# Soil carbon storage controlled by interactions between geochemistry and climate

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Soils are an important site of carbon storage<sup>1</sup>. Climate is generally regarded as one of the primary controls over soil organic carbon<sup>1,2</sup>, but there is still uncertainty about the direction and magnitude of carbon responses to climate change. Here we show that geochemistry, too, is an important controlling factor for soil carbon storage. We measured a range of soil and climate variables at 24 sites along a 4,000-km-long north-south transect of natural grassland and shrubland in Chile and the Antarctic Peninsula, which spans a broad range of climatic and geochemical conditions. We find that soils with high carbon content are characterized by substantial adsorption of carbon compounds onto mineral soil and low rates of respiration per unit of soil carbon; and vice versa for soils with low carbon content. Precipitation and temperature were only secondary predictors for carbon storage, respiration, residence time and stabilization mechanisms. Correlations between climatic variables and carbon variables decreased significantly after removing relationships with geochemical predictors. We conclude that the interactions of climatic and geochemical factors control soil organic carbon storage and turnover, and must be considered for robust prediction of current and future soil carbon storage.

Soil organic carbon (SOC) is one of the most important terrestrial C pools, with spatially variable but large annual C exchanges with the atmosphere<sup>1,2</sup>. Single and interactive effects of climatic and biotic factors on SOC dynamics have been studied intensively at various spatial and temporal scales, but are still poorly represented in current Earth System Models (ESMs; refs 3-6). Generally, climatic factors have been regarded as primary controls in empirical and modelling approaches<sup>1,2,7</sup>. Consequently, ESMs predict a significant contribution of SOC to future climate change. However, recent model-based observations indicate that geochemical factors very likely play crucial roles in SOC turnover and large uncertainties remain<sup>8,9</sup>. These uncertainties are explained partly by ESMs poorly representing the current (observed) global SOC distribution<sup>1</sup> and partly by inadequate parameterization of the temperature sensitivity of SOC, microbial carbon use efficiency, and mineral surface sorption of organic matter<sup>1,8,9</sup>. The latter indicates shortcomings in the current approaches that focus on climatic controls and neglect other factors, such as the geochemistry of soils and effects of soil mineralogy on carbon stabilization<sup>10,11</sup>. The geochemistry of the reactive mineral phase of a soil depends on the composition of its parent material and weathering status. Weathering is crucially driven by the time since the onset of weathering, resilience of minerals to weathering, vegetation cover, local climate, and hydrologic conditions. Owing to the difference in scales between climate research and geochemical-related soil research (mostly large and local scale, respectively), the interactions of these key factors for SOC dynamics have rarely been assessed.

Here, we contribute to the debate on the importance of various environmental factors for global SOC dynamics by assessing the degree of direct versus indirect effects of geochemical and climatic factors on SOC stocks (SOC<sub>stock</sub>), concentrations (SOC<sub>%</sub>), specific potential respiration rates (SPR) and SOC fractions along an approximately 4,000 km north-south transect across Chile and the Antarctic Peninsula spanning a large range of climatic and geochemical parameters. All sites were under grassland and/or shrubland vegetation<sup>12</sup> to keep C input as similar as possible (Supplementary Table 2). However, differences in net primary productivity (NPP) could not be excluded; biomass production along the transect ranged between 800 to 4,500 kg dry weight ha<sup>-1</sup> yr<sup>-1</sup>, with extreme values of 300 kg ha<sup>-1</sup> yr<sup>-1</sup> in hot arid climates and up to 8,000 kg ha<sup>-1</sup> yr<sup>-1</sup> in temperate humid climates<sup>13,14</sup>.

Our data reveal strong connections between geochemical and climatic drivers of global SOC dynamics, demonstrating a need to consider their interactions when addressing current spatial patterns of SOC storage and turnover, as well as future global responses of SOC to climate change. We sampled topsoil (0-10 cm) at 24 sites, in triplicate, along this transect (Supplementary Table 1). To study the effects of geochemistry on the selected SOC variables (SOC<sub>%</sub>, SOC<sub>Stock</sub>, SPR and SOC fractions), we determined the following key geochemical characteristics of the soil samples: base saturation (BS) of the potential cation exchange capacity (CEC<sub>pot</sub>); soil texture; contents of silicon (Si) and abundant metals (Fe, Mn, Al); Si/Al ratio; the total reserve in 'base' cations (TRB); and geochemical soil fertility parameters (pH<sub>KCl</sub>, P, K) (Supplementary Table 3). We used mean annual precipitation and temperature as indicators of climatic conditions (see Supplementary Fig. 3). The predicting variables used here are thus proxies for environmental conditions controlling SOC dynamics (for a detailed discussion see Supplementary Information). We assume that geochemical

