


RESEARCH ARTICLE

Crop traits drive soil carbon sequestration under organic farming

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Abstract

1. Organic farming (OF) enhances top soil organic carbon (SOC) stocks in croplands compared with conventional farming (CF), which can contribute to sequester C. As farming system differences in the amount of C inputs to soil (e.g. fertilization and crop residues) are not enough to explain such increase, shifts in crop residue traits important for soil C losses such as litter decomposition may also play a role.
2. To assess whether crop residue (leaf and root) traits determined SOC sequestration responses to OF, we coupled a global meta-analysis with field measurements across a European-wide network of sites. In the meta-analysis, we related crop species averages of leaf N, leaf-dry matter content, fine-root C and N, with SOC stocks and sequestration responses in OF vs. CF. Across six European sites, we measured the management-induced changes in SOC stocks and leaf litter traits after long-term ecological intensive (e.g. OF) vs. CF comparisons.
3. Our global meta-analysis showed that the positive OF-effects on soil respiration, SOC stocks, and SOC sequestration rates were significant even in organic farms with low manure application rates. Although fertilization intensity was the main driver of OF-effects on SOC, leaf and root N concentrations also played a significant role. Across the six European sites, changes towards higher leaf litter N in CF also promoted lower SOC stocks.
4. Our results highlight that crop species displaying traits indicative of resource-acquisitive strategies (e.g. high leaf and root N) increase the difference in SOC between OF and CF. Indeed, changes towards higher crop residue decomposability was related with decreased SOC stocks under CF across European sites.

5. *Synthesis and applications.* Our study emphasizes that, with management, changes in crop residue traits contribute to the positive effects of organic farming (OF) on soil carbon sequestration. These results provide a clear message to land managers: the choice of crop species, and more importantly their functional traits (e.g. leave and root nitrogen), should be considered in addition to management practices and climate, when evaluating the potential of OF for climate change mitigation.

KEYWORDS

climate change mitigation, crop residue, ecological intensification, leaf nitrogen, meta-analysis, organic farming, resource economics traits, soil carbon stocks

1 | INTRODUCTION

Soil organic carbon (SOC) stocks represent the largest terrestrial C pool, although these stocks typically decline after agricultural conversion of natural areas (Guo & Gifford, 2002). Agricultural soils comprise a major proportion of the earth's land surface, thus restoring SOC sequestration in these systems plays an important role in mitigating climate change (Lal, 2004). Additionally, accelerating SOC sequestration can also enhance the fast-cycling of particulate organic matter that serves as a source of nutrients for crop yield (Janzen, 2006). Land management via the ecological intensification of agricultural systems claims that optimizing key ecosystem processes, such as soil C cycling, will maintain food provision while enhancing SOC sequestration (Bommarco, Kleijn, & Potts, 2013). In fact, organic farming (OF), one of the largest existing models of ecological intensification world-wide in terms of surface area (Tittonell, 2014), increases top SOC stocks by 3.50 Mg C/ha as a global average, compared to conventional farming (CF) (Gattinger et al., 2012). The driving factors of such increase are not fully understood, but the high rates of external C inputs (e.g. manure) typically applied in OF certainly contribute to such increase (Kirchmann, Kätterer, Bergström, Börjesson, & Bolinder, 2016; Leifeld & Fuhrer, 2010). However, increments in SOC stocks are also detected when comparing conventional vs. organic farms with low manure application rates (LMR; European livestock units per hectare ≤ 1 , Gattinger et al., 2012). Furthermore, C inputs to the soil via main crop residues are lower in OF, since crop yield is on average 20%–25% lower (Ponisio et al., 2014; Seufert, Ramankutty, & Foley, 2012). Thus, farming system differences in the quantity of C inputs entering to the soil (manure and crop production) cannot fully explain the increased SOC stocks found under the organic management of agricultural lands.

