderón et al. 2011a; Erhagen et al. 2013). DRIFT spectra can provide semi-quantitative information on mineral and organic functional groups in soils (Parikh et al. 2014), which for similar soil types enables relative differences to be enhanced across samples (Calderón et al. 2011a; Demyan et al. 2012). SOM cycling entails the transformation of organic C via processes of decomposition and mineralization that are manifested in functional group chemistry (Hsu and Lo 1999; Calderón et al. 2011b; Ernakovich et al. 2015). Limitations of DRIFT spectroscopy include reduced sensitivity to organic functional groups as a result of mineral dominance of spectra (Parikh et al. 2014; Margenot et al. 2015). DRIFT spectroscopy has shown sensitivity to small changes in quality and quantity of labile organic matter (Calderón et al. 2013) sufficient to help explain SOM transformations and stabilization (Chefetz et al. 1998).

DRIFT spectra were collected on neat soil samples (i.e., no KBr dilution) loaded into wells (10 mm diameter, 2.3 mm depth) and surface smoothed. Absorbance spectra were corrected against a solid aluminum blank in ambient air as the background using a Nicolet 6700 spectrometer (Thermo Scientific, Waltham, MA) with a deuterated triglycine sulfate (DTGS) detector diffuse reflectance accessory (Pike AutoDIFF, Pike Technologies, Madison, WI). Spectra were collected as the mean of 400 scans across 4000–650 cm^{-1} at 4 cm^{-1} resolution. Triplicate spectra were collected on separate soil samples and averaged into one final spectrum for each soil. Spectra were corrected by calculating a linear tangential baseline with zero points representing local absorbance minima (Capriel et al. 1995; Haberhauer et al. 1998; Smidt et al. 2002) using the OMNIC 7.0 software (Thermo Scientific, Waltham, MA).

Five DRIFT spectra absorbance bands were used to assess relative differences in SOM composition. We selected these bands because they have been shown to reflect differences in soil C stabilization in weathered soils (Lehmann et al. 2007; Verchot et al. 2011): aliphatic C–H stretch at 2921 cm^{-1} , carbonyl C=O stretch at 1725 cm^{-1} , ketone and/or quinone C=O and/or aromatic C=C with possible amide C=O contributions at 1610 cm^{-1} , carboxylate C–O symmetric

stretch and/or phenolic C–O stretch and/or aliphatic C–H bend at 1369 cm^{-1} , and polysaccharide C–O at 1020 cm^{-1} (Supporting. Figure 3). Absorbance for these bands includes mineral contributions, but constant mineralogy, similar soil texture, and relatively high SOC content enable absorbance differences to be attributed to organic functional groups (Verchot et al. 2011; Demyan et al. 2012; Parikh et al. 2014). To assess relative changes in DRIFT spectroscopy absorbance corresponding to organic functional groups in soil, we normalized the absorbance intensity of each of the five bands of a single spectrum as the percent absorbance intensity of the sum of absorbance intensities of the five bands (Haberhauer et al. 1998). While there are other approaches to normalize absorbance in soil spectra such as ratios of absorbances to a single absorbance band, the approach used here and by others (Chefetz et al. 1998; Haberhauer et al. 1998) enables comprehensive assessment of relative shifts in absorbances corresponding to organic functional groups.

Statistical analyses

We used Violin plot analysis, which combines a boxplot and a double kernel density plot, to compare the distribution of the variables measured among the different sites, with an ANOVA followed by Tukey's tests at 95% of significance. To explain differences in the ordination among soil variables of SOC, POXC and β -glucosidase and the relative proportion of organic functional groups derived from DRIFT spectra, we performed principal component analysis (PCA) using these variables. The Pearson's correlation coefficient was calculated to evaluate the relationship among soil physical properties and other soil C-related variables measured in this study. All procedures were performed in the R platform using the packages VioPlot (Adler 2015), FactoMineR (Lê et al. 2008), corplot (Wei 2017) and Hmisc (Harrell Jr 2017).

