

RESEARCH ARTICLE

Land use drives the distribution of free, physically protected, and chemically protected soil organic carbon storage at a global scale

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Abstract

Soil organic carbon (SOC) sequestration is increasingly emphasized as a climate mitigation solution, as scientists, policy makers, and land managers prioritize enhancing belowground C storage. To identify key underlying drivers of total SOC distributions, we compiled a global dataset of soil C stocks held in three chemical forms, reflecting different mechanisms of organic C protection: free particulate organic C (fPOC), physically protected particulate organic C (oPOC), and mineral-protected soil organic C (mSOC). In our dataset, these three SOC pools were differentially sensitive to the effects of climate, soil mineralogy, and ecosystem type, emphasizing the importance of distinguishing between physical and chemical C protection mechanisms. C stocks in all three pools varied among ecosystems: cropland soils stored the least amount in each pool, with forest and grassland soils both containing significantly more fPOC (40%–60% greater in each ecosystem) than croplands. oPOC stocks did not significantly differ from zero in croplands but were substantial in forest and grassland soils. Meanwhile, mSOC stocks were the greatest in grasslands and shrublands (90%–100% greater than croplands). In cropland soils, there were no major effects of tillage on C storage in any of the three pools, while manure addition enhanced mSOC stocks, especially when added with inorganic N. Thus, the human land use intensity in croplands appears to reduce SOC storage in all major pools, depending upon management; retaining native vegetation should be emphasized to maintain current global SOC stocks.

KEYWORDS

climate mitigation, land use, MAOM, POM, soil density fractionation, soil organic carbon, tillage

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1 | INTRODUCTION

Soils are integral in our fight against the climate crisis, as they store nearly 3000 Pg carbon (C) globally, and these C stocks may be further enhanced through changes in management practices (Sokol et al., 2022). The majority—up to 65%—of SOC is in the mineral-associated organic C (MAOC) pool (Sokol et al., 2022), which is more resistant to microbial decomposition than the particulate organic C (POC) pool (Six et al., 2002). MAOC consists of microbially processed organic matter bound to mineral surfaces, and it can persist for thousands of years (Mikutta et al., 2006; Rabbi et al., 2013; von Lützow et al., 2007). POC, on the other hand, is made up of non-mineral-bound—though more chemically complex—compounds that typically persist in the soil for months to decades (Denef & Six, 2005; Lavalley et al., 2020; von Lützow et al., 2007). Fundamental differences in the chemistry, microbial processing, and turnover times of POC and MAOC make predicting global carbon-climate feedbacks of the total SOC pool challenging because its constituent pools respond differently to climate change. For example, a meta-analysis found that warming and elevated CO₂ cause losses and gains in POC, respectively, while MAOC is projected to be relatively unaffected by these global change drivers (RoCCI et al., 2021).

Climate, vegetation, and land management influence the magnitude of total soil C stocks by controlling the microbial processing of SOC, thereby regulating the chemical form in which C is stored. Grasslands and arbuscular mycorrhizal forests store more C in MAOC, whereas ectomycorrhizal forests—typically dominated by coniferous trees and having a thick soil organic horizon—store more of their C in POC (Cotrufo et al., 2019). Meanwhile, agricultural practices cause SOC depletion, as reduced inputs decrease POC content, and physical disruption from tillage promotes the decomposition of MAOC (Kan et al., 2020; Li et al., 2021). Understanding C dynamics in agricultural soils is especially critical because these are the focus of efforts to enhance soil C storage, for example, through the “4 per

mille initiative,” to reduce atmospheric CO₂ concentrations (Griscom et al., 2017; Minasny et al., 2017; Paustian et al., 2016). Modifications to conventional agriculture such as reduced tillage, cover cropping, and organic amendments can promote SOC storage by increasing inputs and reducing physical disruption (Crystal-Ornelas et al., 2021; Li et al., 2021; Wulannityas et al., 2021), providing management options to utilize soils for climate mitigation.

Increased focus on soil C sequestration has fostered research into the biogeochemical factors controlling SOC stability and accumulation. Recent analyses have explored how global SOC stocks are distributed among POC and MAOC pools, allowing for a more accurate assessment of the total SOC vulnerability to global change (Cotrufo et al., 2019; Lugato et al., 2021; RoCCI et al., 2021). Often overlooked within studies examining POC and MAOC stability; however, is the functional importance of a third pool, occluded POC (oPOC). oPOC is composed of organic matter physically protected from decomposition inside soil aggregates, which are bound together and cemented primarily through roots, microbial structures, such as hyphae, and extracellular polymeric substances (Godbold et al., 2006; Liang et al., 2019). As an intermediate in stability between “free” or non-occluded POC (fPOC) and directly mineral-bound carbon (mSOC), C in oPOC is physically inaccessible to many microbes, but not chemically bonded to mineral particles (Jastrow, 1996). The distinctions among fPOC, oPOC, and mSOC thus reflect variation in the major mechanisms that guard organic C against decay: fPOC is completely unprotected, oPOC is physically protected through spatial separation from decomposers, and mSOC is chemically protected via organo-mineral bonds (Figure 1; Cambardella & Elliott, 1992; Six et al., 1999). The mechanism of SOC protection matters for its long-term stability. fPOC, oPOC, and mSOC vary in their vulnerabilities to disturbance, with the persistence of each pool differentially influenced by physical disruption, soil moisture/temperature regimes, and nutrient availability (Balesdent et al., 2000; Sokol

