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Depth-Dependent Controls Over Soil Organic Carbon Stock across Chinese Shrublands

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Abstract

Soil organic carbon (SOC) in shrublands is an important component of global carbon cycling. However, there is a dearth of large-scale systematic observations of SOC stocks at different soil depths, and it remains uncertain whether and how the relative importance of biotic and abiotic variables in regulating SOC stocks changes with soil depth. Here, we quantified large-scale patterns and controlling factors of SOC storage per area (SOCD, kg m^{-2}) for both topsoils (0–30 cm) and subsoils (30–100 cm) by taking full advantage of a consistent stratified random sampling study of one-meter soil profiles across 1211 sites in Chinese shrublands. We found that subsoils stored about 53.30% of total SOCD, falling into the range of previously reported values for terrestrial ecosystems. SoilGrids250m model-derived assessments overestimated SOCD by 13.72 and 65.49% for topsoils and subsoils, respectively. The effects of climate means and seasonality on SOCD were equally strong in both topsoils and subsoils. The predominant effects of edaphic properties on SOCD were more robust in subsoils than in topsoils. Belowground biomass of shrublands was the only significant predictor of topsoil SOCD, but it did not predict subsoil SOCD accurately. These findings have refined our understanding of the pivotal role of shrublands in SOC storage and sequestration potential and could serve as an ecologically valuable baseline for large-scale improvement and validation of depth-dependent SOC dynamics for multilayer SOC modules in Earth Systems Models.

Key words: soil carbon storage; subsoil layer; climate-vegetation-soil relationships; climatic control; edaphic properties; vegetation attributes.

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Highlights

- Shallow soil sampling of shrublands underestimates carbon stocks by > 50%.

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- The importance of climate seasonality, and in particular precipitation, should be taken into account in subsoil carbon assessments.
- The effects of edaphic properties on organic carbon stocks are more robust in the subsoil than in the topsoil.
- Vegetation attributes predict organic carbon much more accurately in topsoils than in subsoils.

Introduction

Soil organic carbon (SOC) makes up approximately two-thirds of the terrestrial carbon pool, storing more carbon than the atmosphere and plant biomass combined, and consequently plays a key role in regulating climate change (Jackson and others 2017; Billings and others 2021; García-Palacios and others 2021), Therefore, a well-developed understanding of large-scale patterns and drivers of SOC stocks has important implications for predicting soil carbon-climate feedbacks in current Earth System Models and for the development of strategies for SOC sequestration in response to climate change (Scharlemann and others 2014; Rasmussen and others 2018; Wiesmeier and others 2019).

Because SOC is so important to terrestrial ecosystem carbon cycling, scholars have increasingly been investigating the main determinants of SOC storage. Existing studies have demonstrated that SOC storage is primarily driven by C inputs (such as aboveground litterfall and root turnover) and by C protective mechanisms (such as litter biochemical quality and environmental constraints that affect SOC decomposition rates, as well as interactions with minerals that together with biochemical recalcitrance control microbial decomposition of SOC) (Jackson and others 2017; Gaitán and others 2019; García-Palacios and others 2021). Recent findings have demonstrated that climate, edaphic and physiochemical properties, and vegetation attributes could all strongly control SOC storage at different spatiotemporal scales. For example, warmer and more humid conditions, deeper soils, and soils with higher clay content are usually associated with higher SOC storage (Wiesmeier and others 2019; Hartley and others 2021).

Despite extensive research, existing knowledge of SOC dynamics remains inadequate in several respects. Previous investigations have focused strongly on the topsoil above 30 cm, with relatively limited evidence from the subsoil. In fact, subsoil below 30 cm could store more than 50% of total SOC stocks (Jobbágy and Jackson 2000; Jackson and others 2017; Luo and others 2019), sequester up to 20% of new carbon globally (Balesdent and others 2018), and differ considerably from topsoil, with higher total volumes and bulk densities, lower SOC concentrations, and longer SOC residence times (Rumpel and Kögel-Knabner 2011; Shi and others 2020; Jílková and others 2021). These different properties of subsoil SOC also raise questions about whether and how the dominant drivers of SOC storage could vary between topsoil and subsoil. Existing studies have demonstrated that SOC stored in both top- and subsoils is strongly controlled by climate, edaphic properties, and vegetation conditions. However, the relative importance of these controlling factors remains largely unknown and is incompletely represented in current Earth System Models (Jackson and others 2017; García-Palacios and others 2021; von Fromm and others 2021; Yu and others 2021). This uncertainty has further resulted in a gap between the theoretical understanding of depth-specific SOC dynamics and our ability to improve terrestrial biogeochemical projections. It is therefore imperative that we better understand the distinct mechanisms controlling SOC storage in top- and subsoils, as this will help to develop unbiased strategies to effectively enhance whole-soil vertical profile carbon sequestration.

Shrublands are among the most poorly represented biomes in terms of SOC stock (Kramer and Chadwick 2018; Nie and others 2019) and could sequester more SOC than previously thought, and are thus an important potential carbon sink (Jobbágy and Jackson 2000; Piao and others 2009; Nie and others 2019). For example, shrublands have stored the deepest organic carbon and contribute greatly to inter-annual variability of the global terrestrial carbon sink among terrestrial ecosystems (Ahlström and others 2015; Terrer and others 2021). However, shrubland SOC storage has been seriously biased in large-scale empirical and modeling studies, while the high potential SOC sequestration capacity of shrublands has been recognized (Jackson and others 2017; Tang and others 2018; Shi and others 2020). Large-scale observational data availability on SOC storage in these shrublands remains insufficient, and shrubland soils are less well-described in current soil digital mapping (Tifafi and others 2018; Dai and others 2019). Most existing studies have not discriminated shrublands from other ecosystems (Jackson and others 2017; Luo and others 2021) and generally use relatively small datasets with limited geographical coverage, focusing on the surface soil layers (Wang and others 2004; Nie and others

2019). These shortcomings have further hampered firm conclusions on the quantitative relationships between SOC stocks and their environmental drivers and have restricted our robust understanding of the potential role of shrublands in SOC sequestration under climate change (Billings and others 2021).

