Understory vegetation management regulates soil carbon and nitrogen storage in rubber plantations

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Abstract Effective management of understory vegetation is crucial for forest biodiversity conservation and ecosystem functions. However, the impact of various understory management practices on key ecosystem processes, such as soil nutrient cycling in tree crop plantations, remains poorly understood. This study quantified the 7-year cumulative effects on soil organic carbon (SOC) and total nitrogen (STN) stocks in rubber plantations under four understory management practices: (i) conventional management (RC) as the control, (ii) herbicide application (RH), (iii) natural regeneration (RN), and (iv) replacement with leguminous shrub (RA). Compared to RC, RN and RA increased the average number of native and invasive species and produced high above- and belowground biomass. Conversely, RH decreased the species number and belowground biomass. More SOC and STN were stored in 0.0–0.2 m topsoil in both RN ($+9.6$ Mg C ha^{-1}; $+0.7$ Mg N ha^{-1}) and RA ($+10.7$ Mg C ha^{-1}; $+0.6$ Mg N ha^{-1}) than RC, while they remained stable in RN but declined in RA from deeper layers of 0.2–1.0 m. Across the entire 1 m soil profile, the annual increment of SOC stocks in RN and RA reached 1.7 and 1.0 Mg C ha^{-1} yr^{-1}, respectively, and of STN stocks reached 0.02 and -0.14 Mg N ha^{-1} yr^{-1}. However, RH decreased SOC and STN stocks and corresponding annual increments for the entire profile. The variations in SOC

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and STN stocks in the topsoil were attributed primarily to aboveground biomass and determined by belowground biomass in the deeper soil. Moreover, litter depth also effectively reflected SOC and STN dynamics. These results suggest that the implementation of natural regeneration and agroforestry system in the understory of rubber plantations offers significant potential for increasing soil C and N stocks. Our findings imply that sustainable understory management practices, especially natural regeneration and agroforestry system, will benefit for understory plants conservation and soil nutrient supply in tree crop plantations.

Introduction

Soils play a crucial role as the primary habitats of life activities in forest ecosystems, providing essential nutrients for plant growth, development, and regeneration. They also have a significant impact on greenhouse gases emissions, such as CO_2, CH_4, and N_2O, which can affect terrestrial carbon (C) and nitrogen (N) cycles and contribute to climate change (Le Quéré et al. 2016). Forest soils account for approximately 44% and 85% of global forest C and N stocks, respectively, which are estimated to be 383 Pg C and 95 Pg N in soil up to 1 m depth (Pan et al. 2011; Post et al. 1985). Soil organic C (SOC) and total N (STN) are critical indicators for assessing soil quality, as they play a significant role in determining long-term C and N budgets (Wang et al. 2021). Anthropogenic management and land use changes can directly or indirectly influence the spatial–temporal variability of SOC and STN, which are important factors in regulating the stability and multifunctionality of forest ecosystems (Maris et al. 2021; Liu et al. 2021b; Zhang et al. 2021). Assessment of the stocks of C and N in forest soils is critical for mitigating climate change and promoting forest conservation and management. Despite this, few studies have attempted to determine soil C and N storage in response to changes in understory vegetation (especially in tree crop plantations), and the potential drivers involved in this process.

Understory vegetation is a vital stratum of forest ecosystems, consisting of seedlings (<1.5 m tall), shrubs, herbs, lianas, epiphytes, and cryptogamic plants like bryophytes and lichens. It plays an indispensable role in forest ecosystem functions and services (Deng et al. 2023; Jin et al. 2022). Management practices for understory vegetation, including mechanical or manual removal, herbicide use, or a combination of both (Ashton-Butt et al. 2018; Zhou et al. 2018), replacement with non-tree species (i.e., establishment of agroforestry systems) (Feliciano et al. 2018; Ma et al. 2020; Liu et al. 2021a), and natural regeneration (Dong et al. 2022; Ming et al. 2019), are common and effective silvicultural strategies for sustainable forestry development. Understory practices can reduce or increase above- and/ or belowground competitive ability in interspecific interactions involving light, soil water, and nutrients between understory vegetation and overstory trees and alter the allocation of limited resources to target trees, which can ultimately influence stand productivity and yield. The effects of these practices on soil C and N accumulation and their fractions availability vary from positive (De Stefano and Jacobson 2018; Liu et al. 2018b), neutral (Li et al. 2019; Wang et al. 2014; Xiong et al. 2008), to negative (Rifai et al. 2010; Yang et al. 2018; Zhang et al. 2014), depending largely on factors such as understory species composition, litter input quantity and quality, soil biochemical processes (e.g., microbial composition, enzyme activities, and nutrient turnover rate), and microenvironments at the stand level (Fang et al. 2021; Li et al. 2020). Furthermore, these effects differ across forest types, climates, and experimental durations at a regional scale (Ma et al. 2020; Zhang et al. 2022b). Therefore, the evaluation of multi-purpose understory management is urgently needed to accurately predict soil C and N storage rates based on long-term observations.

Rubber (*Hevea brasiliensis*) is a typical tropical tree crop that provides various raw materials for industrial products (Liu et al. 2017). The rubber planting area in Xishuangbanna of Southwestern China is estimated to be 0.298 million ha in 2021, accounting for approximately 25.7% of all rubber plantations in China and 2.6% globally. Its expansion rate is expected to quadruple by 2050 owing to the growing worldwide demand for natural rubber (Liu et al. 2021b). Since the 1950s, the majority of large-scale

monoculture rubber plantations in this region have expanded rapidly at the expense of tropical rainforests (Lin et al. 2023), resulting in biodiversity loss, soil erosion, and other environmental problems (Liu et al. 2019). Furthermore, the cutover of rubber plantations and their replacement by other cash crops due to the falling latex price and intensive application of fertilizers and herbicides exacerbate environmental degradation (Liu et al. 2018a). As a result, it is vital to improve the ecological function of monoculture rubber utilizing diverse strategies that do not reduce latex yield, such as rubber-based agroforestry (i.e., understory intercropping) and near-natural management practices (i.e., understory regeneration) (Langenberger et al. 2017; Warren-Thomas et al. 2020).

