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Assessing soil functioning: What is the added value of soil organic carbon quality measurements alongside total organic carbon content?

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ABSTRACT

Soil organic carbon (SOC) content is the most widely used soil health indicator, but many soil functions are also influenced by the quality of SOC. Yet, standardized SOC quality parameters that can be used in soil health assessments in addition to SOC content are still in development. Here, we investigated the relationships between various SOC parameters (both quantity and quality) and soil functions.

We collected 223 soil samples from arable fields in two contrasting Dutch soil types i.e., marine clay and sand. For each sample, we assessed three soil functions (i.e., biological population regulation, element cycling, and soil structure and water regulation) by measuring five indicators per function. We also analyzed SOC quality with four techniques (C:N-ratio, POX-C, Rock-Eval, POM-MAOM fractionation), resulting in 21 SOC quality parameters, and measured SOC content. We then determined for each soil type how much variation in each function indicator was explained by the SOC parameters and other measured intrinsic soil properties.

We found that SOC parameters and intrinsic soil properties explained at most 30 ± 22% of the variation in soil function indicators. SOC content explained 9 ± 16% of the variation across functions and soil types. Including one single SOC quality parameter alongside SOC content never had significant added value in explaining soil functions. Only including multiple Rock-Eval parameters alongside SOC content significantly increased the explained variation compared to SOC content alone, as well as combining multiple parameters from the four different SOC quality techniques.

We conclude that the relationships between the SOC quality parameters and soil functions are insufficiently straight-forward to add significant explanatory power to SOC content alone. We recommend that before including SOC quality parameters in soil health monitoring, more emphasis should be put on evaluating their relation to soil functions and their potential redundancy when used alongside SOC content.

1. Introduction

Soils play a key role in providing multiple ecosystem services to society, such as water regulation, carbon and nutrient cycling and the provision of food, fiber and fuel (Schulte et al., 2014; Bünemann et al., 2018). These ecosystem services are underpinned by soil functions, that can be defined as bundles of soil processes that arise from the interactions between physical, chemical, and biological properties of the soil (Creamer et al., 2022). Soil organic matter (SOM) plays a key role in many of these soil functions, especially those that are related to soil structure, soil biota, and element cycling (Hoffland et al., 2020; Kopittke et al., 2022b). Some soil functions mostly result from the decomposition of SOM, whereas others derive more from the retention of SOM (Janzen, 2006). The decomposition of SOM provides energy and nutrients to soil organisms that are involved in at least 26 processes underlying soil functioning (Creamer et al., 2022; Zwetsloot et al., 2022). The retention of SOM improves habitat for plants and soil life, contributes to soil structure and water retention, enhances the reactive surface in soils and

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thus the capacity to hold nutrients and contaminants, and underlies soil carbon sequestration (Hoffland et al., 2020). Often, soil functions result from both the decomposition and the retention of SOM, since for example biota need both fuel and a favorable habitat (Hoffland et al., 2020). Trade-offs between different functions may also occur, for example management practices that inhibit microbial activity, such as no-tillage, may increase carbon sequestration but reduce nutrient provisioning to plants (Janzen, 2006; Vrebos et al., 2021; Zwetsloot et al., 2021). Optimizing all soil functions simultaneously is therefore difficult, if not impossible, and instead it has been recommended to target land management based on a selected set of prioritized soil functions (Vazquez et al., 2021; Zwetsloot et al., 2021). A higher content of SOM is generally assumed to indicate a higher potential to perform multiple soil functions and hence to improve overall soil health (Reeves, 1997; Deb et al., 2015; Herrick and Wander, 2018; Kopittke et al., 2022a). Yet, the role of SOM characteristics, or in other words the SOM quality, in determining individual soil functions is not well understood (Hoffland et al., 2020). This understanding can support developing land management practices that target specific soil functions. Moreover, parameters that represent labile SOM fractions may serve as early indicators to evaluate impacts of management practices on soil health, since they respond faster to changes in management and land use than total soil organic carbon (TOC) content (Lefroy et al., 1993; Marriott and Wander, 2006). The development of parameters that reflect the characteristics, or quality, of SOM and that can be included in soil health assessment has therefore received increasing attention in recent years (Duval et al., 2018; Bongiorno et al., 2019; Ramírez et al., 2020; Pulleman et al., 2021; Liptzin et al., 2022).

The properties of SOM that are relevant to soil functioning are often related to biological degradation and therefore indirectly relate to the stability of SOM. Biological degradation depends on the chemical complexity, nutrient density and accessibility of SOM and prevailing environmental conditions, besides the metabolic characteristics and trophic interactions of the soil community (Schmidt et al., 2011; Raczka et al., 2021). Regarding SOM properties, the following considerations are relevant: 1) the chemical complexity of SOM influences the required energy and diversity of metabolic pathways that microbes employ to decompose SOM compounds, and the energy reward upon decomposition (Raczka et al., 2021), while this complexity can in case of pyrogenic carbon render biochemical stability (Six et al., 2002; Schmidt et al., 2011); 2) the nutrient density derives from the content and stoichiometric ratio of the main nutrients present in SOM, i.e.: nitrogen (N), phosphorus (P), and sulfur (S) (Tipping et al., 2016); and 3) the accessibility of SOM is influenced by the association of SOM with the soil mineral matrix into aggregates or organo-mineral complexes, providing physical and chemical stability, respectively (Six et al., 2002; Schmidt et al., 2011). The term "soil organic carbon", abbreviated as "SOC", is often used as synonym for SOM, which consists for 48–58% of carbon (Nelson and Sommers, 1983). In this study, we will focus on the carbon component, and we will therefore use the term "SOC quality" when referring to the three described properties of SOM that relate to soil functioning, i.e. the complexity, nutrient density, and accessibility of SOM. We will use "SOC" without further specification when referring to soil organic matter or carbon in general, and will use total SOC content (in $g.kg^{-1}$) as measure for the quantity of SOC. We will use "SOC parameters" when referring to the selected SOC quality and quantity parameters of this study.

The techniques that are currently available to characterize SOC quality can be grouped into physical and chemical SOC fractionations, thermal analyses, and molecular characterizations (Hoffland et al., 2020). SOC fractionations aim at isolating SOC pools with contrasting turnover times, based on physical (i.e., size/density) or chemical (i.e., extraction, hydrolysis, oxidation, destruction of mineral phase) methodological principles (Haynes, 2005; Poeplau et al., 2018). Thermal analyses assess the energetic barriers experienced by the decomposer community by estimating the required activation energy to decompose SOC (related to thermal stability) and/or the energy release (Differential scanning calorimetry (DSC)) upon SOC decomposition (Barré et al., 2016). Molecular characterizations encompass a wide variety of wet chemical, spectroscopic and chromatographic techniques that identify the molecular structure of SOC at varying levels of detail. Molecular features relevant for soil functioning include elemental ratio's that proxy the nutrient density of SOC for biota, or functional groups and properties that define the reactivity of SOC towards the mineral matrix and other soil compounds among which nutrients and contaminants. Most of these characterization techniques provide operationally defined parameters that mainly assess the stability of SOC or assess "what sits where", but these parameters do not necessarily directly relate to soil functioning (Hoffland et al., 2020). Moreover, it is not yet clear what is the added value of SOC quality beyond SOC content and soil intrinsic properties (e.g., texture, pH) that are commonly measured in soil health assessments.

Unraveling what operational metrics for SOC quality relate to which soil functions can be highly useful to better support the assessment of, and advice for, farm practices that seek to strengthen specific soil functions by managing SOC quality. We therefore aimed to assess the relationship between SOC and soil functions related to SOC degradation and stabilization, i.e., 1) biological population regulation; 2) element cycling, 3) soil structure and water regulation. Soil functions cannot be measured directly and instead are assessed using indicators that are based on the mechanistic processes underlying soil functions (Bünemann et al., 2018). Therefore, we investigated how well those indicators for different soil functions were explained by SOC content and different SOC quality parameters in sandy and clay soils. We hypothesized that including SOC quality parameters in addition to SOC content is especially relevant for explaining soil functions that strongly depend on biotic processes, i.e. element cycling and biological population regulation.

2. Materials and Methods

2.1. Site selection

Soil samples were collected as described in (van Rijssel et al., 2022). In short, we collected soils from arable fields of organic farms that had been converted from conventional arable agriculture between 1 and 69 years ago, and paired fields of neighboring conventional farms. All fields, irrespective whether they were conventionally or organically managed, had undergone inversion tillage at least once during the last 5 years, were part of a wider crop rotation that included at least one tuber crop, and had a cereal, grass or legume crop at the moment of sampling. Fields were located on sandy and marine clay soils, classified in the Dutch soil system as Hn21/zEz21 and Mn25a/Mn35a, respectively. According to FAO World Reference Base WRB (WRB, 2022), sandy soils are classified as Anthrosols with $\leq$17.5% silt (<50 μm) and an A-horizon of at least 30 cm. Clay soils were Fluvisols that derive from clay deposition in an originally marine environment, and had a clay content between 10 and 31%. We sampled 48 arable fields (of which 50% organic farms) on clay and 26 fields (50% organic) on sand in July 2017. Three subsamples were taken per field, resulting in a total of 222 soil samples.

2.2. Sample collection, field measurements and storage

At each sampling point, within an area of 1 × 1 m, we measured 4 times penetration resistance and took two disturbed (one of ±1 kg, one of ±5 kg) and two undisturbed soil samples, and one bulk density ring (100 cm^3) from the 5–15 cm mineral top soil. We collected the undisturbed soil samples for the analysis of water stable aggregates with a spade by cutting a ±15 × 15 × 10 cm cube at 5–15 cm depth, removing the cutting edges and crumbling the insides carefully into a flowerpot to protect the soils from compaction during transport. Both field moist, disturbed soil samples were stored cool, and passed within a week through a 10 mm mesh to remove coarse elements from the sample. The

±1 kg disturbed soil sample was air-dried and subsequently sent to the commercial laboratory Eurofins-Agro for analysis of soil texture and cation exchange capacity. The ± 5 kg disturbed soil sample was stored at 4 °C, from which three subsamples were taken. A first subsample of 6 g was sieved over 4 mm, of which 1 g was stored in an Eppendorf tube at −80 °C within a week, for soil microbial community characterization. A second subsample was used to measure pH-H_2O and potential nitrogen mineralization within 2 months. A third subsample was used within 5 months as soil inoculum for a laboratory incubation in which the decomposition of three different substrates was measured. The undisturbed soil samples were pooled within a week and crumbled gently through a 10 mm sieve, air-dried (±25 °C), and stored dark at 4 °C. From the undisturbed soil samples, a subsample was taken for the isolation of water stable aggregates, and another sub-sample was sieved over 2 mm for carbon characterizations and oxalate extractions. For elemental C:N analysis, samples were ground with a ball-mill for 1 min with frequency 18.0 s^{-1}. The 2-mm sieved soils and ground soils were stored dark at 4 °C in between analyses.

2.3. Definitions of soil functions, function indicators and intrinsic properties

For the purpose of this study, we focused on three soil functions that are expected to be directly or indirectly influenced by SOC degradation or stabilization (based on (Bünemann et al., 2018; Hoffland et al., 2020; Creamer et al., 2022; Zwetsloot et al., 2022) and that are important for arable farming: 1) "biological population regulation"; 2) "element cycling"; and 3) "the regulation of soil structure and water". We decided not to consider carbon sequestration as function, since we only measured SOC content at a single soil depth (i.e., 5–15 cm).

We assessed soil functions with indicators that either measure the process itself (e.g., potential nitrogen mineralization), a characteristic of the actor(s) performing the process (e.g., fungal diversity), or the result of the process (e.g., water-stable aggregates). Some function indicators, especially those that represent actors, could represent processes that contribute to more than one of the selected soil functions. However, we wanted to have independent measures and an equal number of indicators (n = 5) for each soil function for statistical analyses. We therefore used each indicator only once for the most representative soil function, similar to (Li et al., 2023) (for an explanation of this classification: see Table 1).

2.4. Measurements of soil function indicators

2.4.1. Biological population regulation

Disease suppression (DisS) was measured based on the number of cauliflower seedlings infected with the widespread soil-borne fungal pathogen *Rhizoctonia solani AG 2-1,* known to cause severe yield losses (Domsch et al., 2007). Cauliflower was chosen as crop species to exclude soil legacy effects as much as possible (Philippot et al., 2013; Hannula et al., 2021), as most agricultural fields of our study did not include cabbage species in the rotation. We followed a method modified from (Postma et al., 2010): For each soil sample two 203 × 54 × 28 mm trays were filled with 150 g dry soil, totaling 444 trays. Sixteen pre-germinated cauliflower seedlings (*Brassica oleracea* var. *botrytis* Flora Blanca) were transplanted into these trays. The seedlings were planted in two parallel 8-seedling rows with 2 cm space between seedlings and 2 cm space between rows. Trays were then placed in a greenhouse (21/16 °C day/night, no additional light provided) and watered every other day. After one week, half of the trays were inoculated with *R. solani* by placing two *R. solani* AG 2-1 infested agar-plugs 1 cm deep into the soil in contact with seedling roots at one end of the tray. The other half of the trays were not inoculated with *R. solani,* but instead had a sterile agar-plug placed on their roots as a control, resulting in 222 trays with cauliflower + *R. solani* and 222 trays with only cauliflower as

Table 1
Overview of the selected indicators for each soil function that includes firstly a short explanation of each function indicator, followed by a motivation for the selection of the indicator for the corresponding soil function.