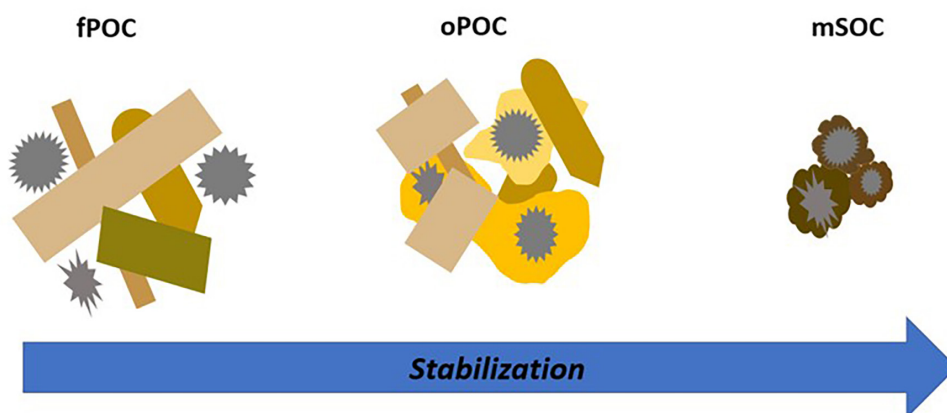


FIGURE 1 Conceptual model for gradient of SOC stabilization. Plant-derived compounds (represented by light brown structures) are found in free particulate organic carbon (fPOC) unbound to mineral surfaces (silt and clay; represented by spiked grey bodies). Microbial biomass (e.g., extracellular polymeric substances, biofilm, hyphae; yellow structures) in occluded particulate organic carbon (oPOC) loosely holds dead plant and microbial molecules to mineral surfaces and promotes stabilization into mineral soil organic carbon (mSOC; grey and dark brown complexes).

et al., 2022). Furthermore, “lumping” oPOC with mSOC into a single pool (MAOC) is likely to obscure important soil carbon-climate feedbacks: oPOC is likely to be much more dynamic than mSOC on annual timescales, but also generally represents a much smaller, and therefore less detectable, C pool (Virto et al., 2010). However, even small changes in SOC storage, extrapolated over large areas, can account for significant ecosystem C loss. Unfortunately, however, isolating oPOC from mSOC requires soil dispersion, sonication, and density fractionation. This is more time-consuming and resource-intensive than quantifying only POC and MAOC, which can be done through size separation (i.e., sieving)—as a result, to date, there have been no attempts to understand large-scale drivers of oPOC stocks. Given the role that oPOC structures have in promoting mSOC formation, though, it is important to account for each pool's biogeochemical characteristics and responses to edaphic and climatic drivers when modeling and managing soils.

To address uncertainties surrounding the distribution of C pools in the soil and their differences across land management types and climate, we compiled a global dataset of C stocks in the fPOC, oPOC, and mSOC fractions, as measured through soil density fractionation, the only approach that allows the empirical quantification of each pool. This allowed us to explore two hypotheses: First, we hypothesized that fPOC and oPOC exhibit more variation in response to climatic and edaphic factors than mSOC, given their higher turnover rates and greater vulnerability to disturbance. Second, we hypothesized that C stocks and distributions among pools differ significantly across land use types, reflecting ecosystem-level differences in the processes that promote (or impede) microbial processing of organic matter, the formation of soil aggregates, and the eventual stabilization of microbial residues on mineral surfaces. Specifically, we predicted that unprotected fPOC pools should be largest in ecosystems with high inputs of fresh plant litter (forests), and smallest in ecosystems with low rates of litterfall (shrubland, cropland). oPOC pools should be greater in ecosystems with high fine root biomass that promotes aggregate formation (forests, grasslands) and lowest in ecosystems where aggregates are frequently disrupted (croplands). Because the mechanisms that promote MAOC formation are highly dependent on soil parent material, texture, and pH (Rasmussen et al., 2018), we predicted that these factors should have the greatest influence on the mSOC pool.

2 | METHODS

2.1 | Data mining and harmonizing

We collected data from papers which utilized a density fractionation methodology to measure soil organic C (SOC) within the three fraction pools: free particulate organic fraction (fPOC), occluded particulate organic fraction (oPOC), and mineral soil organic carbon (mSOC). To filter through published studies reporting SOC stocks, we chose to extract data from papers which cited one of the following rigorous and influential fractionation methodologies: (Golchin

et al., 1994; Shaymukhametov et al., 1984; Six et al., 1998; Sollins et al., 1984, 2006, 2009; Spycher et al., 1983; Steffens et al., 2009). On Google Scholar, there were 3915 papers citing one of the above papers through September 2020. We examined each publication and only extracted data from empirical studies, published in a peer-review journal in English, that measured SOC via density fractionation. When recording oPOC or mSOC data, we only collected data from papers which utilized sonication, sodium hexametaphosphate dispersion, or physical disruption (e.g., from glass beads) to separate oPOC from mSOC (Figure S1). Unless it was specified for a particular soil and reported in the respective study, we set a density cutoff of 1.85 g cm^{-3} for classifying mSOC. Since some studies isolated C pools along a density gradient, we summed SOC stored in fractions above or below the density cutoff.

To make meaningful global comparisons, we chose to only include papers which reported enough information to calculate the C stock in units of g C m^{-2} . In cases where C concentrations but not stocks were reported, we used soil depth and bulk density (BD, g cm^{-3}) to calculate the C stock in a given pool (fPOC, oPOC, mSOC). Data were recorded separately for different locations, ecosystem types, treatments, soil depths, and fractions. Because there was a wide range in soil depth increments used within studies, we summed C stocks from specific depth intervals (e.g. 0–10 cm, 10–30 cm) into two categories: top soil (0–30 cm) or subsoil (31+ cm). Soil volume associated with each observation was calculated assuming a $1 \times 1 \text{ m}$ sampling area and the sampling depth increment reported by the study authors (e.g. 0–10 cm, 15–30 cm). Therefore, because the sampling depth increment would affect the magnitude of the calculated C stock, we included soil volume (depth increment $\times 100 \text{ cm}^2$) as a covariate to account for differences in sample depth. The list of publications from which we extracted data is available in the [Supplementary Materials](#).

