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RESEARCH ARTICLE

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Distinct, direct and climate-mediated environmental controls on global particulate and mineral-associated organic carbon storage

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Abstract

Identifying controls on soil organic carbon (SOC) storage, and where SOC is most vulnerable to loss, are essential to managing soils for both climate change mitigation and global food security. However, we currently lack a comprehensive understanding of the global drivers of SOC storage, especially with regards to particulate (POC) and mineral-associated organic carbon (MAOC). To better understand hierarchical controls on POC and MAOC, we applied path analyses to SOC fractions, climate (i.e., mean annual temperature [MAT] and mean annual precipitation minus potential evapotranspiration [MAP-PET]), carbon (C) input (i.e., net primary production [NPP]), and soil property data synthesized from 72 published studies, along with data we generated from the National Ecological Observatory Network soil pits ($n=901$ total observations). To assess the utility of investigating POC and MAOC separately in understanding SOC storage controls, we then compared these results with another path analysis predicting bulk SOC storage. We found that POC storage is negatively related to MAT and soil pH, while MAOC storage is positively related to NPP and MAP-PET, but negatively related to soil % sand. Our path analysis predicting bulk SOC revealed similar trends but explained less variation in C storage than our POC and MAOC analyses. Given that temperature and pH impose constraints on microbial decomposition, this indicates that POC is primarily controlled by SOC loss processes. In contrast, strong relationships with variables related to plant productivity constraints, moisture, and mineral surface availability for sorption indicate that MAOC is primarily controlled by climate-driven variations in C inputs to the soil, as well as C stabilization mechanisms. Altogether, these results demonstrate that global POC and MAOC storage are controlled by separate environmental variables, further justifying the need to quantify and model these C fractions separately to assess and forecast the responses of SOC storage to global change.

KEYWORDS
climate, environmental controls, primary productivity, soil organic carbon fractions, soil properties

1 | INTRODUCTION

Maintaining and increasing soil organic carbon (SOC) stores is crucial to mitigating climate change and to enhancing the soil's capacity to provide essential ecosystem services, including nutrient recycling and maintenance of plant productivity. As such, it is imperative that we develop an advanced understanding of the environmental conditions under which SOC is most vulnerable to loss, as well as its responses to deliberate management practices aimed at increasing SOC storage. Although we can now identify how drivers of SOC storage, including climate (Jobbágy & Jackson, 2000), carbon (C) inputs, and soil properties (Hassink, 1997; Six et al., 2002) operate on a variety of spatial scales (Wiesmeier et al., 2019), we lack a quantitative framework of hierarchical controls on SOC storage that incorporates its conceptualization into separate fractions. Such knowledge could give us a more specific understanding of how different forms of SOC can be gained or can be lost across multiple ecosystem types, allowing us to better target "multi-pool management" practices (Angst et al., 2023) towards increasing or maintaining SOC storage in different fractions.

Conceptualizing SOC into particulate (POC) and mineral-associated organic carbon (MAOC) fractions can be particularly useful as a first step in building a more comprehensive understanding of global controls on SOC formation and persistence (Cotrufo & Lavallee, 2022; Lavallee et al., 2020). Particulate organic C is formed via fragmentation of structural plant inputs and is primarily protected by physical occlusion in aggregates (or in the case of pyrogenic C, through chemical recalcitrance). Limited protection from decomposition results in POC having relatively short mean residence times (von Lützow et al., 2007), except in locations where decomposition is limited by physical or physiological constraints on microbial activity (Cotrufo & Lavallee, 2022) where POC is found to accumulate (Herndon et al., 2017). In contrast, MAOC is formed via sorption of microbial necromass and decomposition products, as well as soluble plant inputs, to soil mineral surfaces (Haddix et al., 2016; Kallenbach et al., 2016; Liang et al., 2019). These mineral bonds make MAOC relatively inaccessible to microbial decomposition, leading to, on average, longer mean residence times than POC (von Lützow et al., 2007). Given their distinct mechanisms of formation and persistence, it is likely that global POC and MAOC storage are controlled by contrasting environmental variables.

Climate may be the primary driver of both POC and MAOC storage because of its effects on factors that influence the amount of C that enters (i.e., C inputs) and leaves the soil (i.e., C outputs; Cotrufo et al., 2021). For instance, both temperature and moisture are important controls on annual C inputs to soil (i.e., net primary production [NPP]; Churkina & Running, 1998), with increased C inputs often leading to greater SOC storage (Lajtha et al., 2014; Luo et al., 2017). While we lack an understanding of how C inputs separately affect POC and MAOC storage, MAOC can be expected to be more reflective of C inputs than POC, due to POC's lack of soil matrix protection from decomposition. Independent of inputs, climate may act as an additional control on SOC storage through its effects on microbial activity constraints (Cotrufo & Lavallee, 2022). For instance, POC may be particularly sensitive to climate-driven variations in decomposition (Conant et al., 2011). Temperature and moisture are key controls on microbial activity, with higher temperatures leading to accelerated decomposition (Schimel, 2018), especially for complex structural compounds that require higher activation energy to decompose (Davidson & Janssens, 2006) and when optimum soil moisture levels increase microbial access to substrates through increased diffusion (Schimel, 2018). As such, we may expect lower POC storage in warm compared to cold ecosystems, especially when microbial access to substrates is limited by low diffusion under dry conditions. Additionally, moisture may serve as a direct control on MAOC storage through its effects on dissolved organic carbon (DOC) leaching. As plant-derived DOC can make up nearly half of MAOC storage (Angst et al., 2021), leaching of DOC due to high moisture may contribute to greater MAOC stores (Haddix et al., 2020), especially in ecosystems where the majority of MAOC is plant-derived. However, little work has focused on how temperature, moisture, and C inputs interact with one another to control POC and MAOC storage, especially at large spatial scales.