In general, soil nutrients are enhanced in different rubber-based agroforestry systems relative to monoculture counterparts due to increased litter and root inputs, as well as improved physicochemical properties and microbial activity that regulate nutrient cycling (Chen et al. 2019; Krashevska et al. 2015; Langenberger et al. 2017; Li et al. 2020; Liu et al. 2018b), although understory species diversity may be reduced by perennial-shrub intercropping (Liu et al. 2021a). However, the impacts on soil C and N storage from continuous herbicide application and natural regeneration of rubber understory vegetation, which may represent less or more diversity of understory species, has not been adequately explored (Zeng et al. 2021). Our study aimed to investigate the effects of seven years of understory vegetation management on SOC and STN storage in tropical rubber plantations in Southwest China. To achieve this, we determined the characteristics of understory vegetation and litter, soil C and N concentrations, and bulk density across a 1 m profile. We hypothesized that: i) more understory species would appear as natural regeneration of rubber plantations without human interference; ii) natural regeneration of understory vegetation and agroforestry practices in rubber plantations would improve soil C and N stocks, especially in the topsoil, owing to the thriving understory plant community; iii) understory vegetation biomass is a major driver determining soil C and N stocks, with aboveground biomass primarily contributing to the topsoil and root biomass to the deeper soil.

Materials and methods

Study area

The study area was located in the experimental zone of the Nabanhe National Nature Reserve (NNNR) in Xishuangbanna, Yunnan province, China (22°04'–22°17' N, 100°32'–100°44' E). It covers an area of 21,100 ha surrounded by sloping hills, with altitudes ranging from 539 to 2304 m above sea level. The climate is characterized by a subtropical monsoon, with a dry season from November to April and a rainy season from May to October. Based on long-term meteorological observations for NNNR, the annual mean temperature is between 18–22 °C, and the annual mean rainfall ranges from 1100 to 1600 mm, depending on elevation. However, approximately 81%–95% of the rainfall occurs in the rainy season. Natural forests cover more than 67% of the protected area. Agricultural land use systems in the NNNR include perennial systems, such as rubber and banana plantations, paddy rice fields, and other annual crops. The soil type is typical tropical rainforest Latosol (acidic red soil) with a pH value of approximately 5.0.

Experimental design

Rubber monoculture plantations established by replacing semi-natural tropical montane rainforests at an altitude of approximately 700 m were chosen for this study. The rubber plantation in the experimental area was planted in June 1997 with a 2.5 m × 8.0 m planting size using the GT1 rubber strain. In 2015, four understory management practices were initiated in these rubber planting areas: i) conventional management (RC; considered as the control): understory vegetation in the interrow of rubber trees was cut manually three times a year (May, August, and November) and kept in situ; ii) spraying herbicide (RH): herbicide was applied broadcast to suppress the growth of understory plants at May, August, and November, and then the plants were left in situ field until they dried out and died; iii) natural regeneration of understory species (RN): understory species in the interrow of rubber trees were not cut and allowed to grow naturally to achieve a near natural state; iv) rubber-based agroforestry systems (RA): an N-fixing species-*Flemingia macrophylla* was planted in each

rubber interrow with four rows at 1 m×1 m specification (Fig. S1). At each of the management sites, three 25 m×25 m plots were established with nearly a 100 m spacing buffer. Furthermore, we established six 5 m×5 m shrub quadrants in each plot, and one 1 m×1 m herb subquadrant in the upper right corner of each shrub quadrant. The initial average physicochemical properties of the 0.2 m topsoil were as follows: total C 22.5 g kg^{-1}; total N 1.9 g kg^{-1}; bulk density 1.1 Mg m^{-3}; pH 5.5; total P 0.5 g kg^{-1}; available P 0.5 mg kg^{-1}; total K 3.2 g kg^{-1}; available K 50.1 mg kg^{-1}.

Understory vegetation investigation

Understory vegetation investigation was initiated on May 2022 before treatment. We recorded the name, abundance (individual number), percentage cover, height and basal diameter of both shrubs and grasses. The percentage cover of shrubs and grasses was evaluated by the proportion of the plant's projected area to the total area of the quadrant. In each 5 m×5 m shrub quadrant, the aboveground biomass of each shrub species was estimated using the harvesting method. Five plants of average size were randomly chosen for each shrub species as representatives of the entire quadrant, and each individual aboveground segment was cut to estimate dry matter. In each 1 m×1 m herb subquadrant, the aboveground biomass of all the grasses, including small rubber seedlings, were harvested at 0.01 m above the ground. The belowground biomass of shrubs and grasses was obtained using a hand hoe. Litter on the soil surface was collected within each herb subquadrant after measuring the litter depth. The dry matter of all plant and litter samples were dried and weighed in an oven at 65 ℃ for 48 h.

Soil sampling and chemical analyses

The soil was sampled concurrently with the vegetation survey in each plot. Considering local variations, soil samples were obtained from three random points in each shrub quadrant from depths of 0.0–0.2 m, 0.2–0.4 m, 0.4–0.6 m, 0.6–0.8 m, and 0.8–1.0 m using a 50-mm soil auger after removing the surface litter. Soil at the same depth from the six points in

two shrub quadrants located at the upper and lower interrow of the rubber plantation was combined into a composite sample. Finally, 15 composite samples for each plot and 180 composite samples for all 12 plots were obtained. All composite samples were sieved through a 0.25-mm mesh screen after air dried at 25 ℃ to measure SOC and TN using a CN analyzer (Vario Max CN, Elementar, Germany). Moreover, soil bulk density at each horizon was measured with a steel ring and dried at 105 ℃ for 48 h.

Calculations of SOC and STN stock, annual increment, and relative change

The stocks of SOC and STN (Mg ha^{-1}) in each layer and for the whole 1 m soil profile were calculated according to Eqs. (1) and (2):

$$Stock_{SOC} = \sum_{i=1}^{n} CSOC_i \times BD_i \times D_i \times 10 \quad (1)$$

$$Stock_{STN} = \sum_{i=1}^{n} CSTN_i \times BD_i \times D_i \times 10 \quad (2)$$

where n is the number of soil layers, $CSOC_i$ and $CSTN_i$ represent the concentrations of SOC and STN (g kg^{-1}) of layer i, BD_i is the bulk density (Mg m^{-3}) of layer i, and D_i is the depth (m) of layer i, respectively.

The annual increment (R_i, Mg ha^{-1} yr.$^{-1}$) and relative change (R_c, %) in SOC and STN stocks under RH, RN, and RA compared with RC were calculated according to Eqs. (3) and (4):

$$Stock_{Ri} = \sum_{i=1}^{n} \frac{SRH_i - SRC_i}{7year} \quad (3)$$

$$Stock_{Rc} = \sum_{i=1}^{n} \frac{SRH_i - SRC_i}{SRC_i} \times 100 \quad (4)$$

where n is the number of soil layers, SRH_i and SRC_i represent the stocks of SOC and STN (Mg ha^{-1}) of layer i under RH and RC treatments, respectively. The same calculation was performed for RN and RA.