To close this knowledge gap, we quantified large-scale patterns and controlling factors of SOC storage per area (SOCD, kg m^{-2}) for both topsoils (0–30 cm) and subsoils (30–100 cm) by taking full advantage of a consistent stratified random sampling of extensive soil profiles down to one-meter depth across 1211 shrubland sites in China. Specifically, we aimed to: (1) quantify depth-dependent SOCD, and (2) disentangle the relative importance of climatic, edaphic, and vegetation variables on SOCD stored in topsoil (0–30 cm) and subsoil (30–100 cm) for Chinese shrublands.

Materials and Methods

SOCD Observational Data for Chinese Shrublands

Chinese shrublands cover 0.69 million km^2, accounting for nearly 7.3% of China's total land area, and are widely distributed across geographical and environmental gradients (MEPPRC 2015). Chinese shrublands thus provide an ideal system in which to explore the geographical patterns and the dominant drivers of SOC stocks in shrublands. Here, all site-level SOC stock datasets consisted of 1211 soil profiles, sampled during fieldwork for the ''Strategic Priority Research Program-Climate Change: Carbon Budget and Relevant Issues'' by the Chinese Academy of Sciences, which aimed to quantify the carbon budget of terrestrial ecosystems in China in 2011–2015 (Fang and others 2018; Tang and others 2018). Soil profile samples covered major shrubland types, with a broad range of mean annual temperature and precipitation (Table 1, Appendix S1). Detailed sampling specifications, analytical procedures, and data preprocessing can be found in the Technical Manual Writing Group of Ecosystem Sequestration Project (2015) and Xie and others (2018).

Field investigation and sampling were conducted in the 2011–2015 growing seasons according to a standardized sampling protocol. Sampling sites for shrubland types were selected based on geographic distribution and representativeness of Chinese shrublands following the guidance of Vegetation of China. Shrubland sampling sites ranged from 18.26° to 52.37°N latitude, from 75.60° to 131.70°E longitude, and from 153 to 4634 m in elevation (Table 1). Soil profiles for each site were collected from three plots of 5 × 5 m (10 × 10 m in some cases). For each plot, three one-meter soil pits (or to bedrock for some sampling sites) were excavated along the diagonal line of each plot to measure soil physical and chemical properties. Soil samples were collected along the profile at depths (D) of 0–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm for each plot. A soil sample with an estimated dry weight of 100 g was collected and fully mixed with a small scraper from the same soil depth for each plot. Soil samples for each soil depth were used to determine soil bulk density (SBD), soil organic carbon concentration (SOCC), the coarse fragment content (particle diameter > 2 mm; CF, volume percentage), soil nitrogen concentration (TN), soil phosphorus concentration (TP), and pH (Technical Manual Writing Group of Ecosystem Sequestration Project 2015).

Soil organic carbon concentration was determined by colorimetry after oxidation with a mixture of potassium dichromate and sulfuric acid. Soil TN was measured with an elemental analyzer (Vario MACRO cube, Elementar, Hanau, Germany), and soil TP was measured using the molybdate/ascorbic acid method after H_2SO_4–H_2O_2 digestion (See Tang and others (2018) for more details). Other chemical properties and detailed analytical procedures can be found in the Technical Manual Writing Group of Ecosystem Carbon Sequestration Project (2015).

Current studies have demonstrated that SOC stocks can be calculated using fixed-depth or equivalent soil mass methods (von Haden and others 2020). We selected the former method to quantify SOCD because this method is commonly used in SOC stock inventories and we had determined the SBD and CF for each soil depth. Therefore, following previous empirical studies (Doetterl and others 2015; Tifafi and others 2018), we calculated soil organic carbon density (SOCD, SOC stock per area, g/m^2) for each depth for each site: SOCD = SOCC × SBD × D × (1-CF). See Appendix S4 for more details on the depth-specific distribution of SOCD.

For these plots, we also investigated vegetation characteristics, including species composition, dominant species, and above- and below-ground biomass. In brief, before biomass collection, a survey of species composition was completed for each plot. The shrub layer was surveyed throughout the plot and the herb layer was investigated in four quadrants (1 × 1 m) located at the four corners of the plot. Shrub layer biomass was then estimated

Table 1. Basic Statistics of Above-selected Climate, Edaphic and Vegetation Attributes Used in our Statistical Models across Chinese Shrublands

Type	Variable	Mean	SD	Median	Min	Max
Climate	Solar radiation (SR) KJ/m^2	1489	142	1488	1090	1816
	Mean annual temperature (MAT) °C	12.0	6.72	13.1	− 6.9	25.3
	Temperature Seasonality (TS)	8095	2464	7784	2803	15,728
	Mean annual Precipitation (MAP) mm	899	538	834	10	2347
	Precipitation Seasonality (PS)	82.1	23.4	81	33	160
	Topographic wetness index (TWI)	87.2	16.3	85	54	133
Edaphic	Topsoil N %	0.17	0.16	0.12	0.01	1.58
	Topsoil P mg g^{-1}	0.58	0.41	0.5	0.05	3.72
	Topsoil pH	6.92	1.76	6.85	3.94	10.3
	Topsoil clay %	22.2	7.21	23.3	1	38.3
	Topsoil sand %	41.6	12.2	38.3	21.7	97
	Subsoil N %	0.08	0.07	0.06	0.00	0.56
	Subsoil P mg g^{-1}	0.48	0.33	0.42	0.04	4.16
	Subsoil pH	7.09	1.84	7.06	3.94	10.2
	Subsoil clay %	23.9	8.33	25	0.33	42.7
	Subsoil sand %	41.2	12.8	38	22	97.7
Vegetation	Aboveground biomass (AB) kg m^{-2}	1.21	2.09	0.66	0.01	28.8
	Belowground biomass (BB) kg m^{-2}	0.93	1.3	0.51	0.00	12.9
	Growing season length (GSL) day	188	77.8	186	5	365