In addition to climate, soil physicochemical properties may act as a further control on POC and MAOC storage. For instance, strong associations with soil mineral surfaces may mean that the capacity of the soil to form mineral bonds with organic C molecules is an additional control on MAOC storage, with higher silt and clay contents leading to greater storage of MAOC (Hassink, 1997; Six et al., 2002). Other physicochemical properties, including exchangeable calcium (Ca) and iron (Fe) and aluminum (Al) hydroxides, may operate as additional controls on MAOC storage (King et al., 2023; Kirsten et al., 2021; Rowley et al., 2021), whose importance to C storage may be mediated by soil moisture and pH (Rasmussen et al., 2018). pH may also control POC storage through its inhibitory effects on microbial activity. Like cold temperatures, low pH can slow microbial decomposition (Rousk et al., 2009) and may contribute to greater POC storage in acidic soils. However, little work has investigated the extent to which these soil properties interact with our hypothesized overarching climatic controls in determining global patterns of POC and MAOC storage.

To identify hierarchical controls on global C storage, we synthesized POC and MAOC fraction data from 72 existing studies and databases, along with SOC fraction data we generated from the National Ecological Observatory Network (NEON) "megapit" soils (Hinckley et al., 2016). We included studies conducted in a diversity of climate and land cover types, with the goal of identifying controls on POC and MAOC that are generalizable across a variety of ecosystems. We aimed to assess the extent to which climate, NPP, and soil properties directly versus indirectly control C storage in POC, MAOC, and bulk SOC. Based on the observations described above, we broadly hypothesized that POC and MAOC storage would be governed by distinct, climate-mediated environmental controls (Cotrufo et al., 2021), with POC being primarily controlled by C loss processes related to microbial activity constraints, and MAOC being primarily controlled by a combination of C input limitations and soil properties related to C stabilization. Additionally, we hypothesized that linking environmental variables to POC and MAOC would exhibit greater utility in understanding global patterns of C storage than linking the same variables to bulk SOC alone.

2 | MATERIALS AND METHODS

2.1 | Global synthesis of particulate and MAOC data

We constructed an observational dataset of POC and MAOC by conducting a comprehensive search on Google Scholar using various combinations of keywords including "soil carbon," "soil organic matter," "particulate and mineral-associated," "light and heavy fractions," "density fractionation," and "size fractionation," then collating all relevant data from published studies and existing databases (Figure 1). We chose to use Google Scholar as it may have greater geographic representation than other search engines (Harzing & Alakangas, 2016; Martín-Martín et al., 2018). For studies that fractionated soil by size or density only, we defined POC as >53–63 μm in size or <1.65–1.85 g cm^{-3} in density, and MAOC as <53–63 μm or >1.65–1.85 g cm^{-3}. For studies that fractionated soil by both size and density, we considered POC to be <1.65–1.85 g cm^{-3}, and MAOC to be >1.65–1.85 g cm^{-3} and <53–63 μm. Heavy coarse fraction (>1.65–1.85 g cm^{-3} and >53–63 μm; sensu Leuthold et al., 2022) C and occluded SOC fraction (in the cases in which POC was separated by density before dispersion) data were retained for calculations of total SOC (see Section 2.4, below), but excluded from analyses performed on fraction data only. This was done to maintain as much consistency in SOC fraction definitions as possible, as the fractionation schemes of the studies included in our synthesis varied with both study and ecosystem type. While we focused our synthesis primarily on observational studies, we also included data from control plots (i.e., not receiving experimental treatments) of relevant field studies involving experimental N deposition, CO$_2$ enrichment, climate manipulations, etc. However, for experimental studies in agricultural systems where treatment represented a modified management practice, we included all reported data to account for the fact that management practices vary across the landscape, and may generate different environmental controls (e.g., NPP, pH, etc.) on POC and MAOC storage.

2.2 | NEON data generation

We supplemented our synthesis with additional SOC fraction data we generated by fractionating "megapit" mineral soil samples from the NEON (Hinckley et al., 2016). Soil samples were taken from megapits