Soil organic carbon stocks represent the net result of long-term changes in soil C inputs and outputs (Crowther et al., 2016). Consequently, farming system differences in SOC losses via organic matter decomposition might thus contribute to the increased SOC stocks found under OF, altering SOC sequestration. Soil organic matter decomposition is mainly driven by the site climatic conditions, the morphological and chemical quality of plant residues, and soil decomposers (Cornwell et al., 2008; García-Palacios, McKie,

Handa, Frainer, & Hättenschwiler, 2016; Parton et al., 2007). When comparing SOC sequestration in OF vs. CF within the same climatic conditions, a major driver of soil C losses thus may be the quality of plant residues (e.g. leaf and root N concentrations) feeding soil decomposers (Faucon, Houben, & Lambers, 2017). In this line, labile plant residues (e.g. higher N concentration) are usually related with faster decomposition rates (Cornwell et al., 2008; García-Palacios et al., 2016) and hence higher soil C losses. However, opposite consequences for organic matter stabilization may also take place. The Microbial Efficiency-Matrix Stabilization framework suggests that labile litter decomposition increases microbial residues that are chemically bonded to the mineral soil matrix, increasing the stability of the soil organic matter (Cotrufo, Wallenstein, Boot, Denef, & Paul, 2013). Therefore, considering crop residue traits important for decomposition might help to elucidate the mechanisms controlling SOC sequestration responses to OF (Faucon et al., 2017). A detailed understanding of the processes behind increased SOC sequestration is crucial to evaluate whether ecological intensification should be pursued as an effective land management strategy contributing to mitigate climate change via these higher SOC sequestration rates.

To assess whether the traits of crop residues (leaves and roots) drive SOC responses to OF, the importance of these traits should be assessed relative to major drivers of soil C cycling in croplands, such as climate (Guo & Gifford, 2002), fertilization (Leifeld & Fuhrer, 2010), and crop root to shoot allocation (Kätterer, Bolinder, Andrén, Kirchmann, & Menichetti, 2011). Plants differ in their residue traits in ways that predictably affect litter decomposition and soil C cycling. For example, resource-acquisition strategies are typical of fast-growing species producing labile shoot and root residues with high decay rates (Díaz et al., 2016). In addition, acquisitive species may show a more plastic phenotype than resource-conservative species under changing soil nutrient availability levels (Crick & Grime, 1987; Siebenkäs, Schumacher, & Roscher, 2015). Thus, intraspecific changes in resource-acquisition crops may produce plant residues that are more decomposable with the higher inputs of inorganic N supplied under CF. If this is the case, such intraspecific changes in crop residue traits with land management may speed up SOC losses, and thereby promote lower SOC stocks and sequestration in CF compared with OF.

Our main goal was to assess if crop residue traits consistently determine SOC sequestration rates under OF. To do that, we coupled SOC and crop residue traits data from a global meta-analysis comparing OF vs. CF, with European-wide field measurements. In the meta-analysis, we related crop species averages of resource economics traits important for decomposition (leaf N, leaf-dry matter content, LDMC, fine-root C and N) with SOC sequestration responses in OF vs. CF. We hypothesized that, when the same crop species is used, SOC sequestration is enhanced in the OF plots compared with the CF plots when this species is a resource-acquisitive crop. Then, in a network of field experiments across six European sites, we measured SOC stocks and crop residue (leaf litter) traits after long-term land management comparing ecological intensive (e.g. OF) vs. CF. We hypothesized that management-induced changes in leaf litter traits towards higher crop residue lability under CF promoted higher SOC sequestration when comparing OF vs. CF.

2 | MATERIALS AND METHODS

We followed a systems approach to compare two land-use management types (Klerkx, Van Mierlo, & Leeuwis, 2012). The systems approach is considered most appropriate when evaluating ecosystem services provided in conventionally intensive vs. more sustainable agriculture (Gattinger et al., 2012; Ponisio et al., 2014; Seufert et al., 2012). This study consisted in two differentiated parts. In the global meta-analysis, we focused on SOC studies evaluating the same crop species in OF and CF plots, to isolate the influence of crop residue traits on SOC from that of growing different crop species between farming systems. Thus, we addressed the effects of crop resource strategy (represented with species averages of residue traits from global databases) on SOC responses to OF, but not the change in crop trait values with farming systems. Instead, in the second part of the study, we specifically tested the trait-based mechanism of changes in crop residue decomposability with farming practices as a driver of SOC. To do that, we measured management-induced changes in SOC stocks and crop residue traits after long-term ecological intensive (e.g. OF) vs. CF across a European network, and tested the relationship between the two effect sizes.