Values of solar radiation have been divided by 10.

by taking samples of clipped plants for each plot or by applying allometric equations for each species. For the herb layer, all herbaceous biomass was harvested and oven-dried. We then calculated the root to shoot ratio (RS) for each site. Further details on vegetation characterization and soil surveys can be found in the Technical Manual Writing Group of Ecosystem Sequestration Project (2015) and Xie and others (2018).

Environmental and Vegetation Attribute Data

All environmental and vegetation attribute datasets mentioned in this study were acquired from published databases with a consistent spatial resolution of 30 arcsec (approximately 1 km^2 at the equator) except for soil data, for which a 250 m-resolution dataset was used. See more details on data sources in Appendix S2. This method is common practice in previous large-scale SOC studies. In brief, most climate data were obtained from CHELSA-Climatologies at high resolution for the Earth land surface areas (Version 1.2), which is comparable in accuracy to other temperature data but superior for precipitation data. We also obtained climate data, including solar radiation (SR), for each site from Worldclim2 (Fick and Hijmans 2017). Using the Digital Elevation Model (Yamazaki and others 2017), we obtained the topographic wetness index (TWI), which is an important index of potential soil moisture conditions (Wiesmeier and others 2019).

We also included additional edaphic properties and vegetation attributes to account for geographic variation beyond the above-mentioned climatic variables. Data on soil texture for each site was obtained from the SoilGrids250 dataset (Hengl and others 2017). We used this high-resolution soil dataset based on the following aspects. First, we compared the model results with the SoilGrid250m (a 250 m resolution) (Hengl and others 2017) and SoilGrids1km ((a 1 km resolution) (Hengl and others 2014) datasets and found qualitatively similar results in our preliminary statistical analyses. Second, we also considered the importance of edaphic properties and easy comparison with previous studies. Furthermore, we also used this fine-scale extracted SOCD to facilitate comparison with our observational data and reduce the mismatch in scale (Sanderman and others 2017). For each quantitative soil variable, we calculated the depth-weighted averages from 0–30 and 30–100 cm. We also extracted modeled SOCD from SoilGrids250m using the corresponding geographic locations of observational SOCD.

To complement the statistical analysis of SOCD-plant relationships beyond the vegetation biomass we measured, we also extracted growing season length (GSL) index values for each site from the previous datasets during the field sampling period. Vegetation information was obtained from the Resources and Environmental Science Data Center of the Chinese Academy of Sciences (http://www.resdc.cn/). These datasets generally represent the most accurate, current, globally, and regionally comprehensive, and the finest resolution data available for each study site (Duarte-Guardia and others 2019).

Data Processing and Analysis

Here, we divided our soil profiles into two soil layers and aggregated the SOC stocks for each soil layer for each site: commonly-used depth intervals for topsoil (0–30 cm) and subsoil (30–100 cm) represent an arbitrarily-defined cutoff, but one that is often used in SOC stock inventories and can allow for direct comparisons with previous studies (Jackson and others 2017; Balesdent and others 2018). For example, 0–30 cm is the default soil sampling depth considered in the Intergovernmental Panel on Climate Change (IPCC) Tier 1 type greenhouse gas inventories (Balesdent and others 2018; Billings and others 2021). We acknowledged that soil depth is not a nominal category consisting only of topsoil versus subsoil, but a continuous layer approach would have been a good alternative to better quantify how the relative importance of biotic vs. abiotic factors shifts along six sequential soil layers. Such granularity could help to detect some unseen trends and to generate more insightful depth-specific conclusions when comparing the importance of driving factors of SOC in topsoil versus subsoil. We did not perform such an analysis at this time due to financial constraints and the mismatch with current soil databases.

We applied descriptive statistics to characterize our datasets, including mean, minimum/maximum values, and the coefficient of variation (CV) for SOCD and corresponding environmental features at each soil layer (Table 1). Data on SOCD for each soil layer exhibited significant heteroscedasticity and non-normality (Kolmogorov–Smirnov test, $p < 0.05$). Therefore, these variables were transformed using the natural logarithm for each soil layer in the following statistical analyses.

We conducted multiple linear regression models to identify the associations between SOCD and climatic, edaphic, and vegetation variables. We explored the integrative effects of climatic, edaphic, and vegetation variables on SOCD using stepwise multivariate regression with both forward and backward methods. Subsequently, the Akaike information criterion (AIC) was used to identify the most efficient model. The best model was selected as the one with the highest explanatory power (R^2) and fewest explanatory variables. The difference in AIC values between the best and other competing models was less than two (Zuur and others 2009; Ge and others 2019; Smith and Waring 2019). All explanatory variables entering the final models were centered and scaled so those model coefficients could be directly compared.

