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ORIGINAL PAPER

Natural forests exhibit higher organic carbon concentrations and recalcitrant carbon proportions in soil than plantations: a global data synthesis

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Abstract Different chemical compositions of soil organic carbon (SOC) affect its persistence and whether it significantly differs between natural forests and plantations remains unclear. By synthesizing 234 observations of SOC chemical compositions, we evaluated global patterns of concentration, individual chemical composition (alkyl C, O-alkyl C, aromatic C, and carbonyl C), and their distribution evenness. Our results indicate a notably higher SOC, a markedly larger proportion of recalcitrant alkyl C, and lower easily decomposed carbonyl C proportion in natural forests. However, SOC chemical compositions were appreciably more evenly distributed in plantations. Based on the assumed conceptual index of SOC chemical composition evenness, we deduced that, compared to natural forests, plantations may have higher possible resistance to SOC decomposition under disturbances. In tropical regions, SOC levels, recalcitrant SOC chemical composition, and their distributed evenness were significantly higher in natural forests, indicating that SOC has higher chemical stability and possible resistance to decomposition. Climate factors had minor effects on alkyl C in forests globally, while they notably affected SOC chemical composition in tropical forests. This could contribute to the differences in chemical compositions and their distributed evenness between plantations and natural stands.

Keywords Global data synthesis · Natural forest · Plantations · Soil organic carbon · Soil organic carbon chemical composition

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Introduction

Natural forests can provide benefits of carbon (C) storage, water provisioning, erosion control, and biodiversity; however, plantations have an advantage in uniform wood production (Hua et al 2022). A meta-analysis showed that soil organic carbon (SOC) levels decreased by 36.5% through conversion from natural forests to plantations (Liao et al 2012). Most studies have demonstrated that more SOC is stored in natural forests, while several results have shown that plantations sequester more C in soils (Lemma et al 2006; Pibumrung et al 2008; Zarafshar et al 2020). However, the patterns of SOC stocks between plantations and natural stands could be context-independent. The differences in SOC storage vary in different climate regions and environmental conditions (Liao et al 2012; Hong et al 2020). Therefore, a global synthesis of forest SOC patterns needs to be comprehensively assessed.

Various organic C chemicals constitute SOC (Crow et al 2009), including O-alkyl C, alkyl C, carbonyl C, and aromatic C, and show different levels of resistance to decompose in diverse ecosystems (Lorenz et al 2007). Lignin-rooted litter aromatics are significantly refractory in the process of decomposition (Berg and Meentemeyer 2002). Carbohydrates, such as cellulose, are characterized by abundant O-alkyl C (Baldock et al 1992). Carbonyl C represents the oxidized products of various molecules (Hall et al 2020) and is a labile C functional group rapidly degraded by the microbial community (Kang et al 2021). Generally, the alkyl C signal can be assigned to compositions as the framework of long-chain polymethylene [$(CH_2)_n$] such as lipids, waxes and resins, showing relative stability resistance to microorganism decomposition (Kögel-Knabner et al 1992). Alkyl C often accumulates in the soil to the benefit of increasing the SOC pool stability (Mikutta et al 2006). The "ecosystem property theory" indicates that abiotic and biological controlling factors, instead of chemical structure, affect the stability of soil organic matter (Schmidt et al 2011). The "soil continuum model" proposes that organic debris is in a continuous state and goes into smaller polymers via the decomposer community (Lehmann and Kleber 2015). These perspectives suggest that any organic C compositions would ultimately decay in the presence of appropriate decomposer groups and abiotic environment. Based on these theories, we developed a concept of SOC chemical composition evenness (Wang et al 2019b, 2022a, b, 2023a, b). Specifically, when SOC chemical composition evenness reduces, the risk of C emissions increases because of any one soil chemical composition suffering substantial impacts, since climate changes and other disturbances would rise. The evenness of distribution of chemical compositions of SOC can be used to indicate the potential resistance to decompose (Wang et al 2023a, b). In addition, an analogous view indicated that the significant factor controlling decomposition is the molecular diversity of organic compounds instead of the material properties of individual compounds due to the increasing cost of metabolism along a greater diversity of molecules (Lehmann et al 2020). Low diversity, coupled with a high concentration of individual chemical compositions, potentially contributes to both more effective 'investment strategies' and specialization for soil biota (Kögel-Knabner 2017; Wang et al 2023a). The duration of organic residues tends to increase with the enhanced diversity of chemical particles (Kallenbach et al 2016; Wang et al 2023a).

Previous studies have indicated that vegetation changes associated with long-term land use shifts can result in differences in SOC chemical composition (Quideau et al 2001). When natural forests were converted to hoop pine plantations, O-alkyl C decreased while alkyl C increased in soils (Chen et al 2004). Conversely, in afforested pine forests, O-alkyl C was higher in soils than in natural woodlands in the Mediterranean environment (De Marco et al 2022). Mixed plantations of *Erythrophleum fordii* Oliv. and *Pinus massoniana* Lamb. have a higher proportion of recalcitrant alkyl C and a larger evenness of SOC chemical compositions than the monospecific plantation of *P. massoniana* (Wang et al 2019b). However, the various shifts in SOC chemical compositions between natural forests and planted ones have been primarily based on small-scale experiments. Whether the chemical composition of soil organic carbon and their distributed evenness differ among forest types at a global scale is unclear.