2.1 | Global meta-analysis of OF vs. CF studies

We synthesized studies that evaluated the effects of OF vs. CF systems on top SOC stocks, top SOC sequestration rates and soil respiration using pairwise field comparisons located side by side under the same climatic and soil conditions. To do so, we used a published global meta-analysis comparing SOC in OF vs. CF (Gattinger et al., 2012), and complemented it with (1) 27 recent SOC studies representing a 36% increase in the total number of articles compared with Gattinger et al. (2012), (2) 25 soil respiration studies, (3) 28 net primary productivity, NPP studies and (4) leaf and root traits important for crop residue decomposition (e.g. N concentration). Two literature searches were conducted in the ISI Web of Knowledge, one for soil

respiration studies and one for SOC stocks and sequestration rates studies. We identified as CF those systems that rely on synthetic fertilizers and/or pesticides, and as OF those systems that avoided such chemical inputs (Gattinger et al., 2012). OF encompassed different practices, such as animal manure, reduced tillage, cover crops, crop rotation or green manure. All studies evaluated long-term responses to OF for at least three consecutive years, in agreement with European Union regulations (Council Regulation no. 834/2007). See García-Palacios (2018) for a list of the articles included in the meta-analyses and data used in this study, and Appendix S1 for details on data gathering, criteria for selecting studies and data extraction from articles.

Soil organic carbon stocks were extracted from papers or calculated using SOC concentration, bulk density and thickness of the soil layer. SOC sequestration rates were calculated as the ratio between the increase in SOC stocks since the beginning of the experiment and the study length. The average soil depth surveyed across studies was 0–18 cm, and ranged from 0 to 5 cm up to 0 to 90 cm. Thus, our results only refer to C stored in the top soil layers, which are affected by the drivers considered in this study, but with unknown implications for deeper SOC. A set of methodological and biological covariates were also gathered: land-use type (cereal, vegetable, orchard/viticulture and grassland), continent, latitude and longitude, mean annual temperature (MAT) and crop species (cultivar/variety information was not available from papers). When MAT was not provided in the paper, we obtained it from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

To account for variation in fertilization intensity across studies, we collected annual C and N external inputs ($\text{kg C or N ha}^{-1} \text{ year}^{-1}$) in both OF and CF systems. External C inputs (e.g. manure or compost) data were absent in many studies, and we used amendment-specific standard factors (e.g. C:N ratios) to calculate them from external N inputs, following in Gattinger et al. (2012). We calculated the live-stock stocking density of farms on the basis of manure N inputs as European livestock units per hectare, assuming that a dairy cow produces 77 kg N/year in the form of organic compounds (Eurostat, 2012). Farms with LMR (European livestock units per hectare ≤ 1) were identified as zero net input systems. Theoretically, the amount of fertilization supplied in these organic farms could have been produced at the respective farm. Importantly, this allowed us to assess whether OF increased SOC stocks, SOC sequestration and soil respiration compared with CF, even in organic farms with low manure rates, in principle representing closed systems. To account for differences in the amount of crop residue inputs between systems, we gathered data related with NPP from the same articles providing SOC data. Shoot dry matter (kg/ha) was preferred, as this variable is a better surrogate of crop residues quantity, but crop yield (kg/ha) was used instead when biomass measurements were not available.

In the SOC studies evaluating the same crop species in OF and CF plots, we compiled species averages of leaf N concentration (% of dry weight), LDMC (measured as the ratio of leaf dry mass to fresh mass), and fine-root C and N concentrations from the TRY (leaf traits, Kattge et al., 2011) and FRED (root traits, Iversen et al., 2017)

TABLE 1 Characteristics of the six European agricultural sites. OF and CF = organic and conventional farming

	Switzerland	Sweden	Portugal	The Netherlands	France Lautaret	France Vercors
Coordinates	47°30'N 7°33'E	55°37'N 13°24'E	38°42'N 8°19'W	51°32'N 5°51'E	45°02'N 6°20'E	45°07'N 5°31'E
Elevation (m a.s.l.)	312	34	420	25	1,800	1,000
MAT (°C)	9.7	7.2	16.5	10.2	3.5	7.2
MAP (mm)	791	696	1,483	766	956	1,093
Land-use type	Arable	Arable	Agro-forestry	Arable	Arable	Arable
Ecological intensification comparison	OF vs. CF	Extensive vs. intensive rotation	OF vs. CF	OF vs. CF	Grazing vs. Mowing	Low vs. high grazing and mowing
Management length (year)	37	5	20	10	50	50
Main crop species	<i>Triticum aestivum</i>	<i>Zea mays</i>	<i>Quercus ilex</i>	<i>Secale cereale</i> and <i>Avena sativa</i>	Annual grasses	Annual grasses
Species/community	Species	Species	Species	Species	Community	Community
Type of amendment a under EI	Manure	Synthetic fertilizer	Manure	Manure	Cow manure	Cow manure
N inputs in ecological ^a	88	60	N.A.	250	N.A.	30
C inputs in ecological ^a	890	606	N.A.	2,756	N.A.	N.A.
N inputs in conventional ^a	124	112	56	206	N.A.	70
C inputs in conventional ^a	520	0	0	1,048	N.A.	N.A.
Soil pH ^b	6.3	5.8	5.4	6.3	7.2	6.1
Soil clay (%) ^b	16	4	69	1	31	25
SOC stocks (Mg C/ha) ^b	93.3	20.3	16.3	45.8	41.4	33.7
Soil type ^c	Haplic Luvisol	Eutric Cambisol	Orthic Luvisols	Hortic Podzol	Dytric Cambisol	Histic-mesic Inceptisol