Before performing these statistical analyses, we pre-selected explanatory variables to represent hypothesized ways in which environmental (climatic and edaphic) variables and vegetation attributes could affect SOCD. We examined potential multicollinearity among these environmental and vegetation variables by calculating the variance inflation factor (VIF) (Dormann and others 2013). We then selected these explanatory variables according to the variance inflation factor (VIF). We assessed collinearity within this set of explanatory variables using pairwise correlations since collinearity may reduce our ability to draw robust conclusions. We also implemented principal component analysis (PCA) to further select these variables. More detailed information on the selection of climatic, edaphic, and vegetation variables can be found in Appendix S3.

We further evaluated the relative importance of all explanatory predictors as drivers of SOCD. To do so, we compared the relative effects of the parameter estimates for each of the predictors with the effect of all parameter estimates in the model (García-Palacios and others 2018). This method parallels variance decomposition analysis since we standardized all explanatory predictors before analysis. We also examined the overall relative contribution of climatic, edaphic, and vegetation attributes using the same method. We conducted all statistical analyses in R version 3.6.0 (R Core Team 2019) with the basic statistical package, the ''car'' package (Fox and others 2019), and the ''MuMin'' package (Bartoń 2020) using a 95% significance level when appropriate.

Results

Statistics and Geographic Patterns of Topsoil and Subsoil SOCD

We found high variability in SOCD stored in both topsoil and subsoils. Topsoil SOCD averaged 4.84 kg m^{-2}, ranging from 0.10 to 34.67 kg m^{-2}, while mean subsoil SOCD was 5.08 kg m^{-2}, ranging from 0.14 to 47.63 kg m^{-2}. Topsoil SOCD did not differ from that stored in subsoils (Figure 1). Therefore, more than half of the total SOCD (53.30%) was in subsoils within a one-meter soil profile. We also compared topsoil and subsoil SOCD observations with the corresponding model-derived estimates from the SoilGrids250m database and found that these model-based datasets significantly overestimated topsoil SOCD by up to 13.72% and subsoil SOCD by 65.49% (paired *t*-test, $p < 0.05$) (Figure 2). Furthermore, we also found that SOCD for each soil depth decreased with latitude but increased with longitude, though the strength of such relationships tended to weaken insignificantly for subsoils (Figure 3).

Factors Influencing Geographical Variation in Top- and Subsoil SOCD

We found that factors controlling SOCD varied between top- and subsoils (Figure 4). Topsoil SOCD was positively associated with MAP and PS but negatively correlated with MAT (but not TS) and TWI. Topsoil SOCD correlated positively with soil total nitrogen (TN), but negatively with soil sand content, and exhibited no significant relationship with soil clay and total P content (TP). Soil pH did not significantly affect topsoil SOCD ($p > 0.05$). Topsoil SOCD was greater with higher belowground (rather than aboveground) biomass and a longer GSL (Figure 4A).

Likewise, we found that subsoil SOCD positively correlated with MAP and PS but was negatively linked to MAT, though it exhibited no significant trend with TS and TWI (Figure 4B). Subsoil SOCD correlated positively with TN but negatively with soil sand content. Soil pH was strongly positively

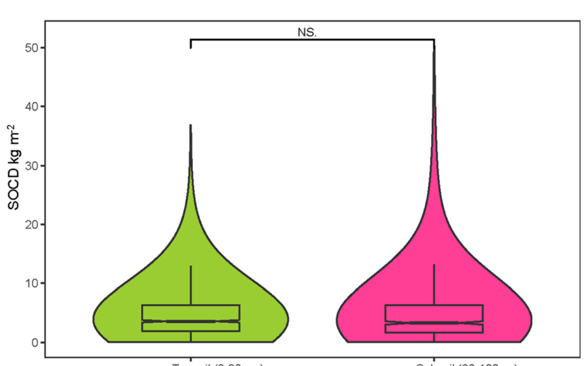

Figure 1. SOCD for topsoil (0–30 cm) and subsoil (30–100 cm) layer in Chinese shrublands. There was no significant difference for SOCD between topsoil and subsoils.

correlated with subsoil SOCD. We detected insignificant effects of soil TP and clay on subsoil SOCD. GSL was the only vegetation attribute that was positively correlated to subsoil SOCD.

The Relative Importance of Climatic, Edaphic, and Vegetation Characteristics

We found that climatic, edaphic, and vegetation characteristics collectively accounted for 73.13 and 64.44% of the variation of topsoil and subsoil SOCD, respectively (Figure 5 and Appendix S5). The relative contribution of climate and soil properties increased from topsoil to subsoil, while vegetation contributions weakened (Figure S5). MAP and TN were the greatest predictors of SOCD in both topsoils and subsoils, whereas the other variables varied in their contributions between topsoil to subsoils. For example, soil pH contributed little in topsoils, but became much more important in subsoils, while belowground biomass (BB) contributed to geographic variation in topsoil SOCD, but its effects disappeared in subsoils.

Discussion

Our large-scale empirical work has substantially expanded previous studies (Wang and others 2004; Yu and others 2007; Nie and others 2019) and provided up-to-date estimates of SOCD in Chinese shrublands. We further identified differences in the strength of the relative effects of climatic and edaphic properties and vegetation attributes on SOCD between soil depths, contradicting previous assumptions that control of SOCD would be consistent across soil layers (Hobley and Wilson 2016; Delgado-Baquerizo and others 2017). Therefore, our study provides a nationwide benchmark of SOCD to refine our understanding of the pivotal role of shrublands in estimating SOC storage and sequestration potential and consequently could serve as an ecologically meaningful baseline for emulating future depth-dependent soil C dynamics in shrublands.