SOC dynamics have been ultimately related to climate; for instance, higher temperatures increase the decomposition of organic matter (Davidson and Janssens 2006; Hall et al 2020). Warming completely alters the organic C chemical compositions and accelerates the degradation of lignin, e.g., aromatic C and carbohydrates, e.g., O-alkyl C (Feng et al 2008; Pisani et al 2015; Guan et al 2018; Wang et al 2019a). Precipitation significantly controls net primary productivity (NPP), shaping plant-rooted C sources (Wynn et al 2006; Nie et al 2021), thus affecting SOC components (Chiti et al 2019). Soil pH has an important role in determining SOC storage (Ramesh et al 2019) and drives the spatial distribution of arbuscular mycorrhizal fungi and soil fauna and the relative abundance of bacterial communities (Liu et al 2007; Cheng et al 2012; Shen et al 2013). Research has shown that pH has a positive relationship with protein and a negative one with lipids in soils at a continental scale (Hall et al 2020). However, the effects of climatic and soil factors on SOC chemicals and their distribution globally are unclear.

In this study, we explore the patterns and drivers of SOC concentration, the individual chemical components of SOC, and their distribution evenness between natural forests and plantations in different climate regions by conducting a global data synthesis. We hypothesized that: (1) natural forests would have more recalcitrant SOC chemical compositions and higher SOC levels concentrations than plantations; and that (2) distributed evenness of SOC chemical compositions would be larger in natural forests because of the more complex plant community structure and the diverse litter carbon inputs.

Materials and methods

Meta-analysis

An extensive literature search was carried out in Google Scholar and the ISI Web of Science on May 13, 2021 using the search terms: nuclear magnetic resonance (NMR); soil organic carbon or soil carbon; chemical composition or composition or fraction or component; and forest or plantation or planted forest. The search initially produced 459 publications (159 from ISI Web of Science and 300 in Google Scholar), of which we focused on SOC chemical compositions in forest topsoil and topsoil sample depth was as < 30 cm (Georgiou et al 2022). To avoid bias in literature selection, studies were chosen according to the following six criteria: (1) studies that estimated soil C chemical composition in mangrove forest ecosystems were excluded; (2) soil C chemical composition was derived only from surface soils, excluding samples from deep soils; (3) the studies explored the effects of various treatments (i.e., nutrient and litter addition, altered temperature or precipitation) on soil chemical composition, and only observations of the control were used; (4) only the method for estimating soil C chemical composition using NMR was employed; (5) studies examining the chemical composition of SOC or SOM were used, and other materials, such as humic substances, particulate organic matter, or light fraction, were excluded; and (6) only studies of the proportion of soil chemical compositions of carbonyl C, aromatic C, O-alkyl C, and alkyl C were used with a sum of 100%. When an original study reported results graphically, SigmaScanPro version 5 (Systat Software Inc., Point Pichmond, CA, USA) was used to extract the data digitally. The subset included 234 sites in 69 publications, covering tropical, subtropical, temperate and boreal forests across Asia, Europe, Africa, America, and Oceania (Fig. S1 and Table S1).

NMR spectra were divided into four shift regions for C chemical composition (Mathers and Xu 2003): alkyl, O-alkyl, aromatic, and carbonyl; the specific chemical shift areas for the four compositions are shown in Table S1 (Condron and Newman 1998; Shrestha et al 2008; Dymov et al 2015; Angst et al 2016; Jiménez-González et al 2016; Fang et al 2017; Cusack et al 2018; Hasegawa et al 2021). Alkyl C/O-alkyl C (A/OA) indicates the substrate quality for microorganisms and the decomposition extent of SOC due to easily decomposed O-alkyl C and recalcitrant alkyl C (Huang et al 2008).

Species evenness refers to how close in numbers each species in an environment is. Pielou evenness index represents the evenness of a community (J'): $J' = H'/H_{max}$; $H' = \sum p_i \log_2 p_i$; and $p_i = n_i/N$, where n_i and N are the mean abundance of ith species and the total abundance, respectively (Shannon and Weaver 1949); $H_{max} = \text{Ln}(S)$, where S is the number of all species. Pielou evenness indicated the evenness of the chemical composition (Wang et al 2019b). $S = 4$ (four chemical compositions of organic C-carbonyl C, aromatic C, O-alkyl C, and alkyl C), N is the total proportion of SOC chemical composition and n_i is the specific percentage of the ith C chemical fraction accounting for the total SOC estimated using relative intensity of every C composition ^{13}C NMR spectra (Wang et al 2019b). A low evenness indicates one or more functional C compositions were relatively low or high, while a high index indicates a more even distribution of different functional C compositions.

In addition, we also collected data on soil properties and climate factors to evaluate their effects on the chemical composition of SOM and its distribution. Both mean annual precipitation (MAP) and mean annual temperature (MAT) were obtained from the global database (http://www.worldclim.org/). Soil organic carbon and pH were derived from corresponding literature or the SoilGrids data of the website (https://soilgrids.org/#!/?layer=TAXNWRB_250m&vector=1). Net primary productivity was extracted from Numerical Terradynamic Simulation Group Data (http://www.ntsg.umt.edu/data).

