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# Direct yield benefits of soil carbon increases in low-carbon soils: A global meta-analysis of cover cropping co-benefits

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## Abstract

Cropland management practices that restore soil organic carbon (SOC) are increasingly presented as climate solutions that also enhance yields. But how often these benefits align at the farm level — the scale of farmers' decision-making — remains uncertain. We examined concurrent SOC and yield responses to cover cropping, including their direct connection, with a global meta-analysis. Cover cropping simultaneously increased yields and SOC in 59.7% of 434 paired observations. Increases in SOC helped increase crop yields in soils with initial SOC concentrations below 11.6 g kg<sup>-1</sup>; for example, a change from 5 g kg<sup>-1</sup> to 6 g kg<sup>-1</sup> increased yields by 2.4%. These yield benefits did not vary with nitrogen inputs or cover crop type, suggesting they are not substitutable with fertilization. Integrating legume cover crops into systems with simplified rotations or with nitrogen inputs < 157 kg N ha<sup>-1</sup> season<sup>-1</sup> led to the largest yield increases (up to 24.3%), with legumes also increasing SOC more than non-legumes (up to 1.5 g C kg<sup>-1</sup>). By simultaneously increasing yields and SOC, targeting cover crops on low carbon soils is an opportunity to benefit both food security and climate.

Soil organic carbon (SOC) is considered a critical component of soil health. In agroecosystems, soil health is a metaphor that describes the degree to which soils support multiple functions beyond just crop productivity<sup>1,2</sup>. SOC influences multiple soil-based ecosystem services, such as nutrient cycling and retention, soil aeration and structural integrity<sup>3</sup>, climate regulation<sup>4</sup>, and possibly crop productivity<sup>5</sup>. The concentration of SOC has thus become one of the most common metrics for assessing the state of a soil's health<sup>6</sup>.

Despite the various benefits that SOC is thought to provide<sup>7</sup>, agricultural expansion and intensification have dramatically depleted SOC across the world<sup>8</sup>. Practices that sequester SOC, defined here as practices where soil carbon inputs are greater than outputs, are garnering increasing attention for their potential to restore soil functionality while simultaneously drawing down atmospheric carbon<sup>9,10</sup>. Cover cropping is one such cropland practice. Grown on fallow soils otherwise left bare, cover crops increase organic matter inputs to the soil in the form of crop detritus and root exudates. Recent meta-analyses showed that cover cropping increases SOC by 0.21-0.56 Mg C ha<sup>-1</sup> yr<sup>-1</sup><sup>11-13</sup>, highlighting its potential to restore some portion of the 116 Pg of global SOC that has been lost since the dawn of agriculture<sup>8</sup>.

But the extent to which farmers will voluntarily adopt C sequestering practices hinges on more than just their potential to mitigate climate change or restore soil health<sup>14,15</sup>. How a practice influences crop productivity and farm profitability is central to farmers' management decisions. Recent meta-analyses show that cover cropping typically increases crop yields<sup>16,17</sup>. Yield increase estimates range from 6% to 33% depending on cash crop type, cover crop type, fertilizer additions and other factors like aridity<sup>18</sup>, although some studies show crop yield decreases as well<sup>16,17</sup>. However, since syntheses of how cover cropping affects SOC and yields have been conducted separately, it is not known how often cover cropping simultaneously increases SOC and yields (co-benefits) at the same location, increases or decreases one but not the other (trade-offs), or even decreases both SOC and yields (co-costs). Perhaps more importantly, it is also not known if there are management, edaphic, or environmental conditions in which the largest yield increases are most likely to align with the largest SOC increases. Understanding the potential for co-benefits will help inform decision-making at the farm level and will help identify areas of overlap between farm level benefits and benefits for society that might occur at regional or global scales.

When yield increases do result from cover cropping, a critical knowledge gap is the relative role of changes in SOC in driving these increases, versus other cover cropping effects, such as nutrient scavenging<sup>19</sup>. Understanding the role that SOC plays in yield changes under cover cropping would contribute to recent calls to better quantify the relationship between SOC and yields generally<sup>5,20</sup>.

The widespread expectation that increasing SOC will increase crop productivity exists<sup>8,21-23</sup> because, as part of soil organic matter, SOC is related to many soil properties and functions that are important for plant productivity like nutrient and water provisioning. However, evidence of a relationship between SOC and yield remains contradictory and inconclusive<sup>5,24-26</sup>. Pot experiments show a positive and causal relationship between SOC and plant growth, up to a threshold of ~3% SOC<sup>27,28</sup>, but limited inference — beyond the direction of causality — is reasonable from few controlled environment studies that artificially manipulate SOC. Other

attempts to circumvent this challenge use observational data, but the lack of controls and covariation between SOC and other environmental and management variables create complex interactions that can be difficult to tease apart even using multivariate approaches<sup>5,24</sup>. Using similar meta-analytic techniques, recent studies have reported positive effects of SOC on yield<sup>5,26</sup>, little to no effects<sup>24</sup>, and negative effects<sup>25</sup>. In addition, observational studies examining SOC-to-yield relationships span very wide ranges of SOC<sup>5,26</sup>. These regional or global SOC-to-yield relationships are generally not applicable to an individual farmer since SOC increases following changes to management are often modest (e.g., relative increases of 5-6% SOC for cover cropping and reduced tillage<sup>29</sup>).

Meta-analysis of studies on agricultural practices expected to shift SOC, such as cover cropping, provides an alternative approach to quantifying the SOC-to-yield relationship<sup>5</sup>. By pairing treatments with relevant control values, relationships between changes in SOC and changes in yield can be quantified in such a way that eliminates the confounding effects that result from observational data (e.g., between climate or edaphic factors that influence both SOC and yields). While other effects can also confound or obscure the SOC-to-yield relationship in this approach (e.g., increases in both nitrogen availability and SOC from legume cover crops or increases in crop productivity that could also lead to SOC increases<sup>30</sup>), building a broad yield model that examines possible confounders can increase confidence in the causality and context-dependence of SOC effects on yield.