To improve future estimates of labile carbon and β -glucosidase activity from the simple measurement of total SOC content, we developed empirical models to predict long-term (100 year) changes in soil C cycling after deforestation. We further evaluated how SOC changed over time since deforestation, and how labile C and enzyme indicators of soil C cycling shifted concurrently with changes in total SOC by

fitting three mixed-effect models. To test whether origin of SOC (i.e., forest-derived) helped predict and β -glucosidase and labile C (POXC), we additionally compared the effects of total SOC concentration and forest-derived SOC in a mixed model. Before subjecting the data to models, predicting variables were standardized by centering and scaling the data to have a mean of zero and a standard deviation of one (Eq. 4). Data were log-transformed to meet assumptions of normality and homogeneity of residuals (Zuur et al. 2011). Since log transformations used base 10, actual values can be obtained by calculating 10^x ; where x is the value generated by the fitted log-based model as in Eq. 4 (Ramette 2007; Legendre and Legendre 2012):

$$S'_k = (S_k - \min) / (\max - \min) \quad (4)$$

For the first model, we fitted a simple mixed-effects model to test the fixed effects of time since conversion and vegetation on log SOC and accounting for plot variability. The conditional predicted plot shows actual values versus values predicted by the model, accounting for the effect of plot used as a random factor (Zuur et al. 2011; Silva et al. 2016). Additional modeling details are described in the Supporting Information.

Results

Changes in SOC cycling indicators associated with LUC

Primary forest (PF) sites were distinct from the secondary forests and pastures, according to PCA (Fig. 1a). The recent conversions (SF and P04) were more similar to the PF when compared with older pastures (P11, P72, and P87) (Fig. 1a). Additionally, certain soil C variables explained a greater proportion of variation among sites (Fig. 1b). SOC, β -glucosidase activity, POXC and DRIFT spectroscopy absorbance at 2921 cm^{-1} (aliphatic C–H) were positively associated with age of pasture sites after 20 years of conversion, whereas DRIFT spectroscopy absorbance at 1020 cm^{-1} (polysaccharide C–O) and 1610 cm^{-1} (ketone, quionine, and/or amide C = O and/or aromatic C = C) were strongly associated with SF and P04 sites (Supporting Table 2). Forest-derived SOC was most strongly associated with PF, and inversely

with older (≥ 24 year) pasture sites (P11, P72, P87). Complementing the PCA results, Pearson's correlations demonstrated that POXC ($R = 0.91$) and β -glucosidase activity ($R = 0.75$) had the strongest positive correlation with SOC, whereas POXC ratio with SOC ($R = -0.62$) and forest-derived SOC ($R = -0.56$) had the weakest negative correlations (Supporting Fig. 4).

Total and labile SOC, and SOC origin

Total SOC and POXC were significantly higher with time ($P < 0.05$) following conversion of primary forest (PF) to older pastures and lower in secondary forest (SF) succession from pasture (P) (Fig. 2a, b). Total SOC was 10.2 (standard deviation ± 3.1) g kg^{-1} under PF and for older pastures (≥ 24 year) was nearly 2- to threefold greater: 18.8 (± 2.5), 29.9 (± 1.4) and 25.9 (± 2.4) g kg^{-1} for pasture established in 1987, 1972 and 1911, respectively (Fig. 2a). Sites following recent LUC of young pasture (7 year) P04 and SF exhibited similar total SOC as PF, with a value of 12.5 (± 3.7) and 15.5 (± 1.6) g kg^{-1} , respectively. There were no detectable differences in total SOC or POXC for SF93 and SF98. POXC values showed a similar trend as total SOC across land uses, with POXC being the greatest for P72 at 930 (± 263) mg kg^{-1} , followed by P87 at 720 (± 89), P11 (708 , ± 47) and P04 (599 , ± 141). Concentrations of POXC in SF (450 , ± 48) were similar to those in PF (495 , ± 108) and P04, but significantly lower from those observed for other pastures ($P < 0.05$).

As an indicator of SOC lability, the POXC demonstrated a similar trend as SOC across the type and duration of LUC (Fig. 2c). The conversion of forest to pasture produced inconsistent changes in the proportion of total SOC as POXC (i.e., POXC:SOC). In soils under PF, 5.1% of total SOC was POXC, and decreased with time in pasture from 4.9% in P04 to 3.8% for P87 to 3.4% for P72 and 3.3% for P11. Mean POXC:SOC was significantly lower under SF (3.9%) compared to the original forest.

Forest-derived SOC decreased rapidly after conversion of PF to pasture, and this trend was reversed in SF following pasture abandonment (Fig. 2d). In pastures, the proportion of SOC derived from forest was 53.1% (± 10.4) for P04, 27.1% (± 6.9) for P87, 21.8% (± 3.9) for P72 and 16.3% (± 2.0) for P11. For SF, up to 97.0% (± 2.9) of SOC was forest-derived.