Statistical models also included site-level coordinates, ecosystem type, soil type (order in the USDA soil taxonomy), soil pH, soil clay content, mean annual precipitation (MAP), and mean annual temperature (MAT) as fixed factors. We removed observations associated with any ecosystem type for which we did not have at least 25 replicates for each SOC fraction, leaving cropland (932 replicates), forest (702), grassland (533), and shrubland (96). Croplands included agricultural land dedicated to grains, whereas pastures were classified as grassland and woody perennial crops were classified as forest. In total, there were 2261 unique datapoints extracted from 198 publications. Of the 2261 datapoints, 1101 were fPOC and ranged from 0 to $36,120 \text{ g C m}^{-2}$, 651 datapoints were recorded as oPOC and ranged from 0 to 9388 g C m^{-2} , and 642 datapoints were recorded as mSOC and ranged from 23 to $27,928 \text{ g C m}^{-2}$.

2.2 | External data collection

We utilized external databases to fill in data gaps for studies that did not report BD, soil texture, soil pH, MAP, or MAT. BD, soil pH, and clay content were extracted from Harmonized World Soil Database,

accessed via the R package *hwsdr* at the coordinate level (Fischer et al., 2008; Team, 2023; Wieder et al., 2014). Similarly, if unreported by study authors, MAT and MAP were collected from *Terra Climate* in R (Abatzoglou et al., 2024; Hijmans, 2023; Team, 2023). Across study-reported and externally collected data, MAT ranged from -2 to 44°C , with a dataset median of 10.1°C . MAP ranged from 215 to 3920 mm and a dataset mean of 830 mm. Although use of global data products to fill in missing data can introduce error, we re-ran models using only author-reported MAT and MAP, and all estimated coefficients were similar. Our conclusions are therefore robust to any imprecision introduced by interpolated climate data.

2.3 | Statistics

Statistical analysis and graphing were done using base R (Team, 2023) and *ggplot2* (Wickham, 2016); schematic diagrams (Figure 1 and Figure S1) were created in Microsoft PowerPoint. We used a linear mixed effects model in the *lme4* package to identify the key drivers in the respective C pools (Bates et al., 2015), with soil horizon (topsoil vs. subsoil), ecosystem type, soil pH, soil clay content, MAT, MAP and volume of soil sampled as fixed effects, and unique study identifier as a random effect. The significance of model predictors was assessed using the *lmerTest* package (Kuznetsova et al., 2017), which uses the Satterthwaite's method to conduct Type III analysis of variance on model outputs. Coefficient estimates were considered significant if they were associated with *p*-values less than .05. The *lsmeans* package was used to conduct pairwise comparisons with Bonferroni correction (Lenth, 2018).

Only ca. 50% of the observations were associated with a reported soil type that could be classified into one of the USDA soil orders, so we did not include this factor in the main models. However, we ran separate linear mixed effects models for each pool which included a "soil type" term, in addition to the factors specified above. Marginal R^2 for these models (which reports variance explained by fixed effects) was assessed using the package *MuMIn* (Burnham & Anderson, 2002). Following Type III analysis of variance on the *lmer* model output (Table S1), the models were further subject to variance partitioning using the reported sums of squares for each model term. Briefly we divided the sums of squares for each term (ecosystem type, climate [MAT + MAP], pH, clay content, soil type, and sampling effects [soil layer + soil volume sampled]), by the total sum of squares for all fixed effects. This enabled us to calculate the proportion of explained variance attributable to each of those key predictors.

For the additional analysis aimed at examining the effects of agricultural management on fPOC, oPOC, and mSOC storage, we focused on observations from croplands only. Models exploring effects of tillage included the fixed effects of soil horizon (top soil vs. subsoil), soil volume sampled, and tillage regime (conventional or "no-till," a category which also included conservation tillage or reduced tillage). Study ID was included as a random effect. Similarly, analyses of nutrient inputs on SOC pools included fixed effects of

horizon, volume sampled, and amendments (none, inorganic N, manure, or inorganic N and manure).

3 | RESULTS

Across all studies (Figure 2; 2261 unique observations from 198 studies), mean C stocks varied among pools within the entire soil column: mean fPOC was $1500 \pm 99 \text{ g m}^{-2}$, mean oPOC was $777 \pm 66 \text{ g m}^{-2}$, and mean mSOC was $3283 \pm 159 \text{ g m}^{-2}$. In studies where all 3 SOC pools were measured simultaneously (1549 unique observations from 100 studies), we were able to calculate the contribution of oPOC to total SOC. This contribution varied enormously, ranging from 0 to 82.5% of total SOC, with a mean contribution of $17.7 \pm 7.2\%$.

Ecosystem type had a large and significant effect on all three SOC pools (Table 1), with C distributions among pools generally conforming to our initial predictions. Model-estimated mSOC stocks were 87% greater in grassland and 102% greater in shrubland, with forest mSOC stocks intermediate (Table 1, Figure 3a). oPOC stocks in cropland soils did not significantly differ from zero, but were 444 ± 338 and 369 ± 349 in forest and grassland soils, respectively. Shrubland oPOC stocks (173 ± 411) did not significantly differ from those in cropland (Table 1, Figure 3b). fPOC stocks in forest and grassland soils were 58% and 38% greater than in cropland, respectively, though not different from each other (Figure 3c).

In the subset of studies for which soil type (USDA soil order) could be determined (1187 unique observations from 124 studies), soil order influenced pools of oPOC and mSOC but had no effect on fPOC (Table S1). mSOC pools were largest in Andisols, Spodosols, and Vertisols, although the effects of the latter two soil orders were nonsignificant given the restricted numbers of observations (Figure S2a). oPOC pools tended to be higher in Andisols, Inceptisols, and Mollisols than other soil orders, although this pattern was influenced by a few outlying data points (Figure S2b) and overall patterns were very weak. Additionally, soil mineralogy also influenced distributions of SOC stocks through its impacts on pH and texture. As we expected, the mSOC pool responded to variation in soil pH, but we observed this pattern for fPOC as well—both pools decreased strongly by $382\text{--}403 \text{ g m}^{-2}$ with every unit increase in pH (Table 1, Figure 4). Soil clay content was not correlated with any C pool in the global dataset (Table 1), but was positively associated with mSOC when soil type was controlled for (i.e., in the analysis on a much smaller subset of observations, Table S1). We found no correlation between MAP or MAT and any of the SOC pools, although fPOC and mSOC had a weakly negative relationship with MAT and a weakly positive relationship with MAP when the proportion of each fraction to total SOC was examined as the response variable from studies that reported all three pools (Table S2).

