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RESEARCH ARTICLE

Drivers of soil organic carbon stock during tropical forest succession

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Abstract

1. Soil organic matter contributes to productivity in terrestrial ecosystems and contains more carbon than is found in the atmosphere. Yet, there is little understanding of soil organic carbon (SOC) sequestration processes during tropical forest succession, particularly after land abandonment from agriculture practices.
2. Here, we used vegetation and environmental data from two large-scale surveys covering a total landscape area of 20,000 ha in Southeast Asia to investigate the effects of plant species diversity, functional trait diversity, phylogenetic diversity, above-ground biomass and environmental factors on SOC sequestration during forest succession.
3. We found that functional trait diversity plays an important role in determining SOC sequestration across successional trajectories. Increases in SOC carbon storage were associated with indirect positive effects of species diversity and succession age via functional trait diversity, but phylogenetic diversity and above-ground biomass showed no significant relationship with SOC stock. Furthermore, the effects of soil properties and functional trait diversity on SOC carbon storage shift across elevation.
4. *Synthesis*. Our results suggest that reforestation and restoration management practices that implement a trait-based approach by combining long-lived and short-lived species (conservative and acquisitive traits) to increase plant functional diversity could enhance SOC sequestration for climate change mitigation and adaptation efforts, as well as accelerate recovery of healthy soils.

KEYWORDS
forest soil, forest succession, functional trait diversity, plant diversity, soil organic carbon, swidden agriculture, tropical forest

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1 | INTRODUCTION

Soil is the largest terrestrial carbon pool and contains more than three times the carbon found in the atmosphere (Lal, 2004). Soil organic carbon (SOC) influences soil function, microbial community composition, water holding capacity, cation exchange and nutrient cycling (Jackson et al., 2017). Hence, SOC impacts the provision of edaphic ecosystem services, making it a key indicator of soil health under sustainable land-use management and for climate change resilience (Lal, 2016). Tropical forests contribute 30% to the total global carbon sink (Harris et al., 2021) and dominate the global carbon pool accounting for 40% of carbon in soil and living plants (Phillips, 1998). In recent decades, the conversion of forest to agricultural land has been a key driver of reductions in SOC leading to declines of 20% to 52% globally (Harris et al., 2021; Smith et al., 2016). Swidden agriculture remains a major agriculture system in the tropics and causes degradation of native vegetation, but not complete removal (van Vliet et al., 2012). Under swidden agriculture, land is cleared by slashing and burning, which increases the surface soil temperature and decreases organic inputs to the soil, reducing soil carbon sequestration and predisposing the soil to nitrogen limitation (Sommer et al., 2004). Currently, swidden agriculture covers 280 million hectares worldwide, including active plots and fallows (Heinimann et al., 2017), and has been the main subsistence cropping system in upland Southeast Asia for centuries (Ribeiro Filho et al., 2013). Intensification of swidden agriculture, through reducing the length of fallows or increasing the duration of cultivation periods, decreases ecological resilience (particularly via soil degradation), increases greenhouse gas emissions and affects the soil seed bank, micro-organisms and macro-faunal communities (Ribeiro Filho et al., 2013).

Conversely, in parallel with intensification of agriculture, some swidden lands are being abandoned and these areas are reverting to forest, creating vast swaths of successional forest (Poorter et al., 2021). During forest succession, plant community composition changes as the forest ages, and different abiotic and biotic factors may drive community assembly across successional stages (Satdichanh et al., 2019). Previous studies have also reported that successional processes affect SOC, soil nutrient availability, below-ground biomass and microbial community composition, and these effects are mediated by biotic and abiotic factors (Li et al., 2013). Because rates of soil carbon loss and sequestration are scale-dependent and reflect the long-term stabilization of organic matter (Trumbore & Czimczik, 2008), examining the interplay between plant biodiversity and environmental factors in the context of land-use change and succession will provide new insights into global soil health. In particular, a better understanding of the effects of plant biodiversity and environmental factors on SOC sequestration in successional forest is needed to enhance soil carbon storage for climate change mitigation and adaptation efforts in Southeast Asia, which currently experiences the highest regional deforestation rates (Miettinen et al., 2011), and elsewhere.

Soil carbon dynamics are predominantly controlled by stabilization and destabilization mechanisms that are not directly linked to plants (Bailey et al., 2019). However, plant biodiversity influences above- and below-ground carbon storage and ecosystem functioning by playing a key role in maintaining carbon inputs, translocating carbon below-ground and mediating soil microbial community composition and activity (Kuzyakov & Domanski, 2000). Plants also control the quantity and quality of plant litter and biomass which drives decomposition rates and may lead to changes in soil carbon dynamic (Augusto & Boča, 2022; De Deyn et al., 2008). Moreover, plant diversity may promote soil fertility indirectly by increasing plant community productivity which in turn accelerates soil nutrient cycling (Cong et al., 2014). Trait composition reflects plant community composition and is likely to shift across forest succession due to changing species coexistence mechanisms and corresponding changes in species abundances (Lohbeck et al., 2012). Previous studies have shown that functional dissimilarity affects soil process rates across trophic levels even when the species richness remains constant (Coulis et al., 2015). The niche complementarity hypothesis states that functional trait dissimilarity enhances ecosystem functioning by promoting resource use complementarity between coexisting species (Garnier et al., 2015). Plant functional trait diversity (FD) has been shown to significantly contribute to carbon storage and mediate nitrogen use efficiency through vegetation cover and soil nutrients (Faucon et al., 2017). Plant traits directly influence soil carbon input, carbon loss (through decomposition and respiration), nutrient cycling/uptake and indirectly mediate plant–soil feedback via litter traits (De Deyn et al., 2008; Faucon et al., 2017). For instance, litter quality plays a key role in driving SOC accumulation in subtropical old growth forests (Xiong et al., 2020); and FD, vegetation cover and above-ground biomass are reported to be positively associated with SOC in degraded agriculture lands in Africa (Augusto & Boča, 2022; Lohbeck et al., 2018).