We use a global meta-analysis to determine how cover cropping affects SOC and crop yields simultaneously, and the extent to which changes in crop yield ( $\Delta_{yield}$ ) are related to changes in SOC ( $\Delta_{SOC}$ ). We thus build on previous meta-analyses that assess how cover cropping affects SOC or yields individually by linking these responses together in a paired treatment-control meta-dataset. We asked 3 questions: 1) Are co-benefits, i.e., simultaneous increases in crop yields and SOC, the most common response to cover cropping? 2) Do changes in SOC link directly to changes in yield and, if so, is this association related to nitrogen (N) inputs? 3) Regardless of direct links between SOC and yield, are there edaphic, environmental, or management conditions where co-benefits of increased SOC and yield from cover cropping are more likely to be maximized? We compiled an exhaustive database of paired yield and SOC responses to cover cropping and constructed models with factors mediating their individual and joint responses. By building comprehensive models to identify and quantify important predictors of yield and SOC changes from cover cropping, our study not only helps with farm-level decisions regarding cover cropping, but also informs policymakers seeking to quantify the impact of cropland carbon sequestration on global food production capacity.

## Results

### *Joint impacts of cover cropping on crop yields and SOC*

Based on 434 observations spanning five continents (Fig. S1), cover cropping had a strong positive effect on both SOC and yield. The linear mixed effect models, based on observations from all management types and sites, predicted yield and SOC changes of +10.9% [95% CI: 7.5 – 14.5] and +1.07 g kg<sup>-1</sup> [95% CI: 0.82 – 1.32], respectively. The average initial SOC concentration of our dataset was 15.5 ± 9.2 g kg<sup>-1</sup> (standard deviation) at an average sampling

depth of 0-18.4 cm  $\pm$  7.3 cm (standard deviation). Mean maize, rice, and wheat yields (the three most common cash crops in the dataset) in control plots were  $7.3 \pm 4.0$ ,  $3.7 \pm 2.0$  and  $4.2 \pm 2.0$  Mg ha<sup>-1</sup> ( $\pm$  standard deviation). The average experiment length (time from beginning of the experiment to sampling of SOC) was 7.7 yrs.

In 59.7% of the 434 paired observations in our dataset, cover cropping increased both SOC and yields (Fig. S2). Trade-offs, in which either SOC or yield increased while the other decreased, accounted for about one-third of observations. In 20.7% of paired comparisons, cover crops increased SOC but decreased yield; in 12.9% of cases, cover crops increased yields but decreased SOC. Co-costs, in which cover cropping negatively affected both yields and SOC, accounted for 6.7% of paired observations.

### *Explaining variability in crop yield responses to cover cropping*

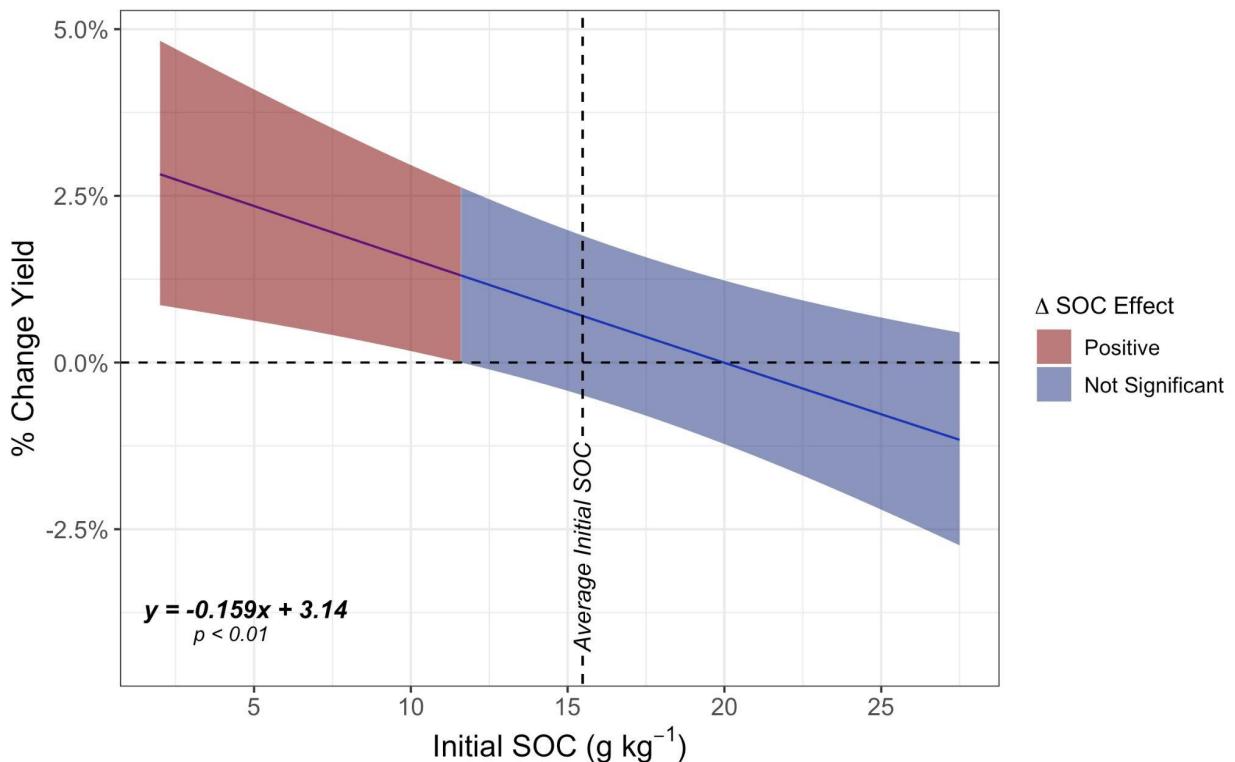
To help explain variation in crop yield responses to cover cropping and drivers underlying patterns of co-benefits and tradeoffs, we considered 29 possible management and environmental variables as moderators (Table S1). Significant predictors in our yield change ( $\Delta_{Yield}$ ) model included an interaction between SOC change ( $\Delta_{SOC}$ ) and initial SOC, in addition to rotational complexity and N fertilizer, with each of the latter interacting with cover crop type (legume vs. non-legume) (Table 1; Table S2). Marginal  $R^2$  of our  $\Delta_{Yield}$  model was 0.25 and conditional  $R^2$  was 0.89, indicating unmeasured site-level effects account for a substantial proportion of variation. Addition of other variables like soil texture, sampling depth, or phosphorus inputs did not improve model fit (Table S2).