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# ETTERS



**Figure 1** | **SOC response variables in geographical context.** Relationship between soil organic carbon stocks (SOC<sub>Stock</sub>, left-hand *y* axis), specific potential respiration (SPR, right-hand *y* axis), mineral-associated SOC (SOC<sub>Mineral</sub>, green circles), microbially available SOC (SOC<sub>Microbial</sub>, blue circles) and latitude (*x* axis). The position of the points relates to the value on the relevant *y* axis, and the size of the accompanying circle relates to SOC<sub>Microbial</sub> and SOC<sub>Mineral</sub> as a percentage of SOC<sub>Stock</sub>. Relative uncertainty is calculated as the mean relative standard deviation of each SOC response variable. An interactive map showing further information on the SOC response and prediction variables in their geographic context is available online (see Supplementary Data). WRB soil orders: DU, Durisol; AR, Arenosol; CH, Chernozem; KS, Kastanozem; PH, Phaeozem; AN, Andisol; CM, Cambisol; GL, Gleysol; AC, Acrisol; LP, Leptosol; CR, Cryosol.

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	MAP	MAT	Clay	Silt	Si	BS	AI	TRB	рН <sub>КСІ</sub>	Fe	К	Ρ	Mn	R <sup>2</sup> <sub>cv</sub>	RMSE <sub>cv</sub>	RMSE unit
Least ang	le linear	regres	sion (l	LARS)	)											
SOC%	5.07	NS	NS	NS	-127.78	-10.75	-72.35	-36.97	NS	-25.62	-13.08	NS	NS	0.95	11.54	SOC g kg <sup>-1</sup>
SOC <sub>Stock</sub>	1.87	NS	NS	NS	-1.61	NS	NS	-2.69	NS	NS	-1.18	NS	NS	0.75	1.3	SOC kg m <sup>2</sup>
SPR	-2.75	NS	NS	NS	5.38	4.58	NS	NS	NS	NS	1.51	NS	NS	0.76	5	$\mu$ g CO <sub>2</sub> -C g <sup>-1</sup> SOC h <sup>-1</sup>
Best subs	et select	ion line	ear reg	gressi	on (BSS)											
SOC%	NS	NS	NS	NS	-0.93	NS	-0.47	NS	NS	-0.36	NS	NS	NS	0.96	11.24	SOC g kg <sup>-1</sup>
SOC <sub>Stock</sub>	NS	NS	NS	NS	-0.56	NS	NS	-0.60	NS	NS	NS	NS	NS	0.71	1.22	SOC kg m <sup>2</sup>
SPR	NS	NS	NS	NS	0.52	0.52	NS	NS	NS	NS	NS	NS	NS	0.86	3.13	$\mu$ g CO <sub>2</sub> -C g <sup>-1</sup> SOC h <sup>-1</sup>

Standardized coefficients indicating variable importance in the LARS and bSS prediction models (see Methods). K<sup>+</sup> and RMSD are computed through cross-validation. MAP, mean annual precipitation; MAT, mean annual temperature; clay, silt, soil clay and silt content; TRB, total reserve in 'base' cations; BS, base saturation of potential cation exchange capacity; Si, AI, Fe, K, P, Mn, soil total content of tested elements; pH<sub>KCI</sub>, soil pH measured in KCI solution; blanks, not selected; SPR, specific potential respiration; SOC<sub>500</sub>, SOCconcentration; SOC<sub>500</sub>, SOC stock (0–10 cm depth); NS, not significant.

differences among soils in the same climate zone are mainly related to the geochemical nature of the parent material and its weathering status<sup>15</sup>. To eliminate the effect of climate on specific potential respiration, we conducted incubation experiments under controlled conditions where temperature and moisture conditions were similar for all samples and only geochemistry varied. To assess the contributions of climatic and geochemical factors to the control of SOC response variables, we used multivariate modelling and (partial) correlations (see Methods).