In this study, we used data from two large-scale surveys of 320 plots (of 1000 m^2 each) and 1280 subplots (of 100 m^2 each) covering a total landscape area of 20,000 ha in Southeast Asia to examine the effects of plant functional diversity, species diversity, phylogenetic diversity, tree above-ground biomass and environmental factors on SOC during forest succession after land abandonment from swidden agriculture. We measured SOC stocks during forest succession to infer sequestration via space-for-time substitution. We asked: (1) How do plant diversity and soil organic carbon stocks vary with forest succession? (2) How do plant diversity, above-ground biomass, forest succession and environmental factors (e.g. soil properties, slope and elevation) influence soil organic carbon sequestration after land abandonment from swidden activities? (3) Does plant functional trait diversity promote soil organic carbon sequestration during tropical forest succession to a greater extent than taxonomic diversity, phylogenetic diversity and above-ground biomass? We hypothesized that plant functional trait diversity may be crucial, because plant trait composition is directly associated with carbon input from plants into soil and reflects resource-use complementarity and its effect on biogeochemical cycles. In contrast, taxonomic and phylogenetic diversity are predicted to have weaker links to SOC due to functional redundancy among taxa, and above-ground biomass alone

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is predicted to increase decomposition activity, with weaker cascading effects on SOC.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study sites are located at Muang Beng, Oudomxay Province, northern Laos (hereafter: Mbeng) with plots ranging in elevation from 857 to 1395 m and Manlaxiang, Xishuangbanna, southwestern China (hereafter: Manla) with plot ranging in elevation from 646 to 1451 m. Manla and Mbeng sites are about 184 km apart (Figure S1) and share a similar typical monsoon climate with mean annual rainfall of 1493 and 1546 mm, and mean annual minimum and maximum temperature are 15°C and 22°C, and 14°C and 24°C, respectively. The vegetation types within both sites are similar and can be characterized as open woodland (plantation), shrub-grassland and grassland (fallow), secondary forest and old growth forest. The main forest types at both of our study sites are tropical montane forest and secondary seasonal tropical forest (Satdichanh et al., 2019), with forest soils dominated by Ultisols soil at Manla (Chen et al., 2019; Shi et al., 2006), and Entisols and Alfisols soils at Mbeng (DALaM, 2020). The upland forests at high elevation (>1000 m) are dominated by Fagaceae species (mainly species in *Castanopsis*, *Quercus* and *Lithocarpus* genera). The main ethnic groups present in both of our study areas are Dai Leu, Hmong, Khamu and a small proportion of Han Chinese and Lao Loum. Traditional swidden practices at both Mbeng and Manla are similar. The cropping period is usually 2–3 years with a fallow period usually 5–7 years. Vegetation is cut and burned to enable the soil to absorb above-ground nutrients in the form of ash prior to cropping, followed by a long period of fallow to allow nutrient levels to recover. At both sites, large areas of formerly swidden agriculture have been abandoned and now comprise successional forests of varying age.

2.2 | Data collection

Field inventories were conducted in 2014 and 2015 with permission granted using the Land Degradation Surveillance Framework (LDSF) methodology (Vågen, Winowiecki, Abegaz, et al., 2013; Vågen, Winowiecki, & Jerome, 2013). LDSF framework used a stratified random sampling design. Each LDSF site is a 100-km^2 with 16 1-km^2 clusters; 10 distinct plots were randomly placed within each cluster. Then the coordinates of each plot were loaded onto a Trimble GPS tablet for navigation. Each plot consists of four 100 m^2 circular subplots that represent a 1000 m^2 (0.1 ha) area. Thus, there are a total of 320 plots (of 1000 m^2 each) and 1280 subplots (of 100 m^2 each) across both of our study sites (Figure S1). Subplot 1 is placed at the centre of the plot, while Subplot 2 is always placed downslope, and Subplots 3 and 4 positioned 120 and 240 degrees from downslope point respectively (Figure S1). The centres of Subplots 2, 3 and 4 are 12.2 m horizontal distance from the centre of Subplot 1. In each subplot, evidence of human disturbance, vegetation cover/structure, elevation, slope, visible erosion and topographic position were recorded. We also interviewed land owners, local people and local authorities that know the area to obtain the land-use history. All individual trees with a diameter at breast height (dbh) ≥ 5 cm were measured for dbh, maximum height and identified (herbarium specimens were collected for unknown species). Cumulative soil mass samples were collected using a soil auger with a diameter of 7.6 cm from each plot at four different soil depths: 0–20 cm, 20–50 cm, 50–80 cm and 80–110 cm. However, soil samples at 50–80 cm and 80–110 cm depth were missing more than 25% of the time, because of soil depth limitations. Therefore, soil data from these two depths were excluded from this study. Topsoil (0–20 cm) and subsoil (20–50 cm) samples were collected from the center of each subplot and combined as one composite sample at the plot level. See Figure S2 for the summary of soil properties used in this study.

From both study sites, we measured a total of 8492 individual tress. At the Manla site, 4825 individual trees were measured belonging to 220 species, 113 genera and 50 families. Out of 220 species, 115 were identified to species-level and 105 species were identified to genus-level. At the Mbeng site we measured a total of 3667 individual trees belonging to 164 species, 104 genera and 42 families. Out of 164 species, 105 were identified to species-level and 59 species were identified to genus-level (Satdichanh et al., 2019). The forest successional stages were classified based on the land-use history and present human disturbance that was observed within each plot. Cropland, rubber plantation plots and plots that contained <three species were excluded from further analyses, resulting in a reduction of 13 species at Manla and 10 species at Mbeng. Cropland and plantation plots were excluded from this study because our interest was to understand SOC sequestration during forest succession. After cropland and plantation plots were excluded, a total of 188 forest plots/752 subplots containing 7654 individual trees were used in this study. On average, there are ~11 individual trees per subplot, representing a range of 0 to >50 individual trees per subplot, depending on forest type or successional stage. Since functional diversity cannot be calculated for plots with <three species, therefore these plots were also excluded from this study. Forty-two percent of the remaining forest plots were early successional stage or pioneer trees stage, <15 years old (31 plots at Manla and 48 plots at Mbeng); 27.7% were mid successional stage or secondary tree stage, 15–30 years old (19 plots at Manla and 32 plots at Mbeng); 20.8% were late successional stage, or mature tree stage, >30 years old (23 plots at Manla and 16 plots at Mbeng); and 10.1% were old growth forest (12 plots at Manla and 7 plots at Mbeng). See Table S1 for summary of forest successional stage characteristics.