Statistical analysis

The Wilcoxon rank-sum test was carried out to determine the differences in chemical composition and evenness of the SOC between natural forests and plantations. Differences were also tested by Wilcoxon rank-sum for various types of tropical, subtropical, temperature, and boreal forests at $P < 0.05$.

Linear mixed-effects models were used to examine the relationships of O-alkyl C and alkyl C on SOC, where O-alkyl C and alkyl C were treated as fixed factors, while studies were treated as random factors.

Structural equation modeling examined the indirect and direct effects of MAT, MAP, pH and NPP on SOC compositions and their distribution evenness, and scaled to mean = 0 and SD = 1. The package "PIECEWISE" performed the structural equation model analysis. All statistical analyses were performed in R 3.2.4 (R Development Core Team 2016).

Results

Concentrations and chemical compositions of soil organic carbon

Higher SOC, a larger proportion of recalcitrant alkyl C, a larger A/OA ratio, and a lower easily decomposed carbonyl C were found in global natural forests than in plantations ($P < 0.05$) (Fig. 1), which supports the first hypothesis. Other chemical compositions, including O-alkyl C and aromatic C, were not significantly different between plantations and natural forests (Fig. 1). Moreover, in tropical forests, SOC levels, recalcitrant SOC composition, A/OA ratio, and evenness of SOC chemical compositions were higher in natural forests (Fig. 2). For subtropical forests, alkyl C of natural forests was significantly larger than that for plantations (Fig. 3). Soil organic carbon in temperate natural forests was significantly larger than in temperate plantations (Fig. 4).

Chemical compositions of SOC were distributed more evenly in global plantations than in natural forests (Fig. 1).

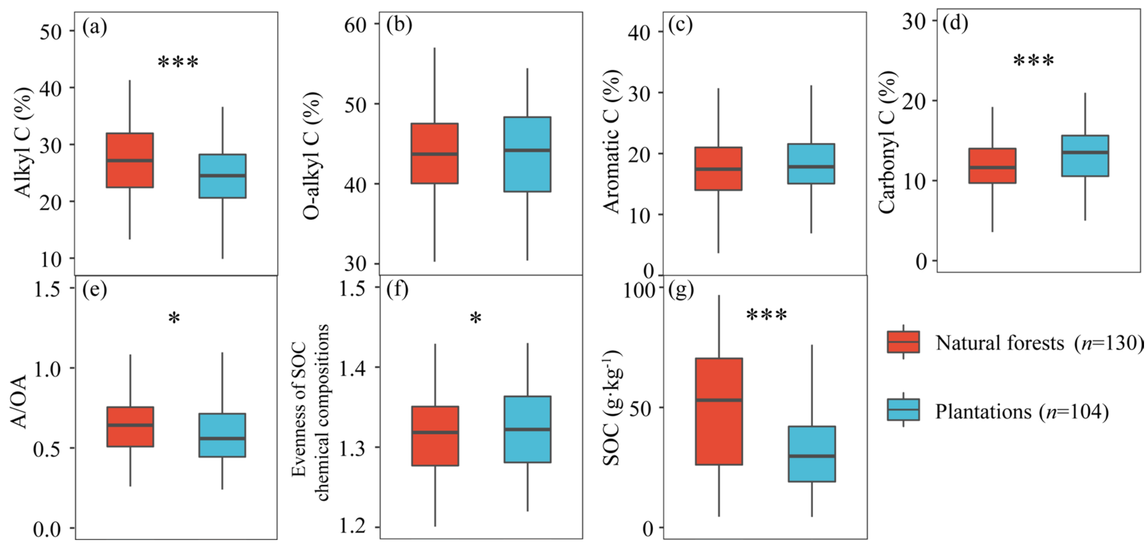

Fig. 1 Percentages of **a** alkyl C, **b** O-alkyl C, **c** aromatic, and **d** carbonyl C, **e** alkyl C/O-alkyl C (A/OA), **f** evenness of SOC chemical compositions and **g** SOC in global forests. Significance levels: $P<0.001$ (***) and $P<0.05$ (*)