The respiration data show that soils with high SOC<sub>Stock</sub> generally respired CO<sub>2</sub> at lower rates per unit C during a 50-day incubation than soils with low SOC contents (Fig. 1 and Supplementary Data Table 3). The quartile of samples with the lowest SOC<sub>Stock</sub> ( $1.4\pm0.3$  kg C m<sup>-2</sup> (0–10 cm depth)), predominantly from arid regions with extremely high or low annual temperatures, respired 2.4 times more than the quartile with the highest SOC<sub>Stock</sub> ( $6.8\pm0.8$  kg C m<sup>-2</sup> (0–10 cm depth)), predominantly from humid regions with mild to warm temperatures. In addition, about

 $38\pm15\%$  of  $SOC_{Stock}$  in the lowest quartile soils is microbially available (SOC\_{Microbial}), whereas this is only 13  $\pm$  15% for the highest quartile. Furthermore, in humid regions with mild to warm temperatures, where (bio)chemical weathering rates are high, SOC is predominantly found in association with the mineral fraction (SOC<sub>Mineral</sub>; see Methods and Supplementary Information 1.4 for details on SOC fractionation results and interpretation). Hence, organo-mineral interactions create physico-chemical barriers for microorganisms to access SOC sources, leading to large, protected SOC stocks in the humid regions with mild to warm temperatures. In contrast, in arid regions with extremely high or low temperatures, where soil weathering is largely driven by physical factors (temperature-driven mechanical shredding of minerals)<sup>16,17</sup>, less SOC is associated with minerals. This finding, together with the high SPR and SOC<sub>Microbial</sub>, suggests that physico-chemical protection of SOC from decomposers is limited in arid soils. Our results show that geochemical parameters have the highest prediction power for the investigated SOC response variables (Table 1). The Si

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**Figure 2** | **Partial correlations between SOC response and climatic variables.** Change of correlation between SOC response and climatic variables controlled for geochemical variables separately and all combined (column 'Geochem'). Difference between zero-order and partial correlations indicate the level of dependency of a given predictor and the SOC response. The colour and numbers shown indicate the strength and sign of the correlation. (No change in colour between controlled variable and zero-order = no dependency; decrease/increase of colour intensity = loss of/gain of correlation.) Significance of the correlations (\*) is evaluated at the 0.05 level. Abbreviations are explained in the caption to Table 1.

concentration was a key predictor and the only variable maintained in all models. In contrast, precipitation was generally of minor importance in all models combining geochemical and climatic predictors; temperature was not important in any model.

Further support for the importance of geochemical soil properties is derived from the partial correlation analysis (see Methods for details). Although the correlations between precipitation and SOC response variables are highly significant (zero-order correlations in Fig. 2) the partial correlation analysis shows that the Pearson correlation coefficients between precipitation and SOC<sub>%</sub>, SOC<sub>Stock</sub> and SPR response variables decreased significantly after removing correlations with all geochemical predictors. In sharp contrast, no such strong decrease was observed in the strength of the correlations between SOC response variables and most geochemical predictors (except for BS and Si) when removing correlations with all climatic predictors (Supplementary Data Table 8). Annual temperature had no effect on the prediction power of geochemical variables (see Fig. 2 and Supplementary Fig. 2). However, annual temperature played a slightly larger role when controlling for the effect of all geochemical predictors combined, as the correlation of temperature with SOC variables increased slightly when controlling for the effect of geochemical variables (Fig. 2). All of these results indicate that SOC response variables partly depend on climatic variables, independently of geochemical soil conditions, but that these relationships are much weaker than those between geochemical predictors and SOC response variables. This conclusion is supported by the identified importance of Si, for which high values are indicative of high SPR and low SOC<sub>stock</sub>, and related to either a lower degree of chemical weathering or felsic geochemistry of the parent material. Overall, precipitation showed high correlations with SOC response variables, but was only a weak predictor of SOC response variables owing to the dominance of geochemical variables. Hence, our results clearly indicate that, in the long-term, climatic variables have predominantly indirect effects on SOC dynamics via their influence on soil geochemistry.