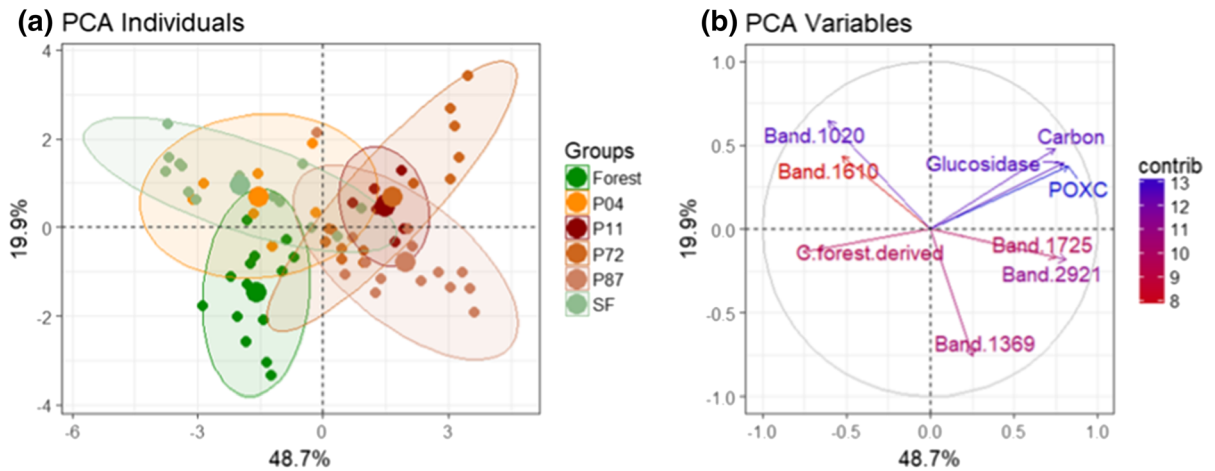


Fig. 1 Principal components analysis of total SOC, forest-derived SOC, POXC, β -glucosidase and organic functional group relative abundance characterized by DRIFT spectroscopy. **a** Dots represent a sample, and the groups and ellipses represent each site of the study. All the ellipses were done with

95% confidence. The group names are PF for Primary Forest, P04 for Pasture 2004, P11 for Pasture 1911, P72 for Pasture 1972, P87 for Pasture 1987 and SF for Secondary Forest. **b** Biplot of the variables as arrows, the color of which indicates the relative contribution of each attribute