Statistical analysis

The homogeneity of variance and normality of all data were checked using Kolmogorov–Smirnov and Levene tests prior to analysis. Differences in plant

species number, coverage, above- and belowground biomass of shrubs and grasses, litter biomass and depth, and annual increment and relative change in SOC and STN stocks between the treatments were evaluated using one-way ANOVA, followed by the least significant difference (LSD) at the significance level of $\alpha = 0.05$. Differences in SOC and STN concentrations and stocks, C: N ratio, and soil bulk density were analyzed using linear mixed-effects models with fixed effects for management practice, soil depth, and their interactions and random effects for blocks. Pearson's correlation analysis was conducted to explore the relationships between plant and soil variables. Linear regression was used to analyze the relationships between SOC and STN stocks and C:N ratio. Redundancy analysis (RDA) was performed to estimate the proportion of variation solely explained by each factor that influenced SOC and STN stocks using CANOCO 5.0 software (Microcomputer Power, Ithaca, NY, USA).

Results

Understory vegetation characteristics

The average number of understory species, above- and belowground biomass and coverage of shrubs and grasses, and litter depth varied significantly among management practices ($P < 0.05$, Table 1). The average species number was larger in RN (4 shrub and 8 grass species) than in other management practices (average 3 shrub and 5 grass species), corresponding to the total species composition-that is, 63 species were observed in RN compared with other strategies that had an average of 45 species. RN and RA were dominated by shrubs such as *Desmos chinensis*, whereas RH and RC had abundant grass such as *Oplismenus undulatifolius* and *Selaginella uncinata*. Each management practice included ferns such as *Cyclosorus interruptus*. The coverage, above- and belowground biomass of shrubs and grasses were higher in RN and RA than in RH and RC, with the exception of grass coverage. The greatest litter depth was observed in RH, although there were no significant differences in litter coverage and biomass among the four management practices.

Table 1 Changes in understory vegetation by management practices

| Site	Average species number	Coverage (%)			Aboveground biomass (g m^{-2})			Belowground biomass (g m^{-2})		Litter depth (cm)
		Shrub	Grass	Litter	Shrub	Grass	Litter	Shrub	Grass	
RC	8.3±0.6b	3.4±2.0c	76.7±4.0a	89.9±1.5	7.6±1.8b	36.4±5.5b	628.6±28.4	151.1±19.4bc	136.8±19.9a	2.2±0.1c
RH	7.2±0.3b	12.8±3.9bc	41.1±4.9c	91.7±1.4	5.8±1.8b	37.5±8.4b	706.7±69.3	101.4±11.9c	72.0±16.0b	4.2±0.3a
RN	12.1±0.6a	43.1±9.7a	66.2±5.6ab	87.7±1.2	37.0±11.2a	94.2±11.6a	644.6±52.1	191.7±14.3ab	176.5±14.2a	2.1±0.2c
RA	8.7±0.5b	28.9±6.2ab	54.3±4.9bc	91.6±1.2	35.3±14.0a	71.9±8.3a	792.4±57.8	244.0±24.7a	156.2±13.9a	3.3±0.4b
F	16.105	8.056	9.837	1.925	3.568	10.408	1.892	10.951	7.803	16.648
P	<0.001	<0.001	<0.001	0.134	0.018	<0.001	0.139	<0.001	<0.001	<0.001

Values are mean ± standard error (SE). Different letters indicate significant differences among four management practices ($P < 0.05$)

RC, conventional management; RH, spraying herbicides; RN, understory natural regeneration; RA, rubber-based agroforestry system

The dominant species in RC are *Cyclosorus interruptus*, *Gynostemma pentaphyllum*, *Diplazium donianum*, *Oplismenus undulatifolius*, and *Spatholobus suberectus*; in RH are *Selaginella uncinata*, *O. undulatifolius*, *C. interruptus*, *Curculigo capitulata*, and *Commelina communis*; in RN are *Angiopteris latemarginata*, *C. interruptus*, *Desmos chinensis*, *S. suberectus*, and *Dioscorea polystachya*; in RA are *Flemingia macrophylla* (planted on purpose), *S. uncinate*, *C. interruptus*, *Aquilaria sinensis*, *D. chinensis*, and *Piper sarmentosum*

Table 2 Linear mixed-effects modeling of the effects of understory management practice, soil depth, and interactions on soil bulk density, SOC concentration, STN concentration, C:N ratio, SOC stock, and STN stock

