Journal of Sustainable Agriculture and Environment

Global Initiative of Sustainable Agriculture and Environment
Harnessing Natural Resources

RESEARCH ARTICLE OPEN ACCESS

The Positive Effects of Soil Organic Carbon on European Cereal Yields Level Off at 1.4%

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Received: 18 July 2024 | **Revised:** 16 October 2024 | **Accepted:** 22 October 2024

Funding: The DUALSOM project was funded through Ministry of Science and Innovation (PID2020-113021RA-I00). The Digging Deeper project was funded through the 2015–2016 BiodivERsA COg call for research proposals, with the national funders Spanish Ministry of Economy and Competitiveness (PCIN-2016-028), Swiss National Science Foundation (grant 31BD30-172466), Deutsche Forschungsgemeinschaft (317895346), Swedish Research Council Formas contract (2016-0194) and French Agence Nationale de la Recherche (grant ANR-16-EBI3-0004-01).

Keywords: cereal production | soil mechanisms | soil organic carbon fractions | sustainable agriculture

ABSTRACT

Introduction: Increasing soil organic carbon (SOC) in croplands is a natural climate mitigation effort that can also enhance crop yields. However, there is a lack of comprehensive field studies examining the impact of SOC on crop yields across wide climatic, soil, and farming gradients. Furthermore, it is largely unknown how water retention, soil microbial diversity, and nutrient availability modulate the SOC-crop yield relationship.

Materials and Methods: We conducted an observational study across 127 cereal fields along a 3000 km north-south gradient in Europe, measured topsoil (0–20 cm) organic C content, and collected data on climate, soil properties, crop yield and farming practices. Additionally, we explored the relationship between crop yield, particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) contents at three soil depths (0–20, 20–40 and 40–60 cm) in a subset of sites.

Results: Relative yield increases levelled off at 1.4% SOC, indicating an optimal SOC content for cereals along a European gradient. The quadratic relationship between SOC and cereal yield was conspicuous even after controlling for large differences in climate, soil and farming practices across countries. The relationship varied significantly across soil depths and C fractions. MAOC dominated the SOC pool, and was significantly related to relative yield up to an optimal level that varied with soil depth. Soil microbial diversity and nutrient availability emerged as main drivers of the SOC-yield relationship, while water retention did not exhibit a notable influence.

Conclusions: Our study demonstrates that SOC is as a key determinant of cereal yield along a European gradient, and identifying this threshold can inform soil management strategies for improved carbon capture based on initial SOC levels.

Nevertheless, the complex SOC-yield relationship highlights the necessity for tailored soil management strategies that consider specific site conditions to optimize C storage and crop yield.

1 | Introduction

Agriculture faces a critical challenge of increasing food production while adopting sustainable farming practices that minimize environmentally costly practices, such as the use of fertilizers, pesticides and tillage (Smith et al. 2019). Soils play a pivotal role in agricultural production, supplying approximately 95% of the global food demand (Tilman et al. 2011). The capacity of soils to store carbon (C) has substantial implications for climate change mitigation (Ma et al. 2023), but also underscores their significant role in sustainable global crop production (Ma et al. 2023). The positive influence of soil organic carbon (SOC) on soil fertility and crop yields has been long acknowledged by seminal papers (Lal 2004) and translated into international programs seeking global agricultural sustainability (Food and Agriculture Organization of the United Nations 2019). Previous attempts to quantify the relationship between SOC and crop yield support a quadratic linkage. These studies suggest that while SOC initially has a positive impact on crop yields, its effects level off beyond a certain SOC content. This pattern has been observed in global literature synthesis (Oldfield, Bradford, and Wood 2019), regional analyses (Kane et al. 2021), plot-level studies (Zvomuya et al. 2008), and experiments with direct manipulations of SOC (Oldfield, Wood, and Bradford 2020). The identification of a threshold in this relationship has direct management consequences, as natural climate solutions based on SOC sequestrations could only co-benefit crop yield up to a certain SOC level.

In understanding the significance of C storage, we commonly distinguish between two primary fractions (Lavallee, Soong, and Cotrufo 2020): particulate organic carbon (POC) and mineral-associated organic carbon (MAOC). The POC fraction consists mainly of partially decomposed organic matter with a high C:N ratio (Wood et al. 2016). Conversely, the slow-cycling MAOC fraction is formed primarily from microbial necromass and plant-derived compounds, and has a lower C:N ratio (Cotrufo et al. 2013). Previous studies highlight that POC can be used as a readily available nutrient source for plant growth, but MAOC is better for long-term SOC storage (Schmidt et al. 2011). Reduced organic matter inputs, combined with tillage and high rates of nitrogen fertilization, may lead to high POC decomposition and an increase in MAOC dominance in croplands compared to natural biomes; in fact, on average, 72% of SOC in cropland is found in the MAOC fraction (Sokol et al. 2022). Also, MAOC usually remains stable and relatively more abundant in deeper soil layers, while POC usually diminishes as soil depth increases (Chenu et al. 2019). Despite the intrinsically different features of POC and MAOC, and the dominance of MAOC in cropland soils, most large-spatial scale assessments of the SOC-yield relationship have focused on overall SOC content (Ma et al. 2023; Oldfield, Wood, and Bradford 2020), neglecting the role of C fractions. Therefore, an evaluation of how POC and MAOC components change with soil depth, and how crop yields respond to such variation may help reconcile climate change mitigation and crop yield goals in croplands (Smith et al. 2000).

The SOC-yield relationship operates through indirect mechanisms, as plants do not directly assimilate C from the soil (Moinet et al. 2023). Widely, SOC is recognized as a key indicator of soil fertility, influencing physical, chemical, and biological properties (Tiessen, Cuevas, and Chacon 1994). For instance, SOC promotes the formation of aggregates and pore spaces, enhancing the filtration, absorption, and retention of water within the soil matrix (Lal 2020). This plays a crucial role in reducing runoff and increasing water accessibility for plants (Rawls et al. 2003). SOC also soil provides nutrients and habitat for soil fauna and microbial communities (Voroney 2007), which in turn improves soil fertility and productivity (Smith et al. 2015). High SOC content can also benefit crop yield acting as a reservoir of macronutrients that positively impact crop productivity (Pan, Smith, and Pan 2009). Quantifying the relative importance of soil mechanisms could improve soil management and provide a new context for a more sustainable agriculture.