Soil functions		
Biological Population regulation	Element Cycling	Soil structure and water regulation
Disease suppression (DisS) The performed disease suppression test is a direct measure of the capability of the soil microbial community to suppress the infection of cauliflower plants by the pathogenic fungus *Rhizoctonia solani*.	*Potential nitrogen mineralization (PNM)* PNM is a direct measure of the potential of the soil community to transform organic nitrogen (N) into inorganic N under aerobic conditions, as measured in a lab incubation of 4 weeks under optimal conditions (21 °C, 70% WHC). The PNM proxies the potential inorganic N release from organic N during a growing season.	*Bulk Density (BD)* BD is the dry soil mass per unit volume, in which solids and pores are combined. BD is a measure for soil porosity in terms of volume, which affects the aeration of the soil, the capacity of the soil to store and transport water and the growth of roots.
Richness bacteria (RB) A higher bacterial richness can support disease suppression via: 1) Prevention of resistance to suppression by increased diversity of the means of disease suppression (Schlatter et al., 2017). 2) Improved adaptability to changing environmental conditions and resilience to disturbances	*Decomposition manure (DM)* The decomposition of organic matter is a primary source of plant nutrients (Sokol et al., 2022), especially in organic farming where all nutrients derive from organic sources. The functional capacity to decompose substrates has been shown to differ between soil decomposer communities (Keiser et al., 2014), which drives variation in decomposition rate of the same organic substrate by different soil communities (Keiser et al., 2011; Veen et al., 2018). A higher capability of microbes to decompose organic substrates of given chemical complexity indicates a faster cycling, hence faster nutrient release, of respective substrates. The applied solid farmyard manure is a relatively complex substrate with a moderate C:N-ratio (12.4) and high lignin content (17.8%). The manure decomposition is measured in a lab incubation of 64 days under optimal conditions (20 °C, 60% WHC), adding 0.5 g of soil to 1 ± 0.1 g of substrate (based on (Keiser et al., 2011; Strickland et al., 2009))	*Water Holding Capacity (WHC)* WHC of < 2 mm disturbed soil. WHC is a measure of the capacity of the soil to retain water in < 2 mm particles, hence excluding water that is retained in the pore network as occurring in the field. This WHC measure is mainly defined by soil texture and organic carbon (Dane and Hopmans, 2002) and determines the capacity to supply water to plants.
Richness fungi (RF) See explanation bacterial richness. Fungi are more	*Decomposition straw (DS)* See explanation manure decomposition. The applied straw had a	*Easy root penetrable depth (D2)* The depth until which plant roots can easily

(continued on next page)

Table 1 (*continued*)

Soil functions		
Biological Population regulation	Element Cycling	Soil structure and water regulation
sensitive to disturbance than bacteria (Six et al., 2006), and hence may serve as an earlier warning.	much higher C:N-ratio (86) and a lower lignin content (8.8%) than the applied manure.	enter the soil, defined here as the depth of the soil with a penetration resistance below 2 MPa (based on (Sinnett et al., 2008)).
Richness protists (RP) See explanation bacterial richness. Protists are more sensitive to disturbance than both fungi and bacteria and may therefore serve as an early warning (e.g. (Du et al., 2022; Zhao et al., 2019)).	*Decomposition cover crop (DCC)* See explanation manure decomposition. Cover crop residues are a relatively simple substrate with a comparable C:N ratio (13.2) and lower lignin content (6.9%) as the applied manure.	*Maximum root penetrable depth (D5)* The depth till which plant roots can enter the soil, below a penetration resistance of 5 MPa. Only the more rigid plant roots will be able to reach this depth (Tracy et al., 2011).
Relative abundance non-pathogenic fungi (RANPF) A higher relative abundance of non-pathogenic fungi indicates a higher proportion of fungal species that can suppress pathogens via competition, antibiosis, parasitism or predation (Hoitink and Boehm, 1999).	*Cation Exchange Capacity (CEC)* CEC is a measure for the capacity of soils to retain and exchange cations (all essential plant nutrients except P, N & S).	*Water stable aggregates (WSA)* We measured the sand-free weight percentage of macro-aggregates of 0.25–10 mm that remain stable when wetted. Larger water stable aggregates consist of smaller aggregates and soil particles (Six et al., 2004), and reflect the capacity of the soil structure and pore network to resist slaking and compaction during drying-rewetting cycles.

control. The disease suppression was quantified as the number of plants that were not damped-off after 21 days. In case both seedling rows had unequal disease spread, the lowest number was reported.

The species richness of bacteria (RB) was measured with DNA sequencing as fully described in (van Rijssel et al., 2022). In short, bacterial community composition was determined by the V4-region of the16S rRNA gene using 515f and 806 rbc. The 16S rRNA gene amplicon reads were analyzed using the dada2 pipeline (version 1.18) (Callahan et al., 2016), and chimeric sequences were removed using the consensus method. The SILVA SSU database (version 138) was used to assign bacterial taxonomy to the sequences (Quast et al., 2012).

The species richness of fungi (RF) was also measured with DNA sequencing according to (van Rijssel et al., 2022). In short, primers and the fungal community composition was determined by the ITS2-region using ITS4 (reverse) and fITS9 (forward) primers. The ITS sequences were analyzed using the PIPITS pipeline (version 2.4, standard settings) (Gweon et al., 2015), and chimeric sequences were removed by comparing UNITE with the UCHIME database (version 8.2) (Edgar et al., 2011). Fungal taxonomy was assigned by aligning sequences to the UNITE fungal database (Kõljalg et al., 2013; Nilsson et al., 2018).

The species richness of protists (RP) was measured with DNA sequencing similar to bacteria and fungi, followed by determining richness of amplicon sequence variants (ASVs) (fully described in Van Rijssel, n.d.). In short, the V4 region of the 18S rDNA was amplified using the universal eukaryotic primers 3NDf and 1132rmod (Cavalier--Smith et al., 2009; Pawlowski et al., 2012; Geisen et al., 2018; Van Rijssel, n.d.). The 18S rRNA amplicon reads were analyzed using the dada2 pipeline (version 1.18) (Callahan et al., 2016) and chimeric sequences were removed with the consensus method. The PR2 database (version 4.12) was used to assign protist taxonomy to the sequences (Guillou et al., 2012).

The relative abundance of non-pathogenic fungi (RANPF) in the community was determined based on information on identified pathogens in the Funguild database (Nguyen et al., 2016). The sum of the relative abundances of all non-pathogenic fungi was calculated per sample.

2.4.2. Element cycling

The potential nitrogen mineralization (PNM) was assessed as the difference between the concentration of nitrate (NO_3) and exchangeable ammonium (NH_4) before and after aerobic incubation. The equivalent of 10 g of dry soil weight was incubated at 70% water holding capacity and a constant temperature of 21 °C during four weeks (Keeney and Nelson, 1982; Griffin et al., 1995). NH_4 and NO_3 were subsequently extracted by suspending the incubated soil in a 1:5 d/w 1M KCl solution, which was shaken in a reciprocal shaker for 2 h at 250 rpm at room temperature, left to settle for 15–30 min, centrifuged for 10 min at 10,000 rpm, after which NH_4 and NO_3 were measured with a Skalar continuous flow analyser according to NEN-EN-ISO 11732:1997 (Keeney and Nelson, 1983).

The decomposition of farmyard manure (DF), straw (DS) and cover crop residues (DCC) was measured in a laboratory incubation that assesses the functional capacity of microbial decomposer communities to decompose organic substrates of different quality, based on (Strickland et al., 2009a, 2009b; Keiser et al., 2011). The different organic substrates were cut into pieces of 0.5–1 cm and were dried at 40 °C for at least 72 h. We then weighed 1 ± 0.1 g substrate in 50 mL plastic centrifuge tubes, and we sterilized the tubes in an autoclave at 120 °C for 20 min to kill microbes native to the substrate. We then added a 0.5g dry weight equivalent of field-moist soil to each tube, serving as inoculum of the soil microbial community. In this way, we incubated 222 soil samples per substrate type, resulting in total 666 different microcosms, at 20 °C at 60% water holding capacity for 64 days. At the end of the experiment, we determined the weight of the freeze-dried samples, from which the dry weights of the tubes and soil inocula were subtracted to obtain the weight loss of the substrates. We used this weight loss as measure for decomposition. The substrates differed in complexity with regards to lignin content (cover crop residues: 6.9%; straw: 8.8%; farmyard manure: 17.8%) and C:N ratio (cover crop residues: 13; straw: 86; farmyard manure: 12). C:N ratio was measured on a Flash EA 1112 elemental C:N analyser. Lignin content was determined by an extraction-hydrolysis procedure that aims to remove all organic compounds except lignin (Poorter, 1994): 0.25 g of dried substrate was extracted with 0.8 mL demineralized water, 2 mL of 99.9% methanol and 1 mL of to 99.8% chloroform, which was repeated for the residue after centrifugation for 10 min at 3800 rpm and discarding the supernatant. After this double extraction, the residue was hydrolyzed for 1 h in 6 mL of 3 M HCl in a hot water bath at 100 °C. After cooling down, the sample was centrifuged again for 10 min at 2500 g, the supernatant was discarded, and the residue was washed with 5 mL demineralized water and centrifuged for 10 min at 2500 g. The residue was extracted twice with the same procedure but without adding the 0.8 mL demineralized water, after which the remaining lignin was dried at 70 °C and measured on a Flash EA 1112 elemental C:N analyser.

Cation exchange capacity (CEC) was measured via Near-Infrared Spectrometry (NIRS) by Agro-laboratory Eurofins-Agro as extensively described in (Reijneveld et al., 2022). In short, the NIRS- absorbance of 125 g soil was measured in a Q-interline FT-NIRS analyzer (http://www.q-interline.com (accessed on 28 November 2021)) in a climate-controlled room at 20°. The spectral absorbance data were subsequently trimmed, to obtain wavelengths between 1000 and 2667 nm with a resolution of 16 cm^{-1}. The trimmed spectra were then related to CEC measurements obtained by the reference method (ISO 23470 (2018) and NEN 6966 (2005)), using a calibration model that is based on > 16000 reference samples ($R^2 = 0.97$, RPD = 5.8) and that has been validated with >1900 soil samples ($R^2 = 0.97$, RPD = 6.0). The calibration was performed with statistical models based on a set of 4 filters

(AMX-S2000, 2018): The Savitzky–Golay method and the partial least squares method were used to transform spectra into a new latent space, and the nearest neighbor method was subsequently subjected to Gaussian processes to obtain the final CEC data (Reijneveld et al., 2022).

2.4.3. Soil structure and water regulation

Bulk density (BD) was calculated after oven-drying (105 °C) of the collected soil in the bulk density ring (100 cm^3) and can be considered as bulk density of fine earth as our soils hardly contained any gravel >2 mm.

The water holding capacity (WHC) was determined by a method based on (Boekel, 1965; Sumner, 1999). Small amounts of water were gradually added to <2 mm, 25 g dry weight equivalent of field-moist soil in a plastic container, and the soil was mixed thoroughly to homogenize the soil water. The soil was then brought to one side of the container, and a line was drawn through the soil to the bottom surface using a spoon. The water content required for water to flow from the soil into the opening of the line was marked as the maximum WHC. Moisture content of field-moist soils was determined by drying the soil overnight at 105 °C in the oven. The WHC was calculated by dividing the total water content (i.e., sum of the initial and added water content) by the 105 °C soil dry weight.

The penetration resistance was measured in the field with an electronic penetrologger of Eijkelkamp with a steel cone of 1.13 cm. We recorded the depth at which the penetration resistance reached 2 MPa, which is the maximum pressure at which plant roots can grow easily (D2) (Sinnett et al., 2008)), as well as the depth at which 5 MPa was reached, which is the maximum pressure at which more rigid plant roots can expand into the soil (D5) (Tracy et al., 2011). We averaged the 4 penetration measurements at each sampling point.

Water stable aggregates (WSA) were determined with a wet sieving apparatus inspired by (Yoder, 1936; Beare and Bruce, 1993). In short, the apparatus consists of a metal arm with two metal frames with a stack of 3 sieves in each frame, from top to bottom: 2 mm, 0.25 mm and 0.053 mm. A subsample of 40 g (sandy soils) or 15 g (clay soils) of air-dried <1 cm undisturbed soil was placed on top of the submerged 2 mm sieve to slake for 5 min. Then, the stack of sieves was moved vertically up and down inside a basin of demineralized water to distribute the aggregates over the different sieves at a sieving frequency of 13 min^{-1} and an amplitude of 100 mm for 8 min. The resulting fractions (2–10 mm, 0.25–2 mm, 0.053–0.25 mm, <0.053 mm) were rinsed into aluminum containers, dried at 105 °C overnight and subsequently weighed. We corrected for the sand that had the same size as the aggregate fraction for the 2–10 mm, 0.25–2 mm, 0.053–0.25 mm fractions according to (Six et al., 2000). We expressed water stable aggregate stability (WSA) as the weight percentage of sand-free 0.25–2 mm and 2–10 mm sized macro-aggregates relative to total soil weight (including sand), with the following equation:

$$WSA(\%) = \frac{FDW_{2-10mm} - SDW_{2-10mm}}{FDW_{rec}} + \frac{FDW_{0.25-2mm} - SDW_{0.25-2mm}}{FDW_{rec}} \quad \text{(Eq. 1a)}$$

With $FDW_{2–10mm}$ and $FDW_{0.25–2mm}$ as the Fraction Dry Weights of the 2–10 mm and 0.25–2 mm fractions after sieving, respectively; $SDW_{2–10mm}$ and $SDW_{0.25–2mm}$ as the Sand Dry Weights of the 2–10 mm and 0.25–2 mm fractions after dispersion, respectively; and FDW_{rec} = Sum of the recovered Fraction Dry Weights of all aggregate fractions (2–10 mm, 0.25–2 mm, 0.053–0.25 mm, <0.053 mm) after sieving, including sand, and all dry weights expressed in gram.