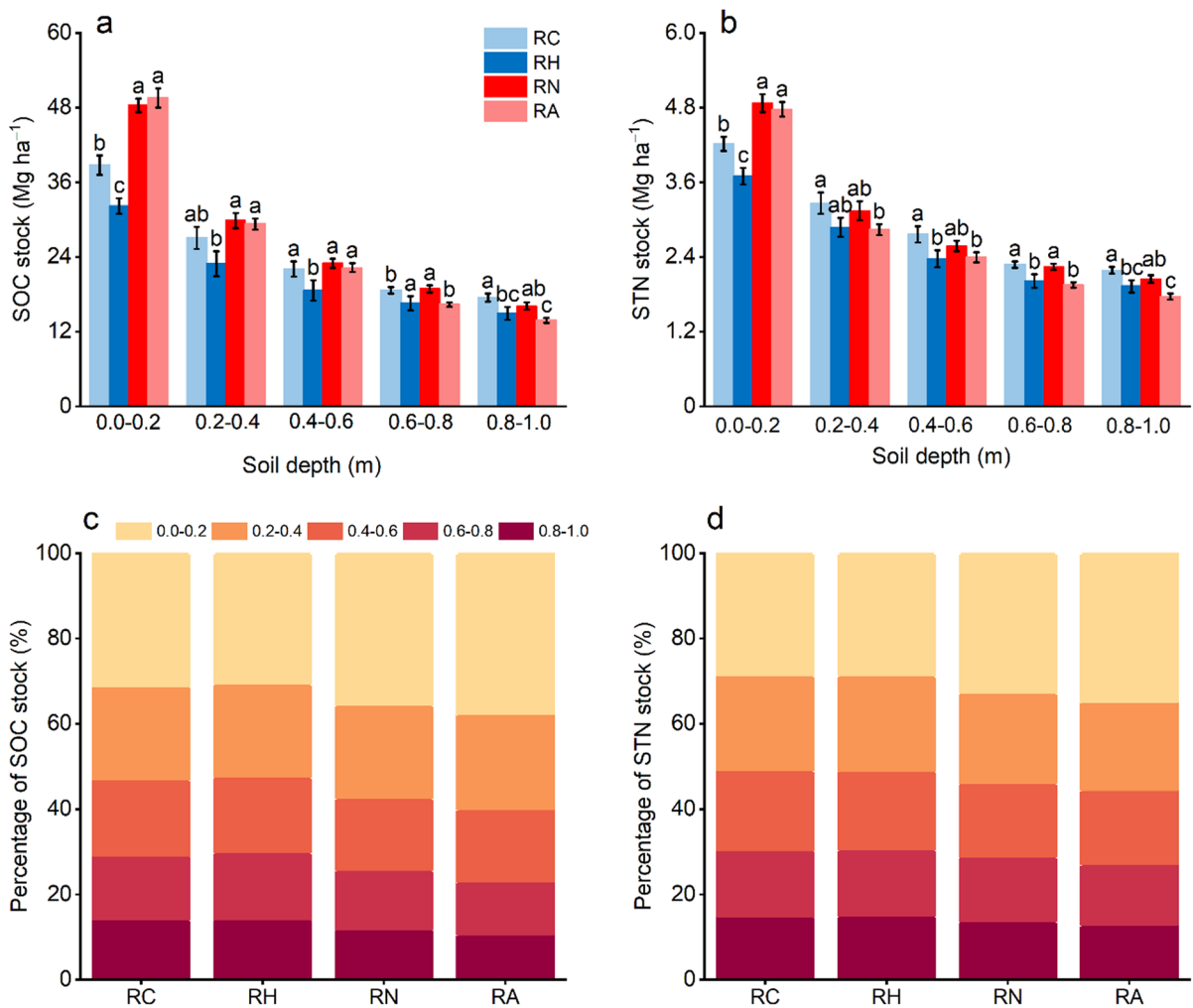| Variables	Management		Soil depth		Management × Soil depth	
	F	P	F	P	F	P
Bulk density	38.89	< 0.001	1.59	0.181	0.39	0.965
SOC concentration	50.40	< 0.001	330.52	< 0.001	11.13	< 0.001
STN concentration	30.80	< 0.001	316.02	< 0.001	7.47	< 0.001
Soil C:N ratio	27.49	< 0.001	30.59	< 0.001	4.20	< 0.001
SOC stock	28.54	< 0.001	352.82	< 0.001	9.44	< 0.001
STN stock	14.44	< 0.001	316.68	< 0.001	5.42	< 0.001
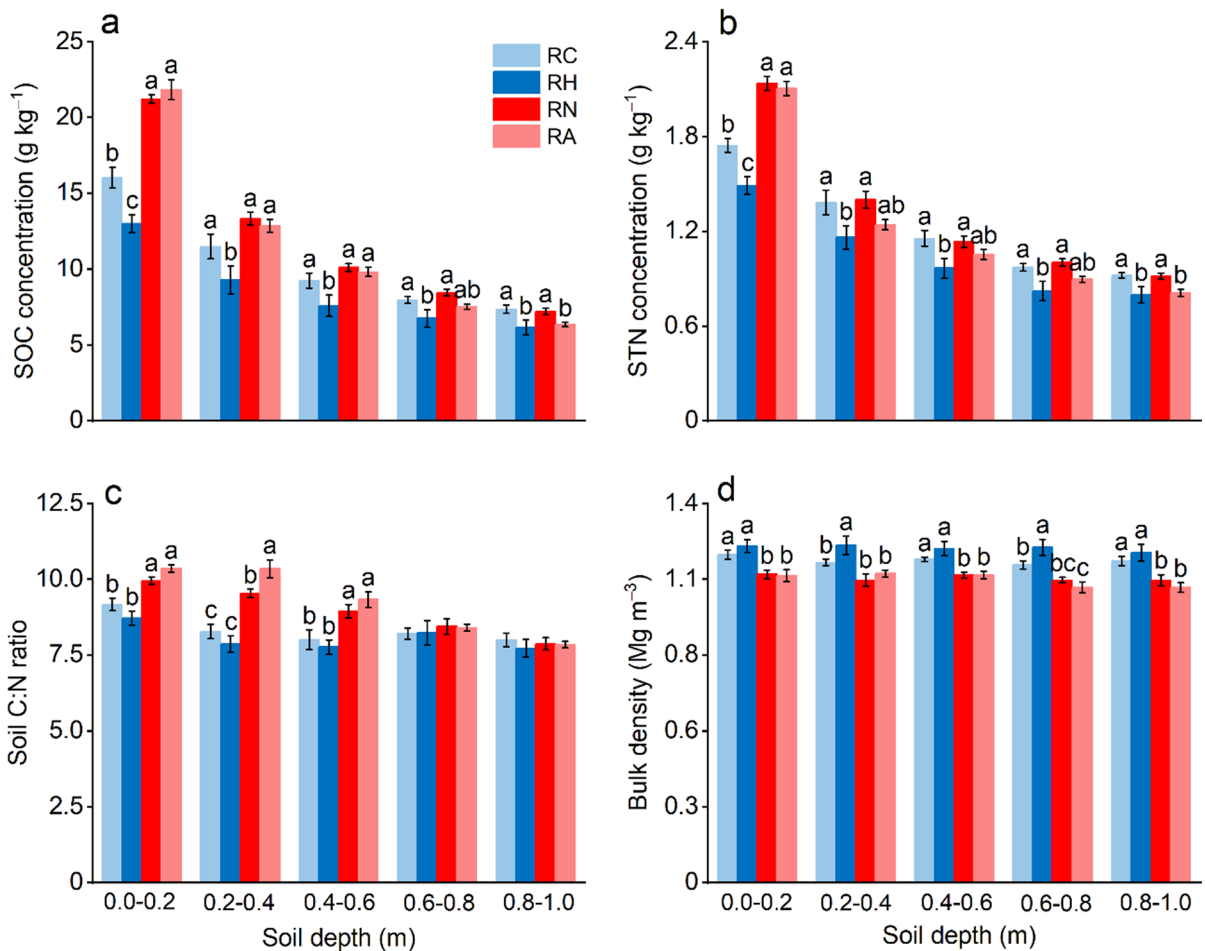
Fig. 1 Concentrations of SOC **a** and STN **b**, C:N ratio **c**, and bulk density **d** at different soil depths under four understory management practices. Different letters indicate significant differences among managements within the same soil depth ($P < 0.05$). Values are means ± SE, n = 9. SOC, soil organic carbon; STN, soil total nitrogen. RC, conventional management; RH, spraying herbicides; RN, understory natural regeneration; RA, rubber-based agroforestry system

SOC and STN concentrations and bulk density

The concentrations of SOC and STN and C:N ratio were obviously affected by management practices, soil depth, and their interaction (*P* < 0.001, Table 2). SOC concentrations were higher in RN and RA than in RC and RH at the 0.0–0.6 m soil depth, whereas they were higher in RN and RC than other management practices at the 0.6–1.0 m soil depth (Fig. 1a). Similarly, RN and RA had greater STN concentrations than RC and RH at the 0.0–0.2 m soil depth, whereas RN and RC contained greater values at the 0.2–1.0 m

soil depth (Fig. 1b). The lowest SOC and STN concentrations were observed in RH, ranging from 6.2 to 13.0 g kg⁻¹ and 0.8 to 1.5 g kg⁻¹, respectively (Fig. 1a and b). On average, RN had the greatest SOC and STN concentrations of 12.1 and 1.3 g kg⁻¹, respectively. The C:N ratios for 0.0–0.6 m soil depth was larger in RN and RA than those in other management practices, while they did not significantly change in other soil depths, ranging from 7.7 to 10.4 in the 1 m soil profile (Fig. 1c). Moreover, SOC and STN concentrations and C:N ratio decreased considerably with soil depth for all management practices, but the differences in either

Fig. 2 Stocks of SOC **a** and STN **b** and their percentage **c**, **d** at different soil depths under four understory management practices. Different letters indicate significant differences among managements within the same soil depth (*P* < 0.05).

