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Restoring particulate and mineral-associated organic carbon through regenerative agriculture

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Sustainability of agricultural production and mitigation of global warming rely on the regeneration of soil organic carbon (SOC), in particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) forms. We conducted a global systematic meta-analysis of the effects of regenerative management practices on SOC, POC, and MAOC in cropland, finding: 1) no-till (NT) and cropping system intensification increase SOC (11.3% and 12.4%, respectively), MAOC (8.5% and 7.1%, respectively), and POC (19.7% and 33.3%, respectively) in topsoil (0 to 20 cm), but not in subsoil (>20 cm); 2) experimental duration, tillage frequency, the intensification type, and rotation diversity moderate the effects of regenerative management; and 3) NT synergized with integrated crop–livestock (ICL) systems to greatly increase POC (38.1%) and cropping intensification synergized with ICL systems to greatly increase MAOC (33.1 to 53.6%). This analysis shows that regenerative agriculture is a key strategy to reduce the soil C deficit inherent to agriculture to promote both soil health and long-term C stabilization.

regenerative agriculture | soil organic carbon | soil health | climate change

Since the development of agriculture, an estimated 133 petagrams of soil organic carbon (SOC) have been lost from soils (1). In addition to contributions to climate change, this SOC loss has imperiled soil fertility and global food security (2, 3), as SOC stocks are positively related to both yield and yield stability (4, 5). "Repaying" this SOC deficit presents a tremendous opportunity to restore soil functioning and reduce atmospheric CO_2 concentrations (6–8). As much of this SOC debt is due to select practices of tillage, bare fallowing, and replacement of diverse perennials with annual crops (9), SOC can be regenerated with climate-smart management (10), also termed regenerative management (11). In contrast to conventional agriculture, exclusively focused on maximizing yields, regenerative agriculture is an approach to farming that aims to improve not only the environmental but also the social and economic aspects of sustainable food production (12).

Principles of regenerative agricultural leverage ecological understanding to build SOC and thereby regenerate soil health (13, 14). These principles include: i) minimizing soil disturbance; ii) maintaining continuous vegetation cover; and iii) increasing quantity and diversity of organic residues returned to the soil (9). Practices that address one or more of these principles include reduced tillage/no-till (NT) (principle 1), cropping system intensification (principles 2 and 3), and the integration of livestock into crop production systems (principle 3). While reduced tillage and NT have received extensive attention as a category of practices that can promote the stabilization of SOC in the topsoil through improved soil structure (i.e., enhanced aggregation) and reduced erosion (15–20), cropping system intensification and livestock integration are more fluid concepts.

We define cropping system intensification to comprise of four main strategies: i) eliminating summer fallow in monocrop systems, ii) increasing the number of annual crops grown per year, iii) planting cover crops, and iv) including perennial crops in rotation. All of these strategies aim to increase SOC by capitalizing on niches in time that would otherwise be left fallow and unproductive (21). Increasing the number of annual crops grown per year increases SOC directly through greater carbon (C) inputs and indirectly through increased microbial biomass and soil aggregation (22). Similarly, cover cropping can increase SOC by enhancing the quantity and diversity of C inputs to soil (23–26). Intensification with perennial crops can greatly increase SOC (13, 27–29). Perennials produce larger and deeper roots than annual crops (30), a key factor for SOC accrual as root C inputs are preferentially retained in soil compared to aboveground C inputs (31, 32).

While a single regenerative practice can build SOC when used in isolation, the potential for synergies between multiple practices is only hinted at in current work. For example, in a dryland system, planting cover crops is more effective at supporting SOC formation when used in combination with NT management (26). As a regenerative practice that

Significance

Regenerating soil organic carbon (SOC) in agricultural soils is one of the most realizable nature-based solutions to mitigate global warming and sustain food production. To better understand SOC formation and persistence we need to separate it into two distinct forms, particulate organic carbon (POC) and mineral associated (MAOC). This study presents results from a global meta-analysis on the response of SOC, POC, and MAOC, to regenerative agricultural practices including no-till, cropping system intensification, and integrated crop–livestock (ICL). We found that regenerative practices increased both POC and MAOC, thus improving soil health and promoting long-term carbon storage. Our most interesting finding was the tremendous potential to increase SOC pools through synergistic interactions between multiple practices especially in ICL systems.

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requires multiple strategies to be simultaneously deployed, integrating livestock into cropping systems has shown promise as a means to increase SOC stocks (33). Crop–livestock integration impacts multiple SOC stabilization pathways by shifting C deposition belowground, modifying N stocks and cycling, and increasing microbial enzyme activity (34–38). Despite the likelihood for regenerative practices in integrated crop-livestock (ICL) systems to increase SOC when adopted in a "stacked" fashion, large-scale studies to evaluate regenerative practice synergies on SOC are lacking.

Although evidence that regenerative agricultural practices can increase SOC stocks is unequivocal, responses are context specific and the moderators of SOC responses to improved management are not yet clear (18). We posit that these system-specific responses arise in part because SOC is not a uniform substance. Separating it into particulate organic carbon (POC) and mineral associated organic carbon (MAOC), its two most contrasting forms, can facilitate understanding and prediction of broad-scale SOC dynamics to provide recommendations to managers and policymakers (39, 40). These two fractions can be separated by size and/or density (41) and show consistent differences in turnover times (42). POC, widely considered a key indicator of soil fertility, cycles faster than MAOC and therefore is more vulnerable to disturbance (39). Conversely, MAOC can be used to assess the capacity for regenerative agriculture to promote SOC sequestration and mitigate atmospheric CO2 (43, 44). Indeed, the millennia of SOC loss from agricultural soils was preferentially from the POC fraction, and a low proportion of POC characterize agricultural relative to unmanaged soils (45). However, until now, the extent to which regenerative agriculture can restore soil health or sequester C long-term by promoting POC and MAOC formation has not been synthesized at the global scale.

With recent emphasis on regenerative agriculture to regenerate soil fertility and mitigate climate change, it is crucial that we understand how these two distinct pools of SOC (POC and MAOC) respond to management. We therefore conducted a global systematic meta-analysis of i) the overall response of POC and MAOC to NT management and cropping system intensification across the soil profile; ii) the impact of agronomic moderators of NT and cropping intensification on POC and MAOC; and iii) the potential synergy of multiple regenerative interventions to build POC and MAOC in ICL systems. We also explored the effects of climate and soil variation on the response of POC and MAOC to management. We focus on meta-analytic comparisons of relative change in SOC, POC, and MAOC concentrations, rather than absolute changes in C stocks, due to paucity of bulk density data available and high variation in soil sampling depth increments. While relative C change does not inform actual soil C sequestration, it allows us to quantify the relative impact of regenerative management on SOC, POC, and MAOC across the soil profile.