2.5. Measurements of SOC parameters

We characterized SOC with four analytical techniques that have been included, or have been recommended to be included, in soil health monitoring programs (Soucémarianadin et al., 2018; Bongiorno et al., 2019; Lavallee et al., 2020; Cécillon et al., 2021; Radočaj et al., 2021; Liptzin et al., 2022): 1) Oxidation with dilute potassium permanganate (POXC), assumed to represent a labile (or biologically active) SOC fraction (Culman et al., 2012); 2) Elemental C:N analysis of bulk soil to obtain the carbon-to-nitrogen (C:N) ratio of SOC reflecting nitrogen dynamics (i.e., immobilization/mineralization); 3) Physical size fractionation into more labile (i.e., fast cycling) particulate organic matter (POM) and more stable (i.e., slow cycling) mineral-associated organic matter (MAOM) and subsequent analysis of organic carbon content and C:N ratio of the POM and MAOM fractions (Poeplau et al., 2018; Lavallee et al., 2020); and 4) Rock-Eval 6 (RE6) thermal analysis, resulting in thermograms from which thermal stability parameters were calculated as proxies for the activation energy of SOC (Barré et al., 2016; Cécillon et al., 2021). We also quantified the SOC released during RE6 pyrolysis, sometimes seen as a proxy for more labile SOM, and approximated the C:H and C:O ratios of SOC that reflect the degree of degradation since biogeochemically stable SOC is more oxidized and H-depleted (Barré et al., 2016; Poeplau et al., 2019; Cécillon et al., 2021). We furthermore applied the $PARTY_{SOC}v2.0_{EU}$ -model with the RE6 data to predict centennially stable and active SOC pools (Cécillon et al., 2021) and calculated the I and R index that have been suggested to represent immature and refractory SOC fractions, respectively (Sebag et al., 2016).

All techniques except that for elemental C:N analysis of bulk soil provided multiple SOC quality parameters based on different operational principles. Together, the different SOC quality parameters can be grouped into for 4 types: Element ratio's (C:N, C:H, C:O), the size (g C kg^{-1} soil) and proportion (g C g^{-1} C) of different SOC fractions, and thermal stabilities (°C). A summary with the description of the different SOC quality parameters, their classification into the different parameter types and their relationship with SOC stability is provided in Table 2. A full description of the indicators and the characterization techniques are provided in (Koorneef et al., submitted to Geoderma).

2.6. Measurements of soil intrinsic property (IP) parameters

We considered intrinsic soil properties as those soil properties that are mainly defined by the origin of the soil, and not by soil management. Soil pH was treated as an intrinsic property in this study since our marine clay soils have naturally a high pH (7–8) due to the presence of shell fragments, and because we could not find a correlation between the time since liming and pH ($R^2 = 0.01$, $p < \alpha$, Fig. S1) in our sandy soils that are naturally low in pH.

The pH was measured after shaking 10 g soils in 25 mL demineralized water for 2 h at 250 rpm.

The content of nano-sized Fe (hydr)oxides and Al (hydr)oxides were measured in an ammonium oxalate extract (Hiemstra et al., 2010), derived from the NEN-5776 protocol (Borggaard, 1992; Schwertmann, 1964). In short, 1.5 g soil was shaken for 2 h in the dark at 180 rpm in 30 mL 0.2 M ammonium oxalate at pH 3. Subsequently, the extracts were centrifuged at 3000 rpm for 10 min, whereafter Fe and Al were measured in the supernatant with ICP-OES (Thermo iCAP 6C500 DV).

The silt and clay contents were assessed via Near-Infrared Spectrometry (NIRS) in a similar manner as described for CEC by Agrolaboratory Eurofins-Agro according to (Reijneveld et al., 2022). Sand and clay weight percentages were measured with NIRS and related to sand and clay measurements obtained by the reference method (NEN 5753 (2018)), using calibration models that were based on > 49000 reference samples in case of clay (R^2 = 0.96, RPD = 7) and >8000 reference samples in case of sand (R^2 = 0.98, RPD = 4.7). Clay models have been validated with >1900 soil samples (R^2 = 0.99, RPD = 8.5), and sand models with >1800 soil samples (R^2 = 0.97, RPD = 5.3). Silt content, expressed as weight percentage, was derived by subtracting the sand and clay weight percentages from 100%.

Table 2
Overview of all soil organic carbon (SOC) quality parameters, and their theoretical relation (positive or negative) with SOC stability. Negative (−) means that a higher value for the SOC quality parameter indicates lower SOC stability, positive (+) means that a higher value for the parameter indicates a higher SOC stability. Table S1 provides an explanation for these theoretical relations. The different quality parameters are grouped in 5 different types: ER: Element ratio; SF: Size of a SOC fraction; PF: Proportion of a SOC fraction; TS: Thermal stability; NA/TS: A typical Rock-Eval index that does not belong to the other 4 SOC quality parameter types, but that was so highly correlated with T50_pyr_CH (R^2 in clay: ≥0.74; sand: >0.94) that the parameter could be considered as a proxy for TS (Koorneef et al., submitted to Geoderma).

Abbreviation	Description	Unit	Theoretical relation to SOC stability (- or +)	Parameter type
POMC_size	SOC present as particulate organic matter (POM, >50 µm), expressed in g C kg^{-1} soil or as proportion relative to total SOC content (g C g^{-1} C)	g C kg^{-1} soil	–	SF
POMC_prop		g C g^{-1} C		PF
ActiveC_size	Centennially active SOC, expressed in g C kg^{-1} soil or as proportion relative to total SOC content (g C g^{-1} C)	g C kg^{-1} soil	–	SF
ActiveC_prop		g C g^{-1} C		PF
PyroC_size	Total pyrolysable SOC, expressed in g C kg^{1} soil or as proportion relative to total SOC content (g C g^{-1} C)	g C kg^{-1} soil	–	SF
PyroC_prop		g C g^{-1} C		PF
POXC_size	Permanganate oxidizable organic carbon, expressed g C kg^{-1} soil or as proportion relative to total SOC content (g C g^{-1} C)	g C kg^{-1} soil	–	SF
POXC_prop		g C g^{-1} C		PF
MAOMC_size	SOC present as mineral-associated organic matter (MAOM, <50 µm), expressed in g C kg^{-1} soil or as proportion relative to total SOC content (g C g^{-1} C)	g C kg^{-1} soil	+	SF
MAOMC_prop		g C g^{-1} C		PF
StableC_size	Centennially persistent SOC, expressed in g C kg^{-1} soil or as proportion relative to total SOC content (g C g^{-1} C)	g C kg^{-1} soil	+	SF
StableC_prop		g C g^{-1} C		PF
Bulk_CN	The carbon to nitrogen ratio (C:N) of the bulk soil	g C g^{-1} N	–	ER
POM_CN	The carbon to nitrogen ratio (C:N) of coarse POM (>50 µm),	g C g^{-1} N	+	ER
MAOM_CN	The carbon to nitrogen ratio (C:N) of fine MAOM (<50 µm),	g C g^{-1} N	–	ER
HI	The hydrogen-index is a proxy for the atomic hydrogen to carbon (H:C) ratio of SOC (Espitalie et al., 1977).	mg CH g^{-1} C	–	ER
OI	The oxygen-index is a proxy for the atomic oxygen to carbon (O:C) ratio of SOC (Espitalie et al., 1977)	mg O_2 g^{-1} C	+	ER
T50_pyr_CH	The temperature at which 50% of SOC has converted to CH during pyrolysis.	°C	+	TS
T50_pyr_CO2	The temperature at which 50% of SOC has converted to CO_2 during pyrolysis	°C	+	TS
T50_ox_CO2	The temperature at which 50% of SOC has converted to CO_2 during oxidation	°C	+	TS
I	The I-index reflects the degree of decomposition of immature SOC fractions (Sebag et al., 2016).	unitless	–	NA/TS
R	The R-index reflects the contribution of refractory SOC fractions (Sebag et al., 2016).	unitless	+	NA/TS

2.7. Statistical analysis

We used multiple linear regression (forward stepwise selection) to determine how much of the variation in the indicator value for each soil function (Table 1) could be explained by the different SOC parameters (Table 2) and IP parameters (i.e., pH, silt content, clay content, Al (hydr) oxides content, Fe (hydr)oxides content).

We performed the multiple regression separately for marine clay and sandy soils, because 1) all intrinsic soil property (IP) parameters, 10 out of 15 soil function indicators, and 19 out of 23 SOC parameters were significantly different between the soil types as determined by two-sided Welch Two Sample t-tests (p-value < Bonferroni-corrected α, Fig. S2, Fig. S3, Fig. S4); and 2) the number of observations was different per soil type (sand: n = 81, clay: n = 144).

2.7.1. Preparing data for forward stepwise selection

In case of our sandy soils, we combined the clay and silt content into one size fraction, because the clay content was always <3%, resulting in too little variation to perform linear regression. We also removed in total 15 outliers present in function indicators that highly skewed the normality and were highly significant with a two-sided Grubbs test ($p \leq 6.7e^{-05}$). All outliers represented measurements of biological processes that can easily result in anomalous results (PNM, DM, DS, DCC), or biological measurements that can be highly influenced by the presence of infected crops during sampling (RANPF). We subsequently checked Pearson correlations among SOC parameters, and among IP parameters, and iteratively removed SOC and IP parameters until the correlation coefficients r among SOC and among IP parameters ranged between −0.9 and 0.9. In the case of SOC parameters, total SOC content was correlated the most to other SOC parameters (Fig. S7, Fig. S8). Due to our study design that puts total SOC content central, we removed the SOC quality parameters that correlated too much ($r > 0.9$ or < -0.9) with total SOC content instead, i.e., StableC_size, ActiveC_size, PyroC_size. This iterative autocorrelation test further led to the exclusion of R and I index (too highly correlated with each other and with T50_pyr_CH, Fig. S7, Fig. S8), and ActiveC_prop (too highly correlated with StableC_prop, Fig. S7, Fig. S8). For the IP parameters, the auto-correlation

test resulted in the exclusion of an additional parameter that combines Al oxide content and Fe oxide content (in mol oxide/kg soil) in both soil types, and of an additional parameter that combines clay and sand content in marine clay soils. We also confirmed that indicators describing the same soil function were not strongly correlated with each other (all correlation coefficients were <0.55; Fig. S4). We z-scaled all selected variables.

2.7.2. Procedure forward stepwise selection

To investigate how much variation in indicator values for soil functions was explained by SOC parameters, we performed forward stepwise selection based on the AIC-criterium (Akaike, 1974). Five different sets of explanatory variables were explored, i.e. 1) All SOC parameters (i.e. SOC content and all SOC quality parameters), 2) all SOC quality parameters, but forcing the regression models to always include SOC content as the first explanatory parameter, 3) all IP parameters, 4) All IP parameters but forcing the regression models to always include SOC content as the first explanatory parameter, and 5) All SOC and IP parameters which was considered to benchmark the maximum explainable variation (MEV). We used the adjusted r-squared (R^2_{adj}) as a measure for how much variation in each function indicator value was explained by each parameter set.

2.7.3. Analyzing the effect of the type (SOC/IP) and number of explanatory variables

We first explored the effect of the type (i.e., SOC and/or IP parameters) and number of explanatory variables on the explained variation in function indicator values with two-way analyses of variance (ANOVA). Different functions and soil types were considered separately. The number of explanatory variables consisted of 4 groups (i.e., 1, 2, 3 or > 3 variables) in the ANOVA analysis, but some function indicators were explained by a maximum of 3 (or less) variables, because the AIC-criterium could not be further lowered. We wanted to keep the number of observations equal for each group (i.e., number of explanatory variables) in the ANOVA. We therefore used the value for R^2_{adj} of the model with the maximum number of explanatory variables (e.g. a model with 2 explanatory variables) as a proxy for the R^2_{adj} to represent the model(s) that should have contained a larger number of explanatory variables (e.g the models with 3 and >3 explanatory variables), but were not calculated as the result of the AIC-criterium procedure. This approach thus resulted in similar R^2_{adj}-values for the models with 2, 3 and > 3 variables, since in this example the function indicator was explained by at most 2 explanatory variables. Since increasing the number of explanatory variables did not significantly affect the explained variation in any of the cases (see Results, Fig. 1), we concluded that models with the maximum number of explanatory variables were not highly overfitted and could be used for further analysis.

We then tested how the explained variation in soil function indicator values differed between soil functions and soil types, for different sets of explanatory variables, i.e., SOC content alone, or SOC in combination with the maximum number of SOC quality and/or IP parameters (sets 1, 2, 3, and 5). For each of these sets, we performed two-way ANOVAs with the explained variation (R^2_{adj}) as response variable and soil type and soil function as explanatory variables.