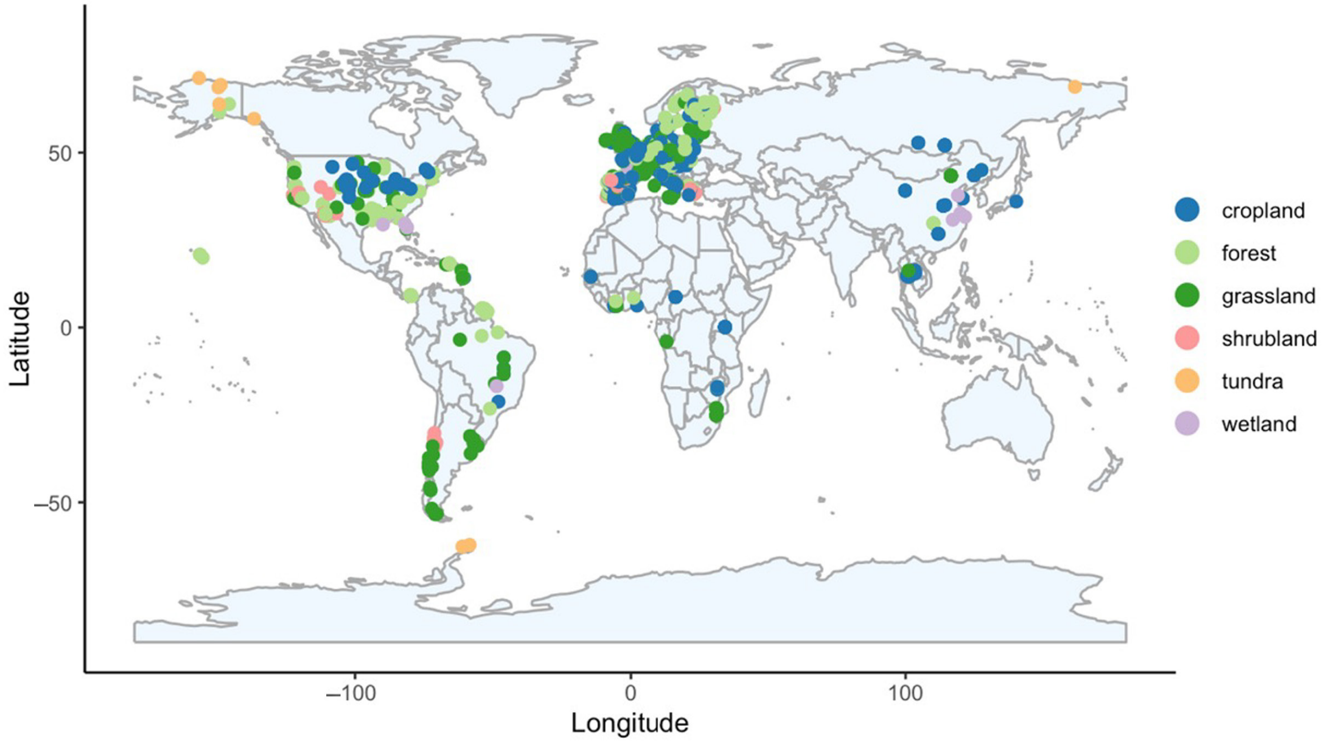

FIGURE 1 Geographic location of all data points included in our synthesis ($n=901$). Different colors represent the land cover type assigned to each point based on author-reported plant community composition and management information. For croplands, $n=312$; for forests, $n=233$; for grasslands, $n=301$; for shrublands, $n=35$; for tundra, $n=7$; and for wetlands, $n=10$. The distribution of our included data across Köppen-Geiger Climate Classification Zones (Beck et al., 2018) can be found in Figure S1. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

or large, temporary soil pits dug to either 2 m depth or bedrock at each of NEON's 47 terrestrial research sites, divided by horizon, then homogenized and characterized according to standard NEON protocols. A subsample of each of the 2-mm sieved, air-dried megapit soil samples was shipped to Colorado State University, where they were de-quarantined for 16 h at 116°C according to APHIS regulation. After de-quarantining, we fractionated all soil samples by both density ($1.85\,g\,cm^{-3}$) and size ($53\,\mu m$) after mechanical dispersion as described in Zhang et al., 2021. Briefly, 5.5–6.0 g subsamples were first shaken in deionized (DI) water for 15 min, then centrifuged at 3400 rpm. Dissolved organic matter was decanted over a 20 μm nylon filter and stored at −20°C. Any particulate material on the filter was set aside as part of the light particulate organic matter fraction ($<1.85\,g\,cm^{-3}$). Twelve glass beads and $1.85\,g\,cm^{-3}$ sodium polytungstate (SPT) were added to the soil residue and shaken for 18 h to disperse aggregates. Soils were then centrifuged for 30 min at 3400 rpm, and the remaining light particulate organic matter was aspirated onto a 20 μm nylon filter. The pellet ($>1.85\,g\,cm^{-3}$) was rinsed multiple times to remove any remaining SPT before wet-sieving to separate it into heavy coarse organic matter (>53 μm), and mineral-associated organic matter (<53 μm). All solid fractions were oven-dried at 60°C, then finely ground to ensure homogenization before being analyzed for %C on an elemental analyzer (Costech ECS 4010; Valencia, CA, USA). Samples that contained carbonates according to the NEON database were acid-fumigated to remove carbonates (Harris et al., 2001), then re-analyzed to obtain organic C values. For this study, we used the light POC and MAOC values from topsoil samples only (see Section 2.4, below), for a total of 47 observations for each of the fractions, as well as bulk SOC.

2.3 | Auxiliary data incorporation

In addition to SOC fraction data, we incorporated auxiliary data including mean annual temperature (MAT; °C), mean annual precipitation (MAP; mm), potential evapotranspiration (PET; mm), aboveground NPP ($Mg\,C\,ha^{-1}\,year^{-1}$) as a proxy for annual soil C inputs, soil texture and pH, bulk density, sampling depth, plant community composition, and any applicable management practices into our synthesized dataset. In all cases, we used the site data as reported in publications or contained within the NEON database. However, if specific site data types such as MAT, MAP, PET, and NPP were not available, we used reported geographic coordinates to extract equivalent 20-year average MAT and MAP values from WorldClim 2.0 (Fick & Hijmans, 2017), and 20-year average PET and NPP values from MODIS (data products MOD16A3GF.061 and MOD17A3HGF.006, respectively; Running et al., 2021; Running & Zhao, 2019). We subtracted PET from MAP to create a metric of effective moisture (MAP-PET; mm; sensu Kramer & Chadwick, 2018). Additionally, we assigned one of six broad land cover types to each soil profile (i.e., cropland, forest, grassland, shrubland, tundra, wetland; Figure 1) based on reported plant community composition and management information.

2.4 | Data processing

After compiling both synthesis and NEON megapit data, we used reported SOC stocks, soil depth, and bulk density values to convert all SOC fraction stocks to SOC fraction concentrations (g fraction-C $kg\,soil^{-1}$). As mentioned above, we did not include organic C in heavy coarse organic matter or in occluded SOC fractions in our downstream analyses of fraction data. However, we retained and used any heavy coarse organic matter or occluded SOC fraction data in calculations of $g\,SOC\,kg\,soil^{-1}$ (i.e., sum of all fraction C values), as well as calculations of MAOC relative to bulk SOC storage (i.e., f_{MAOC}; g MAOC $kg\,soil^{-1}$/g SOC $kg\,soil^{-1}$). While our original intent was to test for variations in SOC storage drivers throughout the soil profile, there was not enough subsoil data available at the global scale to include subsoils in our downstream statistical analyses. As such, we chose to focus our analysis specifically on topsoil. We considered the first sampled depth increment or horizon reported in each study to be representative of topsoil, and applied data from that layer only in downstream analyses. Depending on study site and sampling design, topsoils included both O and A horizons, and spanned different soil depths (Figure S2). This was done to minimize biases associated with variation in maximum topsoil sample depth across our synthesized dataset, as methods of normalizing data to a standardized depth (e.g., Abdalla et al., 2018; Hou et al., 2020; Ogle et al., 2005) across all our data points diluted the effects of driving variables known to change along the soil profile less than, or differently from, SOC (data not shown). After filtering our data so that it contained only topsoil, we averaged all data collected at the plot level such that we had one data point per site. At the end of all data processing, our final dataset included 901 total data points (i.e., $n = 901$ for each SOC fraction as well as bulk SOC) from 72 studies (Figure 1; Figure S1; Table S1; see *Data Sources*, below).