**Table 1.** Standardized coefficients and type III ANOVA results from our  $\Delta_{Yield}$  model (n = 417). df is numerator and denominator degrees of freedom, respectively, with Kenward-Roger approximation for denominator degrees of freedom.  $\Delta_{Yield}$  is the log cash crop yield response ratio.  $\Delta_{SOC}$  is the SOC change from cover cropping (g kg<sup>-1</sup>). Initial SOC is SOC (g kg<sup>-1</sup>) prior to cover cropping. Cover crop type is binary categorical; legume vs non-legume coded 1 and 0, respectively. N fertilization is in-season cash crop N fertilization (kg N ha<sup>-1</sup> season<sup>-1</sup>). Rotational complexity is a categorical variable corresponding to the number of different cash crop species in rotation throughout the experiment. *p*-values in italics are considered significant at  $\alpha = 0.05$ . †Standardized coefficients are not presented for this categorical variable with multiple levels.

$\Delta_{Yield}$ Model Results			
Variable	Standardized Coefficients	df	p-value
Initial SOC	0.01	1,92	0.63
$\Delta_{SOC}$	0.04	1,43	0.06
Cover Crop Type	-0.14	1,24	0.59
Rotational Complexity	†	2,71	<0.001
N Fertilizer	-0.13	1,29	<0.001

Absolute Latitude	-0.05	1,88	0.09
$\Delta_{SOC} \times$ Initial SOC	-0.08	1,71	<0.01
Rotational Complexity $\times$ Cover Crop Type	†	2,25	<0.001
N Fertilizer $\times$ Cover Crop Type	0.17	1,25	<0.001
$\Delta_{SOC} \times$ Cover Crop Type	-0.04	1,32	0.16
$\Delta_{SOC} \times$ N Fertilization	0.0	1,36	0.99

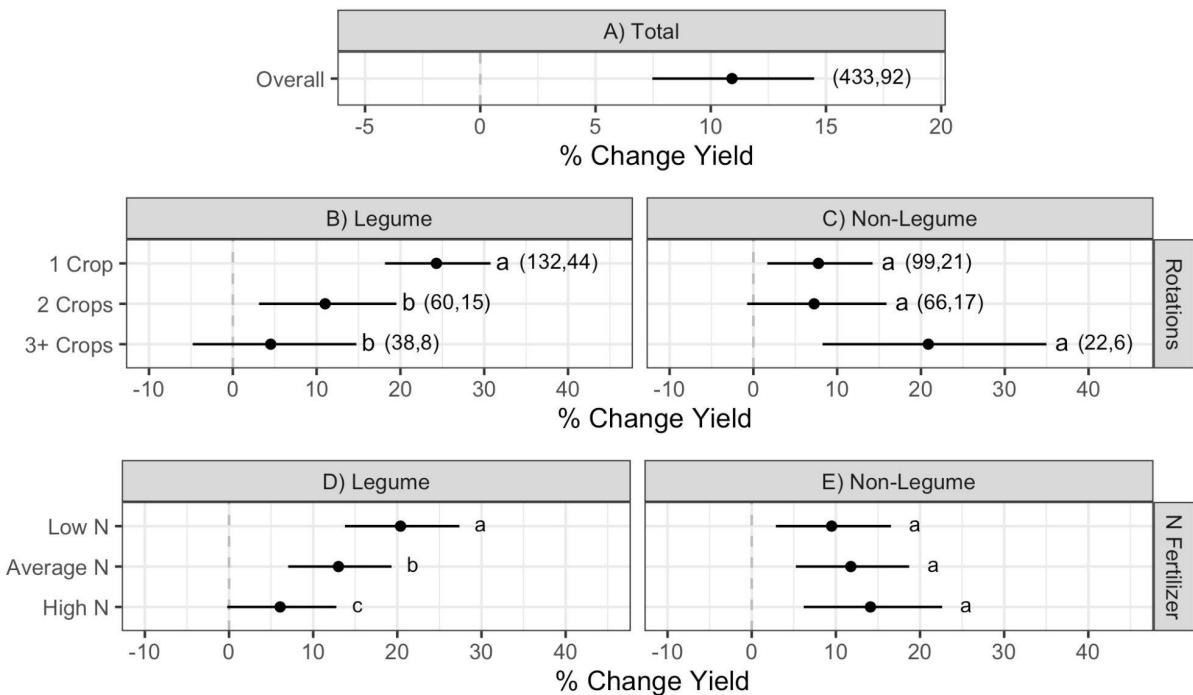
We found that SOC changes from cover cropping ( $\Delta_{SOC}$ ) were associated with yield changes ( $\Delta_{yield}$ ), but only in soils with initial SOC values of  $11.6 \text{ g kg}^{-1}$  or less (Fig. 1). In soils with initial SOC values of  $5 \text{ g kg}^{-1}$ , for instance, a  $1 \text{ g kg}^{-1}$  increase in SOC was associated with a 2.4% yield increase. In soils with initial SOC values greater than  $11.6 \text{ g kg}^{-1}$ ,  $\Delta_{SOC}$  was not significantly associated with  $\Delta_{yield}$ . The  $\Delta_{SOC}$ -to- $\Delta_{yield}$  relationship did not differ between cover crop types (legume vs. non-legume) and did not vary across differing levels of N fertilization.



**Fig 1.** Yield change associated with a  $1 \text{ g kg}^{-1}$  increase in SOC (e.g., from  $5 \text{ g kg}^{-1}$  to  $6 \text{ g kg}^{-1}$ ) at differing levels of initial SOC. Initial SOC is SOC ( $\text{g kg}^{-1}$ ) prior to cover cropping (0-18.4 cm depth on average). Shaded bands are 95% CIs. Increased SOC is positively associated with yield (red) only in sites with below average initial SOC (less than  $11.6 \text{ g kg}^{-1}$ ). 90% of observations fell within the initial SOC range shown. 40 out of 92 study sites in our dataset had initial SOC levels below  $11.6 \text{ g kg}^{-1}$ .