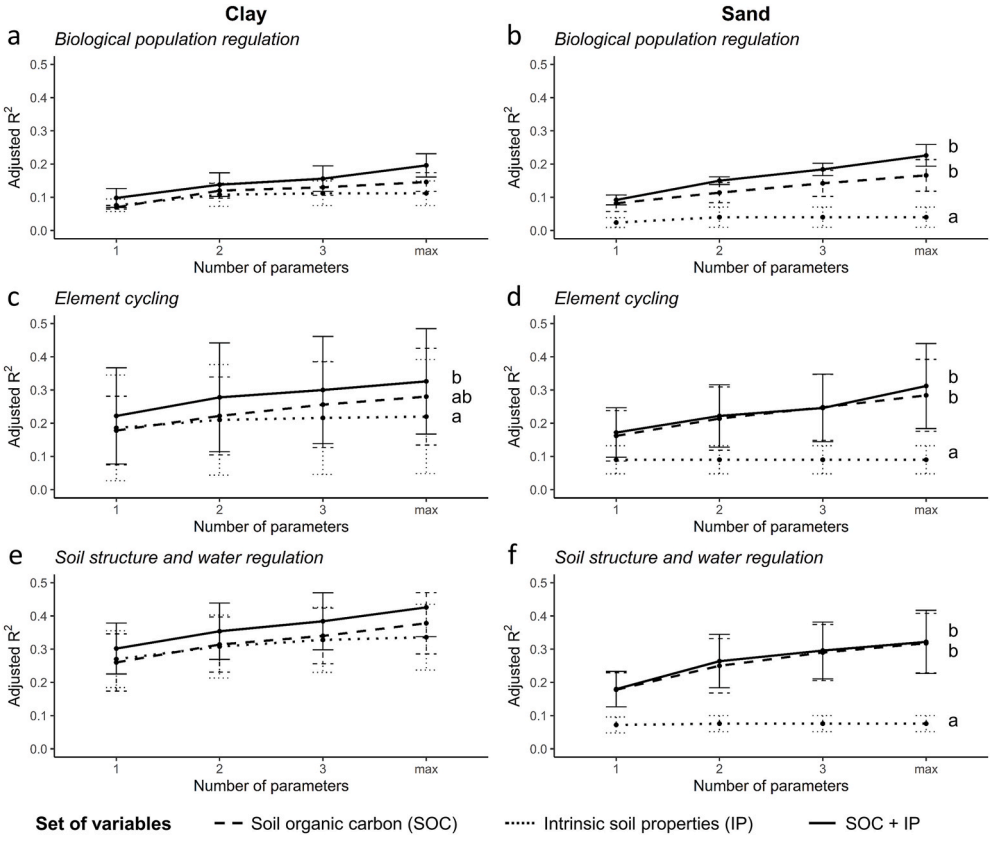

Fig. 1. Soil functions explained by different parameter types and number of parameters in clay and sand: Biological population regulation (a–b), element cycling (c–d), and soil structure and water regulation (e–f)) for each soil type. The explained variation is expressed as the mean adjusted R^2 (y-axis) of the regression models of the five function indicators per soil function, based on forward stepwise regression. The x-axis indicates the number of parameters in the regression models. The different line types indicate the different types of explanatory variables in the regression models, i.e., SOC: SOC quality and quantity; IP: intrinsic soil properties; SOC + IP: all SOC and IP parameters. These sets of variables are described in the Materials and Methods as sets 1, 3, and 5, respectively. The error bars indicate the standard error of the mean. Different letters next to the lines indicate significant differences between the explanatory power of the different types of parameters as assessed by a post-hoc Tukey test after ANOVA (Table S2).

2.7.4. Analyzing the explanatory power of individual SOC quality parameters

To explore the performance of the individual SOC quality parameters, we used Pearson correlations to explain soil function indicators by each SOC quality parameter and SOC content separately, per soil type. We then tested for each function separately whether the explained variation in indicator values differed between SOC parameters or soil types with two-way ANOVA, after combining the results of the regression outcomes of each soil type into one dataset.

A comparable procedure was used to investigate the added value of measuring single SOC quality parameters in addition to SOC content. First, we explained variation in soil function indicators by SOC content in combination with each of the SOC quality parameters using Pearson correlations. Second, we calculated the effect size with the natural log response ratio as a measure for the added value via:

$$Effect\ size = \ln\left(\frac{R^2_{adj-OCQ}}{R^2_{adj-TOC}}\right) \quad \text{(eq. 1b)}$$

With R^2_{adj}-OCQ as the adjusted R-squared of regression models explaining soil function indicators by SOC content in combination with one of the SOC quality indicators, and R^2_{adj}-TOC the adjusted R-squared of regression models explaining soil function indicators by SOC content only. To avoid taking a negative natural logarithm or dividing by 0, we changed all negative values for R^2_{adj}-OCQ and R^2_{adj}-TOC to zero values and subsequently added 0.001 to all values for R^2_{adj}-OCQ and R^2_{adj}-TOC. We then visually assessed whether the effect sizes of the different SOC quality parameters were significantly different from 0 using 95% confidence intervals of the mean. We also assessed for each function separately whether the effect sizes differed between SOC quality parameters or soil types with two-way ANOVA's.

We further assessed the relationship between the added value of the different SOC quality parameters and their redundancy if SOC content has already been measured, for each soil type separately. We first performed Pearson correlations between SOC content and the individual SOC quality parameters per soil type and used the correlation strength (expressed in R^2_{adj}) as measure for redundancy. We then assessed per soil function the relationship between the redundancy (i.e., correlation strength with SOC content) of each SOC quality parameter with its averaged added value for explaining variation in the soil function indicators (i.e., effect size), using Pearson correlations.

Considering that performing SOC characterization with one technique often generates multiple SOC parameters, we also tested the explanatory power when all parameters obtained by the same SOC characterization technique were allowed to enter the models in addition to SOC content. We performed forward stepwise selection as before, to explain variation in each soil function indicator value by multiple SOC quality parameters belonging to the same SOC characterization technique after including SOC content as first explanatory variable. We performed the regressions separately per soil type and combined the results into one dataset to perform a three-way ANOVA with the explained variation (R^2_{adj}) as response variable and SOC characterization technique, soil function, and soil type as explanatory variables.

2.7.5. Checking assumptions

We checked for a normal distribution of the residuals of all models with quantile-quantile-plots and Shapiro Wilk tests, and we assessed the homogeneity of variance with residual plots and Scale-Location plots. We performed data transformations if necessary to meet the assumptions. We used the Bonferroni-correction to adjust significant level α, in case we performed multiple tests.

We used the *stats* package for the ANOVA's and forward stepwise selection. Tukey's Honest Significant Difference test was done as a post-hoc tests after ANOVA, calculated by the *stats* and *multcompView* packages. We used R version 4.2.1.

3. Results

We will first provide a general overview of the relation between soil functioning and SOC vs. IP parameters by presenting results averaged across all soil types and soil functions. This general overview contextualizes the more detailed relations for individual soil functions in each soil type separately, which we will present in the subsequent sections. We will then focus on SOC content only and will present the explanatory power of the different SOC quality parameters in addition to total SOC content, and the performance of the different SOC characterization techniques.

3.1. Explaining soil functions by intrinsic soil properties and soil organic carbon parameters

3.1.1. General overview

The maximum variation in soil function indicators that could be explained by all IP and SOC (i.e., SOC content and SOC quality) parameters was 30 ± 22% (mean ± s.d.), averaged over all soil functions and soil types (Table 3). SOC content alone explained 9 ± 16%, and subsequently adding SOC quality parameters could explain up to 26 ± 21% variation, which was relatively 80 ± 25% of the maximum explainable variation (MEV). The high standard deviations indicate that the amount of variation that could be explained differed strongly between soil function indicators and/or soil type.

3.1.2. Explaining individual soil functions by different types (IP vs. SOC) and numbers of variables

In sandy soils, SOC parameters significantly explained more variation than IP parameters for biological population regulation and soil structure and water regulation (Fig. 1, two ANOVA's: $F > 21.07$, $p < \alpha_{Bonferroni}$ Table S2). Also element cycling tended to be better explained by SOC parameters than IP parameters in sandy soils (Fig. 1, ANOVA: $F = 3.5$, $p < 0.05$ but $p > \alpha_{bonferoni}$, Table S2). In clay soils, only element cycling was significantly better explained by SOC than by IP parameters, but SOC and IP parameters together explained most variation (Fig. 1, ANOVA: $F = 3.69$, $p < \alpha_{Bonferroni}$, Table S2). Increasing the number of SOC and/or IP parameters in the regression models generally explained more variation in soil functioning (Fig. 1), but this was not significant for any of the soil functions (six ANOVA's: $F < 3.27$, $p > \alpha_{Bonferroni}$, Table S2).

3.1.3. Explaining individual soil functions by different sets of SOC and IP parameters

Focusing on the models with the maximum number of parameters, the absolute variation in function indicators that was explained by SOC

Table 3
The absolute (row 1) and relative (row 2) variation explained in soil function indicators by different sets of explanatory variables, averaged over all soil functions (i.e. biological population regulation, element cycling and soil structure and water regulation) and soil types (i.e. clay and sand). The different sets of explanatory variables of the regression models are: SOC: Total soil organic carbon content. IP: Intrinsic soil properties. SOC content + IP: All IP parameters, while forcing the regression models to always include SOC content as first explanatory parameter. SOC content + SOC quality: SOC content and all SOC quality parameters, while forcing the regression models to always include SOC content as first explanatory parameter. MEV: all SOC and IP parameters, benchmarking the maximum explainable variation (MEV). The errors are represented by the standard deviation.

	SOC content	IP	SOC content + IP	SOC content + SOC quality	MEV
R^2_{adj} (%)	9 ± 16	12 ± 18	18 ± 23	26 ± 21	30 ± 22
R^2_{adj}/MEV (%)	21 ± 24	32 ± 27	50 ± 31	80 ± 25	100

content alone and in combination with SOC quality parameters did not significantly differ between clay and sand (Fig. 2a + b, ANOVA's: $F < 1.43$, $p > 0.05$, Table S3). Soil functions in sand tended to be less explained by only IP parameters compared to clay (Fig. 2c, ANOVA: $F = 5.58$, $p < 0.05$ and $> \alpha_{Bonferroni}$, Table S3), but this difference disappeared when additional SOC parameters were included in the regression models (Fig. 2d + e, ANOVA's: $F < 1.59$ and $p > 0.05$, Table S3). The explained variation did not significantly differ between soil functions for any of the sets of explanatory variables that included SOC parameters (four ANOVA's: $F < 2.38$, $p > 0.05$, Table S3). However, among the element cycling indicators, much more of the variation in CEC was explained by IP and SOC indicators than for the other indicators, in both sand and clay (outlier values with $R^2_{adj} > 0.6$ in Fig. 2 a - e). When we repeated the ANOVA and Tukey HSD tests after excluding CEC, this revealed that the function soil structure and water regulation tended to be better explained by IP parameters and SOC content combined with SOC quality parameters than the other two soil functions (two ANOVA's: $F > 4.86$, $p < 0.05$ but $p > \alpha_{bonferoni}$, Table S3), but not by SOC content only, or by SOC parameters combined with IP parameters (three ANOVA's: $F < 3.44$, $p > 0.05$, Table S3). The variation explained by SOC and IP parameters relative to the maximum explainable variation did never differ between soil functions in the soil types, nor when CEC was removed (Fig. 2 f-h, six ANOVA's: $F < 2.84$, $p > 0.05$, Table S3).

3.2. The explanatory power of single SOC quality parameters to explain soil functions

SOC parameters did not significantly differ in their capacity to explain indicators for element cycling and biological population regulation (two ANOVA's: $F < 0.88$, $p > 0.05$, Table S4). Total SOC content had a significantly higher explanatory power than MAOMC_prop in explaining function indicators for soil structure and water regulation according to the post-hoc Tukey HSD test after ANOVA (ANOVA: $F = 2.60$, $p < \alpha_{Bonferroni}$, Table S4), but the explanatory power of all other SOC parameters did neither differ from these SOC parameters, nor from each other.

Regression models based on total SOC content in combination with one SOC quality parameter did not reveal significant differences in the added value (i.e., effect size) of the different SOC quality parameters to explain the indicators of any of the three soil functions (three ANOVA tests: $F < 1.19$; $p > 0.05$, Table S5). Moreover, all confidence intervals of the effect sizes overlapped with 0, except for 1 indicator in sand (i.e., POMC_size for soil structure and water regulation, Fig. S6) that could represent a type I error as 90 confidence intervals were tested. The effect size of the SOC quality parameters was neither significantly negatively influenced by their correlation strength with total SOC content ($p > 0.05$).

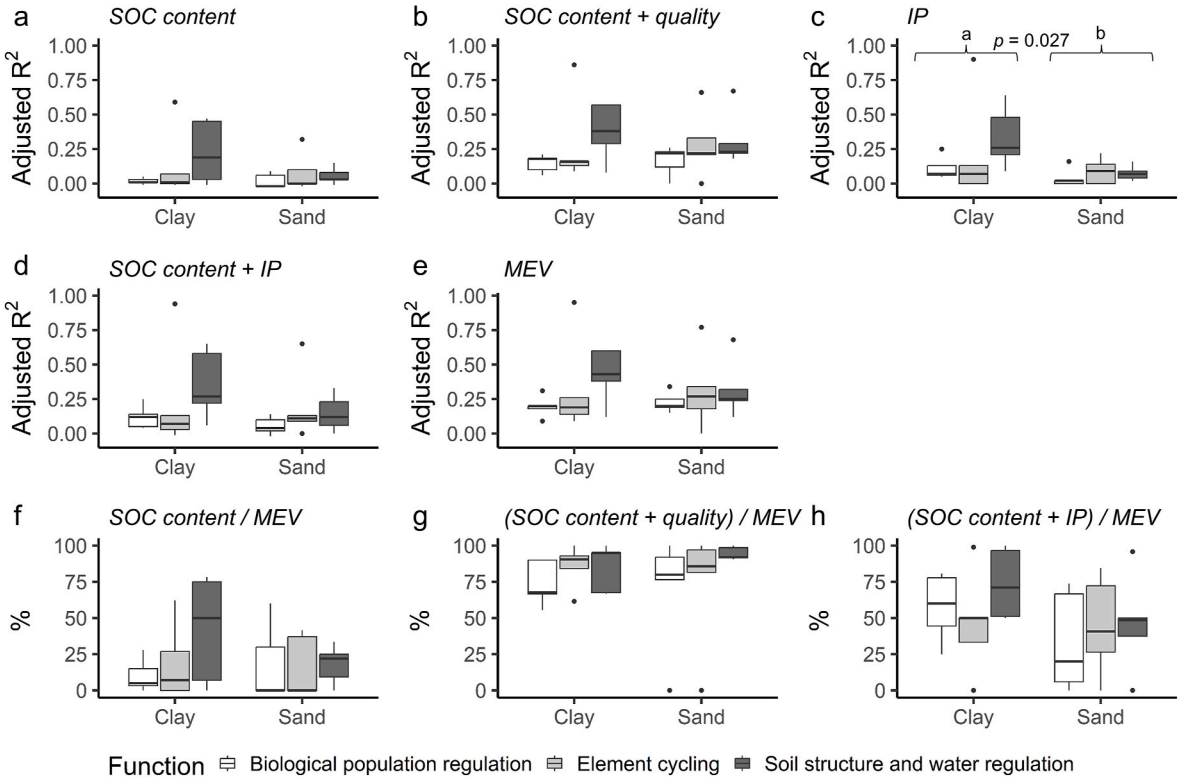

Fig. 2. Absolute (a–e) and relative (f–h) explained variation in indicator values of soil functions by different types of parameters. Each soil function (i.e. biological population regulation, element cycling, and soil structure and water regulation) comprises 5 indicators that are visualized in the boxplots, with a different fill color per function. The different types of explanatory parameters are: SOC content: total soil organic carbon content ($g.kg^{-1}$). SOC content + quality: all SOC parameters, while forcing the regression models to always include SOC content as the first explanatory parameter. IP: intrinsic soil properties. SOC content + IP: All IP parameters, while forcing the regression models to always include SOC content as the first explanatory parameter. MEV: all SOC and IP parameters as a benchmark for the maximum explainable variation (MEV). The R^2_{adj} of the MEV was the denominator to calculate the percentages of the relative amount of explained variation in soil functions (graph f-h). The letters above the boxplots in plot c indicate nearly ($p < 0.05$ and $> \alpha_{Bonferroni}$) significant differences between the explained variation among different soil types as assessed by a post-hoc Tukey test after ANOVA (Table S3).