NA, non-available data.

^aAnnual external C and N inputs from fertilization are in kg N or C ha⁻¹ year⁻¹.

^bSoil physicochemistry are site means between conventional and ecological intensification ($n = 8, 10, 8, 16, 6$ and 16 in Switzerland, Sweden, Portugal, Netherlands, France Lautaret and France Vercors respectively).

^cFollowing FAO (2006).

global databases. We selected these traits because they strongly influence litter decomposition (Faucon et al., 2017), and can be used to characterize the crop species selected in each study based upon its resource-use strategy (Craine, 2009). To account for different biomass allocation strategies between crop species, we performed a literature search and gathered root: shoot (R:S) ratio, since these data could not be obtained from global databases. Data gathering for each crop species ended when we found eight papers to calculate the species average R:S ratio. References used to build the R:S ratio dataset can be found in Appendix S1.

2.2 | Network of European ecological intensification sites

We selected six field sites across different ecological intensification scenarios in Europe (Table 1). At each site, we identified pairwise comparisons of ecological intensive farming vs. CF systems. In 2015–2016, after long-term management (>10 years, except 5 years in the Swedish site), we sampled crop residues (green leaves and leaf

litter) and SOC stocks in the ecological intensive and conventional plots of each site. Since the six sites differed in type of land use, we collected leaf samples at the species level in the four sites with a single crop (e.g. *Triticum aestivum* in Switzerland), or at the community level when different species co-occurred (e.g. grasslands in France). The following traits were measured: litter concentrations of C, N, P, Mg, Ca, lignin and cellulose, C:N, lignin:N and lignin:P ratios, LCI (lignocellulose index = lignin/lignin + cellulose) and LDMC. We also measured surrogates of NPP at each site to assess whether the effects of changes in crop residue traits on SOC were still important after accounting for differences in the amount of crop residues between management systems. We measured wheat straw biomass in Switzerland (kg/ha), *Quercus* spp. leaf litter ground cover in Portugal (%), and above-ground biomass in the Netherlands and the two French sites (kg/ha). NPP data were not available in the Swedish site. After litter collection, top soil was sampled (0–20 cm depth). We measured soil organic matter concentration (% loss on ignition) from air-dried and sieved (2 mm) soil samples, and calculated SOC stocks. See Appendix S1 for more details on leaf and soil measurements.

2.3 | Statistical analyses

First, we explored whether OF increased soil respiration, top SOC stocks and top SOC sequestration rates compared with CF using Cohen's d as a metric of the effect size. Cohen's d is a unit-free estimate of the standardized mean difference between OF and CF that ranges from $-\infty$ to $+\infty$, and estimates the size of the impact and its direction. A positive Cohen's d indicates a higher value of the response variable in OF than in CF. To test whether Cohen's d significantly differed from zero, we assessed whether its bias-corrected 95%-bootstrap confidence interval (CI) overlapped zero, based on 999 iterations. To help the interpretation of the magnitude of the Cohen's d , we calculated the probability of superiority (or "common language effect size") following Ruscio (2008). This is the probability that a randomly sampled OF case study will have a higher observed response variable than a randomly sampled CF case study (Grissom & Kim, 2005). We also tested whether the set of methodological and biological covariates extracted from papers and global databases influenced the effect sizes using weighted random-effects models. The variables significantly related with the effect sizes were selected for further statistical analyses (see Table S1). See Appendix S1 for more details on the meta-analytical procedure. Cohen's d calculations and meta-analyses were conducted with MetaWin v2.1.