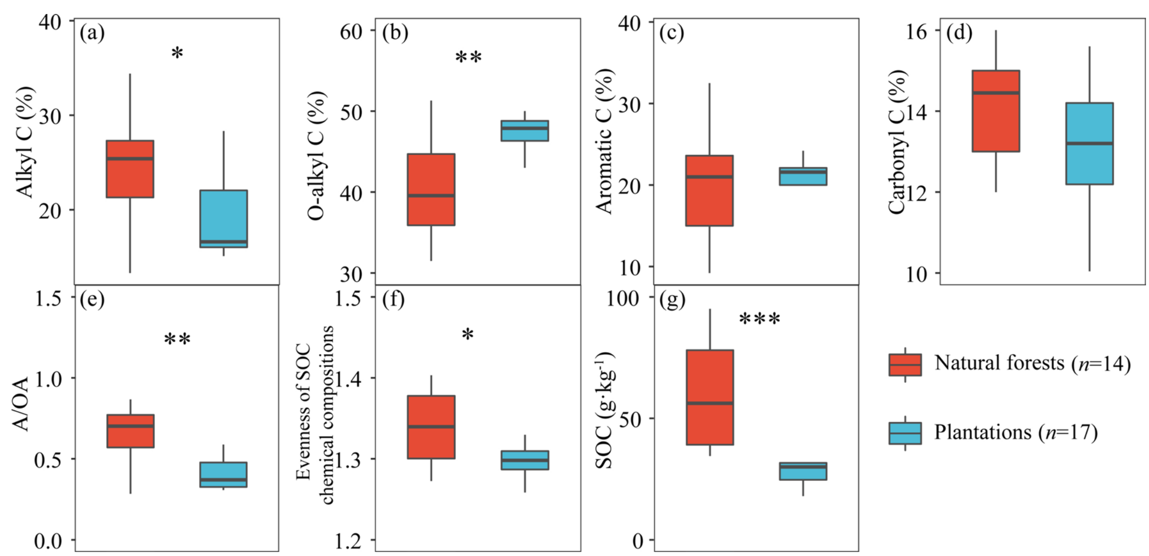

Fig. 2 Sizes of **a** alkyl C, **b** O-alkyl C, **c** aromatic C and **d** carbonyl C, **e** alkyl C/O-alkyl C (A/OA), **f** evenness of SOC chemical compositions, and **g** SOC in global tropical forests. Significant levels: $P<0.001$ (***), $P<0.01$ (**), and $P<0.05$ (*)

Conversely, in tropical forests, SOC was distributed more evenly in natural forests (Fig. 2). This supports our second hypothesis for tropical forests.

Various chemical compositions had different notable relationships with SOC between natural forests and plantations (Figs. 5 and 6). Specifically, with alkyl C, it showed an increasing trend in global plantations, while it was relatively stable in natural forests (Fig. 5). In tropical forests, SOC had decreased O-alkyl C in natural forests and increased in plantations (Fig. 6).

Controls on chemical composition of soil organic carbon and their distribution evenness

Climate factors had various effects on SOC chemicals in different forest types. Generally, they had less consequences on alkyl C and aromatic C, but MAT had negative effects on O-alkyl C but positive effects on carbonyl C and evenness of chemical compositions in global forests (Fig. 7). However, the results showed a different picture in tropical forests. Mean annual precipitation significantly affected

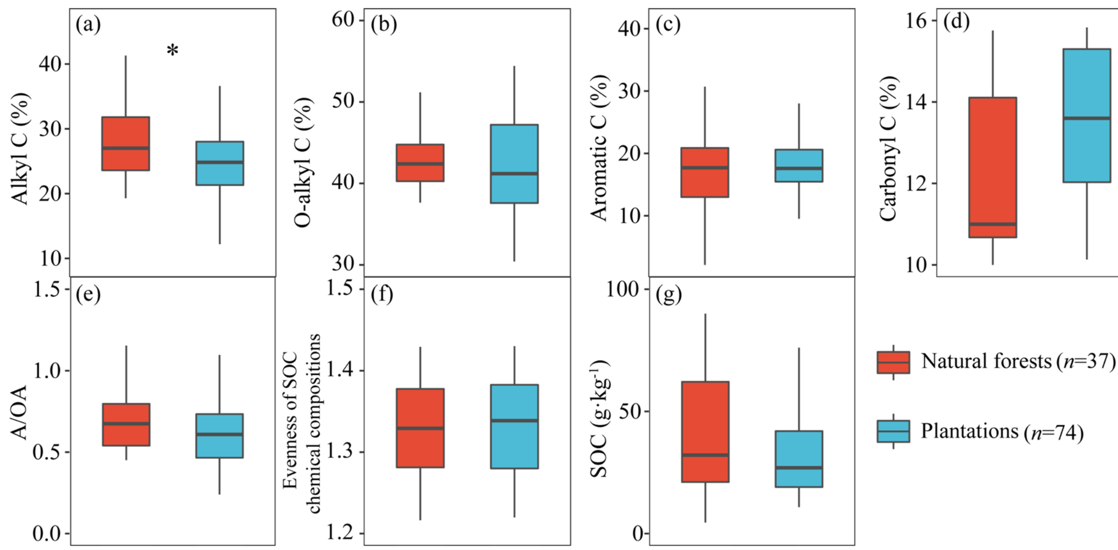

Fig. 3 Sizes of **a** alkyl C, **b** O-alkyl C, **c** aromatic C and **d** carbonyl C, **e** alkyl C/O-alkyl C (A/OA), **f** evenness of SOC chemical compositions, and **g** SOC in global subtropical forests. Significance levels: $P < 0.05$ (*)