3.3. The added value of including multiple SOC quality parameters to explain soil functions: differences between SOC characterization techniques

To assess the full potential explanatory power of the different SOC characterization techniques, function indicators were explained with regression models that were allowed to select from all SOQ quality parameters obtained by each technique separately as well as their combination, after including total SOC content as first explanatory variable. RE6 was the only characterization technique that produced SOQ quality parameters that together could significantly explain more variation than SOC content alone (Fig. 3+RE6, ANOVA: $F = 6.21$, $p < \alpha$, Table S6).

The exact type and number of added RE6 parameters differed per soil function indicator and per soil type (Table 4). Most variation in soil function indicator values was explained when SOC content was combined with multiple SOC quality parameters from different SOC characterization techniques (Fig. 3 +All, ANOVA: $F = 6.21$, $p < \alpha$, Table S6). The explanatory power of the different SOC characterization techniques was not influenced by soil type or soil function, although the absolute amount of explained variation differed per soil function (ANOVA: $F = 12.21$, $p < \alpha$, Table S6) and soil type (ANOVA: $F = 5.25$, $p < \alpha$, Table S6).

4. Discussion

The aim of our study was to investigate to what extent soil organic carbon parameters (i.e., SOC content and different types of SOC quality parameters) can be used to explain soil functions in clay and sandy soils under arable farming. We found that across all functions and soil types, SOC parameters could explain 26 ± 21% of the variation in function indicator values, and additionally including IP parameters increased this percentage to 30 ± 22 %. The explained variation was hence rather low compared to previous studies (Bongiorno et al., 2019; Lucas and Weil, 2021) and varied strongly depending on the soil function indicator under consideration. In general, the function soil structure and water regulation tended to be better explained than element cycling and biological population regulation. Surprisingly, none of the SOC characterization techniques (i.e. POX-C, POM-MAOM, RE6 and C:N-analysis methods) yielded a single parameter that added significant value in explaining the soil functions as additional parameter alongside total SOC content as compared to SOC content alone. When adding multiple parameters generated by the same characterization technique, only RE6 parameters significantly explained more variation than SOC content alone. Combining SOC quality parameters obtained through different, complementary techniques explained most variation, irrespective of soil function and soil type. Below we discuss these unexpected findings in view of our objective and hypothesis provided in the introduction.

4.1. Relationships between primarily biota-driven functions and soil organic carbon

Based on our findings we have to reject our hypothesis that including SOC quality parameters in addition to SOC content would be particularly relevant for element cycling and biological population regulation. In contrast, soil structure and water regulation tended to be the better explained by SOC parameters than element cycling and biological population regulation. SOC parameters explained more variation than intrinsic soil properties across all soil functions, especially in sand, highlighting the importance of SOC for all, and not only the primarily biota-driven, functions.

The supposed relationship between soil life and bioavailable SOC as carbon food source has been a major reason to include a parameter for SOC quality that represents a labile SOC fraction in soil health assessments (e.g. (Stott, 2019; de Haan et al., 2021)). However, we did not find that parameters describing the size or proportion of a labile SOC fraction performed better than parameters based on other SOC properties (i.e., size/proportion of stable SOC fractions, thermal stability and element ratio's) in explaining element cycling and biological population regulation, as the individual SOC quality parameters did not significantly differ in explanatory power for these functions when considered separately or in addition to SOC content. Moreover, regression models for

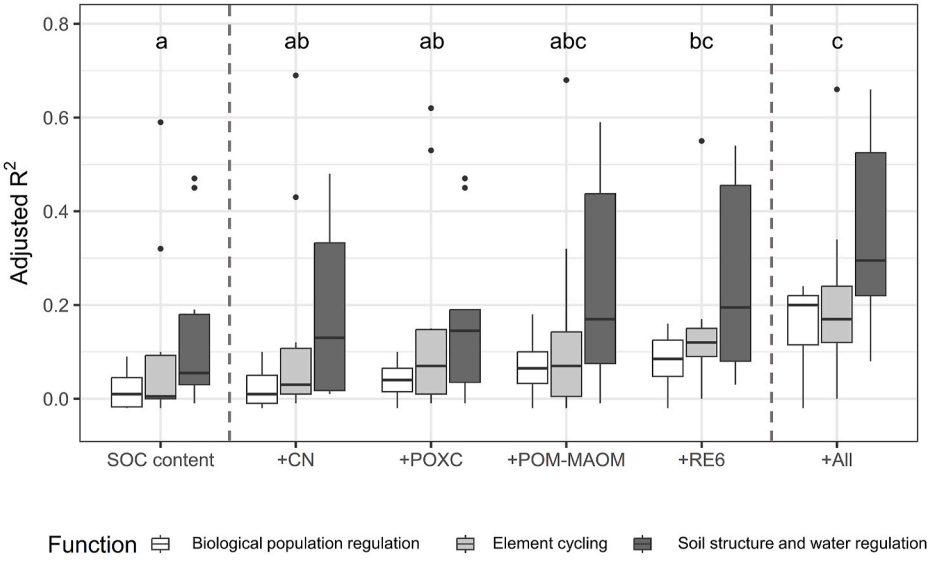

Fig. 3. Soil functions explained by the total soil organic carbon (SOC) content, or SOC complemented with multiple parameters from single SOC characterization techniques and their combination. Each soil function (i.e. biological population regulation, element cycling, and soil structure and water regulation) comprises 5 indicators that are presented as boxplots of different colors. Different letters above the boxplots indicate significant differences between the explanatory power of the different techniques as assessed by a post-hoc Tukey test after ANOVA (Table S6): SOC content: total soil organic carbon content alone; +CN: SOC content and the additional parameter (i.e., bulk_CN) from Elemental C:N analysis; +POXC: SOC content and additional parameters from oxidation with potassium permanganate; + POM-MAOM: SOC content and additional parameters from size fractionation into particulate (POM) and mineral-associated (MAOM) organic matter; + RE6: SOC content and additional parameters from thermal analysis by Rock-Eval 6. + All: SOC content and additional parameters from all the different SOC characterization techniques. The regression analyses were performed separately for sand and clay, but the explanatory power of the different techniques is visualized in one plot as soil type did not influence the explanatory power (Table S6).

Table 4
The complete regression models for explaining the 15 soil function indicators in clay and sand. The models were forced to always include total SOC content (SOC) as first parameter, and were then allowed to select freely from all Rock-Eval parameters. The first 5 function indicators belong to the function biological population regulation, the second 5 parameters to element cycling, and the last 5 parameters to soil structure and water regulation. P-values are marked bold if they were below Bonferoni-corrected significant level $\alpha = 0.002$, and italic if $p < 0.05$ and $> \alpha_{Bonferroni}$. See Table 1 for the description of the abbreviations of the function indicators, and Table 2 for the description of the different SOC quality parameters.

Function	Clay			Sand		
Indicator	Equation	R^2_{adj}	P-Value	Equation	R^2_{adj}	P-Value
DisS	0.05SOC - 0.31T50_pyr_CH	0.03	0.098	0.33SOC	0.10	*0.006*
RF	−0.15SOC - 0.42OI - 0.39T50_pyr_CH	0.16	**4.85E-04**	0.1SOC - 0.38T50_ox_CO2 - 0.26PyroC_prop	0.11	*0.028*
RB	0.15SOC +0.37T50_ox_CO2 - 0.33T50_pyr_CH	0.16	**3.00E-04**	−0.01SOC	−0.02[a]	0.919
RP	−0.24SOC - 0.23PyroC_prop - 0.19T50_pyr_CO2 + 0.26T50_pyr_CH	0.13	*0.002*	0.24SOC +0.22PyroC_prop	0.07	*0.043*
RANPF	0.22SOC +0.39StableC_prop - 0.26T50_pyr_CH	0.07	*0.034*	0.01SOC +0.33T50_ox_CO2	0.04	0.114
PNM	0.1SOC - 0.32T50_ox_CO2 - 0.2OI	0.09	*0.009*	0.11SOC - 0.33T50_pyr_CH + 0.32OI	0.14	*0.004*
DM	−0.23SOC +0.2OI - 0.14PyroC_prop - 0.26T50_ox_CO2	0.15	**4.51E-04**	0.33SOC - 0.26T50_pyr_CH + 0.22T50_ox_CO2	0.17	**0.001**
DS	0.04SOC - 0.22T50_pyr_CH	0.01	0.267	0.11SOC	0.00	0.338
DCC	0.14SOC - 0.35T50_pyr_CH - 0.16T50_ox_CO2	0.09	*0.006*	0.02SOC +0.33T50_pyr_CO2 - 0.26T50_pyr_CH	0.12	*0.007*
CEC	0.75SOC +0.29T50_ox_CO2 + 0.42OI + 0.21T50_pyr_CH - 0.39StableC_prop +0.1T50_pyr_CO2	0.81	**9.14E-34**	0.64SOC +0.33T50_pyr_CH + 0.22T50_pyr_CO2 - 0.18PyroC_prop	0.55	**5.94E-13**
BD	−0.44SOC - 0.2T50_pyr_CO2 - 0.17PyroC_prop - 0.35T50_ox_CO2 - 0.33T50_pyr_CH	0.32	**3.76E-08**	−0.29SOC	0.07	*0.009*
WHC	0.66SOC +0.16T50_ox_CO2 + 0.19OI - 0.41StableC_prop +0.13T50_pyr_CO2	0.52	**2.73E-15**	0.43SOC +0.72OI - 0.28T50_pyr_CH + 0.18PyroC_prop	0.50	**2.19E-11**
D2	0.03SOC +0.25T50_ox_CO2 + 0.26T50_pyr_CH	0.06	*0.031*	−0.03SOC +0.19T50_pyr_CO2 - 0.34StableC_prop	0.03	0.147
D5	0.18SOC +0.45T50_pyr_CH + 0.24T50_ox_CO2 + 0.27OI - 0.21PyroC_prop	0.19	**7.50E-05**	−0.01SOC +0.33T50_pyr_CH + 0.27OI	0.11	*0.011*
WSA	0.66SOC +0.27OI - 0.2T50_pyr_CO2	0.54	**2.81E-17**	0.37SOC +0.37OI + 0.22PyroC_prop	0.20	**2.05E-04**

[a] Negative R^2_{adj}-value caused by penalty term for adding model parameters.

element cycling and biological population regulation did not more often contain a size or proportion of a labile SOC fraction as the first or second SOC quality parameter after SOC content than models for soil structure and water (Table S7).

Potentially, our selection of SOC quality parameters did not include sufficiently labile, fast cycling SOC fractions such as dissolved organic carbon (DOC) (Bongiorno et al., 2019) that more directly relate to microbial activity and corresponding functions, as microorganisms can only assimilate small and dissolved SOC compounds (Lehmann and Kleber, 2015). For instance, potential nitrogen mineralization (PNM), one of the applied soil function indicators in this study, is measured over a short time scale (i.e. 4 weeks) and may hence depend more on the SOC that is bioavailable within that time frame (e.g. DOC) than on the SOC that is relatively labile but is expected to decompose over a longer time, e.g. 7–15 years (Balesdent et al., 1998; Bol et al., 2009) in case of POM, or ca. 30 years in case of ActiveC (Cécillon et al., 2021; Kanari, 2022). Still, POXC has been suggested to represent the small portion of SOC that serves as easily available food source for soil microbes (Weil et al., 2003; Moebius-Clune et al., 2017; Stott, 2019), and has been found to show a small but significant positive correlation ($R^2 = 0.35$) with nitrogen mineralization in the study of (Lucas and Weil, 2021). The low explanatory power of POXC that we found for these biota-driven soil functions does not support this finding and is in line with several previous indications that POXC may not be as labile as often assumed (Culman et al., 2012; Morrow et al., 2016; Woodings and Margenot, 2023).