Values are means ± SE, n = 9. SOC, soil organic carbon; STN, soil total nitrogen. RC, conventional management; RH, spraying herbicides; RN, understory natural regeneration; RA, rubber-based agroforestry system

variable were greater in topsoil than in deeper soil horizons. Soil bulk density differed significantly between management practices ($P < 0.001$, Table 2), ranging from 1.1 Mg m^{-3} in RA and RN to 1.2 Mg m^{-3} in RH (Fig. 1d). There was no significant difference in bulk density among the various soil depths.

Distributions of SOC and STN stocks

The SOC and STN stocks varied significantly among management practices, soil depth, and their interactions ($P < 0.001$, Table 2). The stocks were larger in RN and RA than in RC and RH at the 0.0–0.2 m soil depth (Fig. 2a and b). Except for SOC at the 0.2–0.6 m depth, RN and RC had higher SOC and STN stocks than other management practices at the 0.2–1.0 m soil depth. RH had the lowest SOC and STN stocks, ranging from 15.0 to 32.2 Mg C ha^{-1} and 1.9 to 3.7 Mg N ha^{-1}. For the entire soil profile, the accumulation of SOC stocks in RH, RC, RN, and RA reached 105.3, 124.1, 136.3, and 131.4 Mg C ha^{-1}, respectively, whereas STN stocks were 12.9, 14.7, 14.9, and 13.7 Mg N ha^{-1}, respectively. Their stocks also decreased obviously with increasing soil depth for each management practice, and the differences between the different management strategies gradually decreased with increasing soil depth. In all management practices, SOC and STN were mainly stored in the first 0.2 m of topsoil, accounting for 30.6%–37.7% and 28.7%–34.9% of their storage at a depth of 1 m, respectively (Fig. 2c and d). Moreover, SOC stocks at the 1 m depth were positively

correlated with STN stocks and C:N ratio across all management practices ($P < 0.001$, Fig. 3).

Annual increments and relative changes in SOC and STN stocks

We calculated the annual increments and relative changes in SOC and STN stocks for non-traditional management practices (i.e., RH, RN, and RA) relative to RC. Compared with RC, annual increments of SOC stocks in RN and RA were positive at the 0.0–0.6 m soil depth, while for STN, they were positive only in the top 0.2 m depth (Fig. 4a and b). Negative annual increments of SOC and STN stocks in RH were observable at all depths. Across the soil profile, the annual increment of SOC stocks in RN and RA reached 1.73 and 1.04 Mg C ha^{-1} yr^{-1} and that in STN stocks of RN reached 0.024 Mg N ha^{-1} yr^{-1}. The relative changes in SOC and STN stocks for non-traditional managements exhibited the same trend with annual increments (Fig. 4c and d). The relative change in SOC stocks in RN and RA was 11.3% and 6.9%, while for STN stocks in RN, it was 1.9% at the 1 m depth.

Relationships between SOC and STN stocks and understory vegetation

The SOC and STN stocks in the top 0.2 m depth were positively correlated with the average number of species (SN), shrub coverage (SC), above- and belowground biomass of both shrub (SAB and SBB) and grass (GAB and GBB), and total belowground biomass (TBB) ($P < 0.01$, Fig. S2). By contrast, SOC