The effect of rotational complexity on  $\Delta_{yield}$  differed between legume cover crops and non-legume cover crops (Fig 2B, Fig 2C). Holding other predictors at their dataset average,  $\Delta_{yield}$  in legume cover crop treatments was significantly greater in continuous cash crop monocultures (+24.3%, 95% CI: 18.1 – 30.8) versus rotations with two (+11.0%, 95% CI: 3.1 – 19.5) cash crop species (Fig 2B). For rotations with 3 or more cash crops,  $\Delta_{yield}$  from legume cover crops was not statistically different from zero. For non-legume cover crops, the magnitude of  $\Delta_{yield}$  across rotational complexity groups varied but not significantly so. Holding other predictors at their dataset average, non-legume cover crops significantly increased yield in continuous cash crop monocultures (+7.8%, 95% CI: 1.7 – 14.2) and plots with 3 or more cash crops in rotation (+20.9%, 95% CI: 8.3 – 35.0) (Fig 2C).  $\Delta_{yield}$  from non-legume cover crops in two-crop rotations was positive but overlapped zero (+7.2%, 95% CI: -0.8 – 15.9)

We found that increased N fertilization reduced  $\Delta_{yield}$  in legume cover crop treatments but did not have a significant effect on  $\Delta_{yield}$  from non-legume cover crops (Fig 2D, Fig 2E). Legume cover crops in low N systems ( $12.9 \text{ kg N ha}^{-1} \text{ season}^{-1}$ , one standard deviation below the mean N fertilization of our dataset) increased yield by +20.4% (95% CI: 13.8 – 27.4) and in average N systems ( $85.9 \text{ kg N ha}^{-1} \text{ season}^{-1}$ ) increased yield by +13.0% (95% CI: 7.0 – 19.3) (Fig 2D). In systems receiving more than  $157 \text{ kg N ha}^{-1} \text{ season}^{-1}$ , we found no statistically significant effect of legume cover crops. Non-legume cover crops provided yield increases in low (+9.5%, 95% CI: 2.9 – 16.6), average (+11.8%, 95% CI: 5.2 – 18.7), and high (+14.1%, 95% CI: 6.2 – 22.6) N systems (Fig 2E).



**Fig 2.** Cash crop yield change from cover cropping at different levels of rotational complexity (“Rotations”) and N fertilizer ( $\text{kg N ha}^{-1} \text{ season}^{-1}$ ) in our yield model ( $n = 417$ ,  $k = 88$ ). Selected N fertilizer levels are dataset mean  $\pm$  sd with low, average, and high N corresponding to  $12.9$ ,  $85.9$ ,  $158.9 \text{ kg N ha}^{-1} \text{ season}^{-1}$ , respectively. Rotational complexity (“Rotations”) is a count of the number of different cash crop species rotated on a given plot across the length of the experiment. Yield change estimates are shown for both legume and non-legume cover crops. Letters are pairwise comparison results with different letters indicating significantly different effect sizes at  $\alpha = 0.05$ .

Numbers in parentheses are observations in each grouping followed by the number of unique sites in each grouping (not presented for N fertilizer because displayed estimates correspond to selected values along a continuous axis rather than groupings). Error bars are 95% CIs.

### *SOC responses to cover cropping*

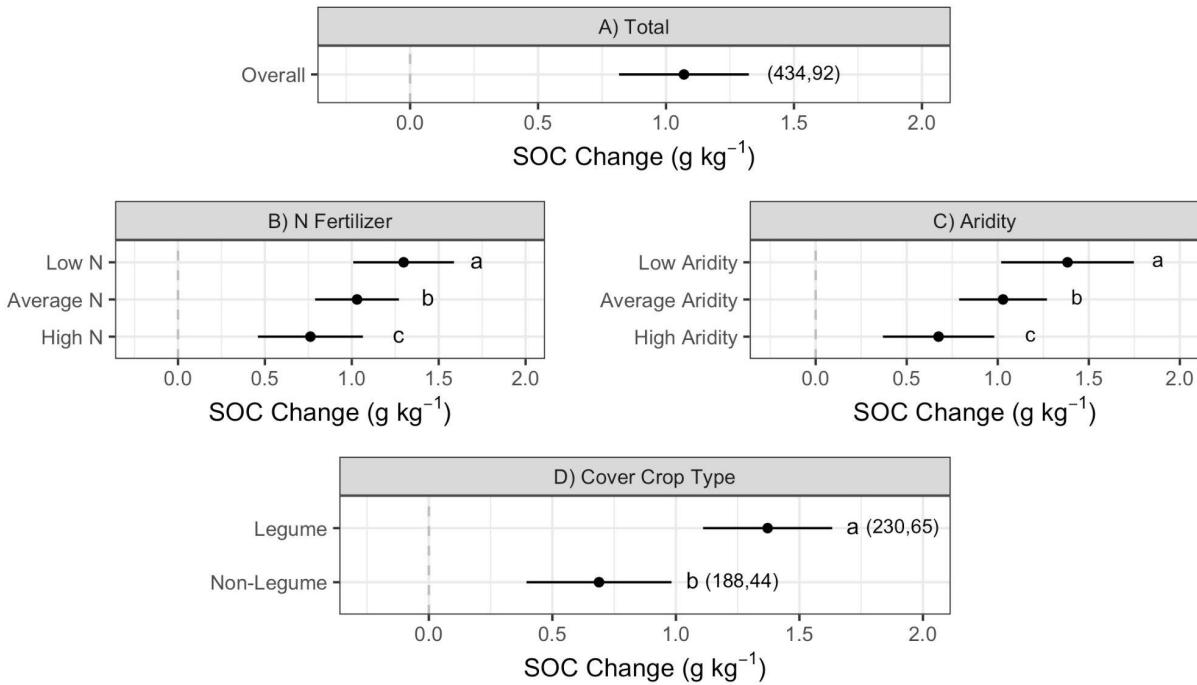
Our  $\Delta_{SOC}$  model included site level aridity and an interaction between cover crop type (legume vs non-legume) and N fertilizer inputs ( $\text{kg N ha}^{-1}$ ) as variables which moderated the effect of cover crops on SOC (Table 2; Fig. 3). Marginal  $R^2$  was 0.15 and conditional  $R^2$  was 0.82. In line with the findings of McClelland et al. (2021), we found that experimental length (i.e., time since introduction of cover crops) was not a good predictor of SOC response. Addition of other variables such as initial SOC, mean annual precipitation, phosphorus fertilization, and tillage did not improve model fit (Table S3).

**Table 2.** Standardized coefficients and type III ANOVA results from our  $\Delta_{SOC}$  model ( $n = 418$ ,  $k = 88$ ). df is numerator and denominator degrees of freedom, respectively, with Kenward-Roger approximation for denominator degrees of freedom.  $\Delta_{SOC}$  is the measured cover crop treatment SOC concentration ( $\text{g kg}^{-1}$ ) minus the measured SOC concentration of the paired control ( $\text{g kg}^{-1}$ ). Cover Crop Type is binary categorical; legume vs non-legume coded 1 and 0, respectively. Aridity is an index of site level aridity (low numbers are more arid). *p*-values in italics are considered significant at  $\alpha = 0.05$ .