2.5 | Statistical analyses

We first assessed broad relationships and patterns among our data using simple linear regressions. Specifically, we used linear regressions to test for relationships of MAT and MAP-PET with NPP, as well as relationships of MAT, MAP-PET, NPP, soil pH, and % sand with POC, MAOC, bulk SOC, and f_{MAOC}. We did not include multiple factors or any interactive effects in these simple regressions, such that we tested for the effects of only one explanatory variable per regression. We then used results from these analyses and literature-supported hypotheses to conduct path analyses investigating direct and indirect controls on C storage in POC, MAOC, and SOC using the R package '*lavaan*' (Rosseel, 2012). Given that many known drivers of soil C storage interact with one another, we chose to use path analyses because of their ability to test for mediation, as well as direct and indirect effects of variables on outcomes of interest (Shipley, 2016). We created two separate path analyses, one which predicted POC and MAOC storage and one which predicted storage in bulk SOC. The fit of different iterations of these path analyses was assessed using Chi square, the comparative fit index (CFI > .9), the root mean square error of approximation (RMSEA < .08), and the standardized root mean square residual (SRMR < .08; Hooper et al., 2008). Our final path analysis structures that exhibited the best fits allowed for direct effects of MAT, MAP-PET, NPP, pH, and % sand, as well as indirect effects of MAT and MAP-PET via NPP, on POC and MAOC storage, or bulk SOC storage. We originally included topsoil sampling depth as a covariate in our analyses to account for differences in it within and across studies but removed it due to poor fit. We assessed effects of our environmental variables (i.e., MAT, MAP-PET, NPP, pH, and % sand) by assigning coefficients to individual pathways, then multiplying coefficients to calculate indirect effects (e.g., for indirect effects of MAP-PET, we multiplied the effect of MAP-PET on NPP by the effect of NPP on MAOC). We summed direct and indirect path coefficients to estimate total effects of each variable on POC, MAOC and bulk SOC storage. In addition to determining controls on SOC storage, we compared our POC and MAOC fraction path analysis with our bulk SOC analysis to assess the utility of separating SOC into POC and MAOC in understanding global patterns of SOC formation and persistence. We also assessed differences in f_{MAOC} among land cover types using Welch's one-way analysis of variance to account for uneven sample size among land cover types, and further investigated our significant test result using Games-Howell post-hoc pairwise comparisons using the R package '*rstatix*' (Kassambra, 2023). All analyses were carried out in R version 4.1.1 (R Core Team, 2021).

3 | RESULTS

3.1 | Broad relationships between climate, NPP, soil properties, and POC, MAOC, and bulk SOC storage

We first explored global patterns of SOC formation and persistence by conducting linear regressions between environmental variables and POC, MAOC, and SOC storage, as well as relationships between climate and NPP. We found significant, positive relationships between NPP and both MAT and MAP-PET (Figure S3a,b; Table S2), reflecting expected associations between climate and NPP. We also found significant relationships between POC and MAT, MAP-PET, NPP, and pH. MAP-PET and NPP were positively associated with POC, while MAT and pH were negatively associated with POC storage (Figure S3c–g; Table S2). Environmental controls on MAOC included MAP-PET, NPP, and % sand, with MAP-PET and NPP being positively related, and % sand being negatively related to global MAOC storage (Figure S3h–l; Table S2). All studied environmental variables were associated with bulk SOC. Specifically, MAP-PET and NPP were positively associated with SOC, while MAT, pH, and % sand were negatively associated with bulk SOC storage (Figure S3m–q; Table S2). We note that the significance of the above relationships may be driven in part by high sample size, as many relationships had relatively small r^2 values (i.e., .0111–.221).

3.2 | Direct and indirect controls on global POC, MAOC, and bulk SOC storage

To assess direct and indirect effects of the above environmental variables on soil C, we constructed separate path analyses to predict C storage in POC and MAOC and bulk SOC (Figures 2 and 3). Our fraction path analysis fit the data well ($\chi^2_{(2,n=649)} = 1.239$, $p = .538$; CFI = 1.0; RMSEA = .068; SRMR = .007; Hooper et al., 2008), and explained 35.8% of the variation in NPP, 12.3% of the variation in POC, and 20.5% of the variation in MAOC (Figure 2; Table S3). Consistent with our linear regression analyses, NPP was positively predicted by both MAT and MAP-PET. Global POC storage was directly predicted by MAT and pH, both of which had a negative effect on POC. Contrary to our linear regressions, however, neither MAP-PET nor NPP emerged as a significant predictor of POC, potentially because path analysis calculates partial regression coefficients that account for correlations and covariance between multiple factors, which likely reduced the already weak relevance (i.e., low r^2) of our linear regression coefficients. Global MAOC storage had direct, positive relationships with MAP-PET and NPP (and as such, indirect relationships with MAT and MAP-PET), as well as a direct, negative relationship with % sand (Figure 2; Table S3).

Our SOC path analysis revealed similar trends in global C storage. Like our fraction analysis, our SOC path analysis fit our data well ($\chi^2_{(2,n=649)} = 1.239$, $p = .538$; CFI = 1.0; RMSEA = .0; SRMR = .007; Hooper et al., 2008) and explained 35.8% of the variation in NPP, with both MAT and MAP-PET once again having direct, positive effects on NPP (Figure 3; Table S4). However, this path analysis explained only 12.3% of the variation in global SOC storage, which was predicted by all included exogenous variables. MAT, pH, and % sand had direct, negative effects on SOC storage, while MAP-PET and NPP had direct, positive effects on SOC. In addition, MAT and MAP-PET had positive, indirect effects on SOC via NPP (Figure 3; Table S4).