The main goal of the global meta-analysis was to evaluate the role of crop residue traits determining the crop resource-use strategy (conservation, low leaf and root N vs. acquisition, high leaf and root N) for SOC responses to OF. To do that, we selected studies using the same crop species in OF and CF systems and compare the relative importance of leaf N concentration, LDMC, crop R:S ratio, two metrics of fertilization intensity (annual C inputs in OF and annual N inputs in CF) and climate (MAT) on driving OF-effects (Cohen's d) on SOC stocks and sequestration rates. N inputs in OF were not included because they were used to calculate C inputs in most of the organic farms. C inputs in CF were not included as conventional treatments did not use organic amendments. We proposed a multivariate *a priori* model of hypothesized relationships within a path diagram (Figure S1), and tested it separately for SOC stocks and sequestration rates using structural equation modelling (SEM). All SEM analyses were performed with AMOS 23.0 (Arbuckle, 2014).

Lastly, we assessed whether the effects of ecological intensification on SOC stocks were driven by the responses of crop residue traits to management. We first evaluated the effects of ecological intensive farming vs. CF on SOC stocks using ANOVA within each site. We also calculated the effect size of ecological intensification on SOC stocks and on each crop residue trait using the response ratio. The response ratio of SOC stocks was calculated as $RR(SOC) = \ln(SOC_{eco}/SOC_{conv})$, where SOC_{eco} and SOC_{conv} are the SOC stocks in the ecological intensification and CF plots respectively. We then addressed whether $\ln RR(SOC \text{ stocks})$ across sites was explained by the effect size of ecological intensification on 11 crop residue traits ($\ln RR(\text{trait } i)$), where i is a particular trait (e.g. leaf litter N concentration), using general linear mixed

model analysis. We constructed all possible models combining all the crop residue traits, and selected the best-fitting models using the Akaike's information criterion (AIC_c). When multiple models were selected ($\Delta AIC_c < 4$), we used a model averaging approach to assess the relative contribution of each variable to this averaged model (Burnham & Anderson, 2002). These analyses were carried out using the PERMANOVA+ module for the PRIMER software (Clarke & Gorley, 2015).

3 | RESULTS

3.1 | OF-effects on soil respiration, SOC stocks and SOC sequestration rates

Our global meta-analysis showed positive OF-effects (standardized difference between OF and CF) in soil respiration (probability of superiority c. 84%), SOC stocks (c. 68%), and SOC sequestration rates (c. 91%; Figure 1). We found a significant relationship between OF-effects on both SOC stocks and SOC sequestration, and external C inputs (e.g. manure) applied under OF (Table S1) in the random-effect meta-analyses. Interestingly, the positive OF-effects shown in Figure 1 were still significant in organic farms with LMR. Leaf N concentration was positively related with OF-effects on SOC sequestration, and LDMC was negatively related with both SOC variables (Table S1). The positive OF-effects on both SOC variables were not related with the effect size on NPP (Figure S2).