Alternatively, a strong involvement of soil biota introduces multiple sources of variation that obscure the relationship between SOC and primarily biota-driven functions such as element cycling and biological population regulation in field context. The activity, diversity and abundance of soil organisms and their interactions are all influenced by various environmental (soil) conditions, of which SOC quality is only one aspect (Bardgett, 2002; Bokhorst et al., 2017; Raczka et al., 2021). Soil organisms also play an important role in the modification of SOC properties and the formation of aggregates (Six et al., 2004), the building blocks of soil structure, so that soil structure and water regulation can also be more driven by biota than we initially expected, and was therefore better explained by SOC parameters.

4.2. The added value of 1 single SOC quality measure besides SOC content

Most published soil health assessments include only one SOC quality parameter besides total SOC content (Stott, 2019; de Haan et al., 2021). Considering that any additional measurement in soil health assessments increases costs and complexity, identifying one master SOC quality parameter would indeed be optimal. However, none of the SOC quality parameters of our study had significant added value in explaining soil functions if SOC content was already considered. Two SOC quality parameters of our study (i.e. the sizes of POXC and POMC fractions) have previously been found to significantly explain several function indicators ((Bongiorno et al., 2019; Lucas and Weil, 2021). However, these SOC quality parameters were directly related to the function indicators and were not considered as additional measurements besides SOC content. Total SOC content alone was found to significantly, or marginally significantly ($p < 0.05$ and $> \alpha_{Bonferonni}$), correlate with 7 out of 15 soil function indicators in our study (Table S8), with 3 out of 3 function indicators in (Lucas and Weil, 2021), and with 17 of 25 function indicators in (Bongiorno et al., 2019). Total SOC content was also highly correlated with all parameters representing sizes of SOC fractions in our study (correlation coefficient r in clay >0.82 and in sand >0. 70 Fig. S7, Fig. S8), with the sizes of especially the POXC and POMC fractions in (Bongiorno et al., 2019), and with the size of POXC fraction in (Lucas and Weil, 2021). Hence, relationships between SOC quality parameters and soil function indicators may be confounded with total SOC content, if these parameters correlate strongly with SOC content. Expressing the size of SOC fractions as proportion to total SOC content (hence converting the unit from g C kg^{-1} soil to g C g^{-1} C) would provide a more independent SOC quality parameter, also suggested by (Bongiorno et al., 2019). However, parameters that represented such proportions (i.e., g C

g^{-1} C), as well as the other more independent types of SOC quality parameters (i.e., thermal stability and element ratio parameters), did not have significantly larger added value in explaining function indicators than the absolute (g C kg^{-1} soil) sizes of SOC fractions in our study. Moreover, the added value of the SOC quality parameters in explaining soil functions was not related with their correlation strength with SOC content. A low correlation between SOC content and a SOC quality parameter will therefore ensure a low redundancy of the respective SOC quality parameter, but may not necessarily increase its explanatory power for soil functions.

4.3. Relation between SOC stability and SOC content

We observed that the total SOC content (g C kg^{-1} soil) was strongly positively correlated with the contents (i.e., "sizes", in g C kg^{-1} soil) of both labile and stable SOC fractions (Fig. S7, Fig. S8), and that the latter (i.e., the sizes of MAOM-C and StableC) were not yet leveling off at higher total SOC contents (Fig. S9) as can be expected in temperate arable soils (Begill et al., 2023). However, where relative proportions (g C g^{-1} C) of labile size fractions were positively correlated with total SOC content, the proportions of the stable size fractions correlated negatively (StableC) or did not correlate (MAOMC) to total SOC content (Fig. S7, Fig. S8). Hence, the sizes of the labile SOC fractions increased more strongly with increasing total SOC content than the sizes of the stable SOC fractions, so that relatively the overall stability of SOC was reduced.

This relatively lower stability at higher SOC contents is supported by other observations in the literature. For instance, SOC content in long-term bare fallow sites has been shown to decline to a constant minimum after ±100 years, which implies that higher SOC contents at earlier time points derive from a larger size of the labile and not from the stable SOC fraction (Cécillon et al., 2018). Moreover, more steps are needed to transform fresh litter inputs to MAOM as compared to POM (Cotrufo and Lavallee, 2022), so that the size of the POM fraction tends to increase more rapidly with SOC content than the MAOM fraction (Cotrufo et al., 2019; Lugato et al., 2021). Where POM can simply increase by fragmentation of fresh litter, the build-up of MAOM requires its association to the soil mineral matrix which is influenced by multiple factors (e.g. mineralogy, pH, competing and synergistic ions (Kögel-Knabner et al., 2008)) and requires more intensive microbial processing with associated needs (e.g., a higher nitrogen input (De Ruiter et al., 1993; Cotrufo and Lavallee, 2022)).

Interestingly, the C:N-ratio of the MAOM fractions correlated positively, and O:C ratio (i.e., OI) of the bulk SOM negatively, with increasing SOC content (Fig. S7, Fig. S8). These result indicate that SOC is relatively less microbially processed at higher SOC contents since microbial processing generally increases the oxygen and nitrogen content of SOM (Lehmann and Kleber, 2015; Barré et al., 2016; Lavallee et al., 2020; Begill et al., 2023). In our arable soils, increasing MAOM contents at higher SOC levels might therefore have been limited by microbial processing, as carbon saturation is unlikely (Begill et al., 2023). The positive correlation between the H:C ratio (i.e., HI) and the C:N ratio of our bulk soils and POM fractions with total SOC content (Fig. S7, Fig. S8), further suggests a relatively higher presence of plant-derived compounds (Sebag et al., 2016; Cotrufo and Lavallee, 2022; Zander et al., 2023), hence relatively lower stability of SOC, at higher SOC contents.

The POXC fraction as expressed relatively to SOC content (i.e., POXC_prop) was the only supposedly labile SOC fraction that was not positively correlated to SOC content in our study (Fig. S7, Fig. S8). Besides the before-mentioned doubts about the lability of POXC (Culman et al., 2012; Morrow et al., 2016; Woodings and Margenot, 2023), the observed negative correlation can also be explained by an underestimation of POXC at higher levels as the rate of the oxidation with permanganate was found to depend on SOC content (Pulleman et al., 2021).

Most RE6 thermal stability parameters were not correlated with SOC content, except for T50_ox_CO2 that negatively correlated with SOC content in sand, supporting a decreased stability at higher SOC contents (Fig. S7, Fig. S8). In clay soils, SOC content was negatively correlated with the immaturity index (i.e., I) and positively correlated to the refractory (i.e., R) index and T50_pyr_CH (Fig. S7, Fig. S8), which all would contradict our hypothesis that a higher SOC content indirectly indicates a decreased stability of SOC. However, T50_pyr_CH, I and R have previously been shown to correlate less strongly and less consistently with the biochemical stability of SOC than other RE6 thermal stability parameters (Cécillon et al., 2021; Delahaie et al., 2023).

The direction of all observed relationships between the SOC quality parameters and total SOC content was similar for both soil types. The convincing majority of these relationships indicated that the stability of SOC decreases with total SOC content, which highlights the need to further investigate the relationship between SOC content and stability, and to assess to what extent the quality of SOC can be considered separately from its quantity.

4.4. Selecting the optimal SOC characterization technique for soil assessments of soil functioning

None of the SOC characterization techniques yielded a single parameter that had significant added value in explaining soil functions if total SOC content was already considered. Still, total SOC content only explained 9 ± 16% of the variation in all soil function indicators across both soil types, although some function indicators were very well explained by total SOC content only (e.g. R^2_{adj} CEC >0.6 in Fig. 2 a). The explanatory power of total SOC content was lower than expected, considering the central role of SOC in soil functioning (e.g (Reeves, 1997; Deb et al., 2015; Herrick and Wander, 2018; Hoffland et al., 2020; Kopittke et al., 2022a)) and that SOC or SOM content is the most frequently included parameter in soil health assessments (Bünemann et al., 2018). Including multiple SOC quality parameters from different characterization techniques besides total SOC content increased the explained variation up to 26 ± 21 %. The repeatedly rather low percentage may derive from our agricultural field context, where SOC parameters are just part of the multitude of factors influencing soil function indicators. The high standard deviation of the explained variation suggests that the relative importance of SOC quality depends on the specific function indicator and environmental context (e.g. soil type, weather conditions). All in all, these findings indicate that the different operational principles of the different SOC characterization techniques led to complementary parameters, and that careful selection of these SOC quality parameters can help in developing a further understanding of the mechanistic processes underlying soil functioning.

For the implementation in soil health assessments, it is practical to use only one SOC characterization technique. Rock-Eval 6 (RE6) was the only SOC characterization technique that resulted in parameters that together explained significantly more variation in soil function indicators values than SOC content alone, although the difference in explanatory power compared to the other techniques was relatively small. The separate RE6 parameters did not differ in effect size compared to parameters from other SOC characterization techniques, so likely the RE6 parameters were more complementary to each other than the parameters derived from the other techniques. This complementarity is supported by the observation that RE6 was the only technique that provided in all types of SOC quality parameters (i.e. element ratio's, thermal stability, and the sizes and proportions of SOC fractions). RE6 also provided the highest number of SOC quality parameters, but after removing highly correlated parameters before multiple linear regression, this number was similar to the number of SOC quality parameters derived from POM-MAOM (n = 6). Moreover, using the Aikake-criterium for forward stepwise regression ensured that SOC quality parameters were only included in the regression models if they had sufficient explanatory power, as the Aikake-criterium includes a penalty term that limits the number of model parameters (Cavanaugh and Neath, 2019). We therefore believe that the diversity (i.e., spanning a

range of different SOC properties) rather than the quantity of RE6 parameters underlies their greater explanatory power compared to models with multiple parameters obtained from the other SOC characterization techniques.

5. Conclusions

We evaluated 22 promising SOC parameters, i.e., SOC content and 21 SOC quality parameters, for their capacity to explain different soil functions that are influenced by SOM degradation and that are relevant for arable farming. Soil structure and water regulation tended to be better explained than element cycling and biological population regulation. SOC content alone explained 9 ± 16% of the variation across soil functions and soil types, and all SOC and intrinsic soil property parameters together 30 ± 22%. We found no evidence that including one single SOC quality parameter in addition to SOC content had significant added value in explaining any of the three selected soil functions. However, the use of multiple SOC quality parameters obtained by Rock-Eval analysis in addition to total SOC content did add significant explanatory value, as well as combining multiple parameters from the four different characterization techniques.

Our results suggest that the relationship between soil functions and SOC quality is not straightforward, and cannot be fully disentangled from SOC content. However, these findings do not dismiss the potential of SOC quality parameters to further identify underlying mechanisms that control soil functioning, which can subsequently be targeted to improve farm management practices. We recommend that in future evaluations of SOC quality parameters for soil health assessments, more emphasis should be put on their (either mechanistic or empirical) relation to soil functions and their potential redundancy when used in addition to total organic carbon content.

CRediT authorship contribution statement

Guusje J. Koorneef: Writing – review & editing. **Mirjam M. Pulleman:** Writing – review & editing. **Rob NJ. Comans:** Writing – review & editing. **Sophie Q. van Rijssel:** Writing – review & editing. **Pierre Barré:** Writing – review & editing. **François Baudin:** Writing – review & editing. **Ron GM. de Goede:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The entire dataset that is collected by the first and fourth author (S van Rijssel) will be made publicly available once she submitted her manuscripts of her PhD as well (expected coming year).

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Appendix A. Supplementary data