2.3 | Soil analysis and soil organic carbon stocks

Soil samples were air-dried and gently crushed to pass through a 2 mm sieve. We measured the mass of coarse material which did not go

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through the sieve, and the fine material which passed through the sieve. Out of 320 soil samples per site, 32 samples (10%) were selected as reference samples and analysed using traditional wet chemistry. SOC was determined via potassium dichromate oxidation following the method described in LY/T 1237–1999. Clay and sand contents were measured using the pipette method described in LY/T 1225–1999. Soil pH was determined using potentiometric method as described in LY/T 1225–1999. Next, ground soil samples were gently crushed to pass through a 0.15 mm sieve and scanned in the Mid-infrared (MIR) spectrum from 4000 to 400 cm^{-1} or 2500 to 25,000 nm with 32 co-added scans per spectra to measure absorbance spectra using a Bruker® Alpha Fourier transform spectrometer equipped with a Drift diffuse acquisition attachment (Satdichanh et al., 2019). Absorbance spectra were collected as log (1/Reflectance) using ground Zn Se for the background reference in the Optics Users Software (OPUS, version 7.5). The measured absorbance spectra of each scanned soil sample were read into R using a script developed by the World Agroforestry (ICRAF), and the calibration models were developed using the *train* function from the *caret* packet, based on the random forest algorithm (Kuhn, 2008). The best-calibrated model was used to predict the soil texture and soil properties of all soil samples (Table S2) using the *predict* function in R (Satdichanh et al., 2019). See Figure S3 for predicted vs observed values of SOC content.

Soil bulk density (BD) of each plot was measured for cumulative soil mass samples (0–20 cm and 20–50 cm depth) following Equation (1) and (2) below (Berner & Law, 2016):

$$\text{BD} = \text{total air} - \text{dried soil weight (g)} / \text{soil volume} \left(\text{cm}^3\right), \qquad (1)$$

$$\text{Soil volume} = 3.14 \times \left(\text{soil auger radius}^2 \times \text{soil thickness}\right), \qquad (2)$$

We then estimated soil organic carbon stock ($\text{SOC}_{\text{stock}}$) in kg C m^{-2} to a depth of 50 cm only for the forest plots using Equation (3) (Li et al., 2019):

$$\text{SOC}_{\text{stock}} = \text{OC} \times \text{BD} \times \text{ST} \times (1 - (\text{CF} / 100)) \times 0.01, \qquad (3)$$

where OC is soil organic carbon concentration ($g\,kg^{-1}$), BD is soil bulk density ($g\,cm^{-3}$), ST is thickness of each soil depth (cm), CF is percent of coarse fragment >2 mm and 0.01 is a unit conversion factor. Finally, cumulative SOC in the 0–50 cm soil depth was used in this study to represent SOC stock per plot.

2.4 | Plant functional traits and above-ground biomass

Tree height (H) was measured individually in the field using a Vertex IV, and the mean of the top 10 tallest trees across the entire sample for each species represented tree maximum height (H; m) for that species. Plant trait data, wood density (WD; g cm^{-3}), specific leaf area (SLA; cm^2 g^{-1}), leaf carbon (LC; g kg^{-1}), leaf nitrogen (LN; g kg^{-1}) and leaf phosphorus (LP; g kg^{-1}) were obtained at species-level for known species and genus-level for species that identified to genus-level from published data, for example global wood density database (Chave et al., 2009; Zanne et al., 2009), global database of plant traits (Kattge et al., 2020), China plant trait database (Wang et al., 2018), ICRAF's Tree Functional Attributes and Ecological Database and other databases (see Supplementary materials-A for detailed references and plant traits data-level of each species obtained for this study). For the Manla site, trait data obtained at species-level for each species accounted for 71%–80% of the total tree abundance at this site. Whereas for the Mbeng site, WD and SLA traits data obtained at species-level accounted for >80% of the total tree abundance at this site; LN accounted for 75%; LC and LP accounted for 68% and 67% of the total abundance respectively (Table S3).

Plant maximum height is a key trait reflecting plant life history, disturbance, competition, resource use and ecological strategy (Satdichanh et al., 2015), while WD is a key stem trait associated with plant water balance and hydraulics (high wood density relates to stress tolerance and a conservative life history strategy; Chave et al., 2009). The SLA, LC, LN and LP relate directly to plant life history strategy via trade-offs between tissue construction, turnover, and efficiency, as depicted by the leaf and wood economic spectra (Wright et al., 2004), while also directly influencing soil properties and soil carbon sequestration via leaf litter decomposition (Augusto & Boča, 2022). See Table S4 for summary of plant traits ecological significance.

Above-ground biomass (AGB) of each species was calculated across each successional stage using *computeAGB* function in BIOMASS package in R following the Equation (4) (Chave et al., 2014), then total AGB per plot was used in this study.

$$\text{AGB} = 0.0673 \times \left(\text{WD} \times \text{H} \times \text{dbh}^2\right)^{0.976}, \qquad (4)$$

where WD is wood density ($g\,cm^{-3}$), H is tree maximum height (m) and dbh is diameter at breast height (cm).