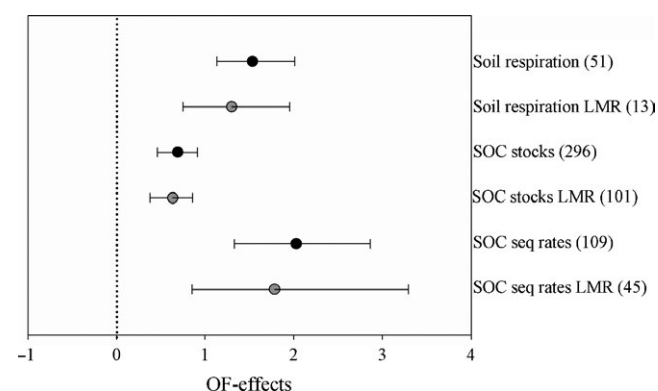
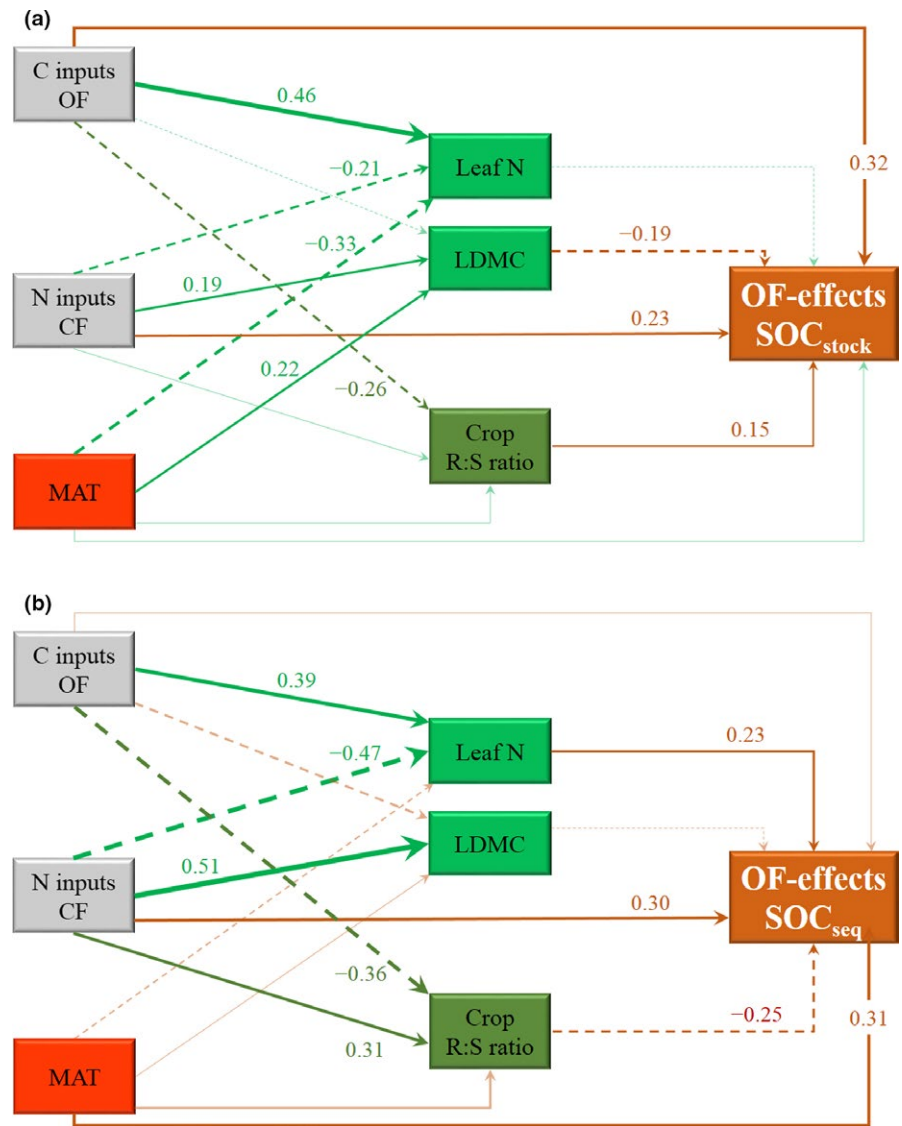


FIGURE 1 Effects of organic compared with conventional farming (OF-effects) on SOC stocks, SOC sequestration rates and soil respiration in a global meta-analysis. Data are standardized mean differences (Cohen's d) in the response variables between OF and CF across farms world-wide. Analyses were conducted separately for all case studies (black circles) and for comparisons where organic farms applied low manure rates (LMR, European livestock units per hectare ≤ 1 , grey circles). The bars around the means are bias-corrected 95%-bootstrap confidence intervals. If they do not overlap with zero, the means between OF and CF are significantly different from zero. Number of study cases are shown in brackets. The probability of superiority for each response variable was: soil respiration (86%), soil respiration LMR (82%), SOC stocks (69%), SOC stocks LMR (67%), SOC seq rates (92%) and SOC seq rates LMR (90%)

FIGURE 2 Structural equation models testing the importance of leaf N concentration and leaf-dry matter content (LDMC) on the effects of organic compared with conventional farming (OF-effects) on SOC stocks (a) and sequestration rates (b) in a global meta-analysis. The response variable in each model (in brown) represents the standardized mean differences (Cohen's *d*) in SOC stocks or sequestration between OF and CF across farms world-wide. The model also includes the influence of fertilization intensity (annual C and N inputs in a particular farming system, in grey), mean annual temperature (MAT, in red), and crop R:S ratio (in dark green). Continuous and dashed arrows are positive and negative relationships respectively. The widths of the arrows are proportional to the strength of the standardized path coefficients. Non-significant ($p > .05$) path coefficients are softened. Goodness-of-fit metrics for each model are: SOC stocks (Bootstrap $p = .251$; RMSEA = 0.035, $p = .476$; GFI = 0.997) and SOC sequestration (Bootstrap $p = .472$; RMSEA = 0.042, $p = .426$; GFI = 0.496). $R^2_{\text{SOCstocks}} = .23$, $R^2_{\text{SOCseq}} = 0.24$. LDMC = leaf-dry matter content [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