3.3 | Relationships between f_{MAOC}, environmental variables, and land cover type

We next aimed to understand the extent to which the above environmental controls are reflected in the fraction of C stored in MAOC relative to total bulk SOC (i.e., f_{MAOC}), as well as across land cover types that are representative of those controls. MAT, NPP, and soil pH were positively related to f_{MAOC} while soil % sand was negatively related (Table S5; Figure S4), though these relationships were relatively weak (i.e., in all cases, $r^2 < .1$). We did not find any relationships between MAP-PET and f_{MAOC} (Table S5; Figure S4). Additionally, land cover was a significant predictor of f_{MAOC} ($F_{5,37.901} = 58.024$; $p < 2\text{e-}16$; Figure 4), with croplands having higher f_{MAOC} than all other land cover types (Table S6). In addition, both shrublands and grasslands had higher f_{MAOC} than forests, wetlands, and tundra (Table S6). Notably, most land cover types spanned

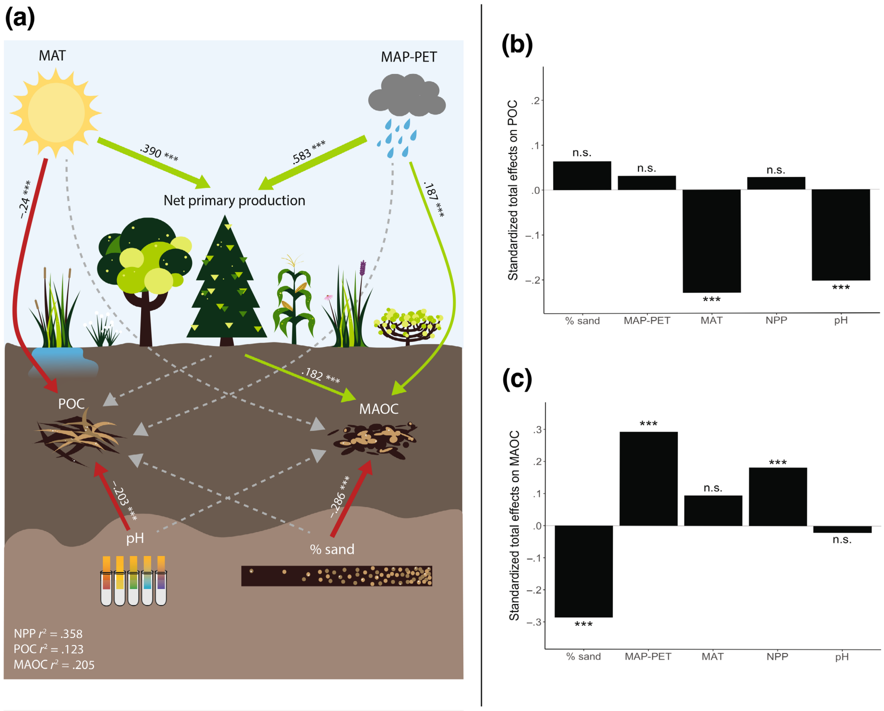

FIGURE 2 Results from path analysis showing direct and indirect effects of mean annual temperature (MAT; °C), mean annual precipitation minus potential evapotranspiration (MAP-PET; mm), net primary production (NPP; Mg C ha^{-1} year^{-1}), soil pH, and % sand on global particulate (POC; g C kg soil^{-1}) and mineral-associated organic carbon (MAOC; g C kg soil^{-1}) storage (a). Green and red arrows indicate significant positive and negative effects, respectively, of the variables described above on POC and MAOC storage. Grey, dashed arrows indicate non-significant paths. The widths of the arrows correspond to standardized path coefficients, shown in numbers above each arrow. Standardized total (i.e., direct plus indirect) effects of the variables described above on POC and MAOC storage are shown in (b) and (c). In all cases, n.s. indicates non-significant, ***$p < .001$. Full results and output are provided in Table S3.

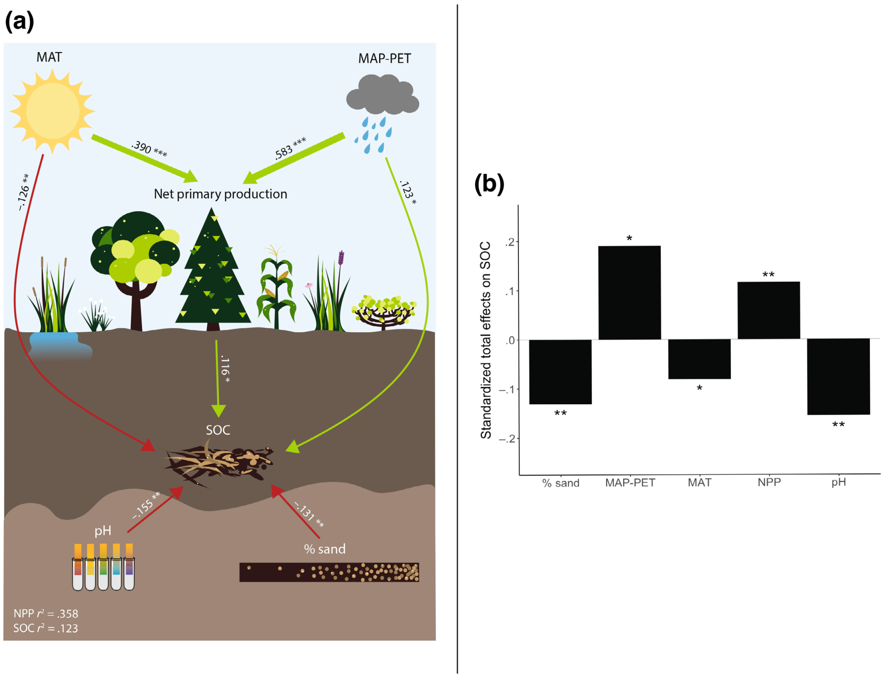

FIGURE 3 Results from our path analysis showing direct and indirect effects of mean annual temperature (MAT; °C), mean annual precipitation minus potential evapotranspiration (MAP-PET; mm), net primary production (NPP; tons C ha^{-1} year^{-1}), soil pH, and % sand on global bulk soil organic carbon (SOC; g C kg soil^{-1}) storage (a). Green and red arrows indicate significant positive and negative effects of the variables described above on bulk SOC storage. The widths of the arrows correspond to standardized path coefficients, shown in numbers above each arrow. Standardized total (i.e., direct plus indirect) effects of the variables described above on bulk SOC storage are shown in (b). In all cases, n.s. indicates non-significant, *$p < .05$, **$p < .01$, and ***$p < .001$. Full results and output are provided in Table S4.