We hypothesized, broadly, due to assorted pathways for regenerative management to augment total SOC, that regenerative practices would differentially affect POC and MAOC. For instance, we expected NT to increase POC through enhanced aggregation, but to leave MAOC relatively unchanged. Cropping intensification was expected to increase POC through increased plant C inputs and reduced erosion and to increase MAOC by increasing living root exudation. Finally, we expected ICL systems to increase MAOC through increased microbial efficiency yet reduce POC by diverting plant C inputs into livestock biomass.

Results

Distribution and Relative Importance of Stock Change for POC and MAOC. Overall, 118 studies comprising 157 experiments were analyzed in this study (*SI Appendix*, SI References). In most soils, POC made up a small proportion (~17%) of total SOC stocks (Mg C ha^{-1}) compared to MAOC (Fig. 1*A*). Consequently, a large relative change in the POC concentration (g C kg $soil^{-1}$) resulted in only a minor absolute change in SOC stocks (Fig. 1*B*). For instance, a 50% increase in POC concentration was associated with an average change of only 2.7 Mg C ha^{-1}, whereas the same percent increase in MAOC and SOC pools was associated with an average stock change of 11.0 Mg C ha^{-1} and 13.2 Mg C ha^{-1}, respectively.

NT and Cropping System Intensification Build POC and MAOC in Topsoil. To compare the impact of regenerative management across the soil profile, we delineated between topsoil and subsoil at 20 cm, as this was the average tillage depth across studies. Regenerative management significantly increased SOC content

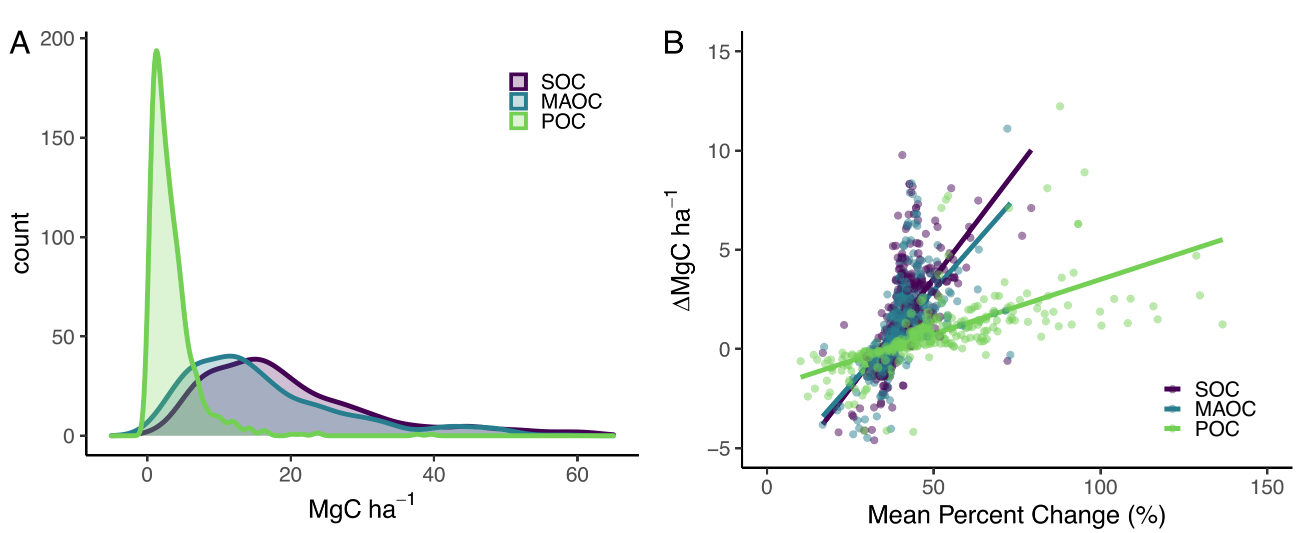

Fig. 1. (*A*) Density plot of carbon (C) stocks (MgC ha^{-1}) in total SOC, MAOC, and POC. (*B*) Plot of linear relationship between MPC of C concentrations (gC kg $soil^{-1}$) and absolute response of C stocks (ΔMgC ha^{-1}) for SOC, MAOC, and POC. These plots were generated from 374 observations (circa 34% of the dataset) for which SOC stock values were available.

in the topsoil but did not significantly affect SOC fractions in subsoil, which had much fewer observations (Fig. 2). Compared to conventional tillage (CT), NT increased topsoil SOC by 11.3%, with an 8.5% increase in MAOC and a 19.7% increase in POC (Fig. 2*A*). The overall effect of NT on topsoil was particularly driven by 0 to 5 cm layer, but the trend was consistent throughout the entire 0 to 20 cm layer (*SI Appendix*, Fig. S1). Cropping system intensification as defined above increased SOC by 12.4%, with a 7.1% increase in MAOC and a substantial 33.3% increase in POC (Fig. 2*A*). These increases, while larger in the 0 to 5 cm layer, were consistent across the profile (*SI Appendix*, Fig. S1). There was a tendency for a large positive response of POC to cropping intensification in subsoil (+22.5%, Fig. 2*B*), but with substantial variation around the mean (CI: −2.76 to 54.5%), indicating the influence of other moderator effects on POC response.

Effects of NT on SOC Fractions Vary with Experimental Duration, Tillage Frequency, and Cropping System Intensity. Since the response of SOC fractions to NT is only significant in topsoil, we analyzed agronomic practices as moderators effecting the SOC, MAOC, and POC response to NT for topsoil only (Fig. 3 and *SI Appendix*, Table. S6). We found that NT significantly increased SOC, MAOC, and POC only in experiments lasting greater than 6 y. Tillage frequency moderated the effect of NT on MAOC (Fig. 3*B*), but not on POC (Fig. 3*C*), resulting in a slight trend toward significance in SOC (Fig. 3*A*). Further, MAOC concentrations under NT were 14.2% higher than those under CT systems with multiple tillage disturbances per year and only 5.0% higher than those under CT systems with only one tillage disturbance per year (Fig. 3*B*).

Cropping intensity of the rotation moderated the effect of NT on SOC (Fig. 3*A*), MAOC (Fig. 3*B*), and POC (Fig. 3*C*). Compared to CT cropping systems, total SOC increases in NT systems with only one cash crop per year (+13.8%) were significantly higher than SOC increases in systems including multiple cash crops in a year (+6.1%, $P = 0.006$) and systems with cover crops (+6.8%, $P = 0.0001$). For MAOC, NT had the greatest effect in systems with multiple crops per year (+13.3%) compared to systems with cover crops (+7.3%, $P = 0.003$) and systems with one cash crop (+8.1%, $P = 0.10$). The effect of NT on POC was only significantly different than zero in systems with a single cash crop (+32.7%). In systems with multiple cash crops per year and systems with cover crops, NT did not increase POC compared to CT.