3.2 | Influence of crop resource economics traits on the effects of OF on SOC stocks and sequestration rates

When evaluating studies in the global meta-analysis using the same crop species in OF vs. CF, fertilization intensity and climate were the main drivers of the OF-effects on SOC_{stock} and SOC_{seq} (Figure 2). Greater OF-effects on SOC stocks were promoted by higher external C inputs in OF and higher N inputs in CF. OF-effects on SOC sequestration rates were positively affected by N inputs in CF and MAT. As hypothesized, crop traits also played a significant role. In farms where the crop species exhibited traits indicative of resource-acquisitive strategies (low LDMC; $r = -.19$, and high leaf N; $r = .23$), the increases in SOC stocks and sequestration rates in OF relative to CF were higher (Figure 2). When addressing whether these patterns also occurred for below-ground plant residues, we indeed found a positive relationship between resource-acquisitive strategies (low fine-root C; $r = .32$, and high fine-root N; $r = .26$) and OF-effects on SOC sequestration (Figure S3).

3.3 | Relationship between changes in crop residue traits and SOC stocks responses to ecological intensification

The comparison of ecological intensification vs. CF in the six European sites showed a general trend of increased SOC stocks under ecological intensification, but a contrasting result was found in the Netherlands site (Figure 3, Table S2). Fertilization N inputs at this site were larger in ecological (pig manure + pig slurry) than in conventional (pig slurry + inorganic fertilizer) plots (250 vs. 206 kg N ha⁻¹ year⁻¹, Table 1), and so was crop leaf litter N (Table S3). When relating shifts in crop residue traits and SOC stocks across sites, the best-fitting model included leaf litter N, cellulose and Mg, and explained 49% of the variability in the effect size of ecological intensification (lnRR) on SOC stocks (Table S4). lnRR leaf litter N had the greatest explanatory power ($R^2 = .35$, $p < .001$; Figure 4) and was included in all best-fitting models (Table S4). lnRR SOC stocks was inversely related to lnRR leaf litter N, indicating that increased SOC stocks in the ecological vs. conventional comparison

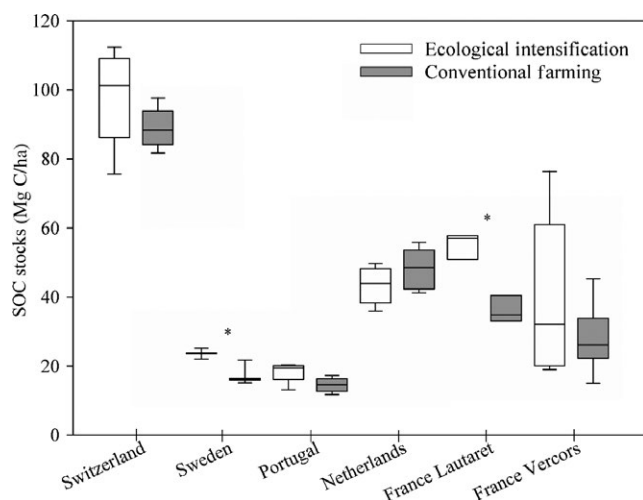


FIGURE 3 Effects of ecological intensification vs. conventional farming on SOC stocks across six European sites. Box plot represents medians, 5 and 95 percentiles, and the minimum and maximum of all of the data (sample size per site as in Table 1). Asterisks indicate significant differences between ecological intensification and conventional farming at $p < .05$. Detailed statistics can be found in Table S2. When present, the effects of other treatments (e.g. permanent vs. temporary grasslands in the France Vercors site) were pooled for clarity if not significant

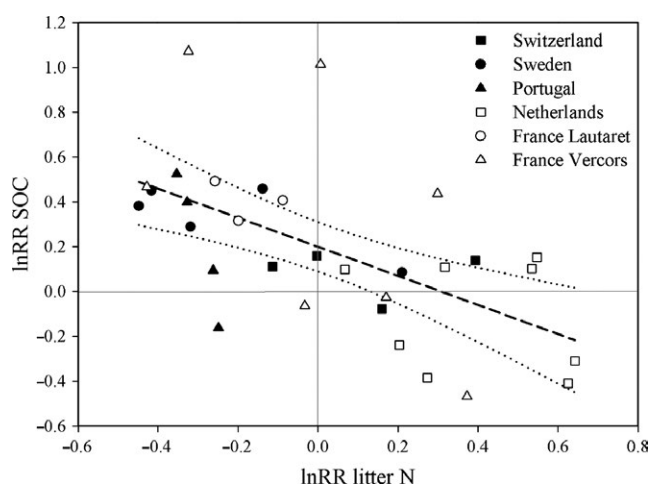


FIGURE 4 Relationship between the effect size of ecological intensification on crop leaf litter N concentration (lnRR litter N) and the effect size of ecological intensification on SOC stocks (lnRR SOC) across six European sites. lnRR is the ratio of ecological intensive to conventional farming. The model predicted-relationship (dashed line, $R^2 = .35$, $p < .001$) and the 95% confidence intervals are shown (dotted lines), $n = 31$. See Table S4 for model details