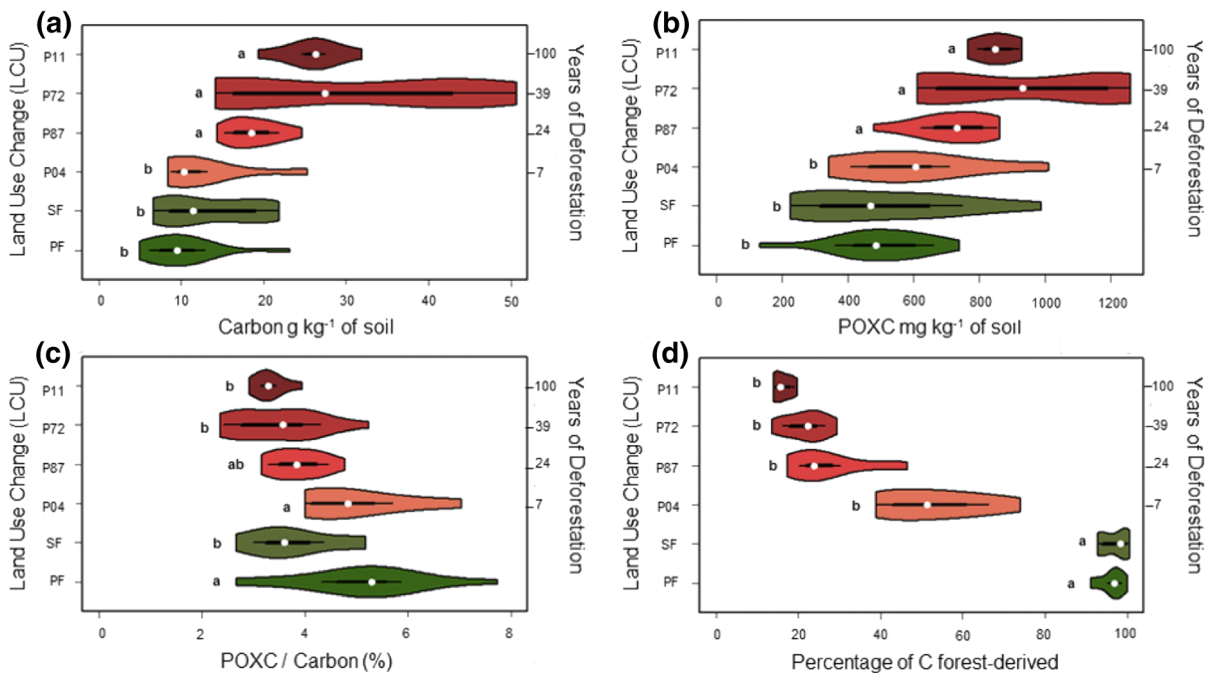


Fig. 2 Violin plot representing (a) total SOC, (b) POXC, (c) the ratio of POXC:total SOC, and (d) percentage of forest-derived SOC (derived from $\delta^{13}\text{C}$ in soils (0–10 cm depth) across chronosequence of forest-pasture and pasture-secondary forest land use change in the Brazilian Amazon, which combines a boxplot represented by the bar and the lines, and a doubled

kernel density plot. Letters on the plot show the groups after the ANOVA, followed by Tukey tests with a 95% of significance. The land uses are primary forest (PF), Pasture 2004 (P04), Pasture 1987 (P87), Pasture 1972 (P72), Pasture 1911 (P11) and secondary forest (SF)

β -Glucosidase activity

The response of soil β -glucosidase activity to LUC was similar to that of SOC and POXC. Conversion of primary forest to pasture significantly increased β -glucosidase activity ($P < 0.05$) in older pastures (≥ 24 year) and decreased in secondary forest (Fig. 3a). Primary forest, secondary forest and the most recently established pasture (7 year) exhibited similar β -glucosidase activities. When normalized to total SOC, β -glucosidase activities were not significantly different across all LUC sites (Fig. 3b).

Modeling SOC, POXC, β -glucosidase activity, and ^{13}C

A mixed-effects model showed significant differences in SOC across land use type and time (i.e., years after conversion) (Fig. 4). This analysis generated positive coefficients for time (i.e., SOC increased over the time) and higher concentrations of surficial SOC in pasture and secondary forests than in primary forest.

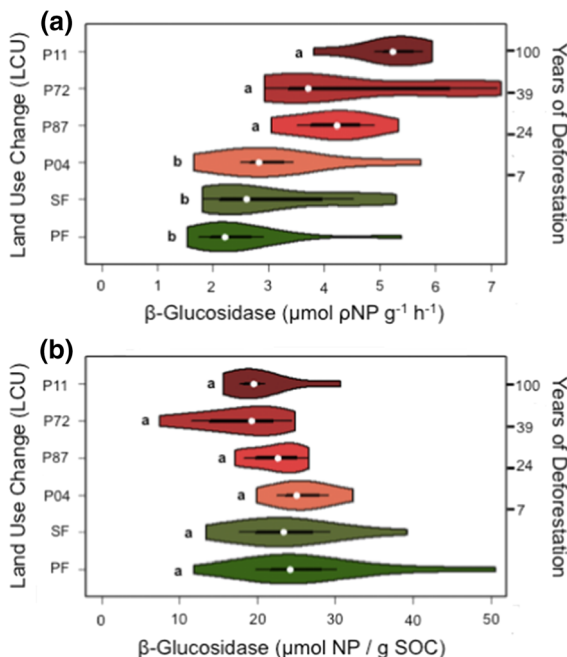


Fig. 3 Violin plot, representing in (a) β -glucosidase activity and (b) β -glucosidase activity normalized to total SOC. Letters indicate significant differences among means (Tukey test, $p < 0.05$). The land uses are primary forest (PF), Pasture 2004 (P04), Pasture 1987 (P87), Pasture 1972 (P72), Pasture 1911 (P11) and secondary forest (SF)