Fig. 3 Linear regression relationships between SOC stocks and C:N ratios **a** and soil STN stocks **b**. SOC, soil organic carbon; STN, soil total nitrogen. RC, conventional management; RH, spraying herbicides; RN, understory natural regeneration; RA, rubber-based agroforestry system
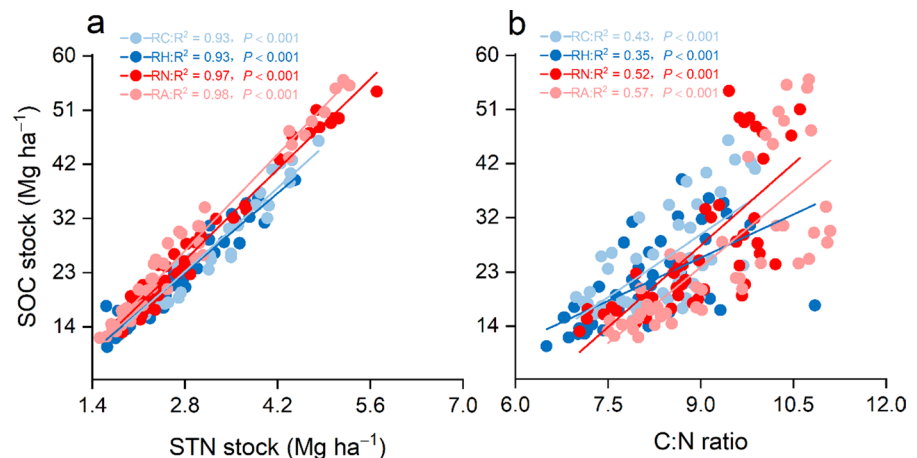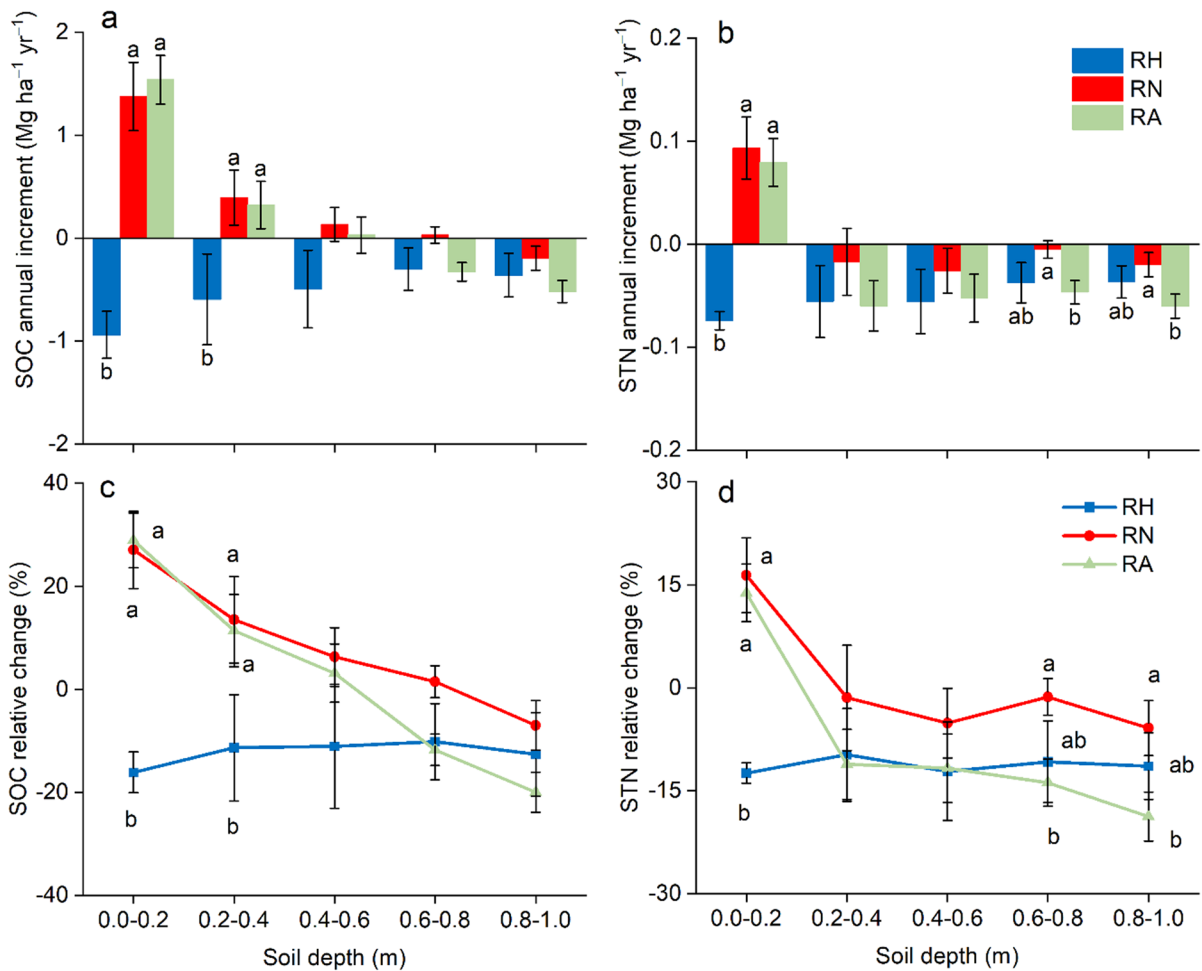
Fig. 4 Annual increment and relative change in SOC **a**, **c** and STN **b**, **d** stocks compared with conventional management (RC). Different letters indicate significant differences among managements within the same soil depth ($P < 0.05$). Values are means ± SE, n = 9. SOC, soil organic carbon; STN, soil total nitrogen. RH, spraying herbicides; RN, understory natural regeneration; RA, rubber-based agroforestry system

stocks for the entire 1 m depth were positively correlated with GBB, SBB, and TBB ($P < 0.01$), while STN stocks was positively correlated with TBB ($P < 0.05$). SOC and STN stored within 0.2 m or the entire 1 m soil profile both had a negative correlation with litter depth (LD) ($P < 0.001$). The effects of understory vegetation factors on SOC and STN stocks were assessed using RDA analysis (Fig. 5). A forward selection of the explanatory variables retained TBB and LD as significant environmental variables ($P < 0.05$). The first two component axes explained 49.3% and 5.2% of the total multivariate variation in SOC and STN stocks, respectively. Among all the understory variables, TBB explained the most

variability in SOC and STN stocks (40.2%), followed by LD (5.5%) and SAB (2.2%), and the other variables explained less than 2.0% variation.

Discussion

Understory management effects on vegetation characteristics

We found a diverse community of understory plants comprises 124 species from 50 families and 77 genera across all sites. However, the composition of understory vegetation varied with four management
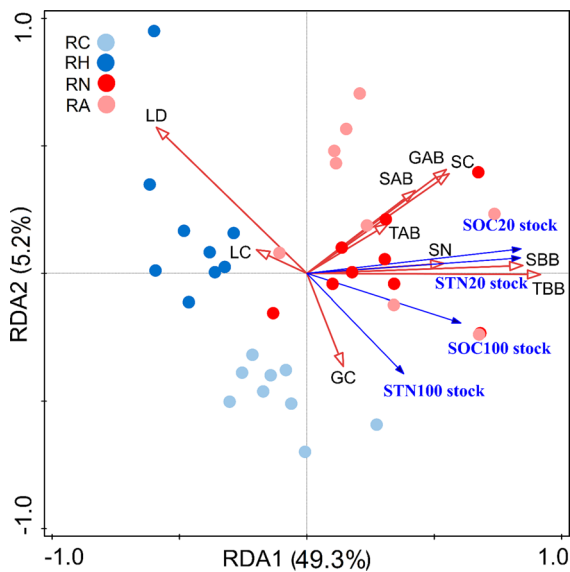
Fig. 5 RDA ordination plot of the soil C and N stocks constrained by vegetation factors. SN, average species number; LC, litter coverage; GC, grass coverage; SC, shrub coverage; LD, litter depth; SAB, shrub aboveground biomass; GAB, grass aboveground biomass; TAB, total aboveground biomass; SBB, shrub belowground biomass; TBB, total belowground biomass; SOC20 and STN20 stocks, carbon and nitrogen storage at the 0.0–0.2 m soil depth; SOC100 and STN 100 stocks, carbon and nitrogen storage at the 0.0–1.0 m soil depth. RC, conventional management; RH, spraying herbicides; RN, understory natural regeneration; RA, rubber-based agroforestry system

practices in structurally simplified rubber plantations (Table 1). Compared with RC, RN and RA exhibited a richer species assemblage, including some ferns and medicinal as well as endangered species (e.g., *Cyclosorus interruptus*, *Spatholobus suberectus*, and *Angiopteris latemarginata*). Although native and beneficial species thrived in RN and RA, invasive species such as *Chromolaena odorata* of the Asteraceae family also appeared sporadically, potentially posing a threat to native plant diversity and altering forest structure in the long term (Lan et al. 2022). However, the dense intercropping of leguminous shrubs in RA suppressed grass growth and resulted in a reduction in species numbers, which is consistent with findings reported by Liu et al. (2021a). RH, on the other hand, decreased the average number and coverage of grass, attributing to the effective inhibition of glyphosate herbicide on herbs. This result is similar to some studies (Ashton-Butt et al. 2018;