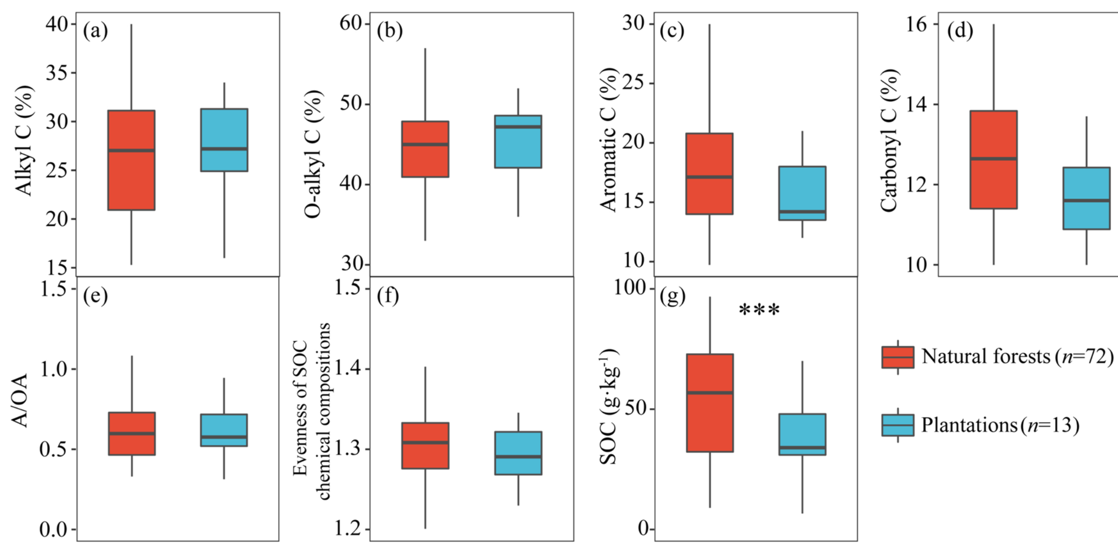

Fig. 4 Sizes of **a** alkyl C, **b** O-alkyl C, **c** aromatic C, and **d** carbonyl C, **e** alkyl C/O-alkyl C (A/OA), **f** evenness of SOC chemical compositions, and **g** SOC in global temperate forests. Significance levels: $P < 0.001$ (***)

the chemical make-up of SOC and evenness of their distributions, and MAT affected alkyl C and aromatic C levels (Fig. 8).

pH and NPP markedly affected the chemical compositions of SOC and their evenness at a global scale (Fig. 7), and in tropical forests (Fig. 8). pH was negatively related with alkyl C and positively with the evenness of chemical compositions across global forests and in tropical forests (Fig. 7). Net primary productivity was positively related with carbonyl C levels and chemical compositions evenness (Fig. 8).

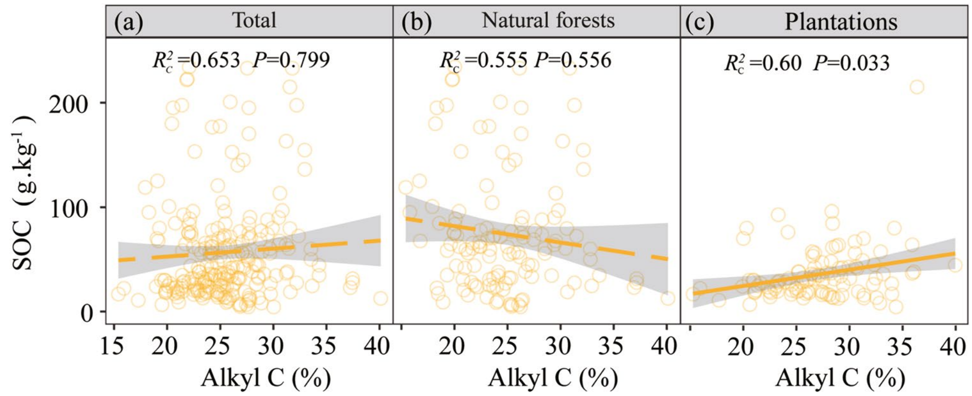

Fig. 5 Relationships between alkyl C and SOC in global forests; **a** total, **b** natural forests, and **c** plantations

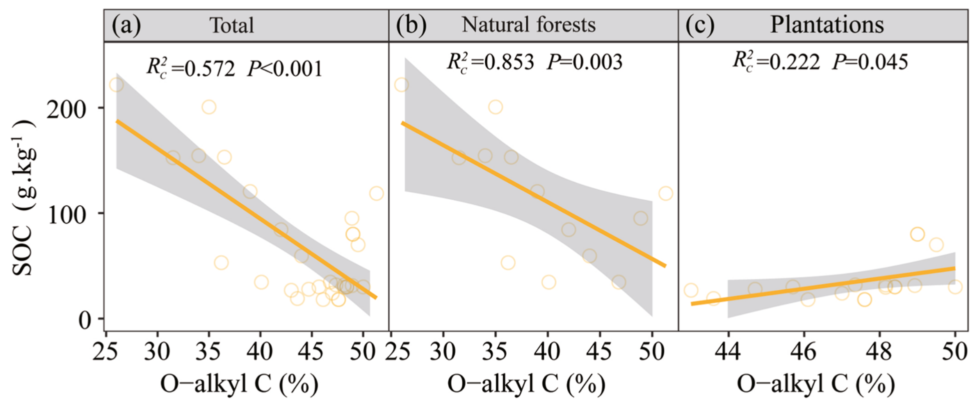

Fig. 6 Relationships between O-alkyl C and SOC in global tropical forests; **a** total, **b** natural forests, and **c** plantations

Discussion

Concentration/chemical compositions of soil organic carbon in natural forests and plantations

Compared with many natural forests, plantations are subject to more anthropogenic disturbances. The simpler stand structure and higher soil temperatures in plantations stimulate SOM decomposition (Li et al 2014). The intense cultivation in plantations leads to a significant loss of SOC (Wu et al 2014). Consequently, it was higher in the natural forests.