Here, we combined standardized field surveys across 127 cereal fields covering a 3000 km north-south European gradient with farmers' questionnaires to quantify the relationship between SOC content and fractions with cereal yield. We first addressed if a quadratic relationship between SOC and cereal yield was conspicuous while controlling for covarying factors related to climate, soil properties and farming practices, and quantified the asymptote. Then, in a subset of sites we quantified the SOC-yield relationship across three soil depths ($n = 22$, 21 and 16 in 0–20, 20–40, 40–60 cm, respectively) and two C fractions (POC and MAOC). Finally, we assessed the relative importance of water retention, soil microbial diversity, and nutrient availability as driving soil mechanisms of the SOC-yield relationship across European croplands.

2 | Materials and Methods

2.1 | European Cereal Fields and Relative Yield

We selected 127 cereal fields across a 3000 km north-south gradient in Europe, including sites in France ($n = 29$), Germany ($n = 25$), Spain ($n = 22$), Sweden ($n = 31$) and Switzerland ($n = 20$). A standardized field sampling campaign was carried out during 2017. We selected conventional cereal fields with closely related C3 cereals such as wheat (*Triticum* sp., $n = 95$), barley (*Hordeum vulgare*, $n = 26$), and oat (*Avena sativa*, $n = 6$) to minimize variation between cereal types. See Garland et al. (2021) for more details on study site selection. Grain yield data was obtained from farm managers of each site through a questionnaire. Since not all fields had the same cereal species, yields could not be directly compared. Therefore, we calculated a relative yield for each crop type by dividing the raw grain yield data obtained from farmers by the average yield value for that crop species among the five countries (i.e., the average of the five average values of barley, oat and wheat for the 2017 growing season according to FAO STAT (https://www.fao.org/faostat/en/#data/QCL), as in Garland et al. (2021).

2.2 | Farming Practices and Climatic Conditions

We collected information on inorganic fertilization, tillage, plant cover duration and crop diversity from the farmer questionnaires. Inorganic fertilization referred to the sum of the total amount of mineral N fertilizers applied in 2016 (kg N ha^{-1} $year^{-1}$), 1 year before sampling. Tillage was quantified using two distinct variables: the number of tillage events and the maximum depth of tillage (cm), both 1 year before sampling. The proportion of plant cover over time was calculated as the number of months with living plants (cash crop, cover crop or forage ley) covering the soil divided by the total number of months over the 10 years before sampling. We calculated the Shannon diversity index to assess crop diversity, which considers all plant species in the last 10 years of crop rotation. This approach aids in standardizing the analysis, acknowledging variations in crop types across different fields. We collected mean annual temperature (MAT) and mean annual precipitation (MAP) from each cereal field using WorldClim (Fick and Hijmans 2017) as the monthly average data.

2.3 | Soil Sampling and Analysis

We sampled topsoil (20 cm depth) during the flowering period (i.e., anthesis), which starts between May in the southern sites (i.e., Spain) and August in the northern sites (i.e., Sweden), to reduce variation in crop-growth stage. At each site, eight soil cores were taken in a circular pattern within a 10 m radius using a 5 cm diameter auger. Three of these (eight) cores were kept intact and used to measure soil physical and structural properties. The remaining five cores were homogenized into a composite sample and sieved to 2 mm. One part of this soil was air-dried for SOC analyses. Another portion was stored at 4°C for ammonium, nitrate, and phosphorus content analyses, and some soil was frozen at −18°C for microbiological analysis (Garland et al. 2021). We measured sand content (%) and pH following the Swiss standard protocols (Swiss Reference Methods of the Agroscope 1996), as major parameters determining soil physicochemistry in regional to global studies (Orgiazzi et al. 2018).

We collected multiple soil variables as indicators of the three mechanisms hypothesized to drive the SOC-crop yield relationship, that is water retention, soil microbial diversity and nutrient availability. Water-holding capacity (g water/g soil) was measured following the Swiss standard protocols (Swiss Reference Methods of the Agroscope 1996) as an indicator of water retention. To assess soil microbial diversity, DNA was extracted using the DNeasy PowerSoil-htp 96-well DNA isolation kit (Qiagen). Amplicon sequencing of bacterial 16S rRNA genes was performed using a two-step bcPCR approach (Berry et al. 2012), using gene-specific PCR primers with sequencing adaptors for GS FLX Titanium chemistry (Life Sciences). 16S rRNA gene sequences were assembled using PEAR (Zhang et al. 2014) with default settings. Further quality checks were conducted using the QIIME pipeline (Caporaso et al. 2010). Reference-based and de novo chimera detection as well as clustering in OTUs were performed using VSEARCH7 and Greengenes' representative set of 16S rRNA gene sequences as the reference database. The fungal internal transcribed spacer (ITS) region was amplified using the PacBio SMRT Sequencing platform (Pacific Biosciences) with the primers ITS1f (CTTGGTCATTTAGAGGAAGTAA) and ITS4 (TCCTCCGCTTATTGATATGC) targeting the entire ITS region (~630 bp). Fungal sequences were then clustered into OTUs using the UPARSE pipeline (Edgar 2013). Taxonomical information was predicted to OTUs based on the UNITE database (V7.2) using SINTAX. Alpha diversity indexes were calculated using OTU abundances, rarefied to match the lowest sequence count across taxa (10,000 and 2000 sequences per sample in bacteria and fungi, respectively). For more information on sequencing and bioinformatic analyses, please refer to Garland et al. (2021). We calculated the Shannon–Weaver index of bacterial and fungal diversity as indicators of soil biodiversity (Garland et al. 2021). Community analyses were conducted using the R package *vegan*. Lastly, we measured ammonium content (μg $N\text{-}NH_4$/g soil) and nitrate content (μg $N\text{-}NO_3$/g soil) following the Swiss standard protocols (Swiss Reference Methods of the Agroscope 1996), and available phosphorus (mg/kg soil) by Olsen et al. (1954), as indicators of nutrient availability. SOC content was determined in 2-mm-sieved soil using a wet-oxidation method in accordance with the Swiss standard protocols (Swiss Reference Methods of the Agroscope 1996). A mass of 0.1–0.5 g of soil was accurately weighed and placed into a 250 mL beaker. Subsequently, 2 mL of potassium dichromate solution ($K_2Cr_2O_7$) and 3 mL of sulphuric acid (H_2SO_4) were combined using a magnetic stirrer. Small funnels were then positioned in the beakers, and the samples were subjected to a heating bath at 150°C for 7 min. Afterwards, the beakers were allowed to cool to room temperature, the funnels were removed, and 100 mL of deionized H_2O was added using a measuring cylinder. The resulting solution was titrated by introducing 1.5 g of sodium fluoride (NaF) and four drops of diphenylamine solution ($(C_6H_5)_2NH$). The titration process involved the addition of titration solution of Fe (II) $(NH_4)_2Fe\ (SO_4)_2 \cdot 6H_2O$, and the colour of the solution transitioned from brown to light green before progressing through grey and ultimately turning blue.