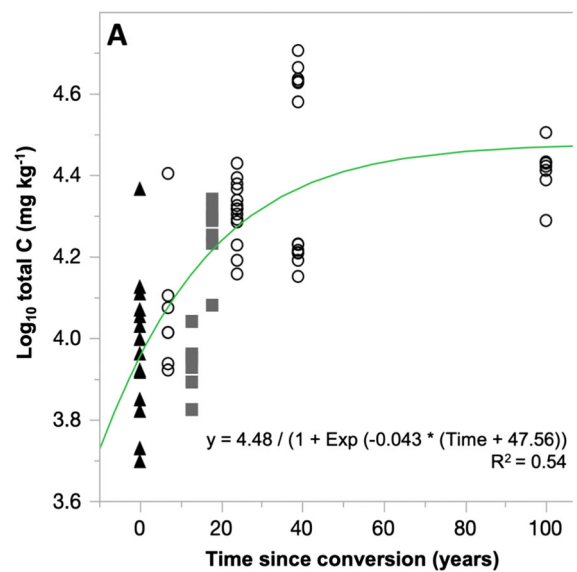


Fig. 4 Logistic models of time series and land use change depicting the log of total soil organic carbon (SOC) over ~ 100 years. Solid lines show predict values and points show measured values. Black triangles represent primary forest, gray squares represent secondary forest, and circles represent pasture. The observed range of Log_{10} total SOC is consistent with typical values found in native forests and savannas across the region Wright et al. 2020 (e.g., ~ 3.8 to $4.5 \text{ Log}_{10} \text{ mg/kg}$ represents ~ 0.6 to 3.2% total SOC, respectively)

Logistic equations used to characterize changes in SOC over time and across land uses plateaued at $4.48 \text{ mg log OC kg}^{-1}$ soil, which corresponds to an actual value of 30.2 g kg^{-1} or $\sim 3\%$ SOC on a mass basis. This asymptote, which is defined as the maximum level of SOC saturation or carrying capacity across the successional gradient, is given by the first term of the equation shown in Fig. 4a. The inflection point of that same model, defined as the point of fastest SOC accumulation following land use change, is given by first term of the equation divided by two (i.e. half way to the plateau) and corresponds to $2.24 \text{ mg log OC kg}^{-1}$ soil, or an actual value of 174 mg kg^{-1} . This model also shows that the vast majority of SOC gains ($\sim 93\%$) occurred within first 25 years of pasture establishment, with 99% of SOC concentration increases occurring within 60 years of pasture establishment (Supporting Table 3 and 4). Total SOC concentration, but not SOC origin (i.e., forest-derived C), was a direct predictor of soil β -glucosidase activity and labile carbon (POXC) across the deforestation

chronosequence (Supporting Fig. 5–7; Supporting Table 4).

Discussion

SOC dynamics under forest-pasture LUC

Our results reveal an impact of LUC on C cycling in surface soils in this region of the Amazon beyond changes in total SOC concentrations, in which forest-to-pasture and pasture-to-forest conversions trigger distinct shifts in biochemical drivers of the soil C cycle. The observed higher SOC concentrations in the first 40 years following pasture establishment is even more remarkable since it coincided with a near-complete replacement of primary forest SOC with C derived from the pasture grass *B. brizantha*. Increments in total SOC concentrations occurred concurrently with (1) nonlinear increases in labile C (POXC), (2) enrichment in organic functional groups associated with organic matter chemical lability (i.e., aliphatic C–H; Hsu and Lo 1999; Ait Baddi et al. 2004; Ali et al. 2012), and (3) for older pastures, a nonlinear increase in the activity of β -glucosidase, a C-mineralizing enzyme. Therefore, we propose that conversion of primary forest to pasture results in a shift in soil C cycling driven by the replacement of C inputs (roots, litter) from tree forest species to pasture grasses. Sustained elevated total SOC concentrations also indicate that pasture establishment modified soil C saturation in the studied surface horizons (0–10 cm) (Six et al. 2002) compared to native vegetation. Net increases in SOC following seeding of weathered soils with improved pasture species (*Andropogon gayanus*, *Brachiaria humidicola*) were also found in the Colombian llanos, attributed in part to greater rooting depth of the introduced grass species (Fisher et al. 1994).

Our measurements of higher C-mineralizing enzyme activity under the first 40 years of pasture establishment are consistent with an elevated turnover of SOC, following the replacement of C inputs from forest species to inputs from pasture grasses. This finding is consistent with the hypothesized role of microbial transformations of OM for the formation and stabilization of SOC (Demyan et al. 2012; Giacometti et al. 2013) and accelerated turnover of SOC with elevated labile C concentrations in pastures.