Undoubtedly, climatic variables directly control the SOC cycle at shorter annual timescales, through processes such as heterotrophic CO<sub>2</sub> respiration and photosynthetic CO<sub>2</sub> fixation. Hence, current research on global scales focuses on changes in NPP and C inputs to soils to assess the consequences of global change. However, we argue

that climate is not the main control for SOC storage on decadal to centennial timescales (see Supplementary Information 1.4) during which the SOC storage potential evolves because of mineral weathering. Instead climate acts largely as a driving factor through governing soil weathering, which results in geochemical changes in soils that directly control SOC stabilization in the longer term. In topsoils, such as the ones investigated here, high SOC stocks are driven predominantly through physico-chemical stabilization of C with minerals (see Supplementary Information 1.5). Climate change on decadal timescales will probably affect NPP and decomposition, but the effects of changing inputs/outputs of C to soils are constrained by geochemical soil properties.

Hence, our data clearly shows that soil geochemistry is a crucial factor for predicting SOC stocks and dynamics at larger scales. Thus, uncertainty around the global distribution and climate feedback of SOC is probably due to inadequate representation of the geochemistry of soils in current global assessments and ESMs. Understanding the effects of climate change on SOC dynamics also requires understanding the relationship between climate and soil geochemistry, because the mineral matrix ultimately controls the fate of SOC. Only recently, first steps were taken to represent some key geochemical mechanisms controlling SOC, such as the stabilization of C by association with minerals and/or within soil aggregates, into ESMs applied at global scales<sup>3,18</sup>. In ESMs, soils are typically considered as simple textural matrices in which heat and water fluxes occur. However, the mechanistic interaction of SOC with minerals is sufficiently understood<sup>19,20</sup> to incorporate them into ESMs and thus further enhance their predictive power. However, in addition to geochemical controls, this will also require an adequate representation of SOC temperature sensitivity, the molecular structure and recalcitrance of molecules to decomposition, potential sources for SOC priming or nutrient limitation in soils, microbial community structures or environmental controls (soil moisture and oxygen limitation; see further discussion Supplementary Information 1.2). Thus, further efforts should focus on obtaining the required global scale biogeochemical and environmental soil data to represent SOC stabilization mechanisms and direct process-related controls in ESMs.

In conclusion, we present evidence that the long-term SOC stabilization potential of soils under similar vegetation depends

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strongly on the reactivity of the soil mineral phase. Whether temperature or precipitation governs the response of mineral reactivity depends on the prevailing climatic conditions under which soils have developed and whether temperature or moisture is limiting soil weathering (see also discussion in Supplementary Information 1.4). Hence, analysing the geochemistry of soils formed under natural conditions, at a global scale, could substantially enhance our understanding of the dynamics of the global terrestrial SOC cycle. Furthermore, including mineral-driven stabilization in ESMs will improve our predictions of SOC feedbacks to warming<sup>1,21</sup>. Data at present informing ESMs on C turnover responses to global change are mostly derived from controlled experiments under elevated  $[CO_2]$  and/or with a focus on climatic and biotic factors<sup>1,3</sup>, implying that minerals have limited importance for SOC dynamics. This contradicts our findings regarding SOC variables of natural soil systems, which reflect long-term (decades to millennia) interactions of factors, varying in both strength and duration. If ESMs consider climate only as a direct control of SOC dynamics, large inaccuracies are likely to arise because predictions for a changing climate will not account for changes in soil mineral phases.

### Methods

Methods and any associated references are available in the online version of the paper.

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#### **Author contributions**

S.D., P.B. and E.Z.V. designed the research. E.Z.V., M.C.P., A.C.-K. and C.M. conducted sampling campaigns. S.D., A.S. and M.B. collected and analysed the data. S.D., P.B. and J.S. interpreted the data. All authors contributed to the writing of the paper.

#### Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to S.D.

#### **Competing financial interests**

The authors declare no competing financial interests.