2.4 | Soil Organic Matter Fractions Across Soil Depths

We sampled 22 sites from Spain at three soil depths ($n = 22$, 21 and 16 in 0–20, 20–40, and 40–60 cm, respectively) following the protocol explained above, to address the influence of soil organic matter fractions on relative yield across a depth gradient. We separated POC and MAOC fractions by a size fractionation method (Cambardella and Elliott 1992). Briefly, 30 mL of sodium hexametaphosphate (5 g/L) was added to soil and shaken for 18 h to disperse aggregates. After dispersion, the mixture was thoroughly rinsed through a 53-μm sieve to separate the particulate (> 53 μm) and mineral-associated (< 53 μm) fractions, using an automated wet sieving system. The isolated fractions were oven-dried at 60°C. Subsequently, all samples were homogenized by grinding with a ball mill for organic carbon analysis. Bulk SOC, POC and MAOC contents were analysed by dry combustion with a TRUSPEC CN628 elemental analyser.

2.5 | Statistical Analyses

The main objective of our study was to address if a quadratic relationship between SOC and cereal yield was conspicuous while accounting for several covarying factors that are also known to influence crop yield. These factors include soil properties (such as soil pH and texture), farming practices (including fertilization, tillage, plant cover duration, and crop diversity), and climate variables (MAP and MAT). Predictors that did not exhibit a normal distribution were transformed by adding 1 and applying the logarithm to the base e. This transformation was applied to variables including fungal diversity, phosphorus content, nitrate content, and water-holding capacity. All variables were then scaled by subtracting the mean and dividing by the standard deviation. Residuals from our model did not violate assumptions of normality and homogeneity of variance.

First, we tested the influence of SOC on relative yield across the European gradient using a linear mixed model (LMM). Besides the SOC versus relative yield relationship, we also observed a nonlinear relationship between MAT and relative yield, so we included a linear and a quadratic term for SOC and MAT in the LMM. In other words, the variable MAT^2 was incorporated in the model because the highest yields were observed at intermediate temperatures (see Supporting Information S1: Figure S2). Our model included the following variables as fixed effects: MAT, MAT^2, MAP, SOC, SOC^2, soil pH and sand content, tillage depth, number of tillage events, plant cover time, mineral fertilization amount and crop diversity of each site, and country as a random factor. Latitude and longitude were not included in the linear mixed model due to high Pearson correlation with MAT (as shown in Supporting Information S1: Figure S1). In this analysis, our main focus was on estimating the regression coefficient of SOC^2 and understanding its impact on relative yield in conjunction with other significant variables in agriculture. Our approach prioritizes obtaining a robust parameter estimate for SOC^2 rather than striving to develop a model that explains a substantial portion of the variance in our data set (Wasserstein 2019). Therefore, we retained all variables in our final model without conducting model selection, as we recognize their importance as controls on crop yield. Thus, if a parameter was not statistically significant in our model, we nevertheless controlled for it, given that our study is observational and we aimed to separate variation in crop yield associated with SOC^2 from variation linked with other variables. The square root of the variance inflation factor (VIF) was < 2 for all effects, indicating low collinearity among the variables. The quantification of the asymptote was performed by calculating the predicted yield values through the extraction of the standardized coefficients from the adjusted LMM using the fixef function in R. Then, the mean values of all independent variables were obtained to calculate the regression line, and we identified the threshold value where predicted yield began to decline with SOC increase.

Second, we assessed the relationship between the POC and MAOC fractions and relative yield across three soil depth intervals (0–20, 20–40 and 40–60 cm) using LMMs. Nonnormally distributed predictors were adjusted by adding 1 and using logarithm base e, creating transformed variables for POC and MAOC. First, we conducted a two-way analysis of variance (ANOVA) to assess whether the POC and MAOC fractions were significantly different from each other and how they changed with soil depth. Subsequently, separate linear mixed models (LMMs) were performed for POC and MAOC to examine their relationships with relative yield and their interactions with the depth gradient as fixed factors, while treating the sites as a random factor. Consistently with our main objective and the LMM addressing the relationship between SOC and relative yield, we included POC and MAOC as linear and quadratic terms. Edaphoclimatic conditions and farming practices were not incorporated as predictors in LMMs, as these were already addressed in the previous analysis of SOC and sample size was small for a model with multiple predictors. All these data analyses were performed using the *lme4* (Bates et al. 2015) and *car* (Fox and Weisberg 2015) packages.

Finally, we assessed the relative importance of three soil mechanisms driving the relationship between overall SOC (which includes both linear and quadratic terms) and relative yield using confirmatory path analysis with a d-sep approach (Grace 2006; Shipley 2013). This method provides a flexible means of examining causal relationships between variables in path analyses, incorporating different distributions, model structures, and assumptions. For instance, this approach allows the inclusion of nonlinear relationships between variables and challenges associated with small sample sizes. We initially built an a priori structural equation model with all possible relationships (Supporting Information S1: Table S1 and Figure S3). Then, we performed a step AICc procedure (Shipley 2013), based on the Akaike information criterion (AIC; Akaike 1998), to simplify and select the best model that includes overall SOC as predictor even when it was not significant. The quantification of the direct and indirect effects of SOC on relative yield, mediated by soil mechanisms, was conducted using the standardized path coefficients (Grace and Bollen 2005). It is important to highlight that the path coefficients from overall SOC were performed using the sum of absolute values of both linear and quadratic effects. These data analyses were performed using the *piecewiseSEM* R package (Lefcheck 2016) with R software version 4.2.2 (R Development Core Team 2022).