To explore the degree of variability in each SOC pool attributable to major differences among ecosystems, soil types, and climate regimes, we conducted a variance decomposition following a Type III analysis of variance on the mixed effect models described above. We found that the oPOC pool exhibited 0.5–5-fold more variance

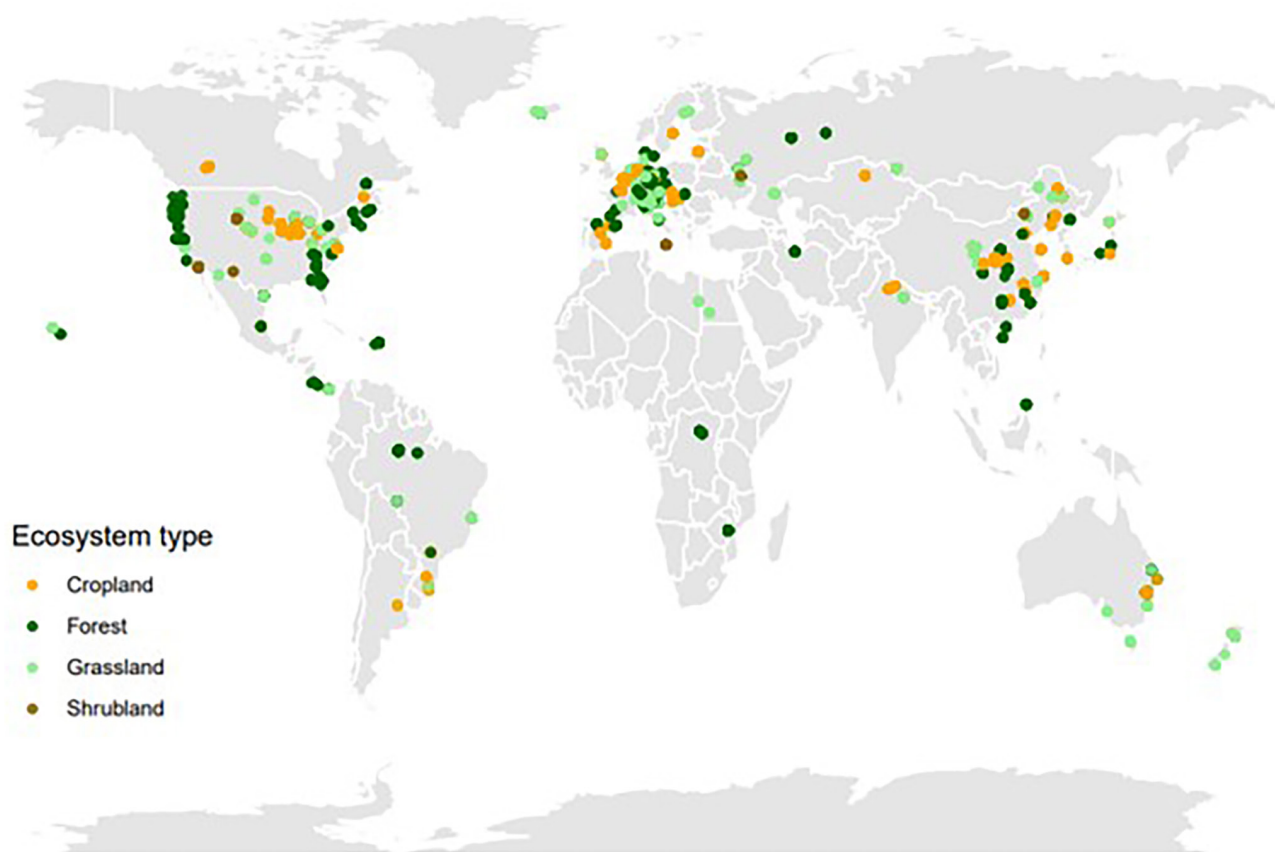


FIGURE 2 Global distribution of sites included in the analysis, colored according to ecosystem type. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

across ecosystems than fPOC and mSOC (Table 2). Additionally, soil clay content had a much more powerful impact on mSOC vs. fPOC and oPOC. Patterns of variance in response to other environmental drivers were relatively similar among pools.

As cropland soils are directly managed, unlike those in other ecosystems, we ran a separate linear model for cropland soils, aimed at examining the effects of tillage and nutrient inputs on SOC storage in each pool. Our goal was to identify whether some of these practices can avert the losses of free, physically protected, and chemically protected C observed across croplands in general. Tillage practices did not have a detectable effect on any of the three pools (Table S3, Figure 5a–c), although there were trends toward higher fPOC (Figure 5a), which were marginally nonsignificant for fPOC stocks in reduced tillage soils ($p=.079$). Soil nutrient inputs did affect C storage: the combination of inorganic N and manure stimulated C storage in mSOC, whereas oPOC and fPOC were unaffected (Table S4, Figure 5d–f).

4 | DISCUSSION

4.1 | Ecosystem type is the predominant driver for changes in SOC stocks

When separated from the unprotected (fPOC) and mineral-associated (mSOC) C pools, physically protected carbon (oPOC)

represents a sizeable SOC pool that has not been explicitly quantified in previous meta-analyses. Consistent with our first hypothesis, across the entire dataset, fPOC and oPOC pools both exhibited a larger coefficient of variation (2.20 and 1.27, respectively) than the mSOC pool (1.08). This indicates that the mechanisms that control the physical protection of SOC are more dynamic than those that control its chemical (organo-mineral) protection.