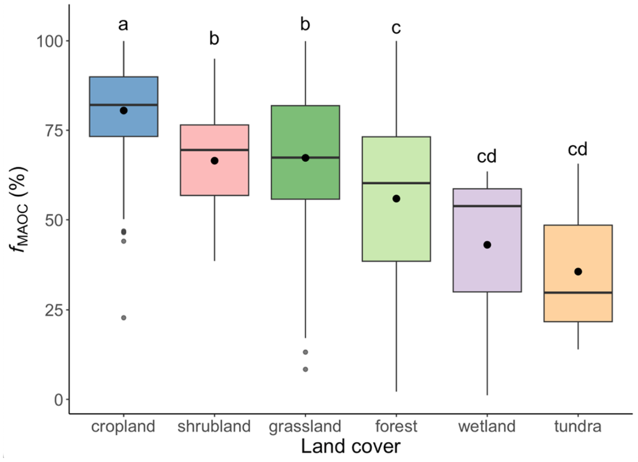

FIGURE 4 Comparison of the fraction of C stored in mineral-associated organic carbon (MAOC) relative to bulk soil organic carbon (SOC), represented as f_{MAOC} (%; (g MAOC kg soil^{-1}/g SOC kg soil^{-1}) × 100), across land cover types (cropland $n = 312$; forest $n = 233$; grassland $n = 301$; shrubland $n = 35$; tundra $n = 7$; wetland $n = 10$). Solid black dots inside each box indicate group means, and letters above bars indicate significant differences between groups. Full post-hoc testing outputs are provided in Table S6. Additional information on the distribution of our mean annual temperature, mean annual precipitation minus potential evapotranspiration, net primary production, soil pH, and % sand data across land cover types is provided in Figure S5 and Table S7.

large ranges of f_{MAOC}, which declined from >75% in croplands to <50% in tundra (Figure 4).

4 | DISCUSSION

In this study, we sought to identify hierarchical controls on global POC, MAOC, and bulk SOC storage by applying path analyses to a large dataset synthesized from published papers and data we generated from NEON megapit soils. We also evaluated the utility of C fractionation in understanding global SOC storage patterns by comparing our POC and MAOC fraction path analysis to our bulk SOC analysis. Overall, climate and soil properties (i.e., pH and texture) emerged as the primary controls on SOC, with climate exerting both direct as well as indirect controls on SOC through controlling plant productivity. Separating SOC into POC and MAOC improved our ability to identify a hierarchy of controls on SOC storage, as demonstrated by identification of distinct environmental drivers of POC and MAOC storage, along with greater % variation explained in our SOC fraction path analysis compared to our bulk SOC analysis. We found that MAT and soil pH were dominant controls on POC storage, while MAP-PET, NPP, and % sand were dominant controls on MAOC storage. These results are echoed in our bulk SOC path analysis, which revealed a similar structure of controls. These results were also echoed in our analysis of f_{MAOC} across land cover types, with land cover types that tend to experience weaker constraints on SOC decomposition (i.e., croplands) having a greater fraction of SOC stored in MAOC than types that experience stronger constraints (i.e., wetlands and tundra). Altogether, these results demonstrate that POC and MAOC are controlled by separate environmental variables, with POC storage being primarily controlled by decomposition (i.e., C output) limitations, and MAOC being primarily controlled by climate-driven plant productivity (i.e., C input) limitations, as well as SOC stabilization.

Consistent with our original hypotheses, we found that global POC storage is controlled primarily by factors that impose limitations on C loss processes (Figure 3; Table S3). The two variables most closely related to POC storage, temperature and pH, are strong controls on microbial activity, with both lower pH (Rousk et al., 2009) and lower temperatures (Schimel, 2018) contributing to slower decomposition. These findings are supported by studies conducted at smaller spatial scales, with low pH contributing to greater POC storage across the United States (Yu et al., 2022) and Europe (Lugato et al., 2021), as well as increased temperatures leading to greater POC compared to MAOC losses in lab incubations (Benbi et al., 2014). Lower POC storage under conditions that promote microbial decomposition is consistent with this SOC fraction's turnover time (von Lützow et al., 2007) and sensitivity to disturbance (e.g., Lobe et al., 2011; Poeplau et al., 2017; Song et al., 2014; Thaysen et al., 2017; Wu et al., 2023), whereby little to no protection from microbial attack makes POC reflective of microbial physical and physiological access constraints (Cotrufo & Lavallee, 2022). This shows that POC may be most vulnerable to C losses from the soil, despite being formed primarily from structural plant inputs, and therefore represents the SOC fraction that requires protection from climate change and management disturbance, such as tillage or draining of wetlands (Ashagrie et al., 2007; Bouajila & Tahar, 2010; Lavallee et al., 2019).