Subsoil SOC Constitutes an Important Carbon Pool and has been Overestimated by SoilGrids250m Database

We found that mean topsoil and subsoil SOCD fell into the previously-documented ranges for terrestrial ecosystems (Table 2) and identified that subsoil SOC represented 53.30% of the topmost meter's SOC stocks, agreeing with reported values for global ecosystems (30–61%) (Jackson and others

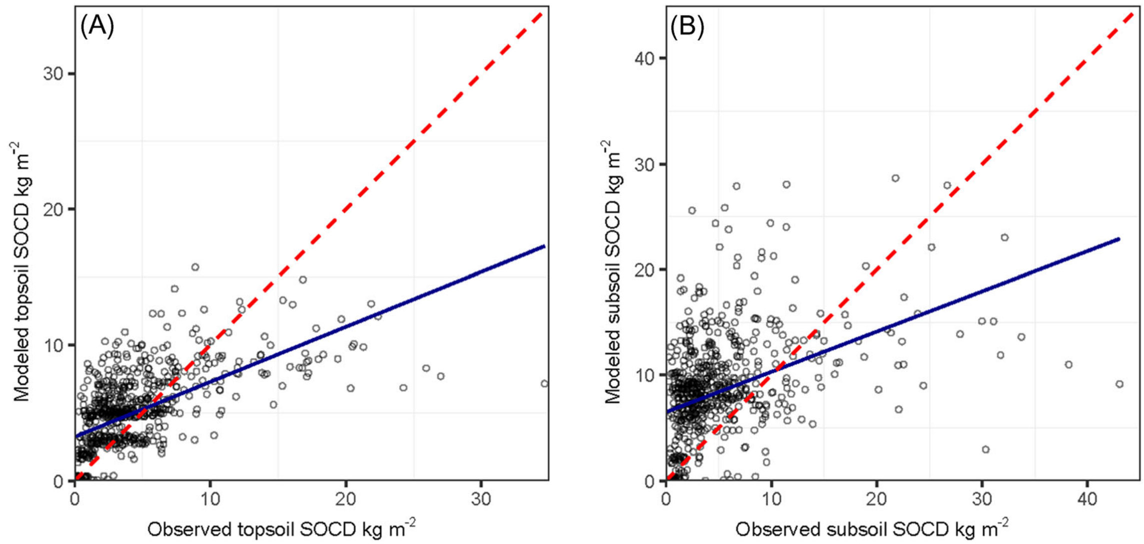

Figure 2. Paired comparisons of SOCD for our ground-based actual observational data for both topsoils (**A**) and subsoils (**B**) with the corresponding model-based estimates from the state-of-the-art SoilGrids250 soil map product across Chinese shrublands. The blue solid line indicates the fitted line between these observed and modeled values from SoilGrids250m database while the red dash line shows the 1:1 relationship.

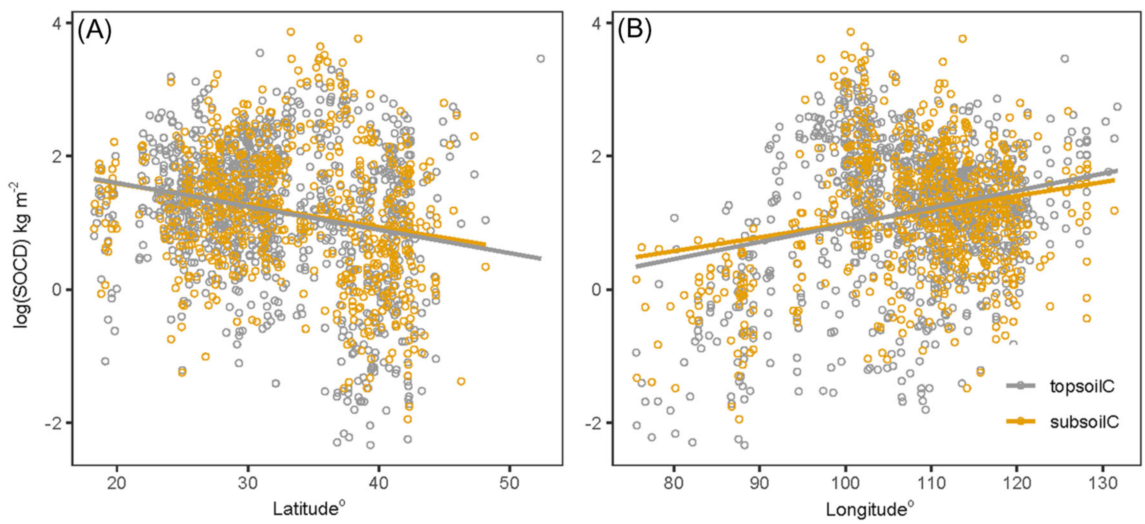

Figure 3. Geographical trends of SOCD for topsoils (0–30 cm) and subsoils (30–100 cm) in Chinese shrublands. Note that SOCD for both soil layers has been transformed using the natural logarithm before performing statistical analyses. All the regression lines were plotted for relationships with $p < 0.05$.

2017; Balesdent and others 2018; Lal 2018) and earlier estimates in Chinese shrublands constructed from a small set of poorly-representative legacy data (54%, calculated from only 91 soil profile samples) (Wang and others 2004). These results underscore that subsoils contribute substantially to total SOC stocks, and the routine surface sampling depth (30 cm) recommended by current protocols of the IPCC could considerably underestimate the actual SOC storage and sequestration potential of shrublands.