# LETTERS

## Methods

Research sites, selection criteria and sampling. Between December 2012 and April 2013, 24 sites were sampled across Chile and the Antarctic Peninsula, covering a vast range of geoclimatic conditions (Supplementary Table 1). We covered all major global climate zones under which natural grassland and shrubland evolve, including hot, temperate and cold, as well as both humid and arid zones to provide a global inference space for our results. Sampling sites were selected that provided: carbonate-free soil samples (null HCl reaction); varying soil moisture regimes (aridic, ustic, xeric, udic and perudic); varying soil temperature regimes (thermic, isothermic, mesic, isomesic and cryic); variation in key geochemical properties of soils related to soil quality, weathering and SOC stabilization via organo-mineral interaction (CEC, BS, total content of Si, Fe, Mn, Al); similar vegetation; and no human disturbance (natural prairie, grassland or shrubland)<sup>22</sup>. Our sites did not include wetlands, where at least part of the year anaerobic soil conditions prevail, reducing rates of decomposition, and the accumulation of large C stocks. Likewise, forest sites were excluded, meaning that the factors important for accumulation of C in forest soil organic layers are not considered. These processes are beyond the scope of our study focusing on comparable grassland/shrubland systems. The sampled soils represent pedons of soil series from the official regional soil surveys conducted by the Chilean Natural Resources Information Centre (CIREN) and cover 11 WRB Soil Taxonomy groups (Durisol; Arenosol; Chernozem; Kastanozem; Phaeozem; Andisol; Cambisol; Gleysol; Acrisol; Leptosol; Cryosol) (Supplementary Table 1). Following published sampling methodology<sup>23</sup>, 20 randomized soil cores (0 to 10 cm depth) were collected from a randomly chosen  $25 \times 25$  m soil plot and mixed. At each study site bulk density was determined using Kopecky cylinders and each composed sample (2 to 3 kg) was sieved to remove soil fauna, rocks fragments (>2 mm) and fine roots, then transported in coolers to laboratories at Concepción University, where they were stored in cooling chambers at -20 °C until analysis.

Climate and vegetation. Mean annual temperature and precipitation data for the sampled sites in Chile were taken from the WORLDCLIM data set<sup>24</sup> records for the period 1950-2000 and for the Antarctic Peninsula from the climate records of the nearest research stations: 'Esperanza' and 'Bellingshausen'. Most grasslands in Chile are derived from the removal of forest since the arrival of European settlers through clearing and fire, or more recently following exotic Pinus or Eucalyptus plantations. Chile has only a small number of native grass species and most were imported by the Europeans. The selected study sites are not intensively managed and are used only for extensive grazing and rangeland. Thus, establishing plant communities similar to natural grasslands in Europe and Western Asia<sup>25</sup>. The principal vegetation formations of the study transect and their main characteristics are described in ref. 26, and dominant and secondary vegetal species were identified for each site (Supplementary Table 2). In the north, the sparse desert coastal scrub vegetation extends into the interior between 24° and 32° S, generating a transition zone from the Atacama Desert in the north towards the winter-wet Mediterranean climatic zone of Central Chile. It encompasses open shrub (matorral) vegetation that gradually changes from 30° S onwards to xerophytic scrub further south. Entering into the Mediterranean climate zone, the vegetation changes to a sclerophyllous scrub. Further south, climatic conditions with areas of high rainfall and modest temperate regimes have led to the development of large areas with deciduous and evergreen broadleaved forests that dominate the natural vegetation of Central and Southern Chile. South of 47° S, precipitation exceeds 4,000 mm yr<sup>-1</sup> and the vegetation becomes increasingly moorland. Further south, along the low Andes in Southern Patagonia and Tierra del Fuego, the vegetation is dominated by gramineous steppe, with characteristics governed by a marked precipitation gradient ranging from 4,000 mm yr<sup>-1</sup> at the western side to 300 mm yr<sup>-1</sup> at the eastern side. The Antarctic Peninsula then closes the gradient of climatic variability within the transect with harsh climatic conditions characterized by short vegetation periods and generally low mean annual temperatures. Vegetation is generally sparse and only two flowering plants occur along the northern and western coasts of the Antarctic Peninsula in areas with the mildest maritime climate in the region.

**Soil analysis.** pH, CEC, BS and soil texture. Soil pH was determined potentiometrically in 25 ml 0.01 M CaCl<sub>2</sub> (1:2.5 soil:solution ratio) with a glass electrode using a portable multi-parameter meter HI9828 (Hanna Instruments US). Potential cation exchange capacity (CEC<sub>pot</sub>) was determined by quantifying NH<sub>4</sub><sup>+</sup> exchanged with 2 M KCl after saturating cation exchange sites with ammonium acetate buffered at pH 7.0 (ref. 27). Exchangeable Al was extracted by 1 M KCl solution and determined colorimetrically. The total percentage base saturation (BS), defined as the relative availability of each cation for CEC<sub>pot</sub>, was calculated as a percentage of CEC<sub>pot</sub>. Soil texture was measured on composite samples of each study site using the hydrometer method following ref. 28. For samples containing >5% organic C, samples were pre-treated with 10% H<sub>2</sub>O<sub>2</sub>.