We found that global MAOC storage is controlled by a different set of environmental controls from POC, including % sand, NPP, and MAP-PET (Figure 3; Table S3). This indicates that MAOC is primarily controlled by climate-driven limitations on C inputs, moisture, and stabilization potential. Soil % sand was the largest control on MAOC. This relationship is broadly supported by the literature, with lower sand (and therefore greater silt and clay) contents contributing to greater MAOC storage (Hassink, 1997; Six et al., 2002). Our additional observed relationship between MAOC storage and MAP-PET is also consistent with previous findings, whereby MAP-PET was found to control the abundance of C retained by reactive minerals (Kramer & Chadwick, 2018). This association with effective moisture may be reflective of the direct sorption pathway of MAOC formation, with increased moisture leading to greater leaching of soluble plant inputs that are capable of sorbing directly to soil mineral surfaces (Haddix et al., 2020). Though large portions of the MAOC pool can be formed from microbial decomposition products and necromass (Huang et al., 2019; Kallenbach et al., 2016; Liang et al., 2019), this direct pathway of MAOC formation from plant compounds is increasingly recognized as a significant pathway of MAOC formation, especially in wet environments (Angst et al., 2021; Yu et al., 2022). Limitation on C inputs (i.e., NPP) represented another constraint on global MAOC storage. We interpret this relationship between MAOC and plant C inputs as the result of MAOC's protection from microbial access, making it less vulnerable to types of disturbance that accelerate decomposition and therefore more representative of C inputs to the soil than POC. Additionally, there could be interactions between the soil matrix and plant productivity not explored in this study that contribute to greater MAOC storage. For instance, recent work indicates that increased soil mineral capacity index (MCI) leads to both greater plant productivity and MAOC storage (King et al., 2023). As Fe and Ca, key components of this MCI, are essential plant nutrients and important for mineral stabilization, factors that promote plant productivity may also promote MAOC stabilization and storage (King et al., 2023; but see Fuhrmann & Zuberer, 2021; Ramos et al., 2018). Similarly, interactions between increased silt and clay content, soil moisture, and plant productivity resulted in higher MAOC storage in dryland soils (Mao et al., in review).

To our knowledge, this analysis is one of the first to assess global, hierarchical controls acting on both POC and MAOC storage (though recent work has investigated the roles of climate and soil minerology in determining MAOC storage and saturation; Georgiou et al., 2022). However, the structure of controls we identified, particularly with regards to climate as an overarching driver of POC and MAOC storage, is generally consistent with studies conducted at smaller spatial scales. For instance, climate and C inputs exerted the greatest influence on total bulk SOC and POC:MAOC ratio, as well as change in bulk SOC storage, in Australian croplands (Luo et al., 2017). Increased moisture has also been associated with greater MAOC persistence at continental (Heckman et al., 2023) and global scales (Heckman et al., 2022), though in contrast to recent work on global patterns of MAOC saturation, we do not find that MAT is a significant control on global MAOC storage (Georgiou et al., 2022), potentially due to differences in data analysis or in distribution of data points among climate zones (Figure S1) between our studies. Our work moves beyond the above studies by expanding our understanding of SOC storage controls through explicit incorporation of both POC and MAOC, the former of which is relatively understudied in comparison to the latter, as well as by including a global distribution of climate, soil, and vegetation types.

In addition to identifying global controls on POC and MAOC storage, we compared our SOC fraction to our bulk SOC path analysis. While we were able to identify similar effects of climate, C inputs, and soil physicochemical properties on SOC storage when we considered SOC as a single pool, the effects of these variables on SOC were stronger in our fraction path analysis than in our bulk SOC analysis. Additionally, our bulk SOC path analysis explained less variation in SOC storage than our fraction path analysis (12.3% for bulk SOC vs. 20.5% for MAOC; Figures 3 and 4; Tables S3 and S4). This demonstrates the utility of separating SOC into distinct fractions to better understand controls on its formation and storage (Lavallee et al., 2020). In this study, separating SOC into POC and MAOC not only conferred greater explanatory power, but also revealed that these separate fractions are controlled by distinct environmental variables—a finding that could not be realized when considering SOC as a single pool. Building upon the findings of previous syntheses that demonstrate that SOC is not created equal, and that its component fractions respond differently to global change and management (Heckman et al., 2022; Prairie et al., 2023; Rocci et al., 2021), this study indicates that separating SOC into POC and MAOC improves our ability to understand and quantify environmental controls on SOC storage at the global scale. As such, we continue to advocate that SOC is not studied as a unique pool. In particular, as the field has gained robust knowledge of SOC dynamics from its separation into POC and MAOC, we advocate for further separation of SOC into, for example, free versus occluded POC and exchangeable versus stable MAOC, as well as further analyses on how fractionation scheme may influence predictions of SOC fraction formation and persistence (e.g., Leuthold et al., in review; Poeplau et al., 2018). Doing so could advance our understanding of how processes like aggregate inclusion as well as sorption and desorption of DOC to mineral surfaces impact soil C storage, thus improving our ability to predict responses of SOC to global change.

Like our bulk SOC path analysis, our comparisons of SOC storage in MAOC relative to total bulk SOC (i.e., f_{MAOC}) across our included environmental variables and across land cover types dovetail our proposed understanding of POC as controlled by C loss processes. We found that land cover types thought to experience weaker constraints on microbial decomposition, such as croplands (e.g., due to the effects of tillage, Balesdent et al., 2000; Lupwayi et al., 2004 and optimal nutrient status, Parihar et al., 2019) had a greater proportion of their total SOC pool stored in MAOC than types that tend to experience stronger decomposition constraints, such as wetlands or tundra (i.e., due to anaerobic conditions (Huang et al., 2020) or cold temperatures (Frøseth & Bleken, 2015; Figure 4; Table S5). This is mirrored in our linear regressions between MAT, pH, and f_{MAOC}, whereby lower temperatures and lower pH confer greater proportions of SOC stored as POC (Figure S3; Table S5). These findings build upon Sokol et al., 2022 through more explicit incorporation of land cover types including wetlands and tundra, who also found that croplands and polar regions tend to have higher and lower f_{MAOC}, respectively, than both grasslands and forests. Given the large variance in f_{MAOC} within land cover types, especially in types that span a wide range of climatic conditions (e.g., grasslands and forests), this trend suggests that constraints on C inputs and losses from the soil may be a larger control on SOC fraction storage than C input quality. However, the large overlap in f_{MAOC} between forests and grasslands may also be explained by large differences in input quality within land cover types, especially for forests (Krishna & Mohan, 2017; Pérez-Harguindeguy et al., 2000). While more work is needed to confirm the effects of plant input quality on f_{MAOC}, these findings generally support the hypothesis that climate, and its effects on C inputs and decomposition-related SOC losses, represent overarching controls on SOC formation and persistence at the global scale (Cotrufo et al., 2021).