$\Delta_{SOC}$ Model Results			
Variable	Standardized Coefficients	df	p-value
Cover Crop Type	-0.68	1,32	<0.001
N Fertilizer	-0.54	1,64	<0.01
Aridity	0.71	1,71	<0.01

We found that non-legume cover crops were less effective at increasing SOC than legume cover crops ( $+0.69 \text{ g C kg}^{-1}$ , 95% CI:  $0.4 - 0.98$  versus  $+1.37 \text{ g C kg}^{-1}$ , 95% CI:  $1.11 - 1.63$ ; Fig 4D).

Cover crops were less effective at increasing SOC in more arid sites (Fig 4D). In higher aridity sites (one standard deviation above the dataset average, roughly in line with areas such as the US Corn Belt or Southern India) cover cropping increased SOC by  $+0.70 \text{ g C kg}^{-1}$  (95% CI:  $0.39 - 1.00$ ) (Fig 4D). In lower aridity sites (one standard deviation below the dataset average, roughly in line with areas such as northern Japan or Southwestern Brazil), cover crops increased SOC by  $1.37 \text{ g C kg}^{-1}$  (95% CI:  $1.00 - 1.73$ ).



**Fig. 3.** SOC change ( $\text{g kg}^{-1}$ ) from both cover crop types (legume vs non-legume) across differing levels of N Fertilizer as well as SOC change estimates at selected values of site level aridity (“Aridity”) in our SOC model. Selected N fertilizer levels are dataset mean  $\pm$  sd with low, average, and high N corresponding to 12.9, 85.9, 158.9  $\text{kg N ha}^{-1} \text{ season}^{-1}$ , respectively. Selected aridity levels are dataset mean  $\pm$  sd. Cover crop type is binary categorical; non-legume vs legume. Letters are pairwise comparison results with different letters indicating significantly different effect sizes at  $\alpha = 0.05$ . Numbers in parentheses are observations in each grouping followed by the number of unique sites in each grouping (not presented for N Fertilizer and Aridity because displayed estimates correspond to selected values along a continuous axis rather than groupings). Error bars are 95% CIs.

## Discussion

In our meta-analysis of 92 experiments spanning 5 continents, we found that cover crops increased crop yields concurrently with SOC in 59.7% of 434 paired observations, thus providing a win-win outcome for farmers and society a majority of the time.  $\Delta_{\text{SOC}}$  was directly associated with  $\Delta_{\text{yield}}$  only in soils with relatively low SOC prior to cover cropping. The yield benefit of increased SOC did not diminish in systems with higher N inputs and did not differ between cover crop types (legume vs non-legume), indicating that N inputs cannot substitute for changes in SOC that link to higher yields. The largest SOC increases occurred in legume cover crop treatments ( $+1.5 \text{ g kg}^{-1}$ ) and the largest yield increases also occurred from legume cover crops in systems with low to average N inputs and in 1-2 crop rotations (up to +24.3%).

### *Direct relationships between changes in SOC and yield*

As the source of carbon input to soil, photosynthesis is the most fundamental constraint on SOC sequestration<sup>31</sup>. Cover cropping is considered one of the most promising approaches to increase SOC in agricultural soils, in part because it increases net primary productivity (NPP) relative to a bare fallow, and thus carbon inputs to soil<sup>31,32</sup>. Cover cropping may also increase the carbon use efficiency of the soil microbial community<sup>33</sup>, which determines the proportion of carbon inputs

remaining in soil as microbial necromass, recognized as the primary source of stabilized soil carbon<sup>34</sup>. However, since cover crops not only can help build SOC, but also may increase crop productivity directly, i.e., in ways not mediated through changes in SOC, disentangling whether cover crops build SOC directly or build SOC through their effects on cash crop productivity is challenging<sup>30</sup>. In our study, this is an important question to address in order to interpret the positive association between changes in SOC and changes in yield.

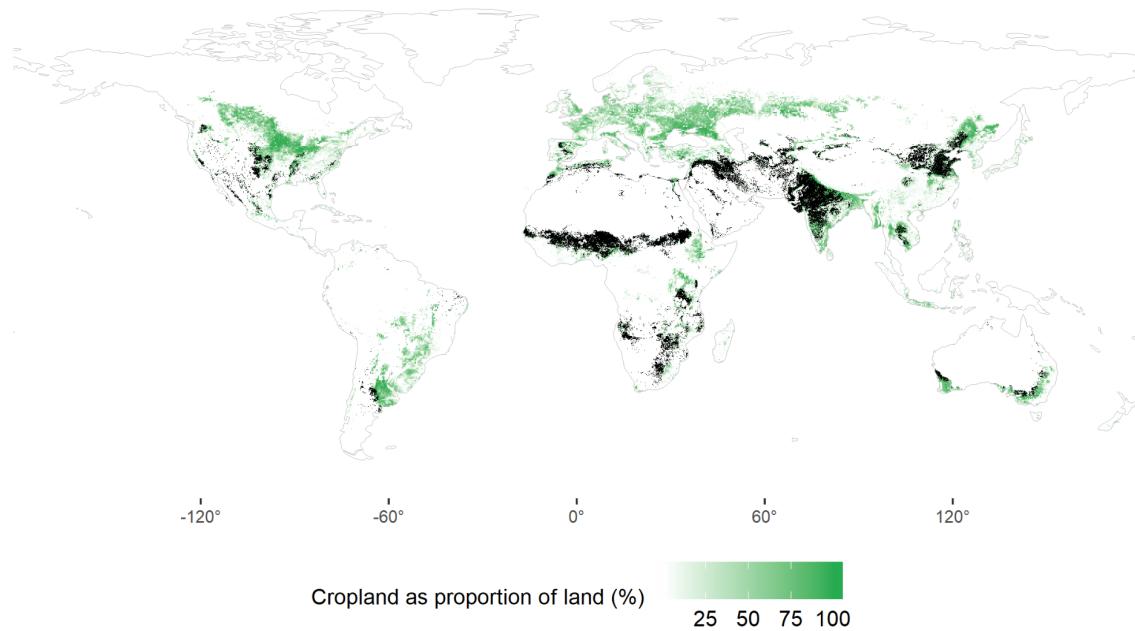
The relative changes in NPP from increases in crop productivity vs. cover cropping suggest that cover cropping is the dominant influence on SOC. In this study, if we assume half of cash crop biomass would be removed as yield<sup>35</sup>, then the average *increase* in cash crop biomass returned to soil as residue for the three most common cash crops in the study was 0.9 (maize), 0.5 (rice), and 0.4 (wheat) Mg ha<sup>-1</sup>. Conversely, cover crop biomass of 3-7 Mg ha<sup>-1</sup> yr<sup>-1</sup> or higher is common<sup>11</sup> and consistent with the average increase of biomass on cover-cropped plots in this study of 5.1 Mg ha<sup>-1</sup> yr<sup>-1</sup> (n=133, k = 47), or 2.2 Mg ha<sup>-1</sup> yr<sup>-1</sup> when winter weeds in fallow plots are taken into account (n = 49, k=18). With all of the cover crop biomass typically returned to the soil, this is ~2.5-5.5 times greater biomass from cover crops directly than from changes to cash crop productivity. As opposed to the non-significant effect of absolute cash crop yield change on  $\Delta_{SOC}$  (p = 0.32), only the difference in cover crop biomass between treatment and control plots was a significant predictor of the absolute change in SOC (p < 0.01; n = 49, k= 18) (Table S4). Thus, we conclude that cover crops directly increase SOC with possible additional but smaller indirect (non-SOC mediated) effects from cash crop productivity.