In this study, natural forests exhibited more recalcitrant SOC, higher A/OA, and lower evenness of SOC chemical compositions at a global scale. Compared with plantations, natural forests had more soil alkyl C, indicating the greater persistence of SOC under current conditions. However, the concept of the molecular diversity of chemical components, instead of material properties of individual organic components controlling the process of decomposition (Lehmann et al 2020) and evenness of SOC chemical compositions, has been suggested to indicate the potential C resistance to decomposition in climate change scenarios and other disturbances (Wang et al 2019b). Therefore, compared with natural forests, plantations had a higher evenness of organic carbon compositions. This suggests that natural forests could be at greater risk of carbon decomposition, while plantations may have higher possible resistance to SOC decomposition in projected climate change scenarios. These results suggest that SOC storage and potential resistance to disturbance exist as a tradeoff between natural forests and plantations at a global scale. The lower alkyl C and the higher carbonyl C in soils in plantations resulted in the greater evenness of chemical compositions. The conception of SOC chemical evenness is based on ecosystem property theory and soil continuum model (Wang et al 2019b). One of the uncertainties was the difficulty of proving the effects of SOC chemical composition evenness on C decomposition in controlled experiments. The experiments could be designed to prove the relationships between SOC chemical evenness and potential C decomposition in the future.

In contrast to the global scale, in tropical regions, natural forests had a higher evenness of SOC chemical compositions due to soil O-alkyl C in plantations. This indicates that tropical natural forests could be at less risk of SOC decomposition to possible disturbances than plantations in the tropics. Combining higher SOC concentrations, the more recalcitrant soil alkyl C and larger soil A/OA in the natural forests in the tropical regions, it is concluded that SOC storage, chemical stability, and potential resistance showed a synergetic relationship between the tropical natural forests and plantations.