3 | Results

3.1 | Relationship Between SOC and Relative Yield

Our analysis indicated that positive SOC effects on relative yield increased up to 1.4% (Figure 1a). After the 1.4% threshold, the positive SOC effects disappeared and even turned negative. Our quadratic relationship between SOC and relative yield was significant even after controlling for climate (MAT and MAP), soil properties (pH and sand) and farming practices (mineral fertilization, tillage, plant cover and crop diversity) (Figure 1b, Supporting Information S1: Table S2). SOC^2 (estimate: −0.58, 95% confidence interval [CI]: −1.08 to −0.09 $p = 0.027$) was the second most influential explanatory variable for relative yield after MAT (estimate: −0.94, 95% CI: −1.73 to −0.17,

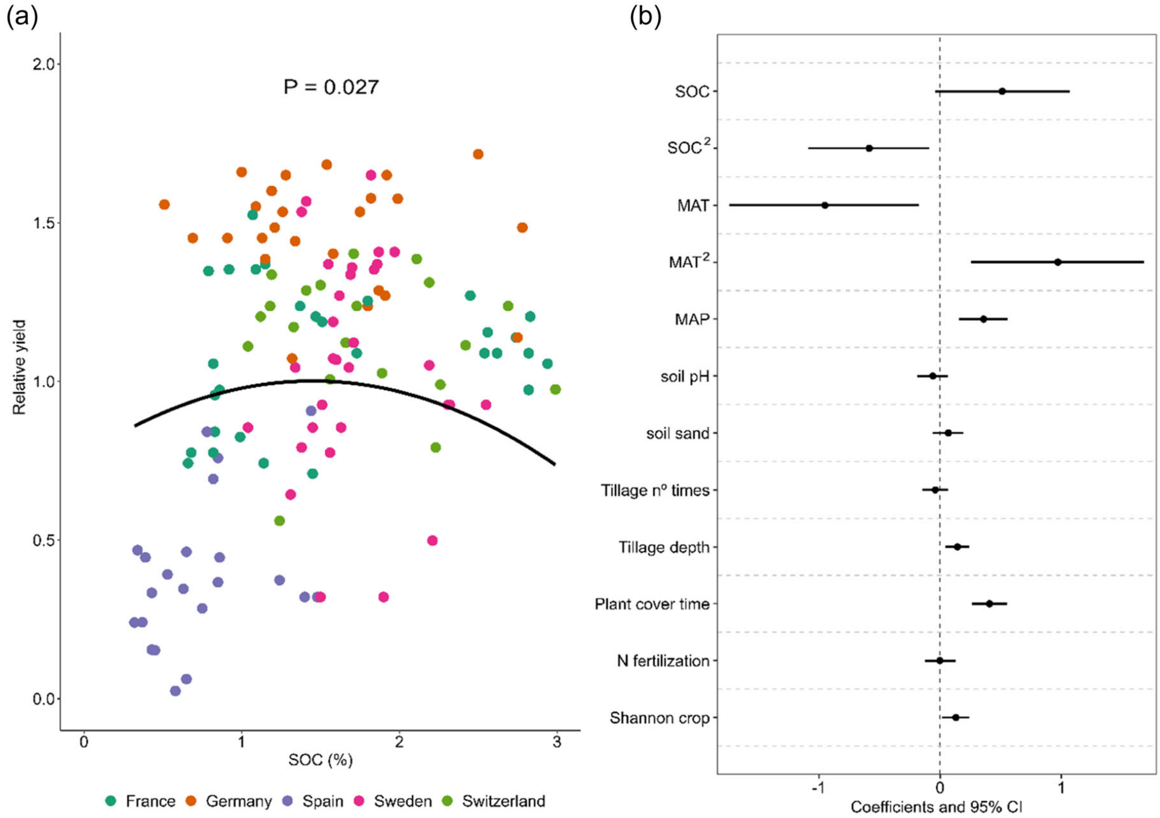

FIGURE 1 | Relationship between SOC and relative yield. The black line represents the modelled relationship between predicted relative yield and SOC across five European countries ($n = 127$) after controlling for edaphoclimatic conditions and farming practices in the linear mixed model (a). The coefficients (dots) and 95% CI, coefficients intervals (lines) of the fixed effects in a linear mixed-effects model (b). MAP, mean annual precipitation; MAT, mean annual temperature.

$p = 0.022$). Mineral fertilization was not associated with yield ($p = 0.977$). Tillage depth (estimate: 0.14, 95% CI: 0.04–0.24, $p = 0.005$), plant cover time (estimate: 0.40, 95% CI: 0.26–0.55, $p < 0.001$), and crop diversity (estimate: 0.13, 95% CI: 0.01–0.24, $p = 0.030$) exhibited positive and significant relationships with relative yield. Our LMM across the European gradient captured a large part of the variation in relative cereal yield ($R_m{}^2 = 0.37$), especially when country random effects were considered ($R_c{}^2 = 0.79$).

3.2 | Relationship Between SOC Fractions and Relative Yield at Different Soil Depths

There was a higher content of MAOC than POC at the three soil depths examined in the subset of Spanish sites (Figure 2). The content of MAOC and POC did not change along the soil depth gradient ($p = 0.47$, Supporting Information S1: Table S3). However, POC and MAOC exhibited a different relationship with relative yield. POC (Figure 3a–c) was not associated with relative yield at any soil depth. In contrast, MAOC showed a significant quadratic relationship with slight variations on soil depth (Figure 3b–d and Supporting Information S1: Table S4). The positive effects on relative yield also disappeared beyond certain point MAOC. When relating the two fractions and three soil depths with relative yield, we found that the main effects captured a small part of the variation in both models (MAOC and POC, respectively, Supporting Information S1: Figures S5 and S6).

3.3 | Relative Importance of Soil Mechanisms Driving the SOC-Yield Relationship

Our confirmatory path analysis accounted for 61% of the total variation in relative yield across the European gradient (Figure 4a). Besides the direct effect of overall SOC on relative yield (Figure 4b), which represented ~72% of the total SOC effects, overall SOC also played a role on relative yield via different soil mechanisms, which represented ~28% of the total SOC effects (Supporting Information S1: Table S5). Overall SOC influenced relative yield via changes in soil microbial diversity and nutrient availability, but not through changes in water retention. Specifically, soil fungal diversity was negatively related with relative yield ($\gamma = -0.12$, $p = 0.047$), whereas soil bacteria diversity showed the opposite pattern ($\gamma = 0.12$, $p = 0.026$). The availability of soil phosphorus and ammonium showed positive ($\gamma = 0.14$, $p = 0.022$) and negative ($\gamma = -0.16$, $p = 0.006$) effects on yield, respectively. Furthermore, soil mechanisms influenced relative yield in a cascading manner. For instance, an increase in water-holding capacity was related with a decrease in bacterial diversity ($\gamma = -0.18$, $p = 0.036$), and greater bacterial diversity was associated with higher phosphorus content ($\gamma = 0.37$, $p < 0.001$). Regarding nutrient