Effects of Cropping System Intensification on SOC Fractions Vary with Experimental Duration, Type of Intensification, and Tillage Management. Intensification increased C in soil fractions only in experiments lasting greater than 6 y (Fig. 4). In experiments that lasted longer than 12 y, intensification increased total SOC by 17.6%, MAOC by 10.8%, and POC by 44.0%. These were significantly higher than increases in experiments 6 to 12 y for SOC (+12.3%, $P = 0.012$) and MAOC (+6.5%, $P = 0.039$).

SOC increases were greatest when perennial cropping systems were compared to annual cropping systems (+16.2%), significantly higher than the effect of multiple crop intensification ($P < 0.001$) and cover crop intensification ($P = 0.024$). The response of POC to intensification was greatest when one-crop systems were compared to crop-fallow systems (+57.5%). This effect was significantly higher than the effect of multiple crop ($P < 0.0001$), cover crop ($P < 0.0001$), and perennial intensification ($P = 0.0001$) on POC. Further, the effect of cover crops and perennial intensification on SOC and POC were significantly higher than the effect of multiple crops ($P < 0.0001$). In contrast to SOC and POC, MAOC increases were greatest when comparing systems with multiple crops per year to one-crop systems (+8.9%).

Increasing cropping diversity did not modify the positive effect of intensification on SOC, but reduced it for MAOC and POC, with polyculture surprisingly showing the least benefit (Fig. 4). The response of SOC, MAOC, and POC to intensification was significantly higher in CT systems compared to NT systems (Fig. 4).

Potential Synergies within Integrated Crop–Livestock Systems. We synthesized the effects of integrating livestock (ICL) in combination with NT and cropping system intensification on SOC, MAOC, and POC in topsoil (Fig. 5). Integrating livestock into annual cropping systems had a tendency to increase SOC (Fig. 5*A*) and POC (Fig. 5*C*), but not MAOC (Fig. 5*B*).

Cropping systems that combined livestock integration with NT practices increased total SOC by 29.9% compared to CT systems without livestock, more than double the effect of NT alone

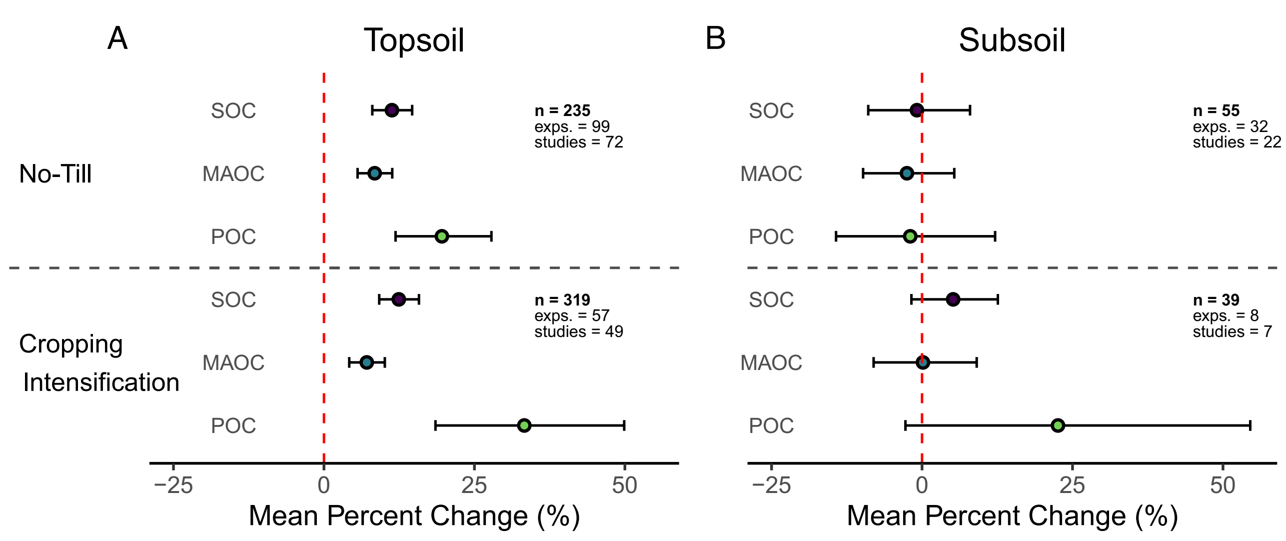

Fig. 2. Overall response of carbon concentrations (g C kg soil^{-1}) in total SOC, MAOC, and POC to regenerative agricultural management in topsoil (*A*, 0 to 20 cm) and subsoil (*B*, 20 to 100 cm). NT systems are compared to CT systems. Cropping intensification includes i) eliminating summer fallow in monocrop systems, ii) increasing the number of annual crops grown per year, iii) planting cover crops, and iv) incorporating perennial crops in rotation. Effect sizes were considered significant if 95% CI did not overlap zero.