Further, if yield increases from cover cropping were driving the positive  $\Delta_{SOC}$ -to- $\Delta_{yield}$  relationship, leading to higher SOC<sup>30</sup>, then this mechanism should increase SOC in soils regardless of initial SOC level, especially since the  $\Delta_{SOC}$  model showed no signs of SOC saturation in soils with higher initial SOC concentrations (i.e., initial SOC was not a predictor of  $\Delta_{SOC}$ ). The best explanation for this interaction is that the positive  $\Delta_{SOC}$ -to- $\Delta_{yield}$  response in low SOC soils is a reflection of decreasing marginal yield benefits from increased SOC in higher initial-SOC soils.

Our experimentally based approach identified a  $\Delta_{SOC}$ -to- $\Delta_{yield}$  response that does not vary based on N inputs or with legume vs. non-legume cover crops, as indicated by the lack of significant interactions between  $\Delta_{SOC}$  and these predictors. A negative  $\Delta_{SOC}$  by N fertilization interaction would have indicated that the yield benefit from SOC was substitutable for N inputs and therefore N related. Likewise, if the  $\Delta_{SOC}$ -to- $\Delta_{yield}$  relationship differed between legume and non-legume cover crops, then some portion of the SOC benefit likely would have been a reflection of yield benefits from N fixation. In the absence of these interactions with  $\Delta_{SOC}$ , the link we found between  $\Delta_{SOC}$  and  $\Delta_{yield}$  is likely better explained by benefits of increased SOC like reduced compaction and increased aeration<sup>3</sup>. Our results thus help to identify and quantify the yield benefits of soil improvement provided by SOC for which fertilization cannot substitute.

We only found marginal yield increases from changes in SOC when SOC prior to cover cropping was less than 11.6 g kg<sup>-1</sup>, which helps clarify contrasting results of prior observational meta-analyses. For instance, in a meta-analysis of Danish farms showing no relationship between yield and SOC<sup>24</sup>, there were very few observations with SOC concentrations below 11.6 g kg<sup>-1</sup>. On the other hand, a study from China reporting positive and linear relationships between yield

and SOC<sup>26</sup> had few observations over  $\sim 15$  g kg<sup>-1</sup>, whereas a global meta-analysis that also showed a saturating yield benefit had a similarly wide range of SOC values as this study<sup>5</sup>. The yield benefit of increased SOC that we identified is slightly less than that reported in the latter study. For a hypothetical increase from 5 g kg<sup>-1</sup> to 8 g kg<sup>-1</sup>, our model predicted a +7.9% yield increase, compared to the +10% yield increase previously reported<sup>5</sup>. An increase of this size may take a number of years of improved management.



**Fig. 4:** Global croplands with SOC concentrations  $< 11$  g kg<sup>-1</sup> in black (5-15 cm). Continent borders are outlined in light gray.

#### *Aligning carbon sequestration goals with yield benefits*

Regardless of direct links between  $\Delta_{SOC}$  and  $\Delta_{yield}$ , we found that incorporation of legume cover crops into systems with one to two cash crops in rotation could build SOC while also increasing crop yields. Legume cover crops provided increases of +1.5 g kg<sup>-1</sup> SOC and +24.3% yield in continuous monocrop cultures. In two crop rotations, legume cover crops increased yield by +11.0% while the +1.5 g kg<sup>-1</sup> SOC increase remained unchanged (i.e., rotation was not a significant predictor of  $\Delta_{SOC}$ ). Yield benefits of crop rotation diversification are well-known<sup>36,37</sup> and based on our results here, appear to be redundant with legume cover crops in more complex rotational systems. This suggests a need for further research on how to optimize cover crops in more complex cash crop rotations, e.g. with mixes of cover crop species<sup>38</sup>.

We identified low to average N input systems as other key farm types where cover crops support alignment between carbon sequestration goals and yield increases. Effects of cover crops on SOC declined as N inputs increased, and yield benefits from legumes were highest in low N input systems. Legumes could thus allow for increasing yields while keeping synthetic N fertilizer inputs low or even reduced<sup>39</sup>, which also comes with environmental benefits. When legume cover crops are introduced, reducing N fertilizer inputs would help counterbalance possible increases in nitrous oxide emissions that can occur in legume systems<sup>40,41</sup>.

The larger SOC response from legumes compared to non-legume cover crops (+1.37 g C kg<sup>-1</sup> vs +0.69 g C kg<sup>-1</sup>) contrasts with no effect of cover crop type found in prior meta-analyses<sup>11,13</sup>, possibly due to their more limited datasets. With relatively more labile plant inputs that microbes efficiently use, legumes may be particularly effective at building soil organic matter pools, including mineral associated organic matter, that are both stable and supply N<sup>33,42-44</sup>. Greater absolute changes in SOC in less arid climates may be due to higher cover crop NPP. While aridity was not in our final  $\Delta_{Yield}$  model, other studies show cover cropping leads to higher cash crop yields in less arid climates<sup>18,45</sup>, suggesting that such areas may be most likely to have co-benefits for SOC and yields.