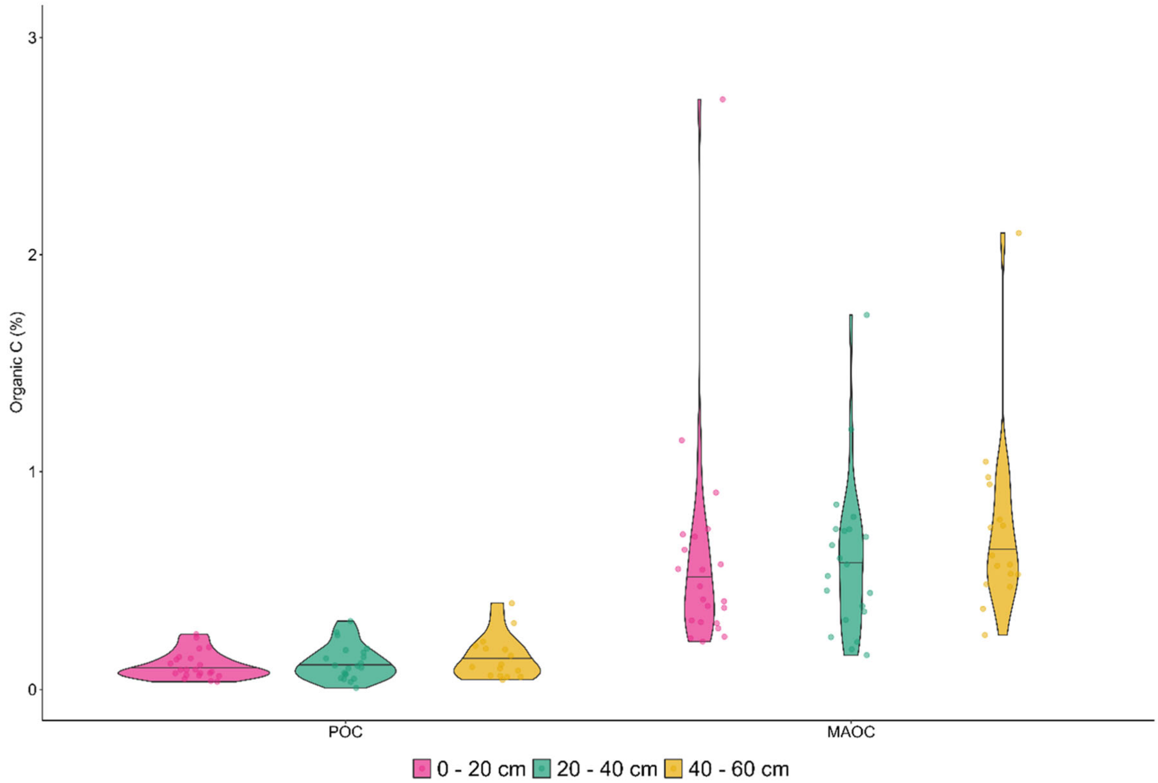

FIGURE 2 | POC and MAOC contents across three soil depth intervals. Violin plots showing the distribution by kernel density of POC and MAOC contents at three soil depths intervals in a subset of sites ($n = 22$, 21 and 16 in 0–20, 20–40, 40–60 cm, respectively). The central horizontal line represents the median.

availability, both variables exhibited a bidirectional relationship, whereby ammonium influenced phosphorus content ($\gamma = 0.17$, $p = 0.028$) and vice versa ($\gamma = 0.25$, $p = 0.006$).

4 | Discussion

Increasing food production under sustainable farming practices is a critical challenge in a climate change context. We observed a quadratic relationship between SOC and cereal yield across 127 sites encompassing a 3000 km north-south European gradient that covers a wide variation of farming practices and edapho-climatic properties, up to a threshold of 1.4% SOC content. Beyond this point, the positive effect of SOC diminishes, and a slight decrease in cereal yield is observed. MAOC dominated the SOC pool, and was positively related with cereal yield from top to subsoils in the subset of Spanish sites. Soil microbial diversity and nutrient availability, but not water retention, were identified as major soil mechanisms driving the SOC-yield relationship.

4.1 | SOC Enhances Cereal Yield and Promotes Sustainable Agriculture Transition

The relationship between SOC and cereal yield was conspicuous even after controlling for the effects of mineral fertilization, crop diversity, tillage, and plant cover duration, showcasing the pivotal role of SOC for soil fertility in croplands. The 1.4% SOC threshold is significant as it marks an optimal point in the relationship between SOC and cereal yield, beyond which the benefits of SOC diminish or even become negative at high values. Based on our quadratic relationship, the increase in SOC does not linearly translate into increased cereal yield, consistent with findings from global (Oldfield, Bradford, and Wood 2019), regional (Oldfield et al. 2022), and experimental studies (Oldfield, Wood, and Bradford 2020). Instead, the positive effects of SOC levelled off at 1.4%. Specifically, a cereal field with SOC 1.4% has a 15.3% higher relative yield that a cereal field with SOC 1.0%. The 1.4% SOC threshold is similar to previous large-scale observational studies that found an optimal value of 2.0% (Oldfield, Bradford, and Wood 2019) and 1.3% (Ma et al. 2023) for C3 cereals. After that threshold, the positive SOC effect on yield disappears. Consistently with previous studies, the negative yield effects observed at high SOC content might be attributed to microbial competition for essential nutrients, particularly N (Oldfield, Wood, and Bradford 2020; Keiser, Knoepp, and Bradford 2016) and/or changes in soil properties (Schjønning 2018; Hassink 1997; Oelofse et al. 2015). However, about 80% of the cereal fields evaluated had SOC below 1.4%, limiting our ability to fully assess the SOC-yield relationship at high SOC content.