2.5 | Plant biodiversity metrics

To quantify tree biodiversity, we examined multiple metrics of functional, taxonomic and phylogenetic diversity. First, we calculated functional trait diversity (FD) indices using a distance-based framework to estimate functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis; Laliberté & Legendre, 2010; Villéger et al., 2008). FRic is a measure of the amount of the functional trait space filled by co-existing species in a community, FEve is a measure of the regularity of abundance distribution in filled multivariate trait space across all species in the community (Villéger et al., 2008). FDis is a measure of mean distance of each species within multivariate trait space weighted by relative abundance to the centroid of all species in the community (Laliberté & Legendre, 2010). FRic, FEve and FDis were calculated from a species dissimilarity-by-traits matrix using the *dbFD* function in the FD package (Laliberté & Legendre, 2010). The species dissimilarity

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matrix (Gower, 1971) was generated using the *gowdis* function in the FD package based on species presence-absence data across all plots. Species diversity (SD) was generated using Fisher's alpha index (Fisher et al., 1943). Fisher's alpha was calculated using the *fisher. alpha* function in the VEGAN package (Oksanen, 2008). To estimate phylogenetic diversity (PD) we first reconstructed phylogeny for each of the study sites using Phylocom v4.2 (Webb et al., 2008) based on Megatree R20120829 as a backbone. Each phylogeny was generated with branch lengths using the *bladj* algorithm in Phylocom and node ages (Wikstrom et al., 2001). Next, phylogenetic species richness (PSR; Helmus et al., 2007) was used to examine PD based on phylogenetic species variability and species richness in a given community. PSR was generated using the *psd* function in the PICANTE package (Kembel et al., 2010). Please note that, in this study we used the same phylogenies as in Satdichanh et al. (2019).

2.6 | Statistical analysis

We performed one-way ANOVA, followed by Tukey post-hoc analysis to examine the significant differences of mean SOC_{stock}, species diversity, functional diversity, elevation, slope and soil properties among successional stages. We used Pearson's Chi-square Test to test the relationship between forest successional stages and environmental factors (elevation, slope and soil texture).

We used Structural Equation Modelling (SEM) to detect the direct and indirect effects of plant diversity (SD, FD and PD), above-ground biomass, environmental factors and land-use history on SOC_{stock} across the successional trajectory. SEM models were fitted using the *psem* function in the PIECEWISESEM package (Lefcheck, 2016) based on generalized least squares to account for spatial autocorrelation among successional stages. The SEM model with smallest AIC score and model chi-square p-value > 0.05 (Hoyle, 2012; Lefcheck, 2016) was selected as best fitted model (minimal adequate model). We found that, at both of our study sites, SEM models with an exponential correlation structure has lowest AIC score and highest model chi-square p-value. We started with a full hypothetical model (see Figure 1 for SEM conceptual framework), and then simplified the model by removing insignificant predictors. For instance, we did not detect any significant relationship between AGB and SOC_{stock}; therefore, AGB was excluded from further analyses. All of the statistical analyses were implemented using R version 4.1 (R Core Team, 2022).

3 | RESULTS

3.1 | Plant diversity and soil organic carbon stocks, and soil properties during forest succession

Our results showed that species diversity and functional diversity increase as forest age increases, but only SD and FD (FRic of Mbeng, and FEve of both study sites) of young successional stage were significantly different from the older successional series (Figures 2 and 3). In contrast, SOC_{stock} was lower in the older forest successional series, although mean SOC_{stock} of early-mid and-late successional stages did not differ significantly from one another (Figure 2). Our SEM model showed that, soil pH was negatively associated with forest succession (Figure 4).

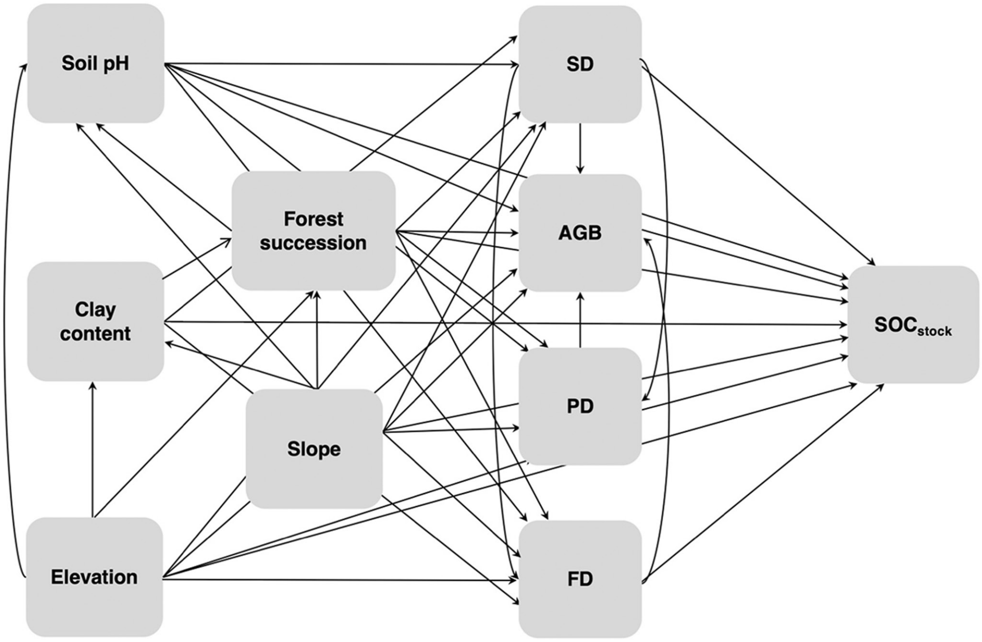

FIGURE 1 Conceptual model for structural equation modelling (SEM). We used this conceptual SEM model to quantify the effects of plant biodiversity, environmental factors and forest succession on soil organic carbon storage (SOC_{stock}). SD, species diversity; AGB, above-ground biomass; PD, phylogenetic diversity; FD, functional diversity.