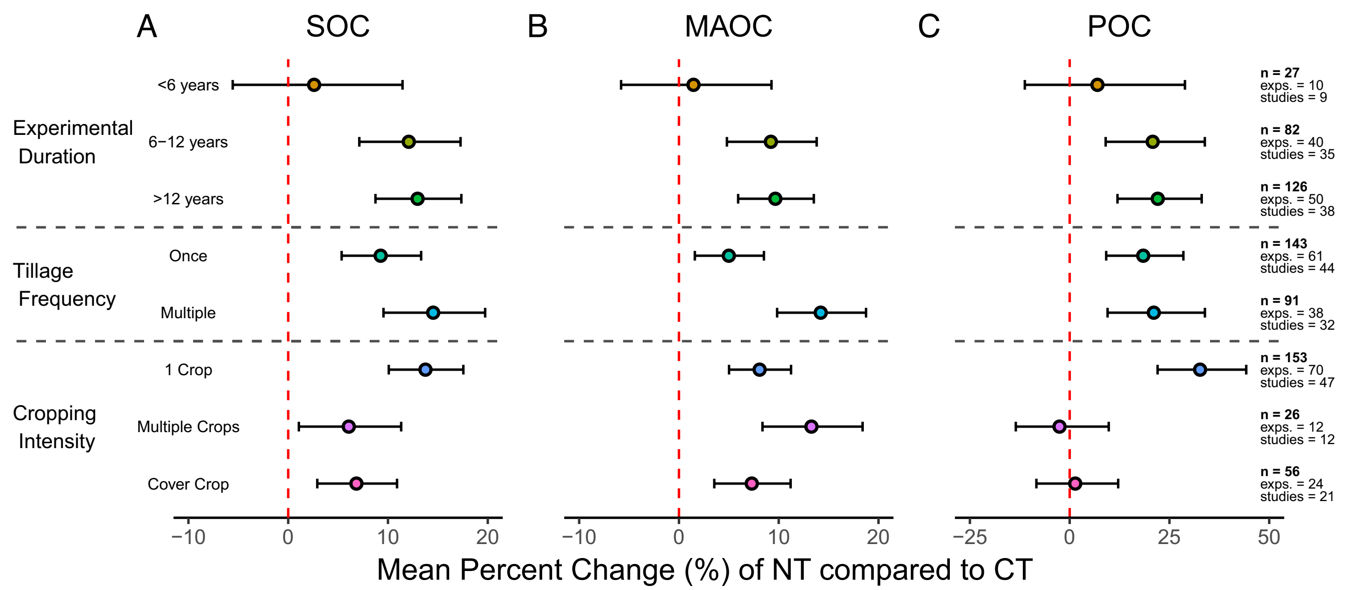

Fig. 3. Effect of NT compared to CT on topsoil (0 to 20 cm) carbon concentrations (g C kg soil^{-1}) in total SOC (*A*), MAOC (*B*), and POC (*C*), as moderated by experimental duration, tillage frequency, and cropping intensity. Cropping rotation, residue management, fertilization regime, and environmental variables held constant. Tillage frequency and cropping intensity on per year basis. Effect sizes were considered significant if 95% CI did not overlap zero. The number of observations (n), experiments (exps.), and studies analyzed for each moderator variable is displayed on the far right of the figure.

(+11.3%). This SOC increase occurred primarily through increases in POC (+38.1%), suggesting an additive effect of combining ICL (+17.0%, ns) with NT (+19.6%). There was a tendency for increased MAOC under NT + ICL (+9.1%) compared to CT without ICL; however, the response was not significantly different from zero.

When livestock integration was used in conjunction with cropping system intensification, C increases were greater than the sum of individual practices. Combing ICL with cover crops has the potential to significantly increase SOC, MAOC, and POC (Fig. 5). The 33.1% increase in MAOC suggests a potential

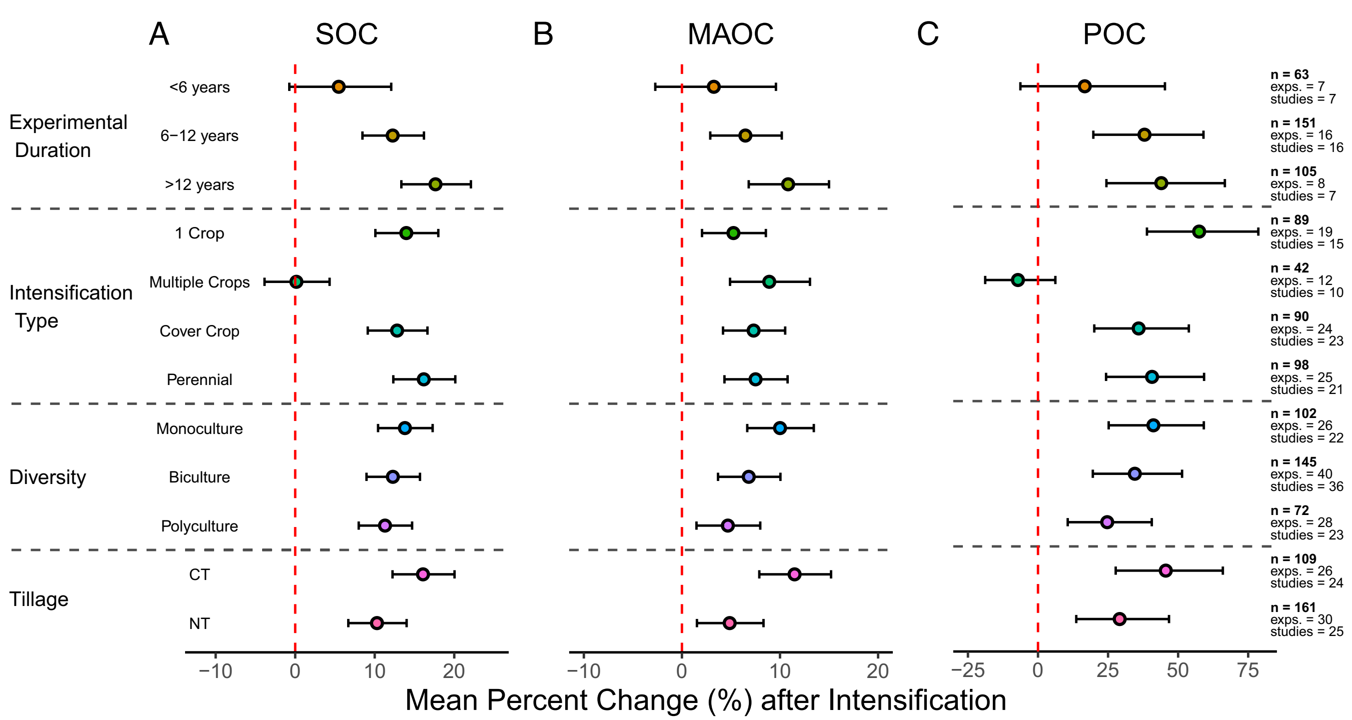

Fig. 4. Effect of cropping system intensification on topsoil (0 to 20 cm) carbon concentrations (g C kg soil^{-1}) in total SOC (*A*), MAOC (*B*), and POC (*C*) as moderated by experimental duration, type of cropping intensity, rotation diversity, and tillage management. Tillage management, residue management, fertilization regime, and environmental variables were held constant. "Intensification type" signifies type of intensification (i.e., "1 crop" = intensification of crop-fallow to rotation of 1 annual cash crop per year, "multiple crops" = intensification of 1 cash crop per year to multiple cash crops per year, "cover crop" = intensification of annual cash crop system to annual rotation + cover crop, "perennial" = intensification of annual cropping system to system with a perennial crop included in rotation). Effect sizes were considered significant if 95% CI did not overlap zero. The number of observations (n), experiments (exps.), and studies analyzed for each moderator variable is displayed on the far right of the figure.