Previous evaluations of soil microbial diversity in the study region have demonstrated losses of microbial diversity and functionality following forest-to-pasture conversion (Rodrigues et al. 2013; Paula et al. 2014). These results corroborate our hypothesis that despite SOC increase after forest-pasture LUC, the conversion results in a shift in soil C cycling driven by the replacement of C inputs (roots, litter) from tree forest species to pasture.

Although the forest-derived SOC fraction in the oldest pastures (< 16%) indicates the potentially long-term persistence of some components of the native carbon pool, it also underscores the susceptibility of the majority of the forest SOC to rapid loss under LUC, even for a low-impact (e.g., no soil disturbance, low stocking density) perennial agricultural system (Solomon et al. 2007b). This rapid turnover of native SOC may be related to changes in microbial community following forest conversion to pasture. For example, functional microbial diversity has been shown to decrease in some areas where primary forest was converted to pasture, with functional gene differences in the first 7 years being larger than differences observed 38 years after conversion (Paula et al. 2014). The mechanisms driving such changes are not well understood and should be investigated in future studies.

SOC origin and quality

Previous studies have indicated decreases, increases, or no change in total SOC concentrations and/or stocks following pasture to forest conversion in Amazonia and other tropical forests (Guo and Gifford 2002; Murty et al. 2002; Fujisaki et al. 2015). While generally native SOC is lost following deforestation (Danuse et al. 2002), as we demonstrate here using ^{13}C measurements, interactions of drivers of SOC cycling can lead to net increases or decreases in total SOC.

The persistence of forest-derived SOC (16%) in surface soils over a century post-conversion likely reflects its biochemical stabilization as pyrolyzed C or via chemical and/or physical protection (e.g., mineral-bound or intra-aggregate C) (Six et al. 2002; Schmidt et al. 2011). Previous studies at these same sites (e.g., Cerri et al. 2004) found that after 80 years of conversion to pasture the remaining forest-derived SOC, as assessed using $\delta^{13}\text{C}$ ratios, was found largely in the silt- and clay-sized fractions, which suggests

chemical protection of forest-derived SOC via stabilization with clay minerals (Feigl et al. 1995; Six and Paustian 2014; Silva et al. 2015). It is also possible that relic forest-derived SOC persists as a refractory pool of pyrolyzed C generated by burning of forest biomass during initial deforestation. Pyrolyzed C can have a half-life 10- to 100-fold greater than native SOC (Singh et al. 2014) with turnover rates estimated at the centennial scale (Spokas 2010; Singh et al. 2012), and is therefore considered a major contributor to long-term SOC storage, including in the Amazon basin via ancient natural fires (Silva et al. 2021), despite being a minor fraction of total SOC in most ecosystems today (Lehmann et al. 2008; Reichstein et al. 2013).

The change in C input source with conversion of forest to pasture is expected to have implications for SOC stabilization due to differences in degradability and the route by which plant detritus enters soil (e.g., forest litter deposition on soil surface versus fine-root turnover within the subsurface). Pasture grasses at our sites may have provided greater subsurface inputs of C, and with a different composition than inputs under forest. The greater surface distribution and turnover rates of *Braccharia* roots in Amazon pastures compared to forest entail increased fine-root density in surface soils of pastures (Trumbore et al. 1995, 2006; De Camargo et al. 1999). Distinct pathways of C entry and thus stabilization as SOC under pasture grasses could explain elevated SOC relative to forest. *Braccharia*-derived SOC has been found to be allocated in finer soil fractions (silt- and clay-size) compared to coarser fractions for primary forest-derived SOC, which likely reflects direct addition of root-derived C from grass species (Rasse et al. 2005). Root-derived C (e.g., exudates, senesced roots) is thought to have greater potential for stabilization and persistence as SOC than shoot-derived C due to greater interaction with soil minerals, in contrast to surface-deposition litter in forest (Gale et al. 2000; Rasse et al. 2005; Cotrufo et al. 2013).