We found that subsoil SOCD estimates have been biased to a greater extent than topsoils when we compared topsoil and subsoil SOCD observations with the corresponding model-derived estimates from the state-of-the-art SoilGrids250m database (Hengl and others 2017; Dai and others 2019). Two potential factors could explain these large discrepancies between the model-derived SOCD and our actual observations. First, the SoilGrids250m products are based on advanced automated mapping and machine learning techniques, but this

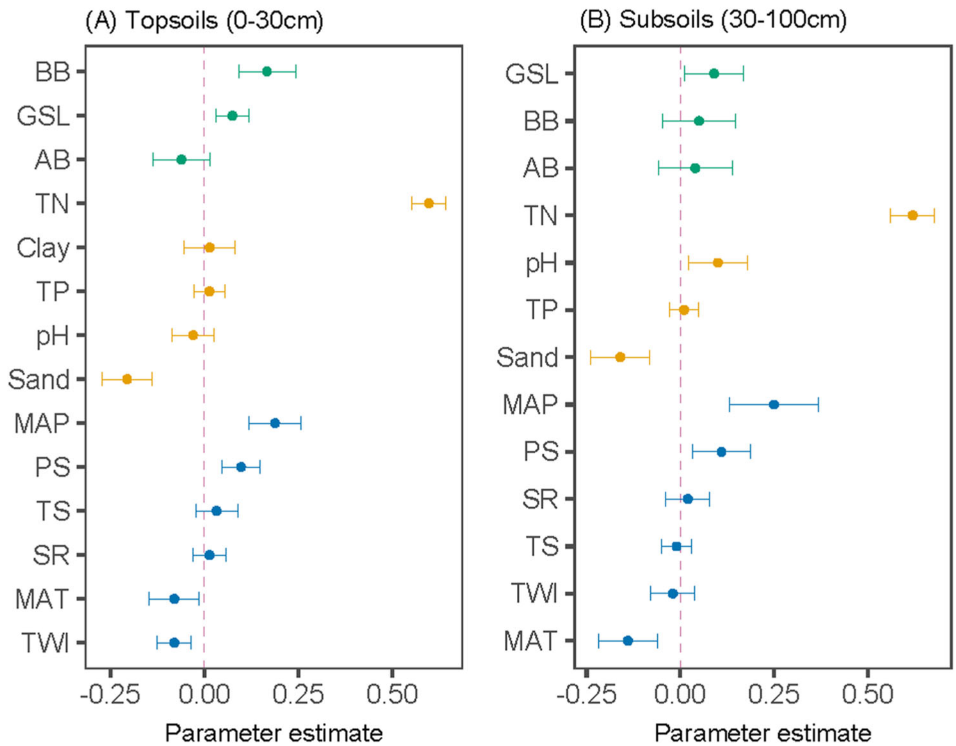

Figure 4. Summary of effects of the climatic and soil and vegetation drivers on SOCD for top and subsoils. The points represent the standard regression coefficients of each predictor included in the best model. Whiskers in **A** and **B** represent the 95% of confidence intervals of the parameter estimates. Coefficients with 95% CI that do not overlap zero can be considered statistically significant. *TWI* Topographic wetness index, *SR* solar radiation, *MAT* mean annual temperature, *TS* temperature seasonality, *MAP* mean annual precipitation, *PS* precipitation seasonality, *TP* soil phosphorus concentration, *TN* soil nitrogen concentration, *AB* aboveground biomass, *BB* belowground biomass, *GSL* growing season length.

approach has the inherent drawback that it calculates SOCD from soil properties such as bulk density, soil organic matter, and particle distribution, which has much a higher uncertainty than SOCD measured directly from empirical field data like the current study (Hengl and others 2017; Tifafi and others 2018; Dai and others 2019). Another issue is that this SOCD map is developed to predict current SOC stocks without considering anthropogenic impacts. Most data used in the SoilGrids250 database are derived from the compilation of legacy soil information of SOC stocks. But SOC stocks have been greatly altered, and these methods preclude any consideration of possible human-induced disturbance effects on SOC stocks over recent decades (Sanderman and others 2017; Dai and others 2019; Wiesmeier and others 2019). This result further underscores that prior estimates did not adequately reproduce finer-scale variability of SOCD. Given that soil inorganic carbon (SIC) is another crucial component of soil carbon, we should also incorporate such information into the future development of the production of SOC and SIC stocks maps for shrublands.

Climatic Controls of SOCD are much Stronger in Both Topsoils and Subsoils

Current studies pinpoint climate as among the most dominant variables that control SOC stocks, but the crucial distinction between top- and subsoils remains poorly resolved (Jackson and others 2017; Wiesmeier and others 2019). Climatic seasonal variations have been commonly neglected when assessing potential SOC drivers in large-scale models, despite the fact that they are important determinants of plant production and microbial enzymatic activity, and thus SOC mineralization and microbial residue carbon accumulation in soils (Doetterl and others 2015; García-Palacios and others 2021). We found that both climate means and seasonality controls over SOCD were equally strong in both topsoils and subsoils. Both MAP and MAT played important roles in topsoil and subsoil SOCD. The pronounced negative effects of TS on topsoil SOCD diluted in subsoils, while the prominent positive effect of PS in topsoils persisted in subsoils. This may be attributed to the fact that Chinese shrublands are mainly precipitation-lim-