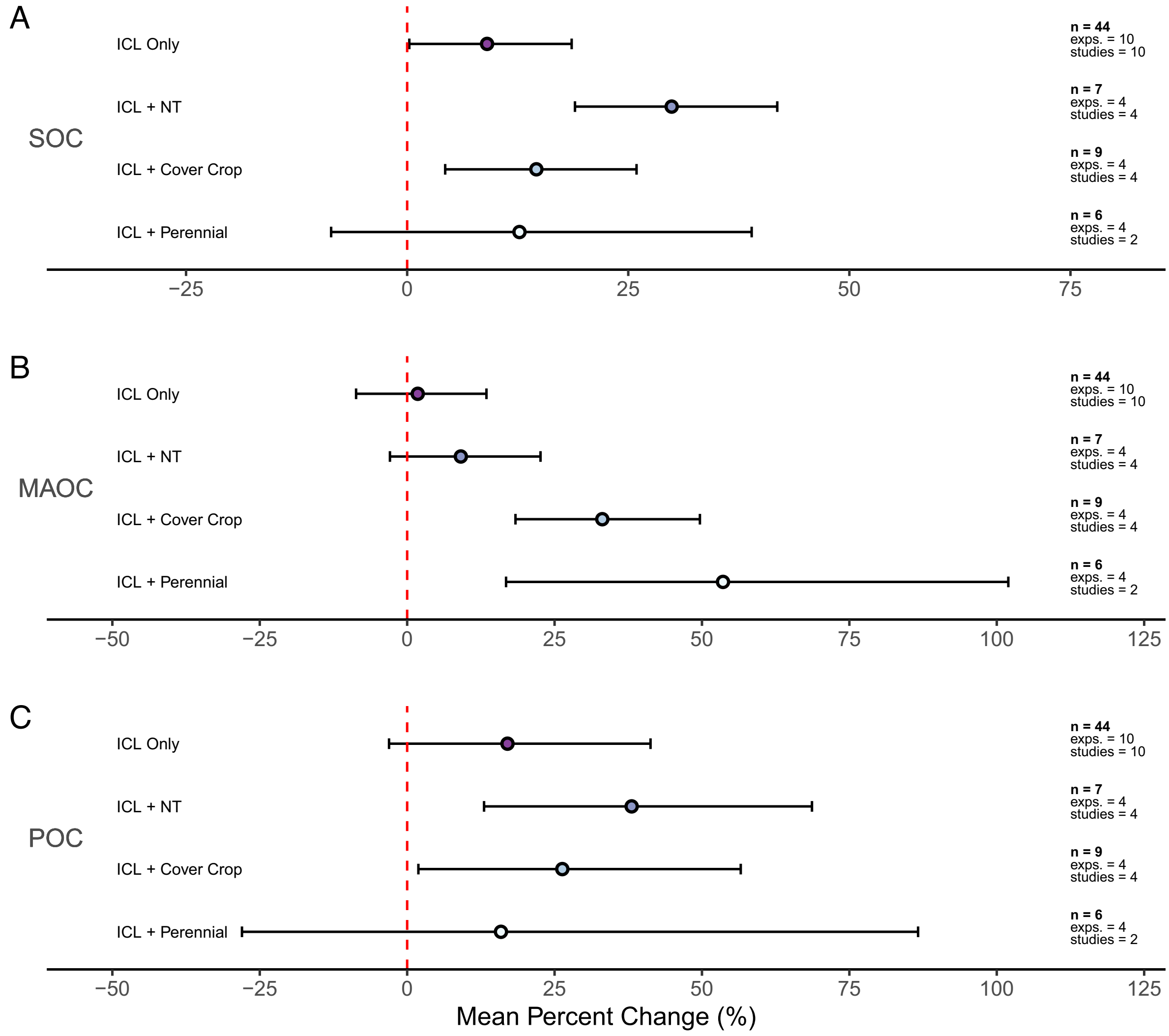

Fig. 5. Potential synergistic effects between Integrated Crop–Livestock (ICL) with NT and cover crop intensification on topsoil (0 to 20 cm) carbon concentrations (g C kg soil^{-1}) in total SOC (*A*), MAOC (*B*), and POC (*C*). "ICL only" compares ICL systems to annual cropping systems without livestock. "ICL + NT" compares ICL systems that are NT to annual systems without livestock that are conventionally tilled. "ICL + cover crop" compares ICL systems that have been intensified using cover crops to less intense systems without livestock. "ICL + perennial" compares ICL systems that have been intensified using perennial grass to annual systems without livestock. Residue management, fertilization regime, and environmental variables were held constant. Effect sizes were considered significant if 95% CI did not overlap zero. The number of observations (n), experiments (exps.), and studies analyzed for each moderator variable is displayed on the far right of the figure.

synergy between ICL (+1.8%, ns) and cover crops (+7.3%) as it greatly exceeded the additive increase of individual practices. However, the 26.3% increase in POC with ICL + cover crops is lower than POC increases with cover crops alone (+35.9%). The differential responses of POC and MAOC under ICL + cover crops resulted in a 14.6% increase in SOC which was comparable to SOC increases under cover crops alone (+12.8%). Similarly, ICL in combination with perennials increased MAOC by 53.6%, showing signs of synergetic effects far exceeding the effects of ICL (+1.8%, ns) and perennial intensification alone (+7.5%). This synergy was not observed for POC or SOC (Fig. 5).

Regenerative Practices Are Effective across a Range of Soil and Climate Conditions. Our synthesis included soils with a wide range of sand content (1.0 to 89%), soil pH (4.2 to 8.6), mean annual temperature (MAT; −2.8 to 30.1 °C), mean annual precipitation (MAP; 302 to 3,100 mm y^{-1}), and potential evapotranspiration (PET; 787 to 2,145 mm y^{-1}). MAT was the only significant moderator of the effect of NT on SOC, MAOC, and POC (*SI Appendix*, Table S6). For every 10 °C of MAT, the effect of NT was increased by 8.3% for SOC, by 6.3% for MAOC, and by 14.2% for POC (Fig. 6*A*). For cropping system intensification, the only significant environmental moderator was sand content for SOC and POC, but not MAOC (*SI Appendix*, Table S7). For every 10% increase in sand content, the effect of intensification was increased by 3.7% for SOC and by 10.6% for POC (Fig. 6*B*).

Discussion

Overall Effects of Regenerative Agriculture on SOC Pools and Stocks. Our global synthesis provides clear evidence for the ability of regenerative practices to increase both MAOC and POC in topsoil (0 to 20 cm) compared to conventional management. As MAOC was the larger fraction (~80% of C) in all soils, any changes to this fraction correlated with changes in total SOC. The absolute response of POC to regenerative practices was smaller and more variable than that of MAOC, suggesting that moderating factors are more important in governing the persistence and stabilization of POC compared to MAOC under regenerative management. MAOC is often positioned as a target for soil C