Luke et al. 2019) but inconsistent with others (Miller and Chamberlain 2008), primarily due to immediate and short-term (recover quickly after banning herbicide) or long-term (unable to recover to original level) adverse effects on the understory composition from herbicides (Zhou et al. 2018), depending on the type, frequency, and range of herbicides applied. Variation in understory species have induced substantial differences in biomass and its nutrient storage, as evidenced by higher aboveground biomass and stock in RN and RA than RC, but lower belowground values in RH (Table 1 and Fig. 6), These findings suggest that repeated broadcast herbicide application has accumulated in the soil, leading to the destruction of plant roots. While an increase in understory biomass and nutrient enrichment could benefit broader biodiversity (Ashton-Butt et al. 2018; Zhang et al. 2022b), it is important to note that ground arthropod diversity may decline due to the loss of the number of understory plant species rather than biomass in a rubber-based agroforestry system (Liu et al. 2021a). Therefore, it is critical to adopt a stand management approach that increases understory species diversity to sustain ecosystem functions.

Understory vegetation management effects on soil C and N stocks

Understory management practices strongly affected the SOC and STN storage capacity in rubber plantations (Fig. 2). Compared with RC, RN and RA increased C and N stocks in the topsoil (0.0–0.2 m) primarily by preserving more understory species and increasing new plant-derived inputs and shrub coverage (Table 1), supporting our second hypothesis. However, SOC and STN stocks from the subsoil below 0.2 m layers generally remained constant in RN but decreased in RA (with the exception of SOC at the 0.2–0.6 m depth). This likely because either nutrient from plant residues is the first to enter the topsoil or because the ground cover of leguminous shrub causes soil nutrient losses, particularly in terms of N emissions, to a certain extent (Aulakh et al. 2001; Rao et al. 2021). These findings coincide with previous studies indicating that higher plant diversity in the understory promotes SOC and STN storage in the topsoil, while specific plant functional group (i.e., deep-rooting tall species) decreases their stocks from the subsoil downward by enhancing organic matter
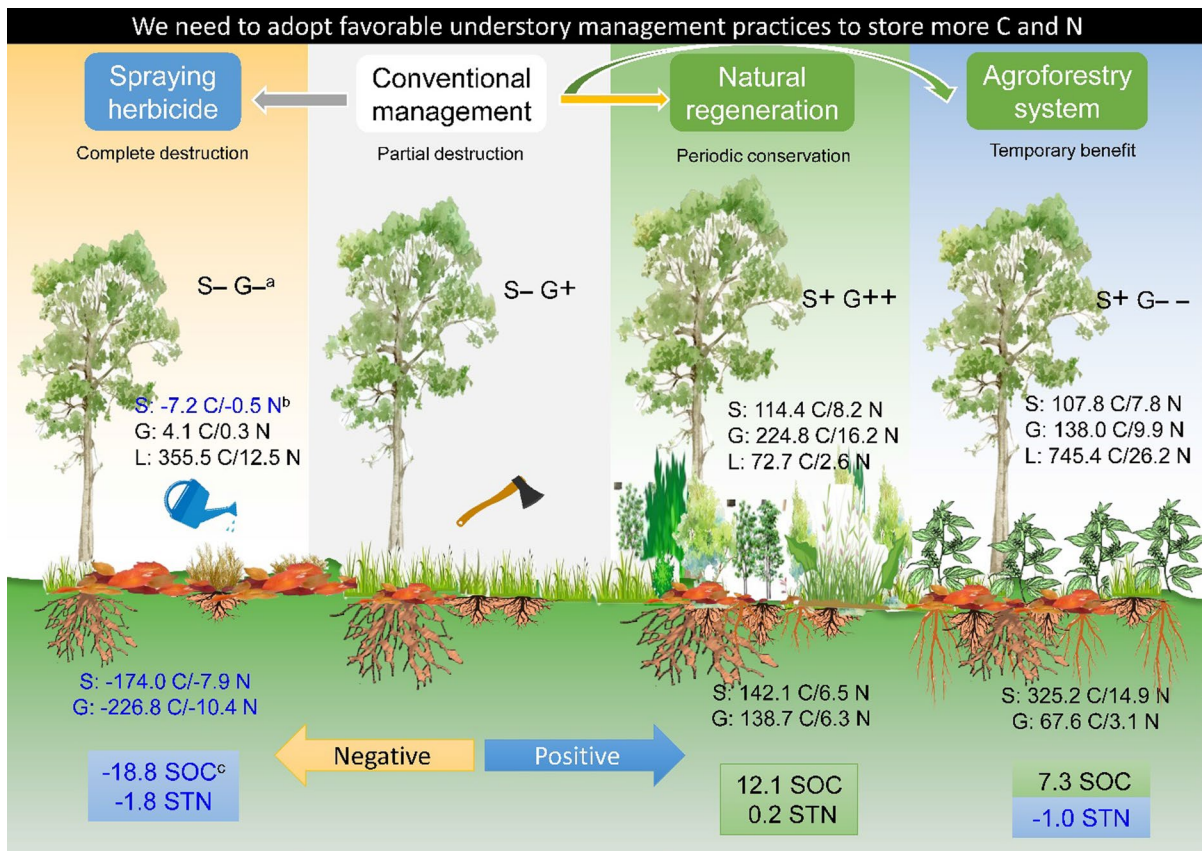
Fig. 6 Schematic diagram of three non-traditional understory management practices on vegetation characteristics and soil C and N stocks relative to conventional management in rubber plantations. Note: [a]the average number of understory species; [b]the relative increments in above- and belowground biomass C and N stocks (kg ha^{-1}) of shrub (S), grass (G), and litter (L); [c]the relative increments in SOC and STN stocks (Mg ha^{-1}) for the whole 1 m soil profile

decomposition (Lange et al. 2023; Qiao et al. 2014; Zhao et al. 2015). Conversely, RH, as reported by others (Rifai et al. 2010), decreased SOC and STN stocks throughout the 1 m soil profile relative to RC due to the detrimental effect of frequent herbicide use on understory vegetation. This slows down the litter decomposition rate, making the unvegetated soil more vulnerable to surface erosion (Nespoulous et al. 2019), which in turn results in losses of C and N. Additionally, observed deviations in soil bulk density due to understory management (Fig. 1d) strongly and inversely control SOC and STN dynamics, as lower bulk density is associated with larger pores and aggregates that promote root growth and various subterranean biological processes, facilitating mineral-related organic C and N storage (Anh et al. 2014; Li et al. 2022).