Moreover, within the context of ongoing calls to focus research efforts on building new, stable SOC to meet climate change mitigation goals (Bradford et al., 2019; Rumpel et al., 2018; Vermeulen et al., 2019), our findings highlight the importance of not just accruing new SOC, but also preventing losses of existing SOC, particularly C that is stored in POC. Our analyses support the notion that POC is highly sensitive to loss (Lobe et al., 2011; Poeplau et al., 2017; Song et al., 2014; Thaysen et al., 2017; Wu et al., 2023), and demonstrate that ecosystems that are especially vulnerable to disturbances associated with global change (e.g., wetlands, tundra) harbor SOC stores that are mostly comprised of POC (e.g., Herndon et al., 2017; Mirabito & Chambers, 2023; Sousa et al., 2015; Xu et al., 2009). Given that C loss processes exert a much greater control over POC than C inputs, and that the soils with the highest C contents (e.g., wetlands and tundra) have high POC stores, large amounts of SOC may be very difficult to rebuild if lost, particularly under a warming climate. As such, a focus on building new SOC, especially in the form of MAOC, is not enough (sensu Angst et al., 2023)—we claim that developing incentives that maintain current SOC stores in natural lands is equally essential to preventing the negative effects of climate change.

Despite our above findings, we note that our path analyses explained only 12.3%, 20.5%, and 12.3% of the variation in POC, MAOC, and bulk SOC storage, respectively (Figure 3; Table S3), indicating that the climate, C input, and soil property variables we included in our analyses were not sufficient to describe global patterns of SOC storage. Several recent studies demonstrate that additional soil physicochemical properties not included in this study, especially exchangeable Ca and Fe- and Al-hydroxides, are better predictors of MAOC storage than % sand alone (King et al., 2023; Kirsten et al., 2021; Rowley et al., 2021). Microbial traits including mycorrhizal type (Craig et al., 2018; Horsch et al., 2023; Keller et al., 2021) and transformation efficiency may be additional modulators of both SOC fraction storage and f_{MAOC}, though the majority of studies on microbial transformations have focused primarily on their effects on microbial-derived MAOC (e.g., Craig et al., 2022; Ernakovich et al., 2021; Kallenbach et al., 2016; Liang et al., 2019). While satellite-based NPP data is often used as a proxy for C inputs to the soil (e.g., Chen et al., 2021; Eclesia et al., 2016; He et al., 2023), it may not be as applicable to agricultural systems, where depending on management strategy, plant residues are often removed from the soil. Additionally, though land cover type may be an indirect indicator of C input quality, specific litter quality traits have demonstrated effects on C storage in POC and MAOC (e.g., Córdova et al., 2018; Craig et al., 2022; Haddix et al., 2016), and may represent a secondary control on SOC fractions, after climate-driven controls. Despite their relevance to this study, there was not enough exchangeable Ca, Fe- and Al-hydroxide, microbial, or litter quality data available in conjunction with C fraction data at the global scale to include them in our synthesis, prohibiting us from testing their effects on global C storage. Furthermore, there was relatively low representation of land cover types including tundra, wetlands, and shrublands in our dataset. In addition to potentially contributing to the relatively low explanatory power of our path analyses, this limited our ability to run more comprehensive analyses of land cover-specific controls on C storage. In combination with an additional lack of standardized data reporting, particularly with regards to SOC and N fraction data, all of the above prevented us from more robustly testing several of the hypotheses presented in the In-N-Out framework (Cotrufo et al., 2021), as was our original intent. Given the difficulties of compiling large datasets for synthesis and meta-analysis projects, we echo recent calls in advocating for more standardized collection and reporting of fraction and ancillary data in SOC studies (Todd-Brown et al., 2022). Successful harmonization of SOC fraction data is an important next step in enabling more comprehensive testing of hypotheses related to SOC storage and N recycling, including the broad, global controls we aimed to test in this work, as well as ecosystem-specific controls that aid in development of site-specific strategies to prevent C loss. Both types of knowledge are critical to realizing the potential of soils to mitigate climate change and alleviate food insecurity.

In conclusion, our analyses revealed that global POC and MAOC storage are driven by separate environmental variables. Specifically, global POC storage is controlled primarily by C loss processes, while global MAOC storage is primarily controlled by constraints on C inputs and C stabilization mechanisms. These resulted in land cover types that tend to experience more rapid decomposition having a greater portion of their total soil C pool stored in MAOC. Despite these findings and demonstrating the effectiveness of fractionation in understanding global patterns of SOC storage, we were only able to explain 12.3% and 20.5% of the variation in POC and MAOC storage. As such, our work highlights the need for increased measurement of variables, including exchangeable Ca, Fe-, and Al-hydroxides, various types of microbial data, as well as fraction N, when conducting studies. Additionally, we invite the soils community to begin separating SOC into fractions beyond POC and MAOC, with the goal of improving our understanding of the likely contrasting behavior of free versus occluded POC and exchangeable versus stable MAOC. We hope that this improved measurement, combined with advancing soils data quality and reporting standards, will aid in effective data harmonization that can enable the field to build upon our findings. Doing so will allow us to develop the robust understanding of controls on soil C and N cycling needed to mitigate climate change and ensure the soil can continue to provide essential ecosystem services well into the future.

AUTHOR CONTRIBUTIONS

Paige M. Hansen: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; validation; visualization; writing – original draft; writing – review and editing. **Rebecca Even:** Data curation; investigation; writing – original draft; writing – review and editing. **Alison E. King:** Data curation; formal analysis; investigation; writing – original draft; writing – review and editing. **Jocelyn Lavallee:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; validation; writing – original draft; writing – review and editing. **Meagan Schipanski:** Conceptualization; formal analysis; funding acquisition; writing – original draft; writing – review and editing. **M. Francesca Cotrufo:**

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.10182813.

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