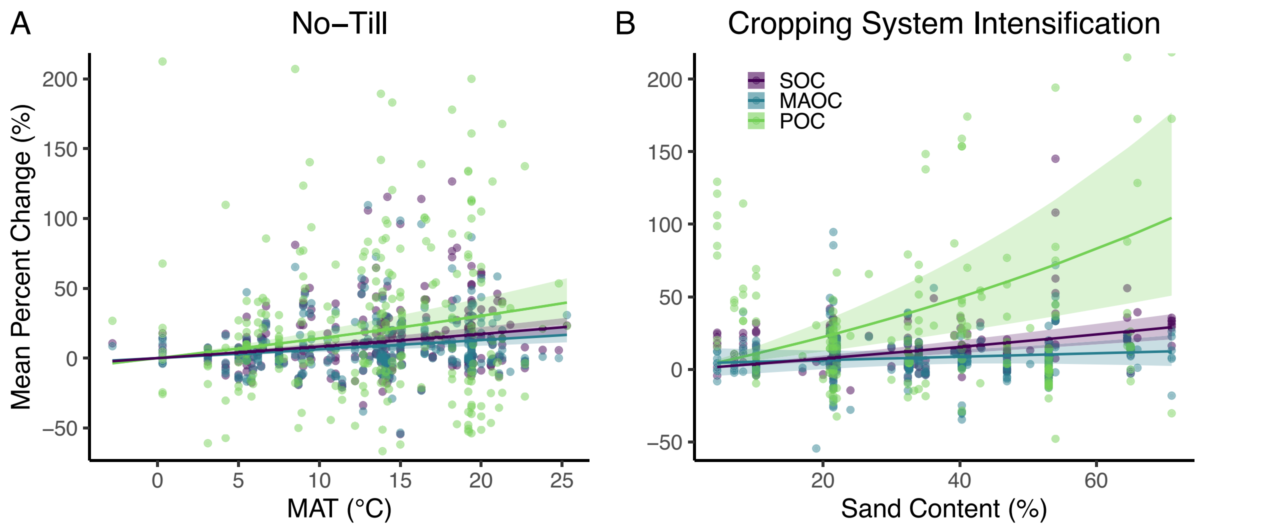

Fig. 6. (*A*) Meta-regression of MAT (°C) against mean response of NT on total SOC, MAOC, and POC concentrations (g C kg $soil^{-1}$) in topsoil (0 to 20 cm). (*B*) Meta-regression of sand content (%) against mean response of cropping system intensification on SOC, MAOC, and POC in topsoil.

sequestration due to its longer turnover times (42). Our results suggest that it is in fact an appropriate target also because of its larger absolute increases under regenerative management. While POC absolute increases are of minor importance to SOC gains (Fig. 1), this analysis pointed to a few practices having high effect on proportional POC accrual (>50% increases). Over time, these large relative increases in POC may regenerate cropland soils to a more balanced distribution of C between POC and MAOC, that is more typical of natural soils (45).

Practitioners of regenerative management are unlikely to see the positive benefits to SOC (POC or MAOC) until after 6 y of implementation. This was particularly evident in CT–NT comparisons, where both MAOC and POC decreased in a significant proportion of studies lasting less than 6 y. Agroecosystems transitioning from CT to NT may take more than 5 y for soil structure to improve under NT before they can accumulate additional SOC (Fig. 3). In contrast, cropping system intensification likely increases SOC steadily over the first 5 y of implementation, but not to a significant degree until after 5 y. Monitoring for fast (1 to 5 y) SOC stock changes under regenerative agriculture should thus not be used to draw conclusions about long-term SOC response.

We did not observe decreases in subsoil (20 to 100 cm) C due to regenerative management, as has been occasionally observed with NT (16). In fact, in many instances, POC was significantly increased in the subsoil from cropping intensification, especially with the inclusion of perennials (Fig. 2 and *SI Appendix*, Fig. S2). While there is evidence of publication bias favoring reporting of positive, significant results, the skew is very slight and likely only minorly impacts our results (*SI Appendix*, Fig. S3).

SOC Changes under NT. Due to the effect of NT on maintaining soil aggregates, an acknowledged mechanism of POC protection (18, 20), we expected that NT would primarily increase POC. However, we found that, in topsoil, NT increases MAOC as well as POC. NT may alter quantity and distribution of C inputs through roots. After initial yield decreases due to soil compaction (46), NT may increase root C inputs, a strong pathway for MAOC formation (31, 32). Alternatively, differences in POC and MAOC could be the direct result of reduced C losses by erosion in NT systems (19).

Surprisingly, the frequency of tillage did not moderate the effect of tillage on POC, possibly because any amount of tillage was enough to disrupt aggregate formation and prevent POC accumulation. MAOC stabilization, however, was greatly affected by the frequency of tillage. This is possibly a result of chronic disturbance which may prevent the recovery of fungal networks and other soil organisms, such as earthworms (47), which have shown to be critical for stable SOC formation (48, 49).

The negative effects of tillage on POC are mitigated by intensifying the cropping system, suggesting that in regenerative systems occasional tillage events will not greatly affect POC stocks. In contrast, cropping system intensity had a synergistic effect with NT on MAOC, with MAOC increases from NT being greatest in systems with multiple crops per year. This is possibly because intact fungal networks are able to efficiently process the continuous plant inputs to form MAOC (50).

SOC Changes under Cropping System Intensification. Consistent with our expectations, cropping system intensification increased both MAOC and POC. With cropping system intensification, C increases are likely the result of increased C inputs (20), and established pathways link POC formation with plant structural residues and MAOC formation with plant exudation through living roots (31).

We found that the most important method of intensification for increasing POC was the elimination of summer fallow with continuous cropping. Additional intensification with multiple crops per year did not increase POC further, although intensifying continuous cropping with cover crops and perennials did further increase POC. Differences in the quantity or quality of belowground inputs with cash crop vs. cover crops or perennial crops may explain this apparent discrepancy. Perennial intensification was especially important for increasing POC as this was the only practice that also increased POC in both subsoil and topsoil. This is likely due to the greater and deeper root system in perennials as compared to annuals (30).

The benefit of intensification on POC and MAOC was lessened as diversity increased. Common choices in research site design may help to explain this finding, as systems that were intensified using perennials often did not increase in diversity (e.g., corn–soy intensified to corn–alfalfa–alfalfa–alfalfa). Similarly, more diverse systems containing summer fallow were frequently compared to continuous annual monoculture (e.g., corn–soy–fallow compared to continuous corn). MAOC formation appears to depend less on diversifying the rotation than on reducing fallow to maintain continuous inputs.

Finally, cropping intensification had a greater effect in CT than in NT systems, especially for MAOC. The explanation could be that SOC concentrations in CT systems are lower than those in NT systems; therefore, the same SOC absolute change due to intensification will be proportionally larger under CT; or that in heavily disturbed CT systems, intensification may reduce bare ground minimizing loss of SOC and nutrients through erosion (51).

Potential Synergies within Integrated Crop–Livestock Systems. As only a limited number of studies explored combinations of regenerative practices with ICL, we consider our results compelling preliminary evidence, with further research needed to provide unequivocal support of synergies. Nevertheless, our results show an enormous potential for ICL to increase SOC, POC, and MAOC, primarily when used in combination with NT and cropping intensification. When ICL was used in combination with NT, we found significant POC increases that exceeded those from NT alone, indicating an additive interaction likely through enhanced aggregation and improved soil structure (37, 52).

We also found evidence of synergy between ICL and cropping system intensification. Though ICL and cover crop together and cover crop alone both raised total SOC to the same extent, the distribution of C increase shifted from POC to MAOC when livestock were included. The synergy between ICL and perennial intensification on MAOC was even more pronounced, yet the variation in effect sizes makes it difficult to draw firm conclusions about the effect on POC. Positive synergies between ICL and cropping system intensification on SOC may occur due to impacts of grazing on root photosynthate allocation (53) and microbial decomposition through changes to C-to-N ratios of plant litter and the addition of animal waste (36, 54).