Changes in SOM composition with LUC

The type of changes in SOM composition by LUC type and duration identified by enzymatic and spectroscopic measurements are consistent with the hypothesized impact of LUC on SOC cycling due to shifts in C input type. Shifts in SOM composition were consistent in the type of functional group (e.g.,

aliphatic C-H) and input source (forest litter versus pasture grass) as well as the rate of this change (abrupt forest-to-pasture vs gradual pasture-secondary forest). Pronounced differences in aliphatic C-H and polysaccharide C-O (bend) across sites is consistent with previous reports of shifts in the relative abundance of these organic functional groups with increasing time post-deforestation (Solomon et al. 2007a), though at our study sites we observed greatest aliphatic C-H (stretch) for older pasture. Relative increases in absorbance of methylene CH₂ and methyl CH₃ attributed to aliphatic compounds (Smidt and Meissl 2007) have been associated with greater chemical lability (i.e., less decomposed state) across a variety of organic matter samples (e.g., plant biomass, manure) (Hsu and Lo 1999; Ait Baddi et al. 2004; Ali et al. 2012).

While the activity of β -glucosidase was greatest in the oldest pastures, the activity of this enzyme per unit of SOC was similar among sites, which we interpret to imply little change in microbially-driven C turnover. This may reflect stoichiometric scaling of enzyme activities with SOC (Sinsabaugh et al. 2008, 2009). Functional bacterial diversity was reduced at the youngest pastures (7 years) at our site, and entailed an increase in two genes families associated with hydrolysis of labile carbon compounds (Paula et al. 2014). Observing the bacterial composition in forest-pasture LUC, occurred homogenization of bacterial diversity due to an increased range of existing taxa and loss of endemic forest taxa post-conversion (Rodrigues et al. 2013; Paula et al. 2014).

Potential impacts of fire used in Amazon LUC

The use of fire to establish pastures at our sites, a standard practice throughout the Amazon basin and other tropical forests globally (Boone et al. 2009), is likely to have impacted post-conversion SOC response (de Souza Braz et al. 2013; Navarrete et al. 2016). The transient liming and fertilization effect of ash deposition following burn-based conversion may have stimulated SOC decomposition in the initial years of pasture establishment (Paradelo et al. 2015). For example, losses of forest-derived SOC were observed within the first nine years of conversion to pasture during which there were significantly elevated pH and soil nutrient cations due to burn-mediated liming and nutrient deposition (de Moraes et al. 1996). The

relatively short-lived effect of liming (< 10 years) that is most acute immediately following burning (< 2–3 years) (de Moraes et al. 1996) may explain the lack of significant changes in soil pH and nutrient cations at our sites, even in the youngest pasture (7 years). The intensity of selective logging and subsequent burning may also entail site-specific differences in the extent of the post-conversion burn liming effect. Periodic burning of pastures for weed management (estimated to occur once per 4–10 years) could also contribute yield pasture-specific differences in the fraction of SOC stabilized as pyrolyzed C.

Secondary forest: an emerging LUC

Our study addresses soil C cycling in response to the emergent Amazon LUC of secondary forest succession. Whereas LUC of forest to pasture is abrupt and entails a sudden change in C inputs due to logging and fire, the reverse LUC is a gradual transition of intrusion and establishment of early-stage forest plant species in abandoned pastures. Similar to conflicting observations of SOC response to LUC of primary forest to pasture, varying relationships of SOC between primary and secondary forests have also been reported within and across studies (Fearnside and Imbrozio Barbosa 1998; Berenguer et al. 2014), which could depend on pasture management and edaphic factors.

At our study site, we identified similar SOC concentrations and source (^{13}C signature) in secondary forests as in primary forest. The dominance of forest-derived SOC ($\delta^{13}\text{C}$) in less than 20 years of reforestation (97%) demonstrates a relatively short half-life of SOC derived from pasture compared to forest, and further supports accelerated rates of SOC cycling under pasture. The decrease in POXC and β -glucosidase activity to values similar to primary forest suggests a lowered rate of SOC turnover with secondary forest succession. However, organic functional groups composition of SOM was distinct from that of primary forest, indicating an incomplete turnover of SOM composition to the primary forest patterns within the short-term (< 20 years) of secondary forest development. Notably, polysaccharide C-O enrichment in secondary forests also occurred in the most recent reverse LUC of newly transitioned pastures (7 years post-deforestation). Given decreased β -glucosidase activity and the importance of this

C-mineralizing enzyme as the final step in cellulose degradation (Stott et al. 2010), relative increases in DRIFT spectroscopy absorbances indicating polysaccharide C-O enrichment in secondary forest could reflect disruption of an SOC decomposition equilibrium by microorganisms following the change in C input. Greater inherent decomposability of litter from early colonizer species that constitute secondary forests in the Amazon (e.g., *Vismia* sp. and *Bellucia* sp.) compared to primary forest species (e.g., *Bertholettia excelsa*) (Barlow et al. 2007) may explain observed alteration of SOC composition at our secondary forest sites. On the other hand, the gradual nature of this LUC compared to the abrupt, fire-mediated forest-to-pasture conversion would be expected to enable greater microbial and thus enzymatic adaptation (Knight and Dick 2004).