Coupling relationship of soil C and N following understory vegetation management

There was a general coupling relationship between SOC and STN stocks for each understory management practice (Fig. 3a), as observed in other land use types (Anh et al. 2014; Pan et al. 2018; Qiao et al. 2014). It is known that the greater SOC storage with forest succession can enhance N retention by stimulating microbial N immobilization and abiotic reaction with mineral N to produce organic N compounds (Lewis et al. 2014). In addition, most soil N exists in organic form as a part of soil organic matter, and thus a high STN pool can promote SOC accumulation (Zhang et al. 2021). Furthermore, increased N availability promotes the transformation of plant residues into stable organic compounds, which are

resistant to further microbial attack and delays new C decomposition by inhibiting enzyme activity, thereby facilitating SOC sequestration (Guo et al. 2020; Li et al. 2022). We also observed significant correlations between SOC stock and C:N ratio (Fig. 3b) because a relatively high C:N ratio could benefit SOC buildup by regulating soil nutrient availability and biological activity (Guo et al. 2020), as reported in previous studies (Li et al. 2020; Zhao et al. 2015). The variations in the effects of understory management on C:N ratios at different depths (Fig. 1c) are likely attributable to differences in the distribution and utilization of C and N within various understory plant–soil systems. However, it remains uncertain whether the C:N ratio can effectively reflect SOC and STN stocks in rubber plantations (Li et al. 2020). Moreover, the correlation coefficient varied among different management practices, with higher and closer coefficients being observed in thriving understory vegetation communities, signifying their greater contribution to C sequestration and N mineralization.

Soil C and N storage driven by understory vegetation

Variations in SOC and STN stocks were closely related to understory vegetation characteristics across all management practices (Fig. 5 and S2). Understory vegetation has a high turnover rate (i.e., low C/N and lignin/N ratios) and can produce a proportionately larger amount of litter input despite relatively lower biomass level (Majasalmi and Rautiainen 2020). It mainly regulates soil C and N dynamics through its litter degradation and mixed effect with overstory litters, root exudates, and associated microbial communities (Pan et al. 2018; Zhao et al. 2015). In general, understory vegetation contributes to SOC and STN conservation. We found that the above- and belowground biomass of shrub and grass based on the abundant species number collectively improved SOC and STN stocks in the topsoil (Pan et al. 2018). Moreover, shrub cover facilitated SOC and STN storage, presumably due to rainfall interception, which promotes soil infiltration and reduces surface runoff (Deng et al. 2023; Zhang et al. 2022a). In contrast, only belowground biomass substantially contributed to SOC and STN storage in the 1 m soil profile, highlighting the importance of effective rooting depth for deep C and N reserves. These findings coincide with

previous studies that has shown varying drivers of SOC and STN stocks derived from understory vegetation based on soil stratification (Dong et al. 2022; Li et al. 2022; Zhang et al. 2022a). Furthermore, the depth of aboveground litter was negatively correlated with SOC and STN storage regardless of soil depth, although it accounted for a high proportion of variation. Most of the litter was produced by overstory rubber trees, which tend to wash away rather than decompose in situ relative to understory litter. This indicates that the decomposability of plant litter is a crucial determinant of SOC and STN stocks, that is, fast-decomposing litter facilitates the mineralization of organic matter, leading to short-term increases in soil C and N concentrations (Craig et al. 2022). However, a review of stable isotope studies suggests that slow-decaying litter supports long-term storage of SOC and STN relative to rapidly decomposing litter (Zheng et al. 2021). Thus, enhanced litter decomposition due to mixed effects with intact understory litter is effective in increasing C and N returns, particularly in rubber monoculture plantations, in addition to improving litter quantity, soil properties, and environmental conditions (Ashton-Butt et al. 2018; Zhu et al. 2022).

Implications of understory vegetation management in tree crop plantations

Tree crop plantations (e.g., rubber, cocoa, and oil palm) are always classified as "green deserts" since they are monocultures with little ability to support complex biodiversity and ecosystem functions (Horák et al. 2019). Unexpectedly, we observed substantial understory plant diversity in these intensively managed plantations (Table 1), as has been reported by others (Lan et al. 2022; Luke et al. 2019). Despite the positive ecological benefits of retaining and restoring understory vegetation, such as topsoil SOC and STN storage potential (Fig. 4), "competing" understory vegetation is frequently eradicated using herbicides to improve overstory tree crop productivity by maximizing water and nutrient utilization (Deng et al. 2023). Consequently, several non-traditional understory management practices have been arbitrarily employed by smallholders, which vary in terms of their effectiveness in supporting understory species conservation and nutrient retention (Fig. 6). When

smallholders have access to alternative sources of income, such as significant off-farm revenue, natural understory regeneration suitable for periodic conservation of tree crop plantations will occur (Bremer and Farley 2010). Understory intercropping with cash crops has been found to maximize the economic benefits of land use and, when combined with cover crops, improve soil conditions, while also preventing C and N losses caused by deep-rooted shrubs in deep soils (Lange et al. 2023). However, smallholders in mountain regions may be reluctant to adopt this approach due to limited labor availability (Langenberger et al. 2017). Remarkably, both practices produce invasive species in the short term, as beneficial species require longer response times, leaving the system vulnerable to climatic shocks. Therefore, we recommend adapting appropriate understory management schemes tailored to local conditions and the willingness of smallholders to target the control of "problem" understory species. Government professionals must assist in achieving sustainable economic maximization and ecological optimization of tree crop plantations. Ideally, herbicide spraying should be applied only around the base of the tree crop and along the working path, so as to retain understory plants in the interrow (Luke et al. 2019).

Conclusions

Seven years following four understory management practices have seen a significant variability in understory vegetation characteristics as well as SOC and STN stocks in structurally simplified rubber plantations. Compared to conventional management, natural and man-made restoration increased native species and coverage of the understory, leading to higher above- and belowground biomass. Meanwhile, these practices also sporadically introduced invasive species, which may have long-term interspecific competition with native species. In addition, successive application of herbicide has caused severe damage to the understory vegetation, even spreading to the roots. These changes induced C and N accumulation in both natural and agroforestry systems but their losses after herbicide spraying, particularly in topsoil, which was driven primarily by understory vegetation biomass and litter depth. In addition, targeted management of

understory invasive species is critical to ensure ecosystem vulnerability and resilience to climate change. Our findings have significant implications for developing sustainable understory management strategies in terms of understory vegetation protection and soil nutrient supply in tree crop plantations. Future research should focus on differences in soil nutrient storage in understory vegetation with different diversity gradients or life forms (e.g., annual and perennial agroforestry systems) and explore underlying microbial mechanisms.

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

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