Regenerative Practices Are Effective across a Range of Soil and Climate Conditions. Environmental moderators explained a minor portion of the variance in effect sizes of regenerative management on SOC, MAOC, and POC. The only environmental variable to significantly moderate the effect of NT was MAT. A greater relative effect of NT compared to CT on POC and MAOC in warm climates may be due to a synergistic interaction between disturbance due to tillage and overall high microbial activity in warmer climates. In other words, when microbes are inhibited by cooler temperatures, soil disturbance would not stimulate additional decomposition (55).

Across environmental moderators, only sand content significantly moderated the effect of cropping intensification on POC, but not MAOC. Since MAOC formation depends on the availability of binding sites in the silt/clay mineral matrix, we expected a negative relationship between percent sand and MAOC gains. However, a recent analysis has shown that agricultural systems are only at ~31% MAOC saturation (56), and indeed we found no evidence for a constraint on MAOC formation in soils with low silt/clay content.

Limitations and Next Steps. Our meta-analysis was constrained by data available in the literature. Although SOC stock change with management can inform about C budgeting, fewer than half the studies reported information needed to calculate SOC stocks, so we focused on C concentrations. The lack of baseline SOC data prevented conclusions about whether true C sequestration, emissions avoided, or a combination of the two was observed with soil C change. The average soil sampling depth in our database was 20 cm, and future studies will enable more comprehensive understanding of soil C if reported across the soil profile. Finally, though all major continents are represented in our analysis, our database revealed data gaps in South America, Africa, Eurasia, and Oceania (*SI Appendix*, Fig. S4).

This analysis shows that crop intensification and NT increase POC and MAOC, thus both improving soil health and promoting long-term C stabilization. However, the optimization of stacked management strategies to enhance POC and MAOC still has specific knowledge gaps, including the mechanisms driving observed synergies in the integration of livestock into cropland in combination with other regenerative practices. Developing a comprehensive understanding of these and other synergies is essential to accurately represent the effect of regenerative management in predictive tools, for maximizing regenerative agriculture's ability to mitigate climate change and provide additional ecosystem services to benefit producers, the environment, and the society at large.

Materials and Methods

Study Selection. We searched Web of Science and Agricultural Online Access Database (AGRICOLA) to conduct a systematic meta-analysis on the response of SOC pools to tillage management, cropping intensification, and ICL management (Table 1). The search included all papers published until January 2021. After removal of duplicates, our search yielded 4,706 publications. We screened publications following Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (57) using the following criteria: i) peer-reviewed, primary literature; ii) measured SOC fractions that are or can be combined to MAOC and POC; iii) measured response of POC and/or MAOC to soil management intervention with a control that was not treated with that intervention; iv) experimental treatments must include one of these soil management practices: tillage management, cropping intensification management, and integrated livestock management. We included search terms related to "conservation" to find studies with these soil management practices; however, the practices of interest for this study extended beyond those included in conservation agriculture, which does not explicitly include cropping system intensification or integrated livestock management. Studies were excluded if the treatment of interest was not isolated within the experimental design (e.g., when corn–soybean crop rotations w/o fertilizer are compared to corn–soybean–wheat-winter rye rotations w/o fertilizer, the causal effects of rotation intensification cannot be disentangled from fertilization treatment).

To be included in this study, at least three replicates of SOC, MAOC, and/or POC are needed to be measured to ensure robustness of the dataset. Soil had to be sieved to 2 mm or less and dispersed using either sodium hexametaphosphate, sonication, or shaking with glass beads such that aggregates would be adequately broken down. For this study, MAOC was defined as the fraction of SOC smaller than 50 to 63 μm, when separated by size, or heavier than 1.6 to 1.85 g cm^{-3}, when separated by density (41). POC was defined as the coarse (>50 to 63 μm) and/or light (<1.6 to 1.85 g cm^{-3}) fraction, the counterpart to MAOC. Heavy, coarse SOC fractions resulting from the combination of size and density fractionation (i.e., >1.6 g cm^{-3} and >50 to 63 μm) were considered MAOC due to having low C:N similar to the fine, heavy fraction (58). Only studies that directly quantified C using direct combustion or wet oxidation methods were included.

Data Collection and Management. In total, we identified 139 studies, 187 experiments, and 1,250 observations across the world (*SI Appendix*, Fig. S4) that met our inclusion criteria. A complete list of publications included in the analysis can be found in *SI Appendix*, SI References.

We extracted information on C concentrations, percent organic C, and C stocks. If only total SOC and one of the pools was measured, the other was calculated by subtraction. If free and occluded POC content were reported in a study, we summed them as POC content. If different-size MAOC content or MAOC chemical extractions (i.e., hydrolyzable and nonhydrolyzable) were reported in a study, we summed them as MAOC content. If C concentrations were reported on per-aggregate mass basis, we converted to per soil mass (g C kg^{-1} of soil). We included data under control and treatment at last sampling time point if the soils were

Table 1. Search terms used Boolean combinations of SOC terms and agricultural management terms

Cropping systems and SOC fractions	TOPIC: (Cropland* OR "cropping system*" OR "agricultur* management" OR "regenerative agricultur*" OR "conservation agricultur*" OR "sustainable agricultur*" OR "soil management" OR "soil management practice*", * OR agro-ecosystem* OR agroecosystem* OR crop OR "field crop*" OR farm* OR "conservation agricult*") AND TOPIC: (MAOM OR MOM OR "mineral-associated organic matter" OR POM OR "particulate organic matter" OR silt and clay OR "light fraction*" OR "heavy fraction*" OR "physical separation" OR "size separation" OR "density separation" OR "physical fractionation" OR "density fractionation" OR "soil organic matter fraction*" OR "soil organic-matter fraction*" OR "soil fraction*" OR "SOM fraction*" OR "organic-matter fraction*" OR MAOC OR POC OR "mineral-associated organic carbon" OR "particulate organic carbon")
Cropping intensification	TOPIC: ("cover crop" OR "cover-crop*" OR "cover crop*" OR "green manure" OR "crop* rotation*" OR "mixed crop*" OR "diverse crop*" OR "crop* divers*" OR "crop* intensity" OR "sustainable intensification" OR rotation OR "double crop*" OR perennialization OR perennial* OR "perennial * crop*")
Tillage management	TOPIC: ("conservation till*" OR "conventional till" OR "no-till" OR "no till*" OR "reduced till*" OR "minimum till*")
Integrated livestock	TOPIC: ("integrated livestock" OR "livestock integration" OR "integrated crop-livestock" OR "integrated crop-livestock system" OR "grazing inclusion" OR "crop grazing" OR "mixed crop-livestock" OR "mixed crop-livestock system" OR crop-livestock OR "integrated grazing")

collected at different times. We extracted data from tables using Tabula software (https://tabula.technology/). If data were only presented in figures, *metaDigitize* package in R (59) was used for the extraction of data.