**TRB and total elemental composition.** We measured the total reserve in 'base' cations (TRB, the sum of total Ca, Na, K and Mg, in cmol<sub>c</sub> kg<sup>-1</sup>) following

published protocols<sup>29</sup>. The TRB can be used to assess the degree of weathering and the weathering potential of soils by assessing the abundance of Ca, Na, K and Mg cations. To express the nature and amount of weatherable minerals and the amount of metals potentially available to form organo-mineral associations, the total elemental content (TEC) was determined for each of these cations as well as for Si, Fe, Al and Mn, by inductively coupled plasma-optical emission spectrometry (ICP-OES) after borate fusion. High TRB indicates a low degree of soil weathering and low TRB a high degree of soil weathering.

**Soil incubations.** We incubated three replicate samples of 80 g soil from each study site. After a 10-day pre-incubation period, respiration was measured during a 50-day period while keeping moisture (at 60% soil water holding capacity) and temperature (20 °C) constant. Each sample was put in a 1,000 ml sealed Mason jar with no further additives, except that evaporated water was replaced during the experiment. Thus, we established stable conditions for microbial activity to induce respiration close to the potential maximum heterotrophic soil respiration rate<sup>30</sup>. To avoid CO<sub>2</sub> saturation effects influencing microbial decomposition processes, the incubation jars were flushed with fresh air after each measurement. Samples of the gas mixture within the incubation jars were taken periodically every three to seven days throughout the experiment and analysed for CO<sub>2</sub> concentration using a gas chromatograph (Shimadzu GC-14B, Shimadzu Scientific Instruments). We calculated specific potential respiration as CO<sub>2</sub>–C per unit SOC.

Soil C fractionation, C measurements and recovery rates. A sample of 80 g of each soil was fractionated in triplicate to derive functional SOC pools. We used a method based on the conceptual SOC fraction model proposed by ref. 31 (Supplementary Fig. 1). Briefly, the scheme consists of a series of physical fractionation techniques applied to isolate SOC fractions, differentiated by stabilization mechanisms (chemical, biochemical and physical), which can also be associated with different turnover times and SOC stability. SOC was fractionated into coarse particulate organic matter (>250  $\mu$ m), micro-aggregate-associated SOC (250–53  $\mu$ m), and non-aggregated silt and clay aggregated SOC (<53  $\mu$ m) using a micro-aggregate isolator.

The microbial available bulk SOC pool (SOC<sub>Microbial</sub>) was estimated using oxidation with 6% sodium hypochloride according to ref. 32 and inversely related to the mineralizable SOC fraction. Note that the fraction of SOC that is extractable with this method cannot be purely compared to biological mineralization, as the fraction of chemically oxidizable SOC is sensitive to soil mineralogical conditions<sup>33</sup> and also related to higher uncertainties between replicates (Fig. 1). Thus, we used the method only as an additional proxy in combination with the measured specific potential respiration (SPR) rates and the measured amount of mineral-associated and particulate organic matter, as the investigated gradient spans a wide range of mineral versus POM-associated C ratios.

 $\rm SOC_{\#}$  was measured in 1 g ground subsamples using a dry combustion analyser (Variomax CN, Elementar GmbH) with a measuring range of 0.2–400 mg C g $^{-1}$  soil (absolute C in sample) and a reproducibility of <0.5% (relative deviation). Recovery rates exceeding 97% and 91% were obtained for the soil mass and C mass, respectively, across all fractions. The isolated fractions were analysed for total SOC using an elemental analyser (ANCA-GSL PDZ) coupled to an Isotope Ratio Mass Spectrometer (2020, SerCon).

**Incentives for applied scheme.** The gross of the annual, short-term soil-atmosphere C fluxes is related to decomposition of labile, non-protected SOC. SOC is not a homogeneous pool but consists of fractions with different turnover times ranging from days to millennia. Soils can vary greatly in their potential to sequester C owing to their physical and geochemical properties. SOC can be stabilized against decomposition by three key mechanisms: inherent biochemical recalcitrance, organo-mineral associations by interaction with mineral surfaces, and physical protection by spatial separation of C from decomposers or inaccessibility of SOC within soil aggregates (for an overview see ref. 20). Derived from fractionating the sampled soils into functional carbon pools (Supplementary Fig. 1), we evaluated with the acquired data the relative importance of different geochemical parameters, taking into account the amount of microbially available C (SOC<sub>Microbial</sub>) and C stabilized through interaction with minerals (SOC<sub>Mineral</sub>), either within aggregates (m) or associated with free silt and clay particles (s+c) and as particulate, non-mineral-associated organic C (CPOM).