The variability explained by the random effect (~47%) indicates the importance of accounting for cross-country variation across a wide range of environmental and management scenarios along European cereal fields. It also suggests that interventions should be tailored to the specific conditions of each region in terms of crop identity, climate and soil parameters. We agree with (Moinet et al. 2023) that the optimal level at which SOC

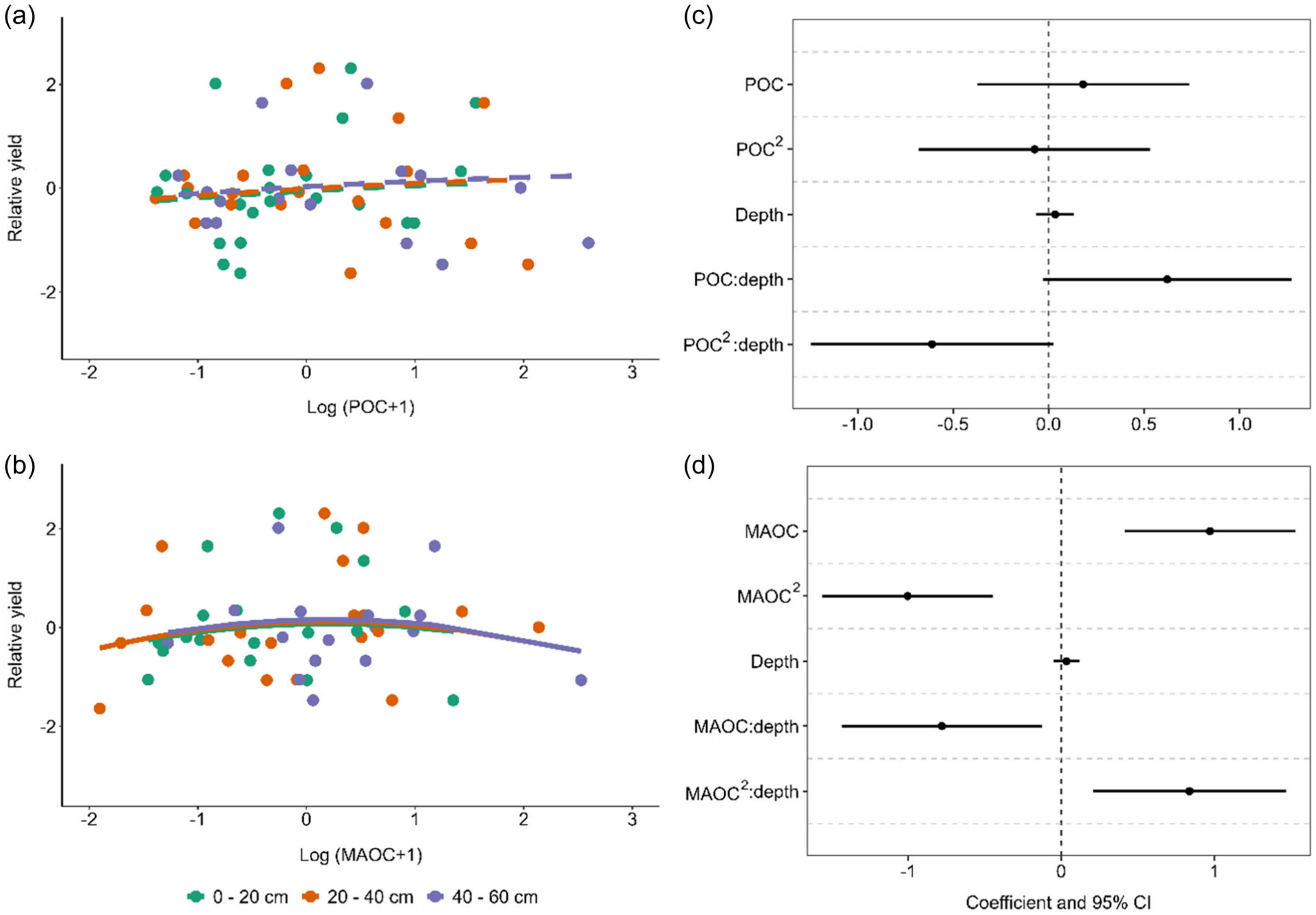

FIGURE 3 | Relationship between POC and MAOC with relative yield. The coloured lines (green, orange and mauve) represent the relationship between predicted relative yield and C fractions (transformed POC and MAOC) at each soil depth intervals (0–20, 20–40 and 40–60 cm) in a subset of sites ($n = 22$). Solid lines indicate significant effects ($p < 0.05$), while dashed lines denote nonsignificant relationships (a, b). Coefficients (dots) and 95% confidence intervals (lines) of fixed effects are presented in a linear mixed-effects model (c, d). Two separate models were run for POC and MAOC.

favours productivity and soil sequestration may be site-specific. However, the magnitude of the effect of SOC on cereal yield at the European scale highlights the importance of monitoring SOC content when farming practices aiming for climate change mitigation also look for crop yield co-benefits. The threshold found can guide soil management strategies towards more active carbon capture, depending on the initial SOC value in consonance with a metanalysis on legume cover crops (Vendig et al. 2023). This may allow farmers to adjust fertilizer inputs appropriately to achieve maximum yields without overspending on fertilizers beyond what is necessary. Future long-term studies and on-farm treatment manipulations under varying climatic conditions should confirm whether building SOC up to a certain level directly enhances yield or if other factors are also involved.

The lack of a strong effect of mineral fertilization on crop yield was not expected, as it is widely documented as a major farming practice increasing crop yield at a local scale (Guo, Liu, and He 2022). We acknowledge that our European gradient may not be adequate to assess fertilization effects, as higher fertilization rates may not be used in the most productive sites, but in those sites where soils are actually nutrient poor, inhibiting a strong fertilization-yield relationship. Tillage depth was positively correlated with cereal yield, in line with previous studies where deep tillage has yield benefits due to enhanced nutrient availability, improved root aeration, and facilitated subsoil water uptake by crops under drought or soil compaction conditions (Schneider et al. 2017). Regarding crop management, we found that the duration of the plant cover through the year mostly determined cereal yield, although crop diversity also played a positive role. While crop diversity is acknowledged for its positive effects on plant growth by facilitating nutrient uptake, disease suppression, and soil structure (Tiemann et al. 2015), a steady supply of carbon and nutrients derived from continuous cover of plant roots and leaves, can be crucial for soil fertility and major cereal yield (Garland et al. 2021).