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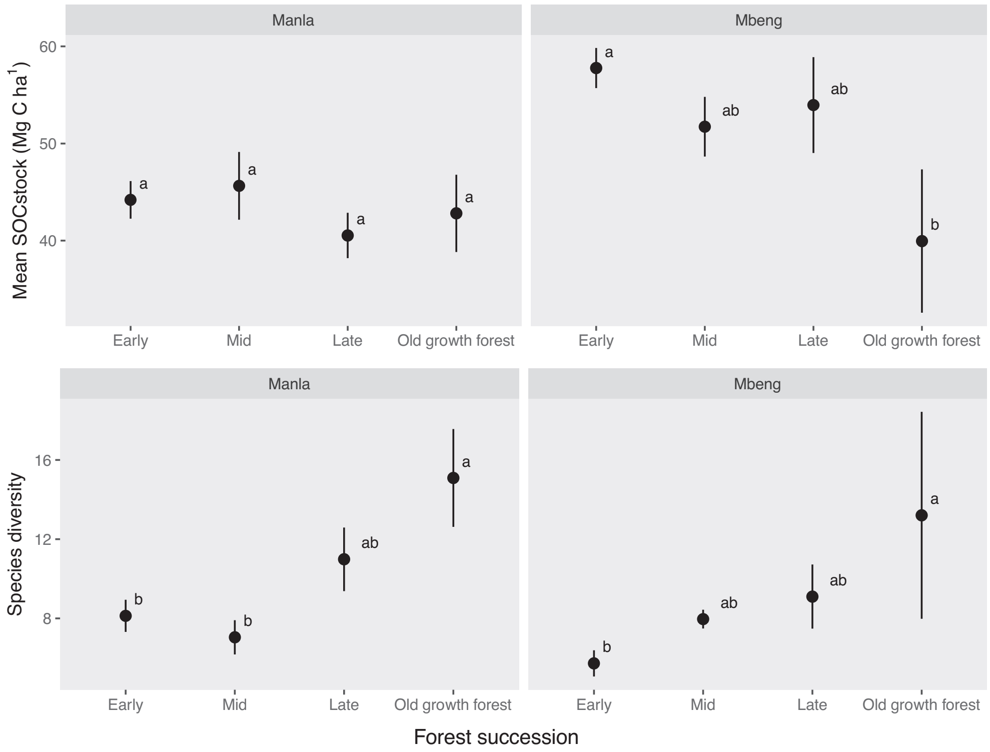

FIGURE 2 Mean soil organic carbon stock (SOC_{stock}) and species diversity (SD) of each successional stage used in this study. Different letters indicate significant differences (at the $p=0.05$ level) detected based on one-way ANOVA and post-hoc Tukey tests.

3.2 | Relationship between plant diversity, above-ground biomass, forest succession and soil organic carbon stocks

At both of our study sites, our SEM models detected consistent significant positive direct effects of functional diversity (FRic and FEve) and negative direct effects of species diversity on SOC_{stock}, as well as indirect positive effects of species diversity on SOC_{stock} via functional diversity (Figure 4). Forest succession had a positive indirect effect on SOC_{stock} via species diversity and functional diversity (Figures 3 and 4). Contrary to our hypotheses, our SEM models did not detect any consistent direct or indirect effects of above-ground biomass and phylogenetic diversity on SOC_{stock} (Figure 4).

3.3 | Relationship between soil properties, environmental gradients and soil organic carbon stocks

Considering the effects of soil properties (soil pH and clay content), elevation and slope on SOC_{stock} across the successional trajectory. At the Manla site our SEM models detected a positive direct effect elevation on SOC_{stock}; and negative direct and indirect effect of clay content on SOC_{stock} via species diversity. Soil pH was not directly associated with SOC_{stock}; but negatively associated with elevation and forest succession (Figure 4). At the Mbeng site, we detected a negative direct effect and negative indirect effect of elevation via soil pH on SOC_{stock}; and a positive indirect effect of slope via functional diversity. SEM further revealed a consistent negative direct effect of soil pH on SOC_{stock} (Figure 4).

4 | DISCUSSION

4.1 | Soil organic carbon stock and forest succession

After lands were abandoned from swidden agriculture at our sites SOC_{stock} was higher in the younger forest and lower in the older forest successional series (Figure 2). We cannot explain with certainty why SOC_{stock} at our sites was lower in the older forests, although our results indicated that soil in the later successional stages initially contains lower clay content (Table S1-Mbeng site), therefore stores lower amount of SOC (Paz et al., 2016). The initial differences of soil quality may influence farmers' land use decision and leads to a bias of the space-for-time approach used in our study (a negative trend of SOC_{stock} across forest successional gradients). However, recent studies have suggested that soil fertility recovers to 90% of old-growth forest values within 10 years of land abandonment from agriculture activities (Poorter et al., 2021), and the highest rate of soil carbon sequestration occurs during the first 15 years (Bautista-Cruz & del Castillo, 2005). Scientists hypothesized that SOC_{stock} increases with forest age (Powers & Marín-Spiotta, 2017), but evidence from field studies on shifting cultivation systems varies and includes

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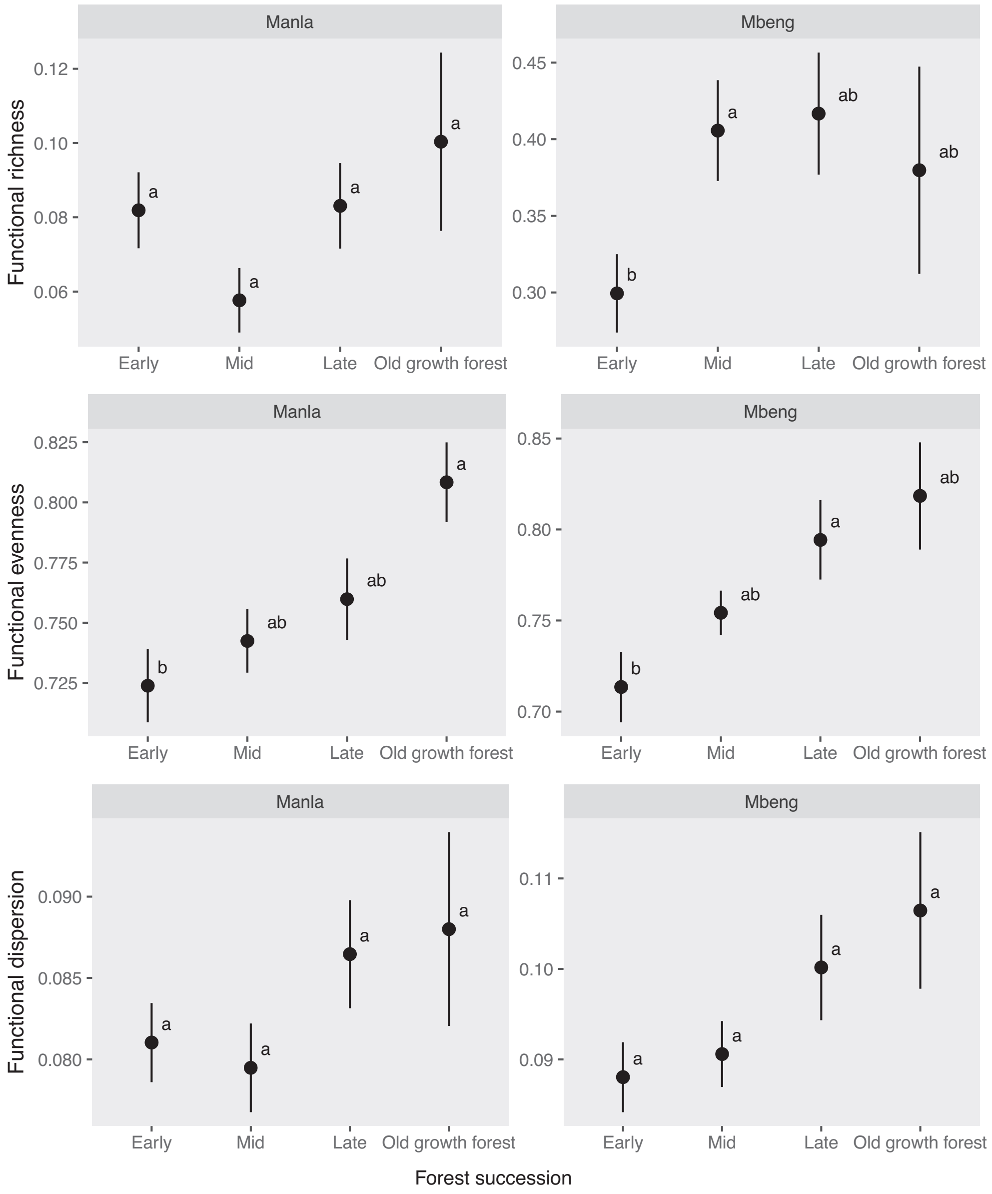