Our global meta-analysis demonstrates that the goal of building soil carbon through cover cropping aligns with the goal of increasing or maintaining crop yields. Importantly, since these goals align at the site level ~60% of the time, benefits of higher yields for farmers are achievable concurrently with the societal benefit of carbon sequestration<sup>10</sup>. Yield benefits related to SOC were only evident in soils with initialSOC concentrations below 11.6 g kg<sup>-1</sup> (43.4% of studies in our dataset). This finding suggests that direct yield benefits from SOC increases could help motivate farmers' adoption of SOC enhancing practices in soils with low SOC. Globally, approximately 20% of cropland has SOC concentrations in the 5 - 15 cm depth of 11 g kg<sup>-1</sup> or lower (Fig. 4). Cover-cropping could improve both productivity and SOC accrual on more than ~40 Mha of maize and wheat cropland which are producing below-potential yield on land predicted to have less than 11 g kg<sup>-1</sup> SOC (Figure S4, Table S5). Other incentives will be needed for farmers with SOC levels greater than ~11 g kg<sup>-1</sup>, especially when socio-economic factors constrain cover crop adoption<sup>46</sup>. Climate factors like short growing seasons and low water availability can also limit cover crop adoption<sup>18</sup>.

We therefore suggest that determining the conditions for which changes to agricultural management provide co-benefits for crop yields and SOC — rather than establishing universal relationships between SOC and yield — will be more useful for spurring agricultural transitions that produce food while also mitigating climate change. To achieve carbon sequestration goals while supporting crop yields, diversifying simplified rotations with legumes is a promising strategy given that legumes often provided the largest benefit to both SOC and yields. Likewise, in low to average N input systems, the greatest yield benefits can be aligned with the greatest SOC benefits through the use of legume cover crops. For systems with complex rotations or high N inputs, non-legume cover crops are a better choice to support yield goals, though SOC changes may be lower. Identifying when and where agricultural management practices deliver direct benefits to farmers and contribute to climate change mitigation will help with the urgent need to increase the carbon sink of agricultural lands.

## Methods

### *Study Selection*

We selected cover cropping studies according to the following criteria: 1) the experimental design includes one or more replicated cover cropping treatments, defined as a non-harvested crop grown between productive seasons; 2) the study includes a clear control as either bare fallow or spontaneous off-season regrowth (e.g., “winter weeds”); 3) data are available for both SOC and cash crop yield, each measured no more than one year apart; 4) cash crop yield is measured as fruit or grain; 5) yield and SOC are available as yearly or monthly values rather than averages across multiple years (for maximum accuracy in matching SOC values with associated yields); and 6) annual fertilizer inputs are equal across control and treatment or are administered based on pre-season soil tests. Potted plant experiments were not included in our dataset.

We began our literature search with the study lists of two recent cover cropping meta-analyses<sup>13,17</sup> and subsequently searched ISI Web of Science for additional studies that matched our criteria using the search string TS=((cover crop\* OR catch crop OR fallow OR green manure) AND carbon AND yield). In October 2020, the date of our final search, our search string returned 2,451 studies. If an article reported only SOC data or yield data, we used key terms related to the experiment to search Google Scholar for articles reporting on the same experiment in order to fill in the missing data. In 11 instances, gray literature sources such as master’s theses, dissertations and conference proceedings were used to supplement data from peer-reviewed publications. In addition to Google Scholar searches, 36 authors were contacted for additional data or methodological clarifications, out of which 8 responded and 3 provided additional data and/or information.

Our final dataset spanned 5 continents and contained data from 92 distinct experiments gathered from 120 sources (107 peer reviewed journal articles, 6 master’s theses, 2 dissertations, 3 publicly available datasets, and 2 conference proceedings). A list of data sources used in the study along with extraction notes is provided in the supplementary material.

### *Data Compilation and Extraction*

We quantified the effect of cover crops on yield using the log response ratio, calculated as the natural log of the cover crop treatment value divided by that of the respective fallow control. For SOC, we used the absolute difference in SOC between the cover crop and control plots, which allowed us to assess the influence of initial SOC without the possibility of statistical artifacts associated with relative differences<sup>47</sup>. Within a given study, a treatment value was matched to a control value only if both groups differed in no other respect than the use of cover cropping (e.g., same tillage regime, same N application, etc.) and if the treatments were sampled at the same time. This aspect of our study design allowed us to control for confounding effects that would otherwise be introduced in a direct comparison of raw values between studies such as environmental conditions, management decisions, or edaphic factors. In the case of the yield response to cover cropping, our use of the RR allowed us to make comparisons across crops with different morphological characteristics (e.g., tomatoes vs. cotton) because weight units are normalized by the ratio. Site-level initial SOC values were not available for some of the studies in our dataset. To approximate missing site-level values, we used the earliest SOC sample

available for the non-cover crop control, assuming that the field had likely been under a no-cover crop planting regime prior to the initiation of the cover cropping experiment. We combined soil metrics and variance measures reported from multiple depths into one single depth using a weighted average which took into account the size of each depth increment relative to the total depth sampled. Fig. S9 shows a histogram of deepest sampling depth. In our model selection process, we assessed the impact of sampling depth as a moderating factor of the effect of SOC on yield. Although differing sampling depths across studies have the potential to obscure trends when comparing raw SOC values, we did not find that sampling depth was a significant predictor of initial SOC values in our dataset. We therefore opted to test initial SOC effects using raw SOC values.