The European Farm to Fork Strategy sets ambitious goals for transforming our food system by 2030, aiming to mitigate climate change while reducing the environmental impacts of synthetic fertilizers and pesticides. Our findings emphasize that C sequestration in arable soils would play a role in these efforts but is not a universal solution due to the nonlinear SOC-yield relationship, and C storage requires achieving significant benefits in both crop yield navigating a complex relationship with

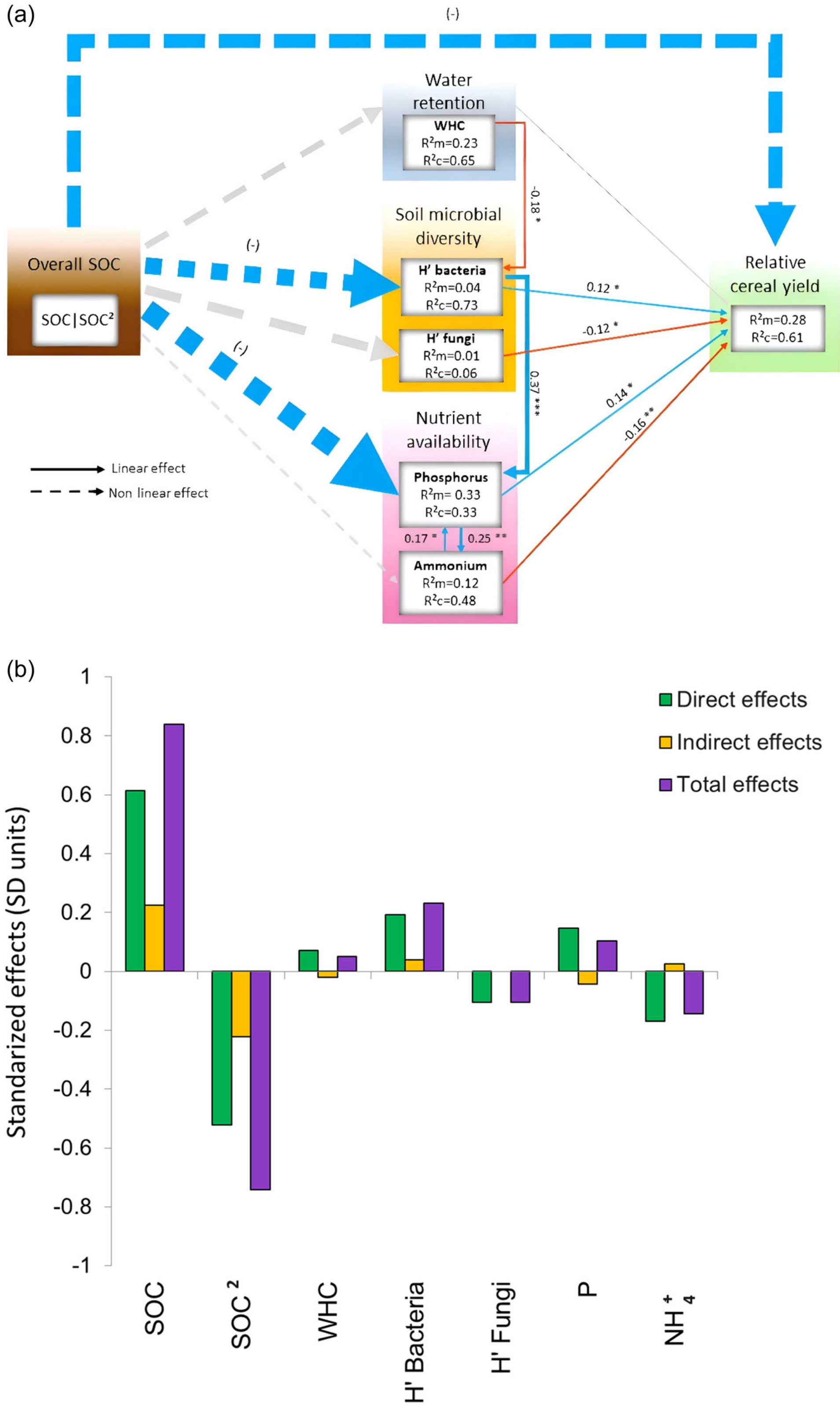

FIGURE 4 | Relationships between overall SOC, soil water-holding capacity, soil bacterial and fungal diversity, soil available phosphorus, soil ammonium and relative yield (Fisher's C statistic: $C = 6.334$, $p = 0.957$, $df = 14$). For each response variable, the marginal variance explained by the fixed effects (R^2m) and the conditional variance explained by the full model (R^2c) are provided. The width of each arrow is proportional to the value of the standardized coefficients (more details see Supporting Information S1: Table S7). The path coefficients from overall SOC were calculated using the sum of the absolute values of both linear and nonlinear effects. Continuous arrows represent linear effects and dashed arrows represent nonlinear effects (quadratic). Red arrow indicates a negative relationship, blue arrow indicates a positive relationship and the grey lines indicates nonsignificative relationship (a). ***$p < 0.001$, ** $0.001 < p < 0.05$, *$p < 0.05$. WHC, water-holding capacity; H', Shannon index. Standarized effect sizes of the direct (green bars), indirect (yellow bars) and total effects (sum of direct and indirect, purple) of SOC, SOC^2, WHC, Shannon index of bacteria and fungi, and ammonium and phosphorus content on relative cereal yield (b).

site-specific management. Nonetheless, as part of broader climate mitigation strategies, soil C accrual in croplands offers promising scalability for C dioxide removal, given historical soil C losses from agricultural activities (Sanderman, Hengl, and Fiske 2017). Integrating C sequestration practices not only enhances climate resilience but also supports a low-input agriculture by reducing reliance on chemical inputs and promoting environmental and economic benefits (Schjønning 2018). As global efforts intensify to achieve net-zero emissions by 2050, alongside deploying scalable negative emissions technologies (Intergovernmental Panel on Climate Change 2023), optimizing soil C management strategies will remain crucial in achieving both agricultural sustainability and climate change mitigation goals effectively.

4.2 | The MAOC Fraction Dominates Croplands and Relates With Cereal Yield Across Soil Depths

The contents of POC and MAOC fractions remained constant across soil depths in the subset of sites. Across the three soil depths evaluated, MAOC (0%–2.7% organic C) consistently exceeded POC content, with MAOC forming 78% of the total SOC pool, which is in line with the 72% dominance found globally (Sokol et al. 2022). This predominance can be attributed to a set of biogeochemical processes triggered by agricultural practices, such as tillage, which favours high aeration that increases microbial decomposition (Lu et al. 2023), and the resulting mineral products associate with mineral soil particles, rapidly forming MAOC from POC (Cotrufo et al. 2013). Indeed, MAOC was higher at 0–20 cm compared to 20–40 cm and 40–60 cm, suggesting the influence of conventional tillage at our sites, where the average tillage depth is 23 cm. Also, if there is no continuous input of plant material into the soil, organic carbon loss occurs. For instance, the POC pool is limited in conventional agricultural systems, where MAOC emerges as the predominant source of bioavailable nitrogen for both plants and microbes (Jilling et al. 2018), as found in our study.