FIGURE 3 Mean functional diversity of each successional stage used in this study. Different letters indicate significant differences (at the $p = 0.05$ level) detected based on one-way ANOVA and post-hoc Tukey tests.

no-change (Bruun et al., 2021), gain (Gogoi et al., 2020) and loss (Sugihara et al., 2019) or fluctuation with fallow age (Chan et al., 2016; Mukul et al., 2022), but SOC tends to recover rapidly during the first 2 years of a fallow period (Lungmuana et al., 2017). Our models did not detect significant direct effects of forest succession on SOC$_{\text{stock}}$ (Figure 4). This result is in line with Eaton and Lawrence (2009), who found that after land was abandoned from decades of shifting cultivation, forest age did not significantly predict soil carbon stock, but was a key factor in predicting above-ground biomass. At global scale, SOC$_{\text{stock}}$ increases with forest age (Laganière et al., 2010), but varies with afforestation types (Berthrong et al., 2009). A global meta-analysis on soil carbon storage during tropical forest succession found a weak positive relationship between forest age and soil carbon stock, but with a lot of local variation in outcomes (Marín-Spiotta & Sharma, 2013). We further investigated a potential source of the error behind space-for-time substitution that could potentially lead to the negative relationship between SOC$_{\text{stock}}$ and forest age detected in this study (Walker et al., 2010). Our results showed that forest succession was not significantly associated with environmental factors (elevation, slope and soil texture; Figure 4 and Table S5). However, slope and topsoil and subsoil sand content of early successional stage were significantly lower than older successional series at both of our study sites (Figure S4 and S5), but we did not detect significant differences of elevation among successional stages (Figure S4). These results suggest that farmers are likely to reuse the sites with better soil (lower sand content and higher SOC) on the gentle slope for agriculture purposes and preferentially abandon inherently poorer soil (higher sand content and lower SOC) on the steeper slope regardless its elevation. As a consequence, SOC$_{\text{stock}}$ is higher in the younger forest with low species diversity, but lower in

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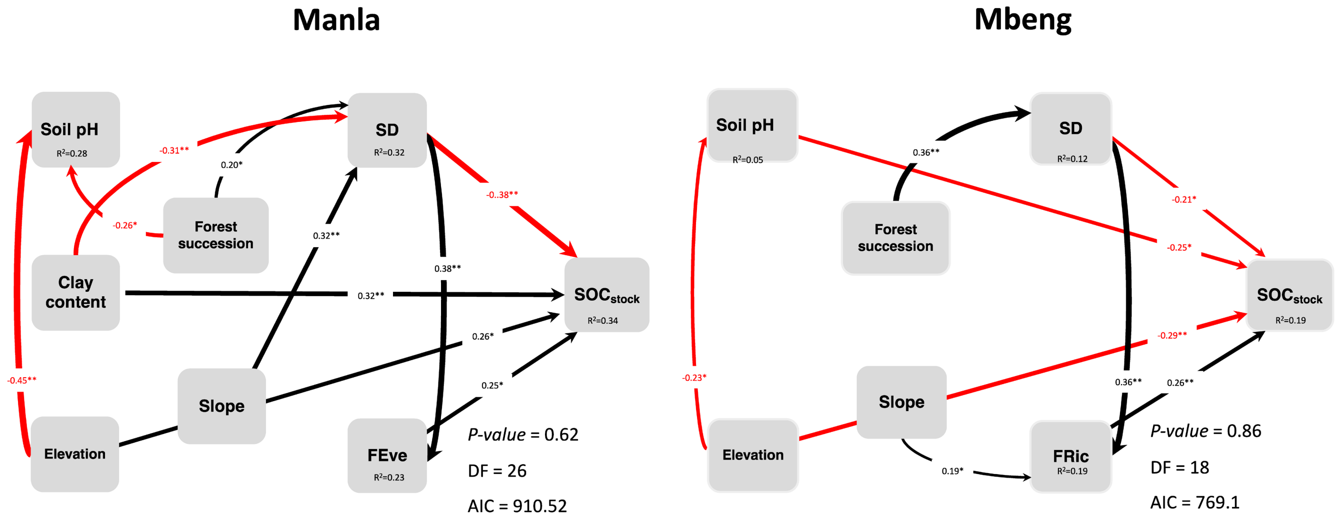

FIGURE 4 Structural equation modelling paths and standardized regression coefficients (ß) of soil organic carbon stocks (SOC_{stock}) of each study site. SD, species diversity; FEve, functional evenness; FRic, functional richness. *p*-value, model chi-square probability. *df*, degree of freedom. $^{**}p < 0.01$, $^{*}p < 0.05$. Black arrows = significant positive paths, red arrows = significant negative paths. Non-significant direct effect predictors and non-significant paths were excluded from the model. The thickness of the arrow denotes the strength of the correlation.

the older forest with higher species diversity, and potentially leads to an apparent negative relationship between SOC_{stock} and forest age and species diversity detected in this study.