In line with our second hypothesis, ecosystem type had a large and significant effect on all three SOC pools, with C distributions among pools generally conforming to our initial predictions. fPOC and oPOC stocks likely reflect greater C inputs and lower C losses from more vulnerable pools in forest and grassland ecosystems as compared with managed systems (croplands). In contrast to croplands, forest and grassland soils tend to have greater root (Hu et al., 2016) and aboveground litter inputs (Hooker & Compton, 2003; Xu et al., 2021), along with less physical disruption from ploughing, tillage, and harvest, allowing for greater retention of SOC in both particulate and aggregate form (Murage et al., 2007; Yoo & Wander, 2008). We also note that oPOC stocks in croplands were not significantly different from 0 g m^{-2} , confirming the instability of aggregates in low-productivity or frequently disrupted soils.

As well as responding strongly to the influence of ecosystem type, all three C pools were influenced by differences in soil geochemistry. Soil texture (clay percentage) did not have a significant effect on any of the C pools in the main analysis, yet oPOC and

TABLE 1 Coefficient estimates (and associated *p*-values, calculated with Satterthwaite's approximation) for linear mixed models of environmental variation in three soil carbon pools.

	fPOC (g m ⁻²), N = 1017	oPOC (g m ⁻²), N = 604	mSOC (g m ⁻²), N = 575
Ecosystem type			
Forest	1289 (<0.001)	444 (<0.001)	412 (0.111)
Grassland	841 (0.004)	369 (<0.001)	1037 (<0.001)
Shrubland	645 (0.296)	173 (0.427)	1213 (0.028)
Climate			
MAT	15.7 (0.586)	8.2 (0.583)	-7.7 (0.867)
MAP	-0.3 (0.308)	-0.2 (0.272)	0.5 (0.233)
Soil factors			
pH	-382 (0.001)	30.8 (0.501)	-403 (0.002)
Clay content	-7.1 (0.485)	-3.6 (0.405)	21.2 (0.098)
Sampling factors			
Soil horizon sampled (topsoil vs. subsoil)	1133 (<0.001)	511 (<0.001)	2291 (<0.001)
Total soil volume sampled	0.0015 (0.010)	0.0009 (<0.001)	0.006 (<0.001)

Note: Study identity was included as a random effect in all models. Continuous predictors with significant slopes, or categorical predictors significantly different from the reference values (croplands, subsoils) are bolded. Because most observations were not associated with information about soil order, we did not include this factor in the models shown here. Results for mixed models including a soil type term can be found in Table S1.

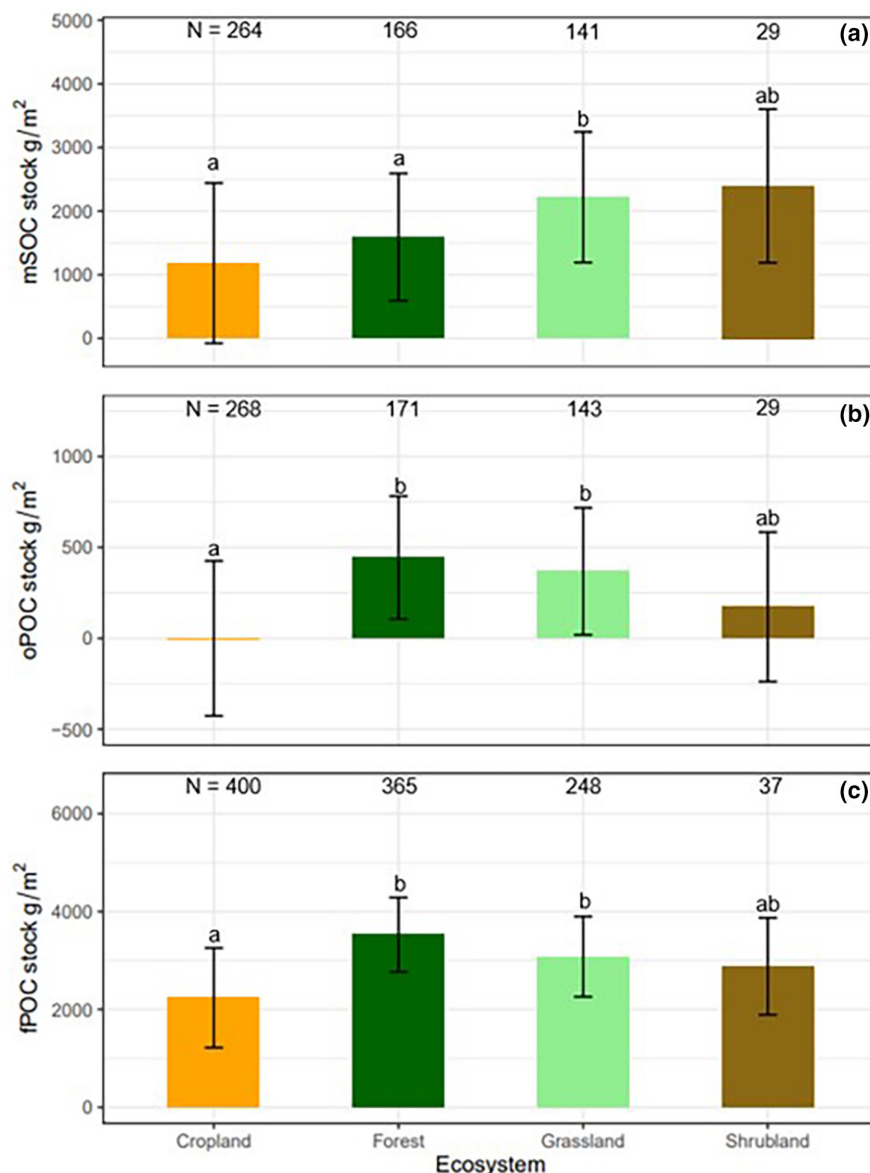
mSOC (but not fPOC) were influenced by soil order. This suggests that mineralogy helps regulate the capacity for C accumulation. Larger mSOC pools in Andisol and Vertisol soil orders are consistent with the high activity of volcanic and shrink-swell clays that characterize these soils. Additionally, mSOC pools increased with soil clay content—after controlling for soil order—suggesting fine-textured soils provide superior chemical stabilization of organic matter. Meanwhile, a significant negative relationship between soil pH, fPOC, and mSOC in our dataset could indicate that decomposition was limited in acidic soils. Previous studies have demonstrated that acidic soils store more SOC (Zhang et al., 2020), as microbial decomposition and efficiency increase above ca. 6.2 pH in forest soils, leading to increased decay of unprotected C. mSOC is likely to be more dynamic than previously conceptualized in response to pH fluctuation, as soil acidification may lead to organic matter stabilization on variable charged mineral binding sites and vice versa with alkalization (Kleber et al., 2021; Lavalley et al., 2020).