The different physico-chemical properties of POC and MAOC may impact crop yield differently (Lavallee, Soong, and Cotrufo 2020). Despite POC is considered a readily available source of nutrients for plants, we only found a significant relationship between MAOC and cereal yield. This finding deviates from the positive POC-yield relationship previously found by Wood et al. (2016) in smallholders African farms. We speculate that the low POC content (0%–0.5% organic C) across our sites is driving the absence of a relationship with cereal yield. It is important to note that the SOC versus yield relationship across soil depths and C fractions was assessed only using sites from Spain. Further investigation across a wider gradient of POC and MAOC should help to elucidate the yield contribution of each C fraction.

Additionally, we observed a quadratic relationship between MAOC and cereal yield across the three evaluated soil depth intervals. However, confirmation across a broader spatial gradient is necessary to substantiate these findings. In natural ecosystems, MAOC has been found to play a major role for long-term SOC storage (Schmidt et al. 2011), as it is less sensitive to climate warming than POC (García-Palacios et al. 2024). Our results indicate that beyond its role in climate change mitigation, MAOC is also important for cereal yield, as it may represent a long-term source of mineral and organic soil nutrients for plant growth in agroecosystems.

4.3 | Soil Microbial Diversity and Nutrients as Major Factors Driving the SOC—Yield Relationship

Soil microbial diversity and nutrient availability were the main drivers of SOC effects on crop yield addressed in the confirmatory path analysis (Figure 4). Specifically, the ability of SOC to improve the habitat for soil bacteria and provide nutrients (P) for cereal yield was of key importance in our European data set. On the other hand, soil water-holding capacity, our surrogate for water retention, did not influence cereal yields. Water-holding capacity was correlated with mean annual precipitation ($r = 0.61$, Supporting Information S1: Figure S1), suggesting that differences in precipitation between sites may obscure the anticipated positive effects of water retention on crop yields. Our results demonstrate that SOC plays a crucial role in improving soil water retention, where previous studies have observed greater crop resilience to climatic stresses such as drought (Kane et al. 2021). However, the variability in precipitation could mask these benefits, which might explain why a significant effect on crop yields is not observed.

SOC has the potential to foster microbial diversity, as distinct microbial taxa can specialize in the decomposition of diverse organic compounds (Siedt et al. 2021). We agree with (Liu et al. 2022) that SOC increased soil microbial diversity (i.e., Shannon index), which in turn improve yield. SOC can regulate bacterial metabolism, growth, and community dynamics (Wang et al. 2015), as bacteria typically experience C limitation in soils (Soong et al. 2020). Then, increased soil bacterial diversity positively impacts yield by transforming and supplying essential nutrients crucial for plant growth, as observed by Garland et al. (2021) in our European data set, where soil N cycling rates escalate with increasing bacterial diversity. This aligns with the long-standing view that soil biodiversity is crucial for soil health (Wall, Nielsen, and Six 2015; van der Putten et al. 2023). Conversely, the diversity of fungi was not influenced by SOC, and showed a negative relationship with cereal yield. Greater diversity of fungi may imply a higher diversity of plant pathogens, especially in low-diversity ecosystems such as cereal fields under conventional farming (Maron et al. 2011).

Our study also suggests a role for soil nutrients as drivers of the SOC-yield relationship. In fact, higher soil P availability with increased SOC was related with higher cereal yield, as a result of an indirect pathway via soil bacterial diversity (Wakelin et al. 2017). We also observed a negative association between soil ammonium content and cereal yields. It is important to note that soil samples were collected during the cereal flowering stage, which may have influenced the observed ammonium content, as actively growing plants may uptake more ammonium, depleting the soil content. Furthermore, the negative impact of soil ammonium content on yields might be also due to an imbalance in the forms of available N to the plants, consistent with previous findings on maize fields (Van der Velde et al. 2014). The interconnected cycles of P and N play a crucial role in agroecosystem nutrient dynamics, particularly through the microbial decomposition of soil organic matter (Keiser, Knoepp, and Bradford 2016; García-Palacios et al. 2013). Overall, our results underscore the important interplay between soil health via soil biodiversity and crop production, suggesting that targeted agricultural practices can leverage soil microorganisms for sustainable yields.

5 | Conclusions

Our study demonstrates that SOC emerges as a key determinant of cereal yield, even when considering variations along a European gradient. Despite potential reductions in yield, farmers can benefit economically from decreased fertilizer usage and increased revenue through mechanisms such as C credits or agro-environmental schemes. The observed MAOC pattern, which warrants confirmation across a broader spatial gradient, underscores the role of this C fraction to support cereal production, beyond its role to increase the resistance of SOC stocks to climate warming. Enhancing soil microbial diversity in croplands through sustainable farming practices is also important given their role in mediating the interconnected CNP cycles via organic matter inputs. Nevertheless, the complex SOC-yield relationship highlights the necessity for tailored soil management strategies that consider specific-site conditions to optimize C sequestration and crop yield in agroecosystems.

Author Contributions

Ana Campos-Cáliz, Pablo García-Palacios, César Plaza and Enrique Valencia designed the study. Marcel G. A. van der Heijden, Matthias C. Rillig, Sara Hallin, Fernando T. Maestre, Laurent Philippot, and Pablo García-Palacios obtained research funding. Ana Campos-Cáliz, Gina Garland, Anna Edlinger, Samiran Banerjee, Pablo García-Palacios, David S. Pescador, Chantal Herzog, Sana Romdhane, Ayme Spor and Aurélien Saghaï contributed to data collection and laboratory analyses. Ana Campos-Cáliz and Enrique Valencia analysed data. Ana Campos-Cáliz drafted the manuscript, with contributions to the writing from all coauthors.

Acknowledgements

We really thank the use of soil samples and data from the Digging Deeper project. We thank Luna McGill for her vital support during soil fractionation and Miguel de Celis for his help in data exploration with R. We acknowledge support of the publication fee by the CSIC Open Access Publication Support Initiative through its Unit of Information Resources for Research (URICI). This work was funded through the 2015–2016 BiodivERsA COg with the support of national funders cited in funding information. A.C.-C. was supported by the Ministry of Science and Innovation (grant PRE2021-097364) under the DUALSOM project.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at https://figshare.com/s/210a8124059f4707ad64.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.