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References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19, 716–723.
Balesdent, J., Besnard, E., Arrouays, D., Chenu, C., 1998. The dynamics of carbon in particle-size fractions of soil in a forest-cultivation sequence. Plant and Soil 201, 49–57.
Bardgett, R.D., 2002. Causes and consequences of biological diversity in soil1. Zoology 105, 367–375.
Barré, P., Plante, A.F., Cécillon, L., Lutfalla, S., Baudin, F., Bernard, S., Christensen, B.T., Eglin, T., Fernandez, J.M., Houot, S., Kätterer, T., Le Guillou, C., Macdonald, A., van Oort, F., Chenu, C., 2016. The energetic and chemical signatures of persistent soil organic matter. Biogeochemistry 130, 1–12.
Beare, M.H., Bruce, R.R., 1993. A comparison of methods for measuring water-stable aggregates: implications for determining environmental effects on soil structure. In: Brussaard, L., Kooistra, M.J. (Eds.), Soil Structure/Soil Biota Interrelationships. Elsevier, Amsterdam, pp. 87–104.
Begill, N., Don, A., Poeplau, C., 2023. No detectable upper limit of mineral-associated organic carbon in temperate agricultural soils. Global Change Biology 29, 4662–4669.
Boekel, P., 1965. Karakterisering van de slempigheid van zavelgronden door bepaling van de consistentie. Landbouwkundig Tijdschrift 77, 306–311.
Bokhorst, S., Kardol, P., Bellingham, P.J., Kooyman, R.M., Richardson, S.J., Schmidt, S., Wardle, D.A., 2017. Responses of communities of soil organisms and plants to soil aging at two contrasting long-term chronosequences. Soil Biology and Biochemistry 106, 69–79.
Bol, R., Poirier, N., Balesdent, J., Gleixner, G., 2009. Molecular turnover time of soil organic matter in particle-size fractions of an arable soil. Rapid Communications in Mass Spectrometry 23, 2551–2558.
Bongiorno, G., Bünemann, E.K., Oguejiofor, C.U., Meier, J., Gort, G., Comans, R., Mäder, P., Brussaard, L., de Goede, R., 2019. Sensitivity of labile carbon fractions to tillage and organic matter management and their potential as comprehensive soil quality indicators across pedoclimatic conditions in Europe. Ecological Indicators 99, 38–50.
Bünemann, E.K., Bongiorno, G., Bai, Z., Creamer, R.E., De Deyn, G., de Goede, R., Fleskens, L., Geissen, V., Kuyper, T.W., Mäder, P., Pulleman, M., Sukkel, W., van Groenigen, J.W., Brussaard, L., 2018. Soil quality – a critical review. Soil Biology and Biochemistry 120, 105–125.
Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: high-resolution sample inference from Illumina amplicon data. Nature Methods 13, 581–583.
Cavalier-Smith, T., Lewis, R., Chao, E.E., Oates, B., Bass, D., 2009. Helkesimastix marina n. sp. (cercozoa: sainouroidea superfam. N.) a gliding zooflagellate of novel ultrastructure and unusual ciliary behaviour. Protist 160, 452–479.
Cavanaugh, J.E., Neath, A.A., 2019. The Akaike information criterion: background, derivation, properties, application, interpretation, and refinements. WIREs Computational Statistics 11, e1460.
Cécillon, L., Baudin, F., Chenu, C., Houot, S., Jolivet, R., Kätterer, T., Lutfalla, S., Macdonald, A., van Oort, F., Plante, A.F., Savignac, F., Soucémarianadin, L.N., Barré, P., 2018. A model based on Rock-Eval thermal analysis to quantify the size of the centennially persistent organic carbon pool in temperate soils. Biogeosciences 15, 2835–2849.
Cécillon, L., Baudin, F., Chenu, C., Christensen, B.T., Franko, U., Houot, S., Kanari, E., Kätterer, T., Merbach, I., Van Oort, F., Poeplau, C., Quezada, J.C., Savignac, F., Soucémarianadin, L.N., Barré, P., 2021. Partitioning soil organic carbon into its centennially stable and active fractions with machine-learning models based on Rock-Eval® thermal analysis (PARTYSOCv2.0 and PARTYSOCv2.0EU). Geoscientific Model Development 14, 3879–3898.
Cotrufo, M.F., Lavallee, J.M., 2022. Chapter One - soil organic matter formation, persistence, and functioning: a synthesis of current understanding to inform its conservation and regeneration. In: Sparks, D.L. (Ed.), Advances in Agronomy. Academic Press, pp. 1–66.
Cotrufo, M.F., Ranalli, M.G., Haddix, M.L., Six, J., Lugato, E., 2019. Soil carbon storage informed by particulate and mineral-associated organic matter. Nature Geoscience 12, 989–994.
Creamer, R.E., Barel, J.M., Bongiorno, G., Zwetsloot, M.J., 2022. The life of soils: integrating the who and how of multifunctionality. Soil Biology and Biochemistry 166, 108561.
Culman, S.W., Snapp, S.S., Freeman, M.A., Schipanski, M.E., Beniston, J., Lal, R., Drinkwater, L.E., Franzluebbers, A.J., Glover, J.D., Grandy, A.S., Lee, J., Six, J., Maul, J.E., Mirsky, S.B., Spargo, J.T., Wander, M.M., 2012. Permanganate oxidizable carbon reflects a processed soil fraction that is sensitive to management. Soil Science Society of America Journal 76, 494–504.
Dane, J., Hopmans, J., 2002. 3.3 water retention and storage. In: Al-Amoodi, L. (Ed.), Methods of Soil Analysis - Part 4 Physical Methods. Soil Science Society of America, Inc., Madison, Wisconsin, USA, pp. 971–973.
de Haan, J.J., van den Elsen, E., Visser, S.M., 2021. Evaluatie van de Bodemindicatoren voor Landbouwgronden in Nederland (BLN),versie 1.0 : BLN, versie 1.1 en de schets

van een ontwikkelpad naar een BLN, versie 2.0. Wageningen Plant Research, Wageningen.
De Ruiter, P.C., Van Veen, J.A., Moore, J.C., Brussaard, L., Hunt, H.W., 1993. Calculation of nitrogen mineralization in soil food webs. Plant and Soil 157, 263–273.
Deb, S., Bhadoria, P.B.S., Mandal, B., Rakshit, A., Singh, H.B., 2015. Soil organic carbon: towards better soil health, productivity and climate change mitigation. Climate change and environmental sustainability 3, 26–34.
Delahaie, A.A., Barré, P., Baudin, F., Arrouays, D., Bispo, A., Boulonne, L., Chenu, C., Jolivet, C., Martin, M.P., Ratié, C., Saby, N.P.A., Savignac, F., Cécillon, L., 2023. Elemental stoichiometry and Rock-Eval® thermal stability of organic matter in French topsoils. SOIL 9, 209–229.
Domsch, K.H., Gams, W., Anderson, T.-H., 2007. Compendium of Soil Fungi, second ed. IHW-Verlag Eching, Germany.
Du, S., Li, X.-Q., Hao, X., Hu, H.-W., Feng, J., Huang, Q., Liu, Y.-R., 2022. Stronger responses of soil protistan communities to legacy mercury pollution than bacterial and fungal communities in agricultural systems. ISME Communications 2 (1), 69.
Duval, M.E., Galantini, J.A., Martínez, J.M., Limbozzi, F., 2018. Labile soil organic carbon for assessing soil quality: influence of management practices and edaphic conditions. Catena 171, 316–326.
Edgar, R.C., Haas, B.J., Clemente, J.C., Quince, C., Knight, R., 2011. UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27, 2194–2200.
Espitalie, J., Madec, M., Tissot, B., Mennig, J.J., Leplat, P., 1977. Source Rock characterization method for petroleum exploration. In: Proceedings Offshore Technology Conference. Volume All Days: OTC-2935-MS.
Geisen, S., Snoek, L.B., ten Hooven, F.C., Duyts, H., Kostenko, O., Bloem, J., Martens, H., Quist, C.W., Helder, J.A., van der Putten, W.H., 2018. Integrating quantitative morphological and qualitative molecular methods to analyse soil nematode community responses to plant range expansion. Methods in Ecology and Evolution 9, 1366–1378.
Griffin, G., Jokela, W., Ross, D., 1995. Recommended Soil Nitrate-N Tests. P.22-29. In: Sims, T., Wolf, A. (Eds.), Recommended soil testing procedures for the Northeastern United States. U. Delaware Agric. Exp. Stn. Bull., p. 493.
Gweon, H.S., Oliver, A., Taylor, J., Booth, T., Gibbs, M., Read, D.S., Griffiths, R.I., Schonrogge, K., 2015. PIPITS: an automated pipeline for analyses of fungal internal transcribed spacer sequences from the Illumina sequencing platform. Methods in Ecology and Evolution 6, 973–980.
Hannula, S.E., Heinen, R., Huberty, M., Steinauer, K., De Long, J.R., Jongen, R., Bezemer, T.M., 2021. Persistence of plant-mediated microbial soil legacy effects in soil and inside roots. Nature Communications 12, 5686.
Haynes, R.J., 2005. Labile organic matter fractions as central components of the quality of agricultural soils: an overview. Advances in Agronomy. Academic Press, pp. 221–268.
Herrick, J.E., Wander, M.M., 2018. Relationships between soil organic carbon and soil quality in cropped and rangeland soils: the importance of distribution, composition, and soil biological activity. In: Soil Processes and the Carbon Cycle. CRC Press, pp. 405–425.
Hiemstra, T., Antelo, J., Rahnemaie, R., Riemsdijk, W.H.v., 2010. Nanoparticles in natural systems I: the effective reactive surface area of the natural oxide fraction in field samples. Geochimica et Cosmochimica Acta 74, 41–58.
Hoffland, E., Kuyper, T.W., Comans, R.N.J., Creamer, R.E., 2020. Eco-functionality of organic matter in soils. Plant and Soil 455, 1–22.
Hoitink, H.A.J., Boehm, M.J., 1999. Biocontrol within the context of soil microbial communities: a substrate-dependent phenomenon. Annual Review of Phytopathology 37, 427.
Janzen, H.H., 2006. The soil carbon dilemma: shall we hoard it or use it? Soil Biology and Biochemistry 38, 419–424.
Kanari, E., 2022. Understand and use the estimation of soil organic carbon persistence by Rock-Eval® thermal analysisComprendre et utiliser l'estimation de la stabilité du carbone organique du sol par l'analyse thermique Rock-Eval®. Sorbonne Université.
Keeney, D., Nelson, D., 1982. Nitrogen-inorganic forms. In: Miller, R.H., DR, Keeney (Eds.), Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. Soil Science Society of America, Madison, WI, USA, pp. 643–698.
Keeney, D.R., Nelson, D.W., 1983. Nitrogen—inorganic forms. Methods of Soil Analysis 643–698.
Keiser, A.D., Strickland, M.S., Fierer, N., Bradford, M.A., 2011. The effect of resource history on the functioning of soil microbial communities is maintained across time. Biogeosciences 8, 1477–1486.
Keiser, A.D., Keiser, D.A., Strickland, M.S., Bradford, M.A., 2014. Disentangling the mechanisms underlying functional differences among decomposer communities. Journal of Ecology 102 (3), 603–609.
Kögel-Knabner, I., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., Eusterhues, K., Leinweber, P., 2008. Organo-mineral associations in temperate soils: integrating biology, mineralogy, and organic matter chemistry. Journal of Plant Nutrition and Soil Science 171, 61–82.
Kõljalg, U., Nilsson, R.H., Abarenkov, K., Tedersoo, L., Taylor, A.F.S., Bahram, M., Bates, S.T., Bruns, T.D., Bengtsson-Palme, J., Callaghan, T.M., Douglas, B., Drenkhan, T., Eberhardt, U., Dueñas, M., Grebenc, T., Griffith, G.W., Hartmann, M., Kirk, P.M., Kohout, P., Larsson, E., Lindahl, B.D., Lücking, R., Martín, M.P., Matheny, P.B., Nguyen, N.H., Niskanen, T., Oja, J., Peay, K.G., Peintner, U., Peterson, M., Põldmaa, K., Saag, L., Saar, I., Schüßler, A., Scott, J.A., Senés, C., Smith, M.E., Suija, A., Taylor, D.L., Telleria, M.T., Weiss, M., Larsson, K.-H., 2013. Towards a unified paradigm for sequence-based identification of fungi. Molecular Ecology 22, 5271–5277.
Koorneef, G.J., Pulleman, M.M., de Goede, R.G.M., Barré, P., Baudin, F., van Rijssel, S.Q., Comans, R.N.J., submitted to Geoderma. Understanding the Effects of Organic versus Conventional Farming on Soil Organic Carbon Characteristics– a Chronosequence Study, In prepr.
Kopittke, P.M., Berhe, A.A., Carrillo, Y., Cavagnaro, T.R., Chen, D., Chen, Q.-L., Román Dobarco, M., Dijkstra, F.A., Field, D.J., Grundy, M.J., 2022a. Ensuring planetary survival: the centrality of organic carbon in balancing the multifunctional nature of soils. Critical Reviews in Environmental Science and Technology 52, 4308–4324.
Kopittke, P.M., Berhe, A.A., Carrillo, Y., Cavagnaro, T.R., Chen, D., Chen, Q.-L., Román Dobarco, M., Dijkstra, F.A., Field, D.J., Grundy, M.J., He, J.-Z., Hoyle, F.C., Kögel-Knabner, I., Lam, S.K., Marschner, P., Martinez, C., McBratney, A.B., McDonald-Madden, E., Menzies, N.W., Mosley, L.M., Mueller, C.W., Murphy, D.V., Nielsen, U. N., O'Donnell, A.G., Pendall, E., Pett-Ridge, J., Rumpel, C., Young, I.M., Minasny, B., 2022b. Ensuring planetary survival: the centrality of organic carbon in balancing the multifunctional nature of soils. Critical Reviews in Environmental Science and Technology 52, 4308–4324.
Lavallee, J.M., Soong, J.L., Cotrufo, M.F., 2020. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. Global Change Biology 26, 261–273.
Lefroy, R.D.B., Blair, G.J., Strong, W.M., 1993. Changes in soil organic matter with cropping as measured by organic carbon fractions and 13C natural isotope abundance. Plant and Soil 155, 399–402.
Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature 528, 60–68.
Li, X., Qiao, L., Huang, Y., Li, D., Xu, M., Ge, T., Meersmans, J., Zhang, W., 2023. Manuring improves soil health by sustaining multifunction at relatively high levels in subtropical area. Agriculture, Ecosystems & Environment 353, 108539.
Liptzin, D., Norris, C.E., Cappellazzi, S.B., Bean, G.M., Cope, M., Greub, K.L.H., Rieke, E. L., Tracy, P.W., Aberle, E., Ashworth, A., Bañuelos Tavarez, O., Bary, A.I., Baumhardt, R.L., Borbón Gracia, A., Brainard, D.C., Brennan, J.R., Briones Reyes, D., Bruhjell, D., Carlyle, C.N., Crawford, J.J.W., Creech, C.F., Culman, S.W., Deen, B., Dell, C.J., Derner, J.D., Ducey, T.F., Duiker, S.W., Dyck, M.F., Ellert, B.H., Entz, M. H., Espinosa Solorio, A., Fonte, S.J., Fonteyne, S., Fortuna, A.-M., Foster, J.L., Fultz, L.M., Gamble, A.V., Geddes, C.M., Griffin-LaHue, D., Grove, J.H., Hamilton, S. K., Hao, X., Hayden, Z.D., Honsdorf, N., Howe, J.A., Ippolito, J.A., Johnson, G.A., Kautz, M.A., Kitchen, N.R., Kumar, S., Kurtz, K.S.M., Larney, F.J., Lewis, K.L., Liebman, M., Lopez Ramirez, A., Machado, S., Maharjan, B., Martinez Gamiño, M.A., May, W.E., McClaran, M.P., McDaniel, M.D., Millar, N., Mitchell, J.P., Moore, A.D., Moore, P.A., Mora Gutiérrez, M., Nelson, K.A., Omondi, E.C., Osborne, S.L., Osorio Alcalá, L., Owens, P., Pena-Yewtukhiw, E.M., Poffenbarger, H.J., Ponce Lira, B., Reeve, J.R., Reinbott, T.M., Reiter, M.S., Ritchey, E.L., Roozeboom, K.L., Rui, Y., Sadeghpour, A., Sainju, U.M., Sanford, G.R., Schillinger, W.F., Schindelbeck, R.R., Schipanski, M.E., Schlegel, A.J., Scow, K.M., Sherrod, L.A., Shober, A.L., Sidhu, S.S., Solís Moya, E., St Luce, M., Strock, J.S., Suyker, A.E., Sykes, V.R., Tao, H., Trujillo Campos, A., Van Eerd, L.L., van Es, H., Verhulst, N., Vyn, T.J., Wang, Y., Watts, D.B., Wright, D.L., Zhang, T., Morgan, C.L.S., Honeycutt, C.W., 2022. An evaluation of carbon indicators of soil health in long-term agricultural experiments. Soil Biology and Biochemistry 172, 108708.
Lucas, S., Weil, R., 2021. Can permanganate oxidizable carbon predict soil function responses to soil organic matter management? Soil Science Society of America Journal 85, 1768–1784.
Lugato, E., Lavallee, J.M., Haddix, M.L., Panagos, P., Cotrufo, M.F., 2021. Different climate sensitivity of particulate and mineral-associated soil organic matter. Nature Geoscience 14, 295–300.
Marriott, E.E., Wander, M.M., 2006. Total and labile soil organic matter in organic and conventional farming systems. Soil Science Society of America Journal 70, 950–959.
Moebius-Clune, B., Moebius-Clune, D., Gugino, B., Idowu, O., Schindelbeck, R., Ristow, A., Abawi, G., 2017. Comprehensive Assessment of Soil Health—The Cornell Framework. Cornell University, Geneva, NY, p. 3.
Morrow, J.G., Huggins, D.R., Carpenter-Boggs, L.A., Reganold, J.P., 2016. Evaluating measures to assess soil health in long-term agroecosystem trials. Soil Science Society of America Journal 80, 450–462.
Nelson, D.W., Sommers, L.E., 1983. Total carbon, organic carbon, and organic matter. Methods of Soil Analysis 539–579.
Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecology 20, 241–248.
Nilsson, R.H., Larsson, K.-H., Taylor, A.F.S., Bengtsson-Palme, J., Jeppesen, T.S., Schigel, D., Kennedy, P., Picard, K., Glöckner, F.O., Tedersoo, L., Saar, I., Kõljalg, U., Abarenkov, K., 2018. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. Nucleic Acids Research 47, D259–D264.
Pawlowski, J., Audic, S., Adl, S., Bass, D., Belbahri, L., Berney, C., Bowser, S.S., Cepicka, I., Decelle, J., Dunthorn, M., Fiore-Donno, A.M., Gile, G.H., Holzmann, M., Jahn, R., Jirků, M., Keeling, P.J., Kostka, M., Kudryavtsev, A., Lara, E., Lukeš, J., Mann, D.G., Mitchell, E.A.D., Nitsche, F., Romeralo, M., Saunders, G.W., Simpson, A. G.B., Smirnov, A.V., Spouge, J.L., Stern, R.F., Stoeck, T., Zimmermann, J., Schindel, D., de Vargas, C., 2012. CBOL protist working group: barcoding eukaryotic richness beyond the animal, plant, and fungal kingdoms. PLoS Biology 10, e1001419.
Philippot, L., Raaijmakers, J.M., Lemanceau, P., Van Der Putten, W.H., 2013. Going back to the roots: the microbial ecology of the rhizosphere. Nature Reviews Microbiology 11, 789–799.
Poeplau, C., Don, A., Six, J., Kaiser, M., Benbi, D., Chenu, C., Cotrufo, M.F., Derrien, D., Gioacchini, P., Grand, S., Gregorich, E., Griepentrog, M., Gunina, A., Haddix, M., Kuzyakov, Y., Kühnel, A., Macdonald, L.M., Soong, J., Trigalet, S., Vermeire, M.-L., Rovira, P., van Wesemael, B., Wiesmeier, M., Yeasmin, S., Yevdokimov, I., Nieder, R., 2018. Isolating organic carbon fractions with varying turnover rates in