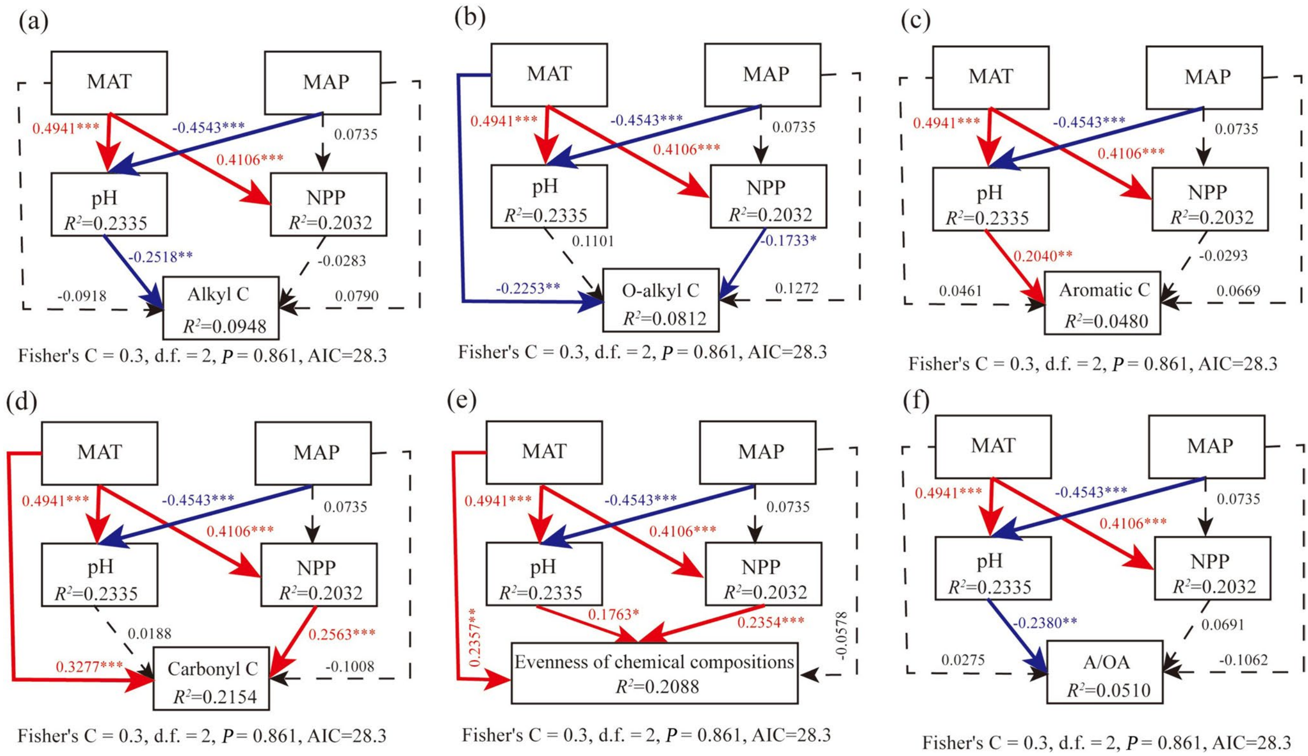

Fig. 7 Structural equation models determining direct and indirect drivers of **a** alkyl C, **b** O-alkyl C, **c** aromatic C, **d** carbonyl C, **e** evenness of chemical composition distribution, and **f** alkyl C/O-alkyl C (A/OA) in global forests; number values are proportional to their relative size of effect. Dashed arrows represent nonsignificant effects, red arrows are positive effects, blue arrows negative effects. Symbols indicate: $P < 0.001$ (***), $P < 0.01$ (**), and $P < 0.05$ (*)

Natural forests play a significant role in SOC storage and sequestration of their higher carbon and alkyl C. Therefore, although plantations can replenish soil carbon loss, protecting natural forests is also significant for improving the storage and sequestration of carbon.

Soil organic carbon levels increased significantly with alkyl C in global plantations and decreased with O-alkyl C in tropical forests. Similarly, O-alkyl C was notably negatively connected with SOC stock in subtropical plantations (Wang et al 2022b). In contrast, in harvested and old-growth forests, the proportion of O-alkyl C in SOC was positively correlated with SOC stock in tropical rainforests (Wang et al 2023b). This inconsistency implies that the relationships between SOC storage and chemical composition are largely dependent on biome and spatial scales.

Controlling factors on chemical compositions of soil organic carbon

In our study, MAT, rather than MAP, significantly affected the chemical compositions of SOC and their even distribution in forests at a global scale. It has been demonstrated that increasing temperature decreases the easily decomposed O-alkyl C in grasslands (Guan et al 2018). Similarly, increasing soil temperature has also been found to decrease O-alkyl C in a soil warming experiment in a subtropical plantation (Wang et al 2019a). Soil warming stimulates microbial decomposition of SOM, and the subsequent release of C into the atmosphere due to warming-induced thawing has been reported (Schuur et al 2015). In this study, soil O-alkyl C was negatively correlated with increasing MAT, while carbonyl C was positively correlated in forests at a global scale. Investments in the use of molecular methods that are rare in the soil solution are energetically less rewarding because of the rapid adsorption or low production rates (Lehmann et al 2020). The larger proportion of the SOC chemical composition, e.g., O-alkyl C, potentially stimulates decomposition for a greater reward (Lane and Martin 2010) than the lower proportion of soil carbonyl C. Therefore, soil O-alkyl C preferentially decomposed with increasing MAT. Increasing temperature can also stimulate decomposition of SOC by increasing C input from plants (Nie et al 2021), which partly shapes the positive relationship between MAT and soil carbonyl C.

In tropical forests, MAP had marked influence on the chemical composition of SOC and its evenness. Precipitation will affect SOC based on indirectly affecting the degree of soil acid (Slessarev et al 2016). Increasing precipitation can