4.2 | Effects of plant biodiversity and above-ground biomass on soil organic carbon stocks

In this study, functional diversity was calculated based on community trait-dissimilarity, and our results suggest that functional dissimilarity consistently promoted SOC sequestration throughout forest succession. These results corroborate previous work revealing that plant traits reflect resource use complementarity among coexisting species and their effects on ecosystem functions (Bu et al., 2019). Functional diversity may drive patterns of ecosystem processes, such as SOC sequestration, but a mechanistic understanding of the underlying processes depends on the specific traits used to quantify functional diversity. The plant traits included in this study represent key plant economic spectra (leaf and wood economic spectra; Chave et al., 2009; Wright et al., 2004) that underpin resource use strategies, nutrient uptake, carbon turnover, and plant life history strategies. These traits also represent response (e.g. response to climates, soil resources, disturbance and water balance) and effect traits (e.g. effects on biogeochemical cycles) enabling us to address the interaction between plant traits and soil biota (De Deyn et al., 2008). For example, previous studies have shown that functional diversity increases soil carbon storage by increasing soil carbon and nitrogen inputs (e.g. root biomass, leaf carbon and nitrogen) through plant functional complementarity (Lohbeck et al., 2018). Our results highlight a temporal/spatial dimension to these trait-soil interactions by revealing that trait complementarity increases SOC_{stock} across successional trajectories. This suggests that at our study sites, plots with higher functional diversity contain both long-lived species with conservative leaf and wood economic spectra (i.e. slow-turnover; low SLA, high WD), as well as short-lived species with acquisitive leaf and wood economic spectra (i.e. fast-turnover; high SLA, low WD). On the other hand, plots with lower functional diversity may have less variation in leaf types (e.g. only conservative or only acquisitive traits), leading to lower variation of inputs to the leaf litter. In successional theory, species with acquisitive traits are often found to dominate early in forest succession as they exploit high resource availability, but later successional stages are often dominated by species with conservative traits (Lohbeck et al., 2013).

Interestingly, our results indicated that species diversity was negatively associated with SOC_{stock}. But species diversity indirectly increased SOC_{stock} by increasing functional trait diversity with a strong support of forest succession (Figure 4). This surprising result contrasts with previous research showing that plant diversity typically increases soil carbon storage via positive effects on microbial growth/activities and root carbon inputs, and therefore increases soil carbon storage (Augusto & Boča, 2022; Chen et al., 2018; Lange et al., 2015); nonetheless, plant diversity showed much less influence on decomposition rate of the existing carbon (Lange et al., 2015). Increases in microbial growth and activity, and higher carbon inputs to soil can stimulate the loss of existing carbon by enhancing decomposition via priming (Kuzyakov et al., 2000). Although we cannot say for sure what drives a direct negative relationship between species diversity and soil carbon storage at our sites, this relationship may be caused by a possible error behind space-for-time substitution approach used in our study as described above, or it may be driven by other factors during the successional processes. For example, it may be a proxy for species competition. Species competition plays an important role in shaping plant community assembly (Aerts, 1999; Satdichanh et al., 2019), influencing plant biomass allocation and

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soil nutrient dynamics (Hartmann et al., 2020). In successional theory, abiotic filtering influences plant community assembly early in succession leading to communities dominated by pioneer species, with lower species diversity and interspecific competition. Fast-growing plant species often invest carbon in roots to recruit beneficial microbial species that can facilitate their growth strategies, and in leaves to maximize resource acquisition (Hartmann et al., 2020). They thus positively influence soil carbon sequestration. In contrast, species competition (competitive exclusion) plays a more important role later in succession resulting in higher species diversity and communities dominated by slow-growing species. However, these species invest carbon mostly in stem growth with weaker cascading impacts on soil carbon sequestration (Aerts, 1999; Chazdon, 2014). Our previous studies confirmed a shift from abiotic to biotic filtering during forest succession at both of our study sites (Satdichanh et al., 2019).

Furthermore, after controlling for diversity, we detected no significant relationship between above-ground biomass (AGB) and SOC_{stock} at both of our study sites (Figure 4). Although above-ground productivity is commonly found to enhance soil carbon (Lohbeck et al., 2018), other studies have reported that higher above-ground productivity may not always result in higher SOC_{stock}. For instance, de la Cruz-Amo et al. (2020) reported that lower altitudes, which have warmer temperatures, promote nutrient cycling and plant growth resulting in higher AGB but low SOC_{stock}. We found that functional trait complementarity plays an important role in soil organic carbon sequestration during forest succession at our sites. The positive relationship between functional trait diversity and soil organic carbon storage detected in this study was strongly supported by positive effects of species diversity and forest succession on functional diversity (Figure 4).

4.3 | Effect of environmental factors on soil organic carbon stocks

Our results showed that, at Mbeng site SOC_{stock} decreased as soil pH increases and soil pH decreases as forest age increases at Manla site. In this study, median soil pH was 4.91 at Manla and 4.93 at Mbeng, suggestive of possible depletion in microbial growth and decomposition rates, thus enhancing soil carbon sequestration. A recent study suggested that land use intensification can cause changes in soil pH, and higher soil pH (>6.2) increases decomposition rates driving declines in soil carbon (Malik et al., 2018). Soil organic matter (SOM) stabilization mechanisms are strongly influenced by soil pH (Rasmussen et al., 2018). In acidic soil systems, SOM stabilization is associated with Al and Fe (Rasmussen et al., 2018), in spite of that our results indicated that clay content played an important role in increasing SOC sequestrate on at one of our study sites (Figure 4). Surprisingly, we detected indirect positive effects of slope via species diversity (Manla) and functional diversity (Mbeng) on SOC_{stock} (Figure 4). This suggests that, forest on the steeper slope with lower human disturbance could maintains species diversity and functional diversity that aid SOC accumulation.