temperate agricultural soils – a comprehensive method comparison. Soil Biology and Biochemistry 125, 10–26.
Poeplau, C., Barré, P., Cécillon, L., Baudin, F., Sigurdsson, B.D., 2019. Changes in the Rock-Eval signature of soil organic carbon upon extreme soil warming and chemical oxidation - a comparison. Geoderma 337, 181–190.
Poorter, H., 1994. The fate of acquired carbon in plants: chemical composition and construction costs. Plant resource allocation 39–72.
Postma, J., Scheper, R.W.A., Schilder, M.T., 2010. Effect of successive cauliflower plantings and Rhizoctonia solani AG 2-1 inoculations on disease suppressiveness of a suppressive and a conducive soil. Soil Biology and Biochemistry 42, 804–812.
Pulleman, M., Wills, S., Creamer, R., Dick, R., Ferguson, R., Hooper, D., Williams, C., Margenot, A.J., 2021. Soil mass and grind size used for sample homogenization strongly affect permanganate-oxidizable carbon (POXC) values, with implications for its use as a national soil health indicator. Geoderma 383, 114742.
Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2012. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Research 41, D590–D596.
Raczka, N.C., Piñeiro, J., Tfaily, M.M., Chu, R.K., Lipton, M.S., Pasa-Tolic, L., Morrissey, E., Brzostek, E., 2021. Interactions between microbial diversity and substrate chemistry determine the fate of carbon in soil. Scientific Reports 11, 19320.
Radočaj, D., Jurišić, M., Antonić, O., 2021. Determination of soil C:N suitability zones for organic farming using an unsupervised classification in eastern Croatia. Ecological Indicators 123, 107382.
Ramírez, P.B., Calderón, F.J., Fonte, S.J., Santibáñez, F., Bonilla, C.A., 2020. Spectral responses to labile organic carbon fractions as useful soil quality indicators across a climatic gradient. Ecological Indicators 111, 106042.
Reeves, D.W., 1997. The role of soil organic matter in maintaining soil quality in continuous cropping systems. Soil and Tillage Research 43, 131–167.
Reijneveld, J.A., van Oostrum, M.J., Brolsma, K.M., Fletcher, D., Oenema, O., 2022. Empower innovations in routine soil testing. Agronomy 12, 191.
Schlatter, D., Kinkel, L., Thomashow, L., Weller, D., Paulitz, T., 2017. Disease suppressive soils: new insights from the soil microbiome: phytopathology®, 107 (11), 1284–1297.
Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56.
Schulte, R.P.O., Creamer, R.E., Donnellan, T., Farrelly, N., Fealy, R., O'Donoghue, C., O'hUallachain, D., 2014. Functional land management: a framework for managing soil-based ecosystem services for the sustainable intensification of agriculture. Environmental Science & Policy 38, 45–58.
Sebag, D., Verrecchia, E.P., Cécillon, L., Adatte, T., Albrecht, R., Aubert, M., Bureau, F., Cailleau, G., Copard, Y., Decaens, T., Disnar, J.R., Hetényi, M., Nyilas, T., Trombino, L., 2016. Dynamics of soil organic matter based on new Rock-Eval indices. Geoderma 284, 185–203.
Sinnett, D., Morgan, G., Williams, M., Hutchings, T.R., 2008. Soil penetration resistance and tree root development. Soil Use & Management: Soil Use & Management 24 (3), 273–280.
Six, J., Elliott, E.T., Paustian, K., 2000. Soil structure and soil organic matter II. A normalized stability index and the effect of mineralogy. Soil Science Society of America Journal 64, 1042–1049.
Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant and Soil 241, 155–176.
Six, J., Bossuyt, H., Degryze, S., Denef, K., 2004. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. Soil and Tillage Research 79, 7–31.
Six, J., Frey, S.D., Thiet, R.K., Batten, K.M., 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. Soil Science Society of America Journal 70 (2), 555–569.
Sokol, N.W., Slessarev, E., Marschmann, G.L., Nicolas, A., Blazewicz, S.J., Brodie, E.L., Firestone, M.K., Foley, M.M., Hestrin, R., Hungate, B.A., Koch, B.J., Stone, B.W., Sullivan, M.B., Zablocki, O., Trubl, G., McFarlane, K., Stuart, R., Nuccio, E., Weber, P., Jiao, Y., Zavarin, M., Kimbrel, J., Morrison, K., Adhikari, D., Bhattacharaya, A., Nico, P., Tang, J., Didonato, N., Paša-Tolić, L., Greenlon, A., Sieradzki, E.T., Dijkstra, P., Schwartz, E., Sachdeva, R., Banfield, J., Pett-Ridge, J., Consortium, L.S.M., 2022. Life and death in the soil microbiome: how ecological processes influence biogeochemistry. Nature Reviews Microbiology 20 (7), 415–430.
Soucémarianadin, L., Cécillon, L., Chenu, C., Baudin, F., Nicolas, M., Girardin, C., Barré, P., 2018. Is Rock-Eval 6 thermal analysis a good indicator of soil organic carbon lability? – a method-comparison study in forest soils. Soil Biology and Biochemistry 117, 108–116.
Stott, D., 2019. Recommended Soil Health Indicators and Associated Laboratory Procedures. U.S. Department of Agriculture, Natural.
Strickland, M.S., Osburn, E., Lauber, C., Fierer, N., Bradford, M.A., 2009. Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. Functional Ecology 23 (3), 627–636.
Strickland, M.S., Lauber, C., Fierer, N., Bradford, M.A., 2009a. Testing the functional significance of microbial community composition. Ecology 90, 441–451.
Strickland, M.S., Osburn, E., Lauber, C., Fierer, N., Bradford, M.A., 2009b. Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. Functional Ecology 23, 627–636.
Sumner, M.E., 1999. Handbook of Soil Science. CRC press, pp. A–21.
Tipping, E., Somerville, C.J., Luster, J., 2016. The C:N:P:S stoichiometry of soil organic matter. Biogeochemistry 130, 117–131.
Tracy, S.R., Black, C.R., Roberts, J.A., Mooney, S.J., 2011. Soil compaction: a review of past and present techniques for investigating effects on root growth. Journal of the Science of Food and Agriculture 91, 1528–1537.
Van Rijssel, S.Q., van der Putten, W.H., Koorneef, G.J., Bakx-Schotman, J. M. R., ten Hooven, F.C., van Vliet, P.C.J. , n.d. Nematode and Protist Responses to Conversion from Conventional to Organic Arable Farming. in preparation.
van Rijssel, S.Q., Veen, G.F., Koorneef, G.J., Bakx-Schotman, J.M.T., ten Hooven, F.C., Geisen, S., van der Putten, W.H., 2022. Soil microbial diversity and community composition during conversion from conventional to organic agriculture. Molecular Ecology 31, 4017–4030.
Vazquez, C., de Goede, R.G.M., Rutgers, M., de Koeijer, T.J., Creamer, R.E., 2021. Assessing multifunctionality of agricultural soils: reducing the biodiversity trade-off. European Journal of Soil Science 72, 1624–1639.
Veen, G.F., Keiser, A.D., van der Putten, W.H., Wardle, D.A., 2018. Variation in home-field advantage and ability in leaf litter decomposition across successional gradients. Functional Ecology 32 (6), 1563–1574.
Vrebos, D., Jones, A., Lugato, E., O'Sullivan, L., Schulte, R., Staes, J., Meire, P., 2021. Spatial evaluation and trade-off analysis of soil functions through Bayesian networks. European Journal of Soil Science 72, 1575–1589.
Weil, R.R., Islam, K.R., Stine, M.A., Gruver, J.B., Samson-Liebig, S.E., 2003. Estimating active carbon for soil quality assessment: a simplified method for laboratory and field use. American Journal of Alternative Agriculture 18, 3–17.
Woodings, F.S., Margenot, A.J., 2023. Revisiting the permanganate oxidizable carbon (POXC) assay assumptions: POXC is lignin sensitive. Agricultural & Environmental Letters 8, e20108.
WRB, 2022. World Reference Base for Soil Resources. International Soil Classification System for Naming Soils and Creating Legends for Soil Maps, fourth ed. International Union of Soil Sciences (IUSS), Austria.
Yoder, R.E., 1936. A direct method of aggregate analysis of soils and a study of the physical nature of erosion losses. Agronomy Journal 28, 337-351-1936 v.1928 no.1935.
Zander, F., Comans, R.N.J., Gebert, J., 2023. Linking patterns of physical and chemical organic matter fractions to its lability in sediments of the tidal Elbe river. Applied Geochemistry 156, 105760.
Zhao, Z.-B., He, J.-Z., Geisen, S., Han, L.-L., Wang, J.-T., Shen, J.-P., Wei, W.-X., Fang, Y.-T., Li, P.-P., Zhang, L.-M., 2019. Protist communities are more sensitive to nitrogen fertilization than other microorganisms in diverse agricultural soils. Microbiome 7 (1), 33.
Zwetsloot, M.J., van Leeuwen, J., Hemerik, L., Martens, H., Simó Josa, I., Van de Broek, M., Debeljak, M., Rutgers, M., Sandén, T., Wall, D.P., Jones, A., Creamer, R.E., 2021. Soil multifunctionality: synergies and trade-offs across European climatic zones and land uses. European Journal of Soil Science 72, 1640–1654.
Zwetsloot, M.J., Bongiorno, G., Barel, J.M., di Lonardo, D.P., Creamer, R.E., 2022. A flexible selection tool for the inclusion of soil biology methods in the assessment of soil multifunctionality. Soil Biology and Biochemistry 166, 108514.