Climate likely exerts its impact on SOC stocks indirectly, by influencing the distribution of forest, grassland, and shrubland ecosystems. Even within ecosystem types, climatic changes can influence

SOC stocks differently, with increased temperature promoting an increase in SOC in some croplands (Wiesmeier et al., 2014), but inducing a negative response in others (Zhang et al., 2019). Similar inconsistent results can be found for precipitation and temperature in forests (Campo & Merino, 2016; Post et al., 1982; Wiesmeier, Prietzel, et al., 2013) and grassland SOC pools (Wiesmeier, Hübner, et al., 2013; Zhao et al., 2017) while SOC stocks in shrubland soils tend to increase with both precipitation and temperature (Doblas-Miranda et al., 2013; Nie et al., 2019). Given that precipitation and temperature are predicted to continue changing in response to rising atmospheric CO₂ levels (Konapala et al., 2020; van der Wiel & Bintanja, 2021), a nonsignificant response of fPOC, oPOC, and mSOC to these factors on the global scale in our analysis is noteworthy. It should not be inferred that SOC stocks are immune to changes in precipitation and temperature; rather, the strong response to the ecosystem indicates that these pools are more influenced by factors locally, while many studies have found a strong response of SOC to precipitation and temperature when examined experimentally (Chen et al., 2020; Nottingham et al., 2020; Soong et al., 2021). We investigated the effects of climate on the proportion of each fraction to the total SOC pool (Table S2), finding that MAT and MAP had weakly positive and negative effect, respectively, on fPOC and mSOC. Within ecosystem types (Table S5)—and found that in forests only—oPOC increased with rainfall whereas mSOC increased with temperature. Although our study cannot shed light on the mechanisms underlying the differential climate sensitivity of carbon pools across ecosystems, the special vulnerability of soil C in forests emphasizes the key role these ecosystems play in the Earth System (Bonan, 2008).

The three SOC pools we examined were differentially sensitive to the effects of ecosystem type, climate, and soil mineralogy, which provides insight into the factors that control soil C accumulation and loss in each pool. For example, the oPOC pool exhibited the greatest degree of variation in response to ecosystem type. This is possibly because the residence time of aggregates is more sensitive to factors that vary among ecosystems, such as plant species identity and physiology. The influence of root density and morphology may be particularly important (Greinwald et al., 2021; Ma et al., 2023; Tisdall & Oades, 1982). Interestingly, clay percentage did not affect any of the SOC pools, yet oPOC and mSOC stocks varied among soil orders and fPOC stocks did not. Additionally, fPOC and mSOC—but not oPOC—responded negatively to increased soil pH. It would be expected that free particulate organic matter pools should not be influenced by soil weathering status, whereas mineral protection mechanisms are strongly tied to the abundance and identity of different clays which predominate across soil weathering sequences (Alberto Quesada et al., 2020; Kögel-Knabner, 2017). Similarly, the oPOC pool may capture SOC protected via flocculation, occlusion in pores within secondary clay structures, or through the recrystallization of carbonates (Rowley et al., 2018; Six et al., 2004; Y. Xu et al., 2022)—all of which are influenced by soil mineralogy and pH. Given the mixed results of all three pools in response to differences in pH, soil order, and soil texture, it is unclear what effect geochemical factors have

FIGURE 3 Mean mSOC, oPOC, and mSOC stocks vary by ecosystem. Bars represent propagated standard error of the mean based on mixed-linear model coefficients. Letters denote significant differences according to a pairwise comparison and Bonferroni correction of *p*-values.



on SOC storage on a broad scale. However, the strong response of the SOC fractions to ecosystem type indicates that vegetation and management are the key drivers of organic C storage.

4.2 | Implications of fPOC, oPOC, and mSOC distributions for climate mitigation via enhanced soil C sequestration

With an international push for global SOC stocks to increase by 0.4% each year to mitigate climate change (Griscom et al., 2017; Minasny et al., 2017; Paustian et al., 2016), we were interested in how land use might impact the distribution of C among pools with different residence times and vulnerabilities to disturbance. Across >250 observations, tillage did not significantly influence the magnitude of any SOC pool. This response is notable, as much debate has gone into the merits of reduced and no-till practices for C sequestration.

Some researchers point to increased aggregation and total SOC under conservation tillage (Liu et al., 2021; Ogle et al., 2019) as evidence that this practice can provide a mechanism for large-scale C sequestration if applied at a global scale. Others are more skeptical (Powlson et al., 2014), acknowledging that topsoil C often increases in no-till soils, but that these gains can be offset by losses deeper in the soil profile (Baker et al., 2007). Given the uncertainty surrounding the effects of tillage across the whole profile, our dataset provides a much-needed comprehensive analysis by examining SOC exclusively in terms of density fractionated fPOC, oPOC, and mSOC pools. This rigorous methodology is more informative than those that only measure aggregate C or total SOC, because it provides a lens onto the mechanisms that may influence SOC accumulation and stability under a change in tilling practices. Our results suggest that tillage is not a key determinant of C stability in any C pool, including the physically protected oPOC pool which is hypothesized to be most sensitive to soil disturbance. There was a relatively strong trend