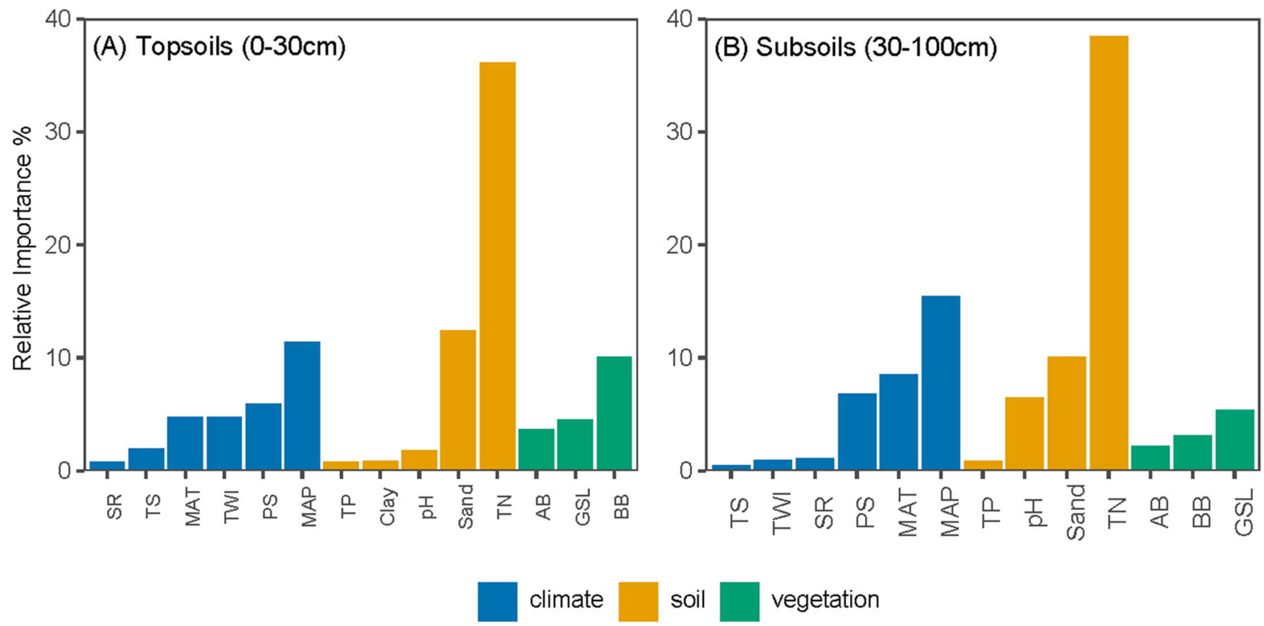

Figure 5. The relative importance of climate, edaphic properties, and vegetation attributes on SOCD for topsoils (**A**) and subsoils (**B**). *TWI* Topographic wetness index, *SR* Solar radiation, *MAT* mean annual temperature, *TS* temperature seasonality, *MAP* mean annual precipitation, *PS* precipitation seasonality, *TP* soil phosphorus concentration, *TN* soil nitrogen concentration, *AB* aboveground biomass, *BB* belowground biomass, *GSL* growing season length.

Table 2. Comparisons of Soil Organic Carbon (SOCD) (kg m^{-2}) in Topsoils (0–30 cm) and Subsoils (30–100 cm) with Earlier Chinese and Global Estimates

Region	Ecosystem type	Topsoil	Subsoil	References
China	All terrestrial ecosystems	3.74	4.66	Yang and others (2007)
Globe	All terrestrial ecosystems*	5.44–5.76	6.18–6.87	Batjes (1996)
Globe	All terrestrial ecosystems*	6.00	5.19	Batjes (2016)
Globe	All terrestrial ecosystems*	5.86	5.91	Jackson and others (2017)
Globe	Grasslands and shrublands*	3.57	3.30	Jackson and others (2017)
China	Open and closed shrublands	1.94–6.55	2.85–3.51	Wang and others (2004)
China	Alpine shrublands	12.78	13.43	Nie and others (2019)
China	Alpine shrublands	16.62	No data	Chen and others (2016)
China	All shrublands	4.84	5.08	This study

The asterisks (*) indicate these data were recalculated from these references.

ited, rather than temperature-limited (Wu 1980; Seddon and others 2016), resulting in the greater response of SOC changes to precipitation perturbations than temperature changes.

Specifically, climate regimes generally impact SOC storage dynamics through direct and indirect controls over C inputs (for example, the quantity and quality of organic carbon), and C outputs (for example, decomposition of plant litter and mineralization of SOC) (Jackson and others 2017; Cusack and Turner 2021). With increasing soil depth, temperature and precipitation regimes become increasingly stable and the impact of soil mineral chemistry becomes more pronounced. However, precipitation-induced moisture varied much more than temperature in subsoils due to the soil's buffering effects on temperature (Hobley and Wilson 2016). High SOC accumulation under high seasonality of precipitation may be caused by high C inputs and low microbial decomposition. Meanwhile, high precipitation amount could induce anaerobic conditions in soils under water-logged conditions, which would further impede microbially-mediated decomposition and increase microbial residues carbon accumulation (Wiesmeier and others 2019; García-Palacios and others

2021). High precipitation conditions potentially favor high plant productivity and plant-derived organic matter inputs by indirectly altering plant biomass distribution, especially in root biomass along soil profiles across Chinese shrublands. Intense seasonal precipitation can also cause great temporal variability in soil moisture and facilitate the vertical transport of labile compounds such as dissolved organic carbon, the colloidal transport of particulate organic carbon, and root carbon exudation from topsoils to subsoils (Kramer and Chadwick 2018; Cusack and Turner 2021). This finding clearly reiterated the importance of considering not only mean climate values but also seasonal patterns and in particular precipitation regimes to accurately model depth-specific SOC dynamics in shrublands. This is particularly important in light of climate change, as we expect greater heterogeneity in precipitation patterns under a changing climate.