### *Data Analysis*

We collected sampling variances when available to assign weights to data points. However, only 30% of studies reported some form of variance. Following previous work, we chose instead to weight our observations using sample size of the treatment and control groups which gave high weight to larger, well-replicated studies<sup>48-50</sup>. Our weighting formula (eq. 1) includes the common weighting ratio based on treatment group sample size ( $n_t$ ) and control group sample size ( $n_c$ ) as well as a correction term dividing by the total number of observations contributed by a given study (N). This additional step is meant to ensure that no study contributes a disproportionate amount to the final model simply because it contained more extractable data points than another<sup>51</sup>.

$$(Eq. 1) \quad W = \frac{n_t \times n_c}{n_t + n_c} \times \frac{1}{N}$$

We modeled study site as a random effect to account for the non-independence of these data points, and nested sampling year within study site to account for temporal non-independence. To build models for both  $\Delta_{SOC}$  and  $\Delta_{Yield}$ , we implemented a model selection process which utilized Akaike Information Criterion (AIC)<sup>52</sup> scores to select final predictors which we had hypothesized may be mechanistically related to  $\Delta_{SOC}$  or  $\Delta_{Yield}$ . Variable relevance was determined by comparing weighted mixed effect models of each variable as a solitary predictor of each response variable against the corresponding model containing only the intercept. Because of incomplete data for certain predictor variables, model comparisons between the solitary predictor and the intercept-only model were done using complete data subsets for the solitary predictor. If the regression containing the solitary predictor variable resulted in an AIC score more than two units below that of the intercept-only regression (i.e.,  $\Delta AIC < 2$ ), the variable was included in our final multiple regression model. We did not perform any further model selection because complex model selection decisions are often subjective and can change results considerably<sup>53</sup>. For our  $\Delta_{Yield}$  model, we tested interaction terms between  $\Delta_{SOC}$  and soil texture metrics, as well as an interaction between  $\Delta_{SOC}$  and initial SOC (SOC concentration prior to cover cropping), as per previous findings<sup>5</sup>. Lastly, we tested interaction terms between cover crop type (legume vs non-legume) and yield predictor variables whose effects we hypothesized may be influenced by N fixation such as N fertilization, rotational complexity and  $\Delta_{SOC}$ .

In both models, we checked for collinearity among variables using generalized variance inflation factors (GVIF) with the following adjustment to allow for comparability across variables with

differing degrees of freedom<sup>54</sup> (df):  $Adjusted\ GVIF = (GVIF)^{\frac{1}{2df}}$ . We considered adjusted GVIF values of 3 and higher to indicate potential collinearity<sup>55</sup>. The only cases of collinearity involved models that included annual temperature and precipitation and the aridity index. These variables were assessed separately in regression models and the final variable chosen based on AIC. We centered predictors so that 0 corresponded with the observed mean of each predictor by subtracting the dataset mean from each observation and subsequently standardized coefficients by dividing by two standard deviations<sup>56</sup>. In our  $\Delta_{Yield}$  model, cover crop type was coded as 1 and 0 to allow for comparison of standardized coefficients<sup>56</sup>.

In order to determine whether changes in cash crop yield from cover cropping were driving changes in SOC vs. changes in SOC from cover cropping driving changes in yield, we built three separate weighted mixed effect regressions for  $\Delta_{SOC}$  (Table S4). We tested cover crop aboveground biomass as a solitary predictor of  $\Delta_{SOC}$  and subsequently cover crop aboveground biomass *difference* (cover crop aboveground biomass minus aboveground biomass of spontaneous off-season regrowth in control plots when this data was available) as a solitary predictor of  $\Delta_{SOC}$ . Finally, we tested absolute cash crop yield change (the measured cash crop yield of the cover crop treatment in  $Mg\ ha^{-1}$  minus the measured cash crop yield of the paired fallow control ( $Mg\ ha^{-1}$ )) as a solitary predictor of  $\Delta_{SOC}$ . For absolute cash crop yield change, only crops with yields reported in constant dry weight and with harvest indexes of approximately 0.5 were included since absolute yields of these crops are comparable (e.g., vs. tomatoes, with yields reported in wet weight) as a proxy for total aboveground biomass.

All analyses were performed using R Statistical Software v4.2.0<sup>57</sup>. We built mixed effect regressions using the package ‘lme4’<sup>58</sup> and determined fixed effect F-values using a type III ANOVA in the ‘stats’ package<sup>57</sup>. We used the package ‘emmeans’ to quantify interaction effects<sup>59</sup>. We used pairwise comparison in the package ‘emmeans’ to determine significant differences among levels of categorical variables using  $\alpha = 0.05$  with a Bonferroni adjustment for multiple comparisons<sup>60</sup>. To determine the significance of different levels of our moderating factors, we checked to see whether their 95% confidence intervals (95% CI) overlapped zero, with no overlap indicating a rejection of the null (zero effect) at  $\alpha = 0.05$ . When reporting response estimates at specific values of predictor variables, we held all other predictor variables at their dataset average. We used the Kenward-Roger approximation for denominator degrees of freedom in all p-value calculations<sup>61</sup>.

#### *Assessing Bias and Outliers*

Using the ‘InfluencePlot’ function in the ‘car’ package<sup>7</sup>, we identified highly influential data points using Cook’s distance and assessed the impact of their removal on our models to gauge robustness to extreme data points. Starting from the full dataset, we sequentially removed the point with the highest Cook’s distance in each model and re-ran the models on each trimmed dataset. Using 10 sets of results for each model, each subsequent one with an additional influential point removed, we compared changes in effect size coefficients and p-values to determine if any were highly influenced by one observation (see Table S1 for full comparison results). We noted one such observation which caused the effect of tillage type on  $\Delta_{Yield}$  to be highly significant. Upon removal of this observation, this effect became non-significant and successive removal of influential points after this produced stable effect size estimates (Table S4). As such, we chose to remove this outlier from our  $\Delta_{Yield}$  model to report robust results which

reflected the dominant trends in our dataset. In addition to influential data point removal, we conducted a leave-one-out sensitivity analysis in which we removed studies from our dataset one study at a time and recalculated coefficient estimates on each trimmed dataset. After performing this removal for all 92 studies in both our  $\Delta_{SOC}$  or  $\Delta_{yield}$  models, we assessed the variability in coefficient estimates among trimmed datasets (Figs. S5 and S6) and looked for outlier estimates which would have indicated that one study was having an outsized effect on model fit. In addition, we looked at each leave-one-out model which pushed coefficient estimates for significant predictors towards the null (0) and away from the null (0) for non-significant predictors to see if the significance of any given predictor was dependent on a single study or if the non-significance of any given predictor was dependent on a single study (either of which would be a sign of unstable coefficient estimates). We found that variability in all coefficient estimates was low and that significance or non-significance of any given predictor was not dependent on any given study. We looked for publication bias in our dataset on both the yield and SOC RRs using funnel plots (see Fig. S3).

### **Author contributions**

I.V., T.M.B., and L.P. conceived the ideas and designed methodology; I.V. and G.D.L.C. collected the data; I.V., A.G., K.E., and A.M. analyzed the data; I.V. and T.M.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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### **Conflict of Interest**

The authors have no conflicts of interests related to this work.

### **Data Availability**

Data used in this meta-analysis are available from the Dryad Digital Repository, accession.

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