Indicators of SOC cycling at secondary forests are consistent with shifts in soil–plant nutrient allocation that accompany forest development from abandoned pastures (Bomfim et al. 2020a, b). Net transfer of phosphorus (P), a key limiting nutrient in the Amazon (Dalling et al. 2016), and base cations such as calcium (Ca) and magnesium (Mg) from soil to above-ground vegetation during secondary forest development have been reported in tropical forests (Lawrence and Schlesinger 2001; Markewitz et al. 2004) – the reverse of primary forest conversion to pasture by burning – may indirectly impact SOC cycling by limiting primary productivity (Chelsea et al. 2017).

Implications for soil C across the Amazon basin

Changes in C input quantity and quality implicit in tropical forest LUC may have pronounced impacts in SOC cycling, as demonstrated in the quarter-century following the currently dominant LUCs of primary forest to pasture and pasture to secondary forest (Bomfim et al. 2020a, b). Of the 750,000 km² of Amazon primary forest converted to agriculture by the first decade of the twenty-first century (Nogueira et al. 2015), only 46% remained in pasture, and pastures in varying stages of abandonment (8%) or secondary forest succession (22%) were far greater than annual crops (5%) (Ometto et al. 2016). Assuming the rapid re-attainment of soil C cycling under secondary forest succeeding pasture at this study site, a potential area equivalent to one-fifth of agricultural land use (161,000 km²) may be able to recuperate from this

initial LUC within another two decades of pasture abandonment (Neeff et al. 2006; Ometto et al. 2016).

As we demonstrate here, changes in the amount and type of C inputs can be used to explain the impacts that LUC may have on soil C cycling and thus total SOC response (Rittl et al. 2017; Chelsea et al. 2018). Repurposing pastures for annual agriculture, in particular by soybean (Macedo et al. 2012), means that secondary forest succession from pasture may be a diminishing LUC in the decades to come. On the other hand, repurposing pastures to soybean (Eugenio et al. 2011; Richards et al. 2014) and sugarcane (Richards et al. 2014) serves as an indirect driver of primary forest conversion via new pasture establishment, meaning that shifts in soil C cycling in the Amazon basin are likely to persist with the expanding agricultural frontier.

Conclusions

Scientists, land managers, and policy makers are interested in predicting and mitigating the impacts of deforestation on tropical soils. A major roadblock hindering progress in this field is the lack of long-term data showing how soil quality changes with land use. Here we provide the first 100-year record of soil C cycling after forest-to-pasture conversion in the Amazon region. We show that forest-to-pasture conversion, and subsequent secondary forest resurgence in abandoned pastures, alters many aspects of soil C cycling as reflected in isotopic ratios ($\delta^{13}\text{C}$), SOC lability (POXC), molecular composition and other biochemical indicators of SOC turnover. Total and labile SOC increased in surface soils (0–10 cm depth) during a century of pasture, and replacement of the majority of forest-derived SOC (85%) by SOC from pasture grass species occurred rapidly with the first quarter century. Following secondary forest succession, total and labile C concentrations rapidly reversed to that of primary forest driven by a near-complete (97%) return to forest-derived SOC sources within the 20 years after pasture abandonment. However, enrichment of polysaccharide C-O in pastures and secondary forest alike, compared to primary forests, suggests a long-lasting alteration of SOM composition which helps explain previous conflicting reports of total SOC response to similar LUC elsewhere in the Amazon basin. To improve future estimates of labile carbon

and β -glucosidase activity from basic measurements of SOC content we propose empirical models to predict long-term (100 years) changes in soil C cycling after deforestation. Regardless of Amazon LUC impacts on surface SOC concentrations or stocks, impacts on the turnover and lability of SOC offers mechanistic understanding of dynamic responses of SOC in tropical forests to LUC globally.

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