Soil profiles were divided into two separate layers for independent analysis, topsoil (0 to 20 cm), and subsoil (>20 cm). We aggregated smaller increments by calculating a weighted mean for concentration. Data were included in the topsoil if the overlapping layer thickness was no more than 5 cm deeper than the specified layer. Similarly, data were included in the subsoil if the overlap was 5 cm or less. Since studies reported soil depth across a variety of different depth layer thicknesses, we included any depth increments less than 20 cm under topsoil. For example, 0 to 15 cm depth increment would be analyzed as topsoil (0 to 20 cm) and a 15 to 30 cm increment would be analyzed as subsoil. Additionally, to assess differences in the response across smaller sample depths, we analyzed separately the overall response for the 0 to 5, 0 to 10, and 0 to 20 cm layers (*SI Appendix*, Fig. S1).

For the moderator analyses, we extracted information on agronomic factors including experimental duration, tillage frequency (tillage events per year), and cropping system. In addition, we extracted information on soil sampling depth, soil properties (e.g., bulk density, soil texture, percent sand/silt/clay, soil pH, and initial concentration of SOC), and climate characteristics [i.e., MAP, MAT, and lat/long]. If percent sand/silt/clay were not reported, we converted soil texture classification into percent sand/silt/clay using the United States Department of Agriculture soil texture calculator. If lat/long were not reported, we estimated coordinates by searching site name on Google Earth. If climate characteristics were not reported, we extracted MAT and MAP from WorldClim v2.1 (60). PET data were extracted from the Global Aridity Index and PET Database (61).

Cropping system was characterized based on total number of species in rotation (diversity), crop species identities (corn, soy, etc.), frequency of crop occurrence, crop functional group (e.g., grass, legume, other), crop life history (e.g., annual or perennial), and crop residue management (e.g., grain harvest, hay harvest, no harvest). Frequency of crop occurrence was calculated as the number of times a crop appeared in rotation divided by the rotation years. Cropping system intensity was calculated as sum of all crop frequencies. For example, the cropping system intensity of a 4-y rotation of corn–soy–corn–wheat would be calculated as $\frac{2}{4}$ (corn) + $\frac{1}{4}$ (soy) + $\frac{1}{4}$ (wheat) = 1. Cover crops were counted the same as other crops. Perennial crops were given an occurrence of 2 for each year in rotation since the crop occurred during both spring/summer and summer/fall growing seasons. For example, the cropping system intensity of a 4-y rotation of corn–alfalfa–alfalfa–alfalfa would be calculated as $\frac{1}{4}$ (corn) + $1\frac{1}{2}$ (alfalfa) = $1\frac{3}{4}$. Effect sizes for cropping intensification were calculated comparing systems with an intensity equal to 1 (one crop per year) to those with an intensity <1 (crop-fallow) and systems with an intensity >1 (multiple crops per year) to rotations with an intensity ≤1. Diversity moderator categories were determined based on the difference in diversity between the more intense and less intense cropping system. Three diversity moderator categories were used: i) intensification with no change in diversity (monoculture), ii) intensification with an increase in diversity of two species (biculture), or iii) intensification with an increase of more than two species (polyculture). The total average diversity of cropping systems analyzed in this study was low (on average two species in rotation). Only four studies compared rotations with high diversity (>5 species) to those with low diversity (one to three species), which we deemed an insufficient number to support a separate analysis.

Data Analysis. We chose C concentration (g C kg soil^{-1}) as the response variable for SOC, MAOC, and POC over C stock (Mg C ha^{-1}) because 66% of the studies did not report stock or bulk density values. If stock and bulk density was reported, we calculated concentration using the following equation:

$$C_c = 10 * C_s / (BD * depth), \qquad [1]$$

where C_c is the C concentration in g C kg soil^{-1}, C_s is the C stock in Mg C ha^{-1}, *BD* is the bulk density in g cm^{-3}, and *depth* is the soil sampling depth increment in cm.

Variance data were frequently not reported. Instead of excluding these publications (28 publications, 219 observations – 18% of total) from analysis, which could introduce bias, we imputed missing SDs using the following equation (62):

$$\widetilde{SD}_j = \overline{X}_j \left(\frac{\sum_i^K SD_i}{\sum_i^K \overline{X}_i} \right), \qquad [2]$$

where $\overline{X}_j$ is the observed mean of the study with missing SD, and K is the number of *j*th studies with SD.

We estimated the effect size of SOC, MAOC, and POC for tillage treatment, cropping intensification, and ICL using the *metafor* package (63) in R ver 4.2.1. The effect size was calculated as:

$$\ln RR = \ln\left(\frac{\overline{X}_{trt}}{\overline{X}_{ctrl}} \right), \qquad [3]$$

where ln*RR* is the natural log of the response ratio, $\overline{X}_{trt}$ is the mean value of regenerative practice (i.e., NT, cropping intensification, livestock integration), and $\overline{X}_{ctrl}$ is the mean value of the conventional control. To improve interpretation, we transformed these values to mean percent change (MPC) using the following equation:

$$\text{Mean Percent Change} = \left(e^{\ln RR} - 1\right) * 100\,\%. \qquad [4]$$

We applied a three-level multivariate approach using the rma.mv function in *metafor* package to account for dependency of effect sizes. The model structure accounts for three levels of variance: i) sampling variance of individual effect sizes, ii) variance between effect sizes from the same study, and iii) variance between studies (64). To account for the level of precision between studies, individual effect size was weighted by the inverse of the sampling variance (65).

We used log likelihood ratio tests to evaluate homogeneity of within-study and between-study variances and found significant variation across effect sizes (64). We tested each individual moderator with each regenerative intervention–SOC pool pairing and performed pair-wise comparisons of each level of moderator using an omnibus test of model coefficients. To determine robustness of these relationships, we added all significant moderators into one model. We considered the relationships robust if moderators were still significant following the multiple moderator test (64).

We tested for publication bias using Egger's regression test by including SE of the effect sizes as a moderator (66). The relationship between the precision and size of studies is considered asymmetrical, and therefore biased, when the intercept of this regression test significantly deviates from zero ($P < 0.1$) (67). To further evaluate publication bias, we visually assessed histograms of lnRR for left or right skew (*SI Appendix*, Fig. S3). Histograms of the overall log response ratio (lnRR) provided evidence for a lack of publication bias. However, Egger's test indicated slight overestimation of effect sizes for SOC (int = 0.111, $P < 0.001$), MAOC (int = 0.059, $P < 0.001$), and POC (int = 0.278, $P < 0.001$) in response to regenerative management.

We conducted a sensitivity analysis to assess the robustness of the overall results. To quantify the impact of each eliminated study, we employed a jackknife approach to remove specific studies from each regenerative intervention–SOC pool pair and recalculate the mean effect sizes (68). The sensitivity analysis indicated these results were robust and that no particular publication drove the overall response (*SI Appendix*, Fig. S5).

Data, Materials, and Software Availability. Dataset data have been deposited in https://www.figshare.com (69).

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