The Predominant Role of Edaphic Properties is more Pronounced in Subsoil SOCD

While the overall effects of edaphic properties on SOCD have recently received much attention, quantitative relationships between these variables have been not identified (Billings and others 2021; Cusack and Turner 2021; Hartley and others 2021). Here, we demonstrate that the overall contribution of edaphic properties consistently outweighed that of climate on both top- and subsoil SOCD. While this finding corroborates some earlier studies (Doetterl and others 2015; Luo and others 2019), it contradicts studies from Chinese forests (Yang and others 2007; Zhou and others 2019) and earlier conclusions that edaphic properties dominated only in subsoils (Jobbágy and Jackson 2000; Wang and others 2004). This finding further contradicts the current climate-driven framework of SOC dynamics in Earth Systems Models (Doetterl and others 2015; Rasmussen and others 2018; Luo and others 2021). We argue that this finding may be ascribed to at least two complementary factors that are ultimately linked to C inputs into and output from soils. First, edaphic conditions can exert prominent direct effects on shrubland growth, impacting the quantity and quality of soil C inputs (Wu 1980; Ge and others 2017; von Fromm and others 2021). Although belowground resource availability has a pronounced effect on plant growth, the actual availability of those resources is largely controlled by edaphic physiochemical environmental properties (Viscarra Rossel and others 2019; Luo and others 2021). Second, soil physical and chemical properties can directly govern carbon outputs via their influence on the transformation and stabilization processes of C inputs into soils, as well as the composition and activity of the soil microbial community (Wiesmeier and others 2019; Cusack and Turner 2021; García-Palacios and others 2021). For instance, SOC can be highly protected from mineralization via tight occlusion within soil aggregates and binding with soil minerals.

Numerous studies have reported strong associations between SOC and soil texture (for example, clay content), and most existing process-based models simulating SOC dynamics make full use of this relationship regarding the fundamental role of soil clays in soil physiochemical processes (Rasmussen and others 2018; Hartley and others 2021). Here, we found that the influence of soil texture became more pronounced in subsoils and that soil clay content was a much weaker predictor of SOCD than sand content in both topsoils and subsoils. This finding is strongly supported by some other studies (Jobbágy and Jackson 2000; Wade and others 2019), but contrasts other studies showing that clay content is a robust predictor of SOCD (Hartley and others 2021). These inconsistent findings exemplified a dual effect of soil clay content on SOCD. On the one hand, the positive effect of increasing clay content can be explained both by the formation of stable, clay-protected organo-mineral associations via the adsorption and aggregation of SOC by clay minerals, which creates physiochemical barriers for microorganisms' access to SOC, and the positive effect on soil water holding capacity (Doetterl and others 2015; Bradford and others 2016; García-Palacios and others 2021). On the other, soil clay can negatively affect SOC when high amounts of soil clay make penetration and growth by deep roots difficult, and available water for plants may be too low in these soils and ultimately result in low below-ground carbon allocation and thus SOC production (Cusack and Turner 2021; García-Palacios and others 2021). Furthermore, the minor role of clay content here also suggests that other edaphic properties, such as the specific type of soil clay and mineral chemistry, may serve as better predictors of SOCD across shrublands and should be reasonably integrated into new Earth Systems Models.

Vegetation Attributes Predict SOCD much more Accurately in Topsoils than Subsoils

While SOC originates predominantly from the decomposition of plant litter both above- and belowground, quantitative relationships between such vegetation attributes and top- and subsoil SOCD remain largely elusive (Manning and others 2015; Soudzilovskaia and others 2019). We found that belowground biomass was a powerful predictor of SOCD in topsoils but not in subsoils, and both above- and below-ground biomass contributed much less to variation in SOCD in subsoils than in topsoils. This finding confirms results from prior studies in grasslands and croplands (Hobley and others 2015) but contrasts with some findings in forests (Li and others 2010; Sanderman and others 2017). This pattern could be caused by the vertical distribution patterns of root biomass across soil profiles in shrublands. Root biomass and resulting litter mainly concentrate in topsoils and consequently promote the efficient interaction of SOC with soil minerals to form relatively stable organo-mineral complexes and/or associations (Rumpel and Kögel-Knabner 2011; Sokol and Bradford 2019; Luo and others 2021). However, subsoil SOC with more slow and stable turnover rates could reflect historical rather than current vegetation conditions (Delgado-Baquerizo and others 2017; Cotrufo and others 2019; Shi and others 2020). Hence, a promising avenue for future research is the incorporation of explicit consideration of multifaceted current and past vegetation characteristics under paleo-climates into Earth Systems Models to shed new light on a more realistic projection of depth-dependent soil carbon dynamics in shrublands.

Concluding Remarks

Collectively, we have quantified the relative importance of climatic, edaphic, and vegetation attributes in governing top- and subsoil SOCD by improving the explicit and accurate geographical representation of shrublands. We showed that shallow soil sampling in shrublands underestimates SOC stocks by more than half, and thus strongly recommended the inclusion of subsoils in shrubland SOC studies. We also found that model-based estimates from the SoilGrids250m soil database overestimated SOCD by up to 13.72 and 65.49% for topsoils and subsoils, respectively. We also revealed that the relative importance of SOCD drivers differed between top- and subsoils. Specifically, mean annual precipitation and temperature played important roles in driving SOCD in topsoils and subsoils, but the pronounced negative effects of temperature seasonality on topsoil SOCD disappeared in subsoils. We additionally reiterated the importance of precipitation seasonality, a typically unappreciated climate variable, in subsoil SOCD. Edaphic properties were much more robust predictors of subsoil SOCD than of topsoil SOCD. Topsoil SOCD was more likely to be driven by apparent belowground carbon inputs, while belowground biomass did not impact SOCD in subsoils. Our work has reinforced that shrubland subsoils could act as significant potential carbon sequestration sites. More importantly, these results refine valuable information for large-scale improvement and validation of depth-dependent SOC dynamics for multilayer SOC modules in Earth Systems Models.

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Declarations

Conflict of Interest The authors declare no conflict of interest.

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