Interestingly, we observed both positive (Manla) and negative relationships (Mbeng) between elevation and SOC_{stock} (Figure 4). As we discussed above, our results suggested that elevation was not a main factor affecting farmers' land use decisions. Furthermore, we investigated whether soil thickness (depth to bedrock) at our study sites vary with elevation and influence SOC_{stock} across elevational gradients. Our results showed that soil thickness at Mbeng significantly decreased as elevation increased (Figure S6) and SOC_{stock} was positively significantly associated with soil thickness (Figure S7). In contrast, we did not find a significant relationship between soil thickness and elevation and SOC_{stock} at Manla (Figures S6 and S7). These suggest that the contrary relationship between SOC_{stock} and elevation detected in this study may be driven by soil thickness. On the other hand, during the dry season, forests at higher elevation at the Manla site often receive heavy fog from November to April (average ~ 150 days/year) that account for ~50% of the total water input beneath the forest canopy during the dry season (Cao et al., 2006). In contrast, forests at higher elevation at the Mbeng site are much drier and receive heavy fog only from December to February. The higher amount of water deposition from fog during dry season at the Manla site may play an important role in maintaining soil moisture, alleviating plant water stress and influence plant–soil feedback and soil carbon cycling (Berrones et al., 2022; Cao et al., 2006; Chung et al., 2017). Our results suggest that soil properties, soil thickness and elevation gradients (as a proxy of water availability and temperature) and slope are important environmental factors affecting SOC_{stock} during tropical forest succession. At the global scale, SOC turnover may be more closely related to soil properties than climatic conditions (temperature and precipitation; Luo et al., 2019), but the vertical distribution of SOC is associated with root distribution (Jobbágy & Jackson, 2000).

5 | CONCLUSIONS

Current global soil datasets are largely inconclusive of what drives SOC sequestration processes in tropical and subtropical regions (Augusto & Boča, 2022; Georgiou et al., 2022; Rasmussen et al., 2018). This study helps to clarify the relationships among different components of plant biodiversity, environmental factors and soil carbon stocks across natural tropical forest succession, particularly after land abandonment from swidden agriculture. Our findings demonstrate that plant functional trait diversity (with a strong support of species diversity and forest succession) not phylogenetic diversity plays an important role in increasing soil organic carbon sequestration during tropical forest succession. Plant trait composition is directly associated with carbon input and output from plants to soil and reflects the resource-use complementary within plant communities and its effect on biogeochemical cycles. Moreover, the significant link between functional diversity and SOC persisted throughout succession, despite underlying complexities in patterns of species richness and phylogenetic diversity. Contrary with our hypothesis, after controlling for diversity we found no relationship between above-ground biomass and soil organic carbon stock at

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both of our study sites. We suggest that, in the mosaic landscape of tropical region, a trait-based approach in restoration and afforestation management practices should be considered. Promoting higher plant trait diversity by combining long-lived and short-lived species (conservative and acquisitive traits) during planting and management may enhance carbon storage in soils for climate change mitigation and adaptation efforts, and for regaining healthy soils to promote forest landscape restoration.

AUTHOR CONTRIBUTIONS

Manichanh Satdichanh conducted fieldwork, collected plant and soil samples, performed plant identification for Mbeng site, conceived the ideas, analysis and led the writing of the manuscript. Manichanh Satdichanh and Gbadamassi G. O. Dossa processed soil samples. Gbadamassi G. O. Dossa and Kai Yan prepared soil samples and carried out the soil mid infrared spectroscopy analysis. Rhett D. Harrison and Manichanh Satdichanh conceived the study and collaborated on the analysis, and development of the manuscript. All authors contributed to the revision and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests. Kyle Tomlinson is an Associate Editor for *Journal of Ecology*, but took no part in the peer review or decision-making process for this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study can be downloaded from the DRYAD Repository at https://doi.org/10.5061/dryad.rn8pk0ph5 (Satdichanh et al., 2023). Plant abundance data can be downloaded at https://doi.org/10.5061/dryad.6ns42cq (Satdichanh et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Satdichanh et al. 2022-Supplementary materials A_traits levels and refenrences.

Table S1. Summary of forest successional stage characteristics. Mean values of elevation, slope, soil pH and clay content at 0–50 cm soil depth of each successional stage. Different letters indicate significant differences (at the $p = 0.05$ level) detected based on one-way ANOVA and post-hoc Tukey tests.

Table S2. Results of the soil spectroscopy calibration models.

Table S3. Number of species and percentage abundance coverage for each plant trait obtained for this study at species-and genus-level.

Table S4. Summary ecological significance of plant traits used in this study.

Table S5. Results of Pearson's Chi-square Test between forest succession and elevation, slope and soil texture.

Figure S1. Map of the study sites. Each study site is a 10 × 10 km (10,000 ha) consists of 160 plots and 640 subplots. Each plot consists of four 100 m^2 circular subplots that represent a 1000 m^2 (0.1 ha) area. Subplot 1 is placed at the centre of the plot, while subplot 2 is always placed downslope, and subplot 3 and 4 positioned 120 and 240 degrees from downslope point respectively (sampling plot layout). The centers of subplots 2,3 and 4 are 12.2 m horizontal distance from the centre of subplot 1.

Figure S2. Summary of soil properties used in this study.

Figure S3. Predicted vs observed of soil organic carbon content of both study sites.

Figure S4. Elevation and slope mean values of each successional stage. Different letters indicate significant differences (at the $p = 0.05$ level) detected based on one-way ANOVA and post-hoc Tukey tests.

Figure S5. Mean value of topsoil and subsoil sand content of each successional stage. Different letters indicate significant differences (at the $p = 0.05$ level) detected based on one-way ANOVA and post-hoc Tukey tests.

Figure S6. Relationship between soil thickness (depth to bedrock) and elevation.

Figure S7. Relationship between soil thickness (depth to bedrock) and SOCstock.

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