**Statistical analysis.** All statistical analyses were performed with R statistical software (R 3.1.1; ref. 34) and the packages 'leaps', 'lars', 'caret', 'psych' and 'relaimpo'.

**Predicting SOC response variables and relative importance of predictors.** To identify variables that have the greatest prediction power for the selected SOC response variables, we used three linear and nonlinear multivariate models: best subset (BSS), least angle regression (LARS) and piecewise linear regression (CUBIST). BSS regression tests all possible combinations of the input variables and finds a subset of size *k* that gives the highest prediction power at the lowest

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prediction error (for example,  $R^2$ , mean squared error, or Akaike Information Criterion). The LARS algorithm provides an efficient way to solve the least absolute shrinkage and selection operator (LASSO) path of solutions. LASSO is a linear regression method that minimizes the sum of squared errors with a penalty on the sum of the absolute values of the coefficients ( $\ell$ 1-norm). Effectively, setting the penalty sufficiently high will cause some of the coefficients to shrink towards zero and ultimately remove the corresponding variables from the set of predictors. An overview of BSS and LARS is given in ref. 35. CUBIST is a model tree approach combined with a nearest-neighbour correction<sup>34</sup>, which creates a tree structure defined by a set of rules with linear models at the terminal nodes. Cross-validation results showed that the two linear models, BSS and LARS, provided the best predictions (Supplementary Table 4). The relative importance of the variables determined by LARS and BSS for predicting the response variables was computed as the standardized regression coefficient. The higher the coefficient, the higher its relative importance for the prediction of the SOC response variables.

**Testing interrelations of climatic and geochemical predictors.** Bivariate relationships between climatic variables (precipitation and temperature) and SOC response variables were estimated using zero-order correlations and partial correlations by controlling for a single geochemical variable and all geochemical variables combined. Similarly, relationships with geochemical variables (Al, BS, clay and silt content, Si and TRB) were controlled for climatic variables.

Partial correlations control the effect of a given predictor on the relationships between other predictors and response variables, and estimate the strength of the linear associations between two variables (for example,  $SOC_{Stock}$  with Si) that cannot be accounted for by the variability in one or several other variables (for example, precipitation). A more detailed interpretation and discussion of the partial correlation results is given in Supplementary Information 1.1.

Level of significance, multicollinearity and model quality assessment. The significance of correlations at the 0.05 level was computed using a *t*-test with the null-hypothesis that there is no correlation. For partial correlation, the test was adjusted by using (n-2)-s degrees of freedom, where n is the number of observations and s is the number of variables partialed out. Before model fitting, high multicollinearity amongst the independent variables was reduced by computing the variance inflation factor (VIF) and iteratively removing variables with the highest VIF (sand content, Al/Si ratio), until only variables with VIF < 10 remained. Linear models were checked for normality and homoscedasticity. Owing to the relatively low sample size (n = 24 plots with three replicates), and to avoid over-interpreting the data, no interaction terms were allowed to enter the prediction models and all models were cross-validated. The same cross-validation partitions were used in all models. For cross-validation, we applied a leave-one-group-out approach with 20 repetitions/data partition having a 0.75 selection probability. Samples were selected by splitting the dependent variable into groups based on percentiles and sampling within these groups. Each data partition was used to fit a model, predict the remaining samples and compute squared errors. The models were sequentially developed on a grid of model parameters (fraction of  $\ell$ 1-norm of the standardized coefficients to the maximum  $\ell$ 1-norm for LARS and

maximum number of variables for BSS regression). To avoid producing complex CUBIST models, the parameters were fixed and set to zero for the number of neighbours and one for the number of committees. Model performance was evaluated with the Root Mean Square Error of Cross-Validation (RMSE<sub>cv</sub>, that is, mean RMSE over the 20 partitions). The best model parameters were defined as those producing the most parsimonious model having a RMSE<sub>cv</sub> within one standard error of the minimal observed RMSE<sub>cv</sub>, as suggested in ref. 36.

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