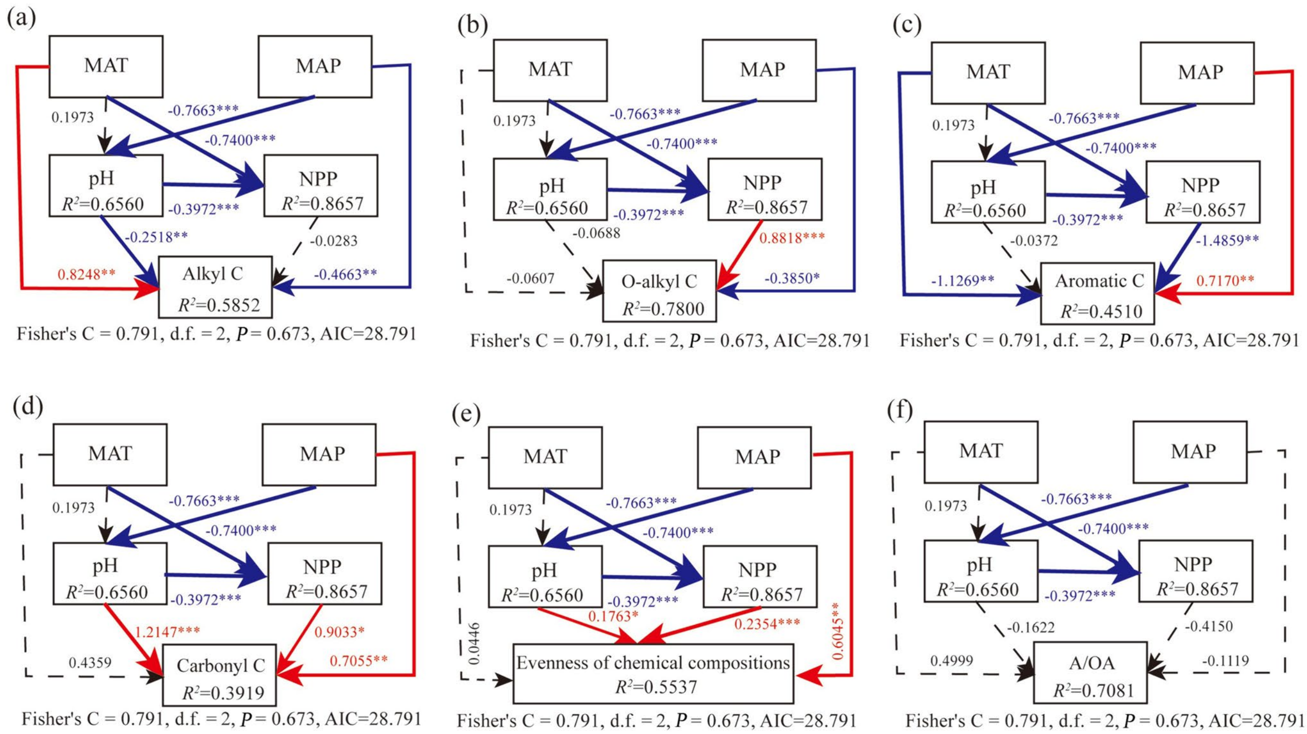

Fig. 8 Structural equation models determining direct and indirect drivers of **a** alkyl C, **b** O-alkyl C, **c** aromatic C, **d** carbonyl C, **e** evenness of chemical composition distribution, and **f** alkyl C/O-alkyl C (A/OA) in global tropical forests; number values are proportional to their relative size of effect. Dashed arrows represent nonsignificant effects, red arrows are positive effects, blue arrows negative effects. Symbols indicate: $P<0.001$ (***), $P<0.01$ (**), and $P<0.05$ (*)

also weather Ca minerals, resulting in greater Ca^{2+} leaching and immobile Al^{3+} accumulation, consequently decreasing pH (Slessarev et al 2016). Ca^{2+} is involved in SOC stabilization (Rowley et al 2018) and decreasing Ca^{2+} partly reduces alkyl C and O-alkyl C and could lead to the increased evenness of SOC chemical compositions.

Compared with global patterns, one of the most significant differences in tropical regions was high temperature and precipitation, and MAT and MAP were 21.6 ± 3.8 versus 12.9 ± 7.2 °C and 1752.2 ± 713.1 versus 1249.6 ± 615.5 mm (tropical values vs. global values) in the study regions, respectively. Furthermore, results from structural equation modeling showed that climate factors had minor effects on soil alkyl C in global forests and significantly affected SOC chemical composition in tropical forests. This could potentially contribute to the differences in chemical compositions of SOC and their distributed evenness between plantations and natural forests globally and in the tropics.

Soil pH has been shown to have a close link with biological processes (Hong et al 2018) and responds to soil properties (Rasmussen et al 2018). It had a negative effect on alkyl C and a positive one on the distribution evenness of SOC chemical compositions in this study (Figs. 7 and 8). Similar results also indicated that soil pH had a positive effect on SOC chemical compositions in Chinese forests (Wang et al 2023a, 2023b). Soil acidity has an important role in regulating microbial activity, biomass, and composition (Tashi et al 2016). The conditions of more acidic soils lead to less diversity of soil bacteria (Shen et al 2013), having significant effects on SOC stabilization and solubility (Özkan and Gökbulak 2017; Nie et al 2021). Soil pH can also affect arbuscular mycorrhizal fungi (e.g., *Acaulospora* and *Glomus*) abundance, substantially regulating SOC decomposition in the scenario of increased CO_2 (Cheng et al 2012). This may partially contribute to the decrease in alkyl C, contributing to increasing SOC chemical composition along with soil pH.

In global nitrogen deposition, an increase will reduce pH in forest ecosystems (Yang et al 2015). Our results indicate that alkyl C increases with decreasing pH in forests globally. These results indicated that in global nitrogen deposition, decreasing pH could change individual SOC chemical composition and enhance its evenness, possibly increasing the potential for carbon loss in forest ecosystems.

Conclusions

Based on a global data synthesis, including 234 field studies across major forest ecosystems, lower SOC levels, less recalcitrant alkyl C, and more evenly distributed SOC chemical compositions were found in plantations than in natural forests. These results suggest that the storage and potential resistance to disturbance of SOC is a tradeoff between natural forests and plantations. The latter could be less at risk of losing SOC and substantially complement the SOC decrease in natural forests in projected disturbances. Specifically, in tropical regions, natural forests had a larger SOC concentration and a higher potential resistance to decomposition in terms of a higher evenness of its chemical compositions. This result highlights that organic carbon storage and chemical stability showed a synergetic correlation between tropical natural forests and plantations. Although plantations can replenish soil carbon loss, protecting natural forests is still important for improving the storage and sequestration of soil organic carbon.

Author contributions Hui Wang conceived the study and designed the methodology; Xiuqing Nie collected the data; Xiuqing Nie and Jian Wang analyzed the data; Xiuqing Nie and Hui Wang led the writing of the manuscript; Shirong Liu provided academic advice. All authors contributed critically to the drafts and gave their final approval for publication.

Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

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