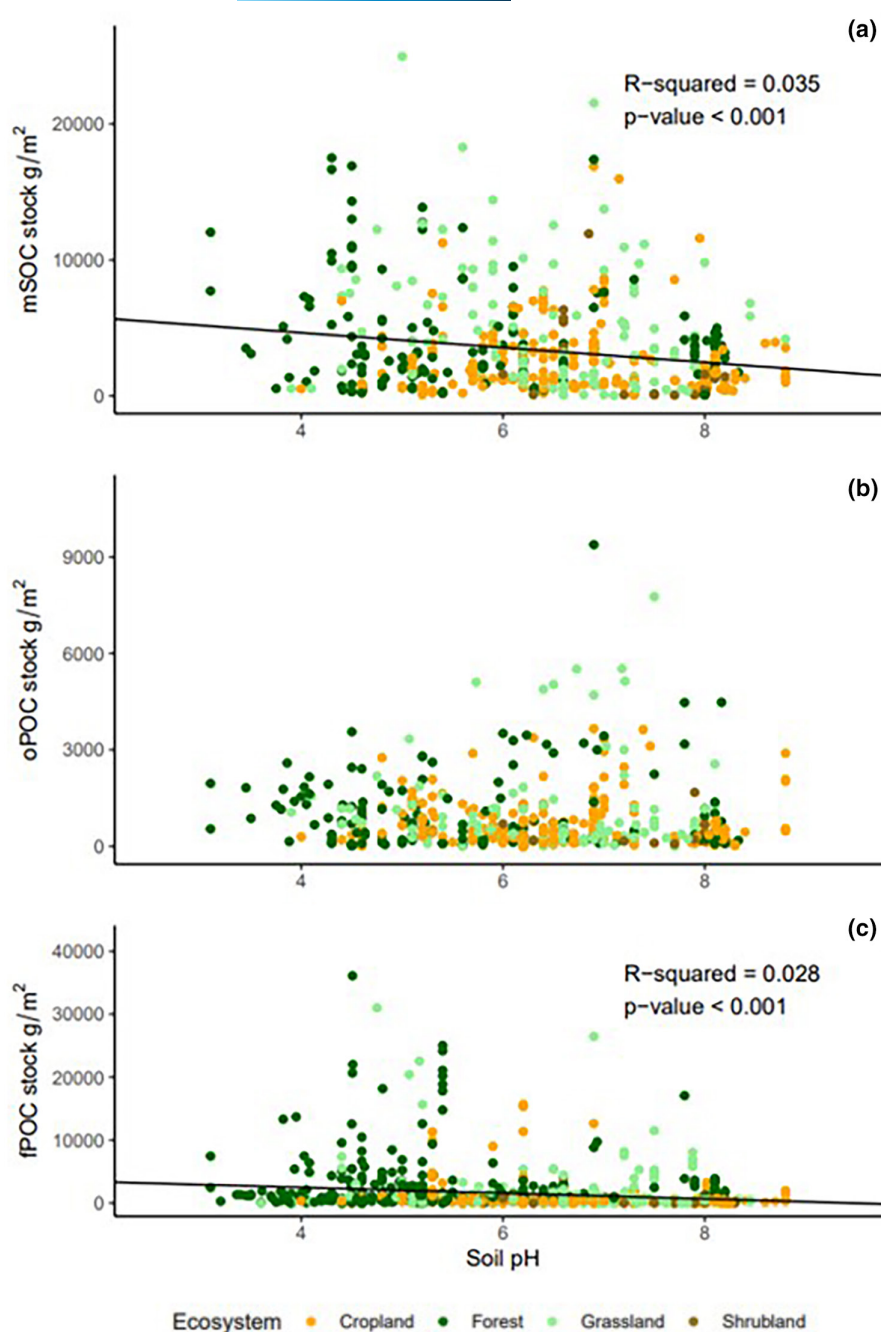


FIGURE 4 SOC storage in mSOC, oPOC, and fPOC pools in relation to soil pH across ecosystem types. Regression lines denote intercept and slope for significant relationships in mSOC and fPOC pools. R^2 , p -values, and regression coefficients were taken from simple linear models of the relevant pool on the individual factor displayed on the X-axis.

toward enhanced fPOC stocks in reduced tillage soils, which indicates that these management practices did influence SOC in some systems and could prove effective at the site level. Yet, the overall results of our global analysis and those of other studies should caution policymakers and land managers against promoting no-till and reduced-till practices as a large-scale C sequestration strategy.

By contrast, N fertilizer and manure inputs had a fairly substantial impact on mSOC stocks. This result is consistent with a recent global analysis, which found a 35% increase in total SOC after manure application, though responses varied substantially depending on manure type (Gross & Glaser, 2021). A nonsignificant change in fPOC stocks in our results could indicate that added organic matter from manure is metabolized immediately, rather than persisting as

fPOC or becoming incorporated into aggregates in the oPOC pool. Furthermore, the only increase in mSOC stocks occurred when inorganic N and manure were added together, meaning that microbes likely relied on resources from both additives (i.e., both C and N) to synthesize the biomass that was subsequently stabilized in mSOC. In sum, our results are informative for conceptualizing the effects that commonly utilized agricultural amendments have on all three SOC pools, while providing insight into the biochemical fates of these additions.

Given the relatively limited capacity for most agricultural interventions to enhance total SOC, we explored how much soil C stocks could be enhanced by converting cropland to forest, grassland, or shrubland soils over a 50-year period. This time frame was

TABLE 2 Proportion of explained variance attributable to ecosystem type, climate (MAT and MAP), soil pH, and soil type (USDA soil order) in mixed effects models of three soil carbon pools.

	fPOC	oPOC	mSOC
Proportion of total variance explained by fixed effects (R^2_{marginal})	0.097	0.138	0.344
Proportion of explained variance attributable to...			
Ecosystem type	0.242	0.357	0.064
Climate	0.013	0.008	0.042
pH	0.051	0.023	0.064
Soil type	0.246	0.524	0.284
Clay content	0.005	0.002	0.086

Note: The remaining fixed effect variance (not shown in the table) is attributable to the effects of soil layer (topsoil vs. subsoil) or the volume of soil sampled (included to control for methodological variation among studies). Individual fixed effects are shown in bold if they were significant predictors in the analysis of variance upon which these figures are based (see Table S1). Patterns of significance vary slightly from those presented in Table 1, due to the inclusion of soil order in the models.

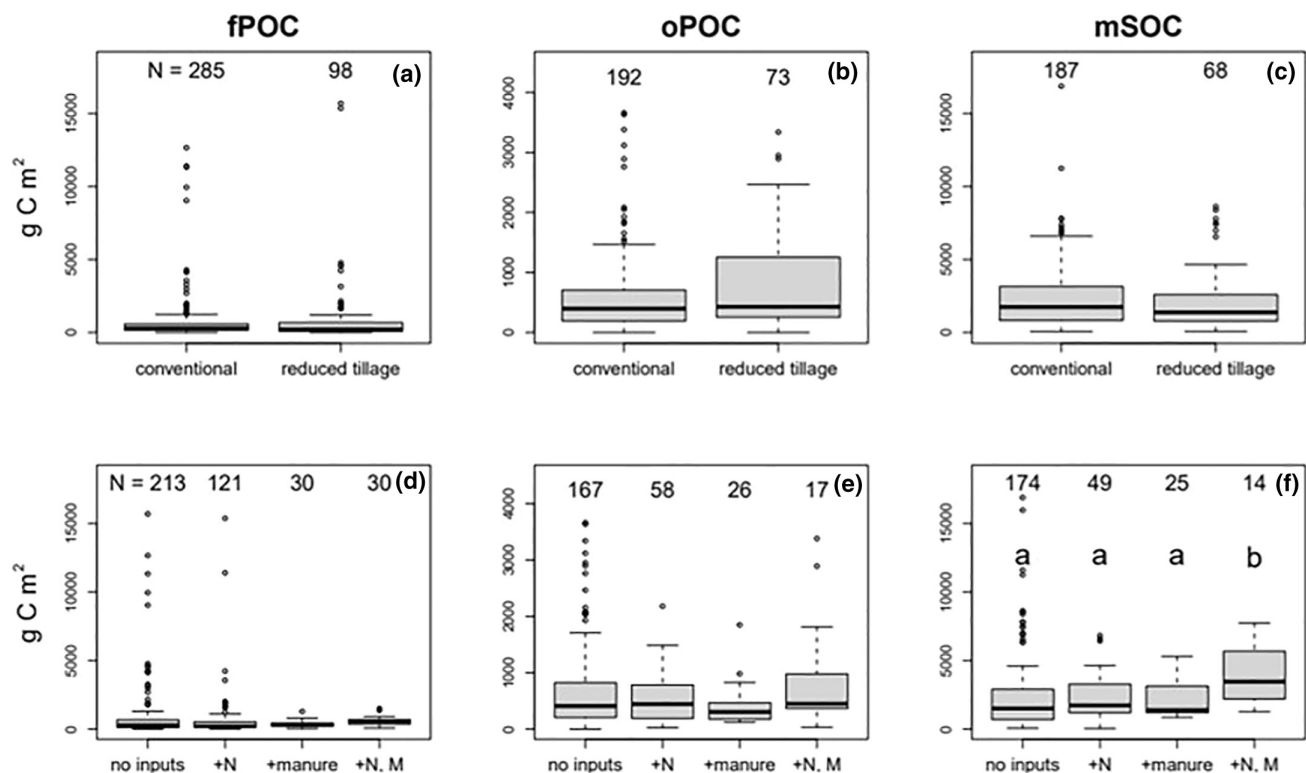


FIGURE 5 C storage in cropland soils as a function of tillage (conventional vs. reduced/no tillage, a–c) and nutrient input regime (d–f). The number of observations in each treatment group is indicated above the boxplots. The impacts of nutrient inputs on mSOC C stocks were significant. Letters denote significant differences according to a pairwise comparison and Bonferroni correction of *p*-values.

chosen as soils can lose SOC during the first 5–15 years after forest and grassland planting (Post et al., 1982), followed by a recovery where stocks can increase by 0.5–1.5% yearly (Post et al., 1982; Yang et al., 2019). Given mean cropland C pool sizes (721 ± 86 g fPOC m⁻², 628 ± 42 g oPOC m⁻², and 2410 ± 147 g mSOC m⁻²) and extrapolating a net gain of 0.4% (4 per mille) yearly results in 880 g fPOC m⁻², 767 g oPOC m⁻², and 2942 g mSOC m⁻² after five decades. These amounts are still far less than the means of those respective C pools in forest and grassland. We conclude that conversion

of cropland to native vegetation under proper management practices could be well within the SOC sequestration goals outlined in the 4 per mille initiative. Large-scale land-restoration initiatives away from cropland should account for a growing human population and must be carefully balanced to avoid food insecurity (Duro et al., 2020; Tscharnkte et al., 2012). However, our results clearly highlight the benefits of retaining and restoring native vegetation where possible to maintain and increase belowground organic C storage.

5 | CONCLUSIONS

Our results provide the most comprehensive assessment of SOC stocks as measured by density fractionation methodology to date. We demonstrated that the physically protected SOC pool, oPOC—which is not explicitly quantified in most studies—makes up a sizeable fraction of the total SOC stock and seems to be the most responsive to environmental variation. It is vital that future quantitative assessments and models differentiate oPOC from mSOC and acknowledge its role in the microbial processing of SOC. Conservation tillage and nutrient amendment did not strongly enhance SOC stocks, whereas all pools were greater in forest and grassland relative to arable soils. This emphasizes the importance of maintaining native vegetation to retain soil C in all its chemical forms.

AUTHOR CONTRIBUTIONS

Samuel J. Willard: Conceptualization; data curation; formal analysis; methodology; resources; validation; visualization; writing – original draft. **Guopeng Liang:** Conceptualization; data curation; methodology; writing – review and editing. **Savannah Adkins:** Conceptualization; data curation; writing – review and editing. **Jessica Murray:** Conceptualization; data curation; writing – review and editing. **Bonnie Waring:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest to report.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.b5mkkwhp0>. The following publicly available datasets were utilized for this study and can be accessed at: Terra Climate (<https://www.climatologylab.org/terra-climate.html>) and Harmonized World Soil Database (<https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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