were driven by an opposite shift in crop leaf litter N concentrations (Figure 4).

4 | DISCUSSION

Soil management in agricultural lands via OF increases top SOC stocks compared to CF (Gattinger et al., 2012). These effects are

largely driven by the higher external C inputs that are applied via manure in organic farms (Kirchmann et al., 2016; Leifeld & Fuhrer, 2010). However, our results showed that the effects of OF on top SOC sequestration were still significant when comparing conventional practices with organic farms using LMR. In fact, the magnitude of the effect size (i.e. *probability of superiority*) on SOC stocks and sequestration rates was very similar between the studies comparing low manure rates in organic farming vs. CF, and the full dataset. Hence, the controversy about whether manure-driven increases in SOC storage can be considered sequestration or not (Leifeld & Fuhrer, 2010; Schlesinger, 2000) is not particularly relevant in our system comparison. We also controlled for the lower soil C inputs that organic farms may get via reduced crop yield (Ponisio et al., 2014; Seufert et al., 2012), and did not find any relationship between the effect size on NPP and that on SOC storage. We conclude that mechanisms other than the higher external C inputs and the lower amount of crop residues applied in OF, contribute to the enhanced SOC sequestration found when comparing OF with CF (average SOC sequestration rates of 0.26 and 0.02 Mg C ha⁻¹ year⁻¹ respectively). The results of our study indicate that crop residue (leaves and roots) traits are one of those mechanisms, which should be considered to predict the effects of farming practices on ecosystem services such as climate change mitigation.

Our global meta-analysis highlighted that, beyond the effects of fertilization intensity, crop resource economics traits (leaf N, LDMC, fine-root C and N) also play a significant role driving the effects of OF on SOC stocks and sequestration rates. The results of our cropland study is in line with patterns previously found in natural ecosystems, from tropical to boreal biomes (De Deyn, Bardgett, & Cornelissen, 2008). Interestingly, the pattern found for leaf traits also emerged when considering root traits, as resource-acquisitive crops (low C and high N concentration in fine roots) were related with higher OF-effects on SOC sequestration (Figure S3). This result and the positive correlation found between N concentration in green leaves and fine roots in our crop species ($r = .54$, $p = .032$) and in other studies (Birouste, Kazakou, Blanchard, & Roumet, 2012; Wang, Wang, Zhao, Yu, & He, 2017), suggest that root traits drive soil C responses to OF similarly to leaf traits. Differences in SOC stocks and sequestration rates are larger in farming systems using fast-growing monocultures (e.g. soybean, clover or barley), or polycultures with fast-growing species (e.g. grass/legume rotation). This supports our first hypothesis, stating that the enhanced SOC sequestration in OF vs. CF is strengthened when growing resource-acquisitive crops. Although most crop species are probably resource-acquisitive species (Donovan, Mason, Bowsher, Goolsby, & Ishibashi, 2014; Milla, Osborne, Turcotte, & Violle, 2015), high variation can be still found, particularly so among crops of different growth forms as in our meta-analysis (vegetables, grasses, grapevines or fruit trees, e.g. from 1% leaf N in *T. aestivum* to 4% in *Vigna unguiculata*).

Resource-acquiring species can be more plastic to changing soil nutrient availability levels than resource-conservative species (Crick & Grime, 1987; Siebenkäs et al., 2015; but see Valladares, Balaguer, Martinez-Ferri, Perez-Corona, & Manrique, 2002). Hence, these

crops might be more responsive to the high inorganic N fertilization rates applied under CF, increasing their residue decomposability (e.g. higher leaf litter N). Consequently, we expect larger soil C losses and lower soil C storage in conventional than in OF, due to higher crop residue decomposition rates and priming effects of labile residues (e.g. high leaf litter and fine-root N, low LDMC, and low fine-root C) on soil organic matter decay (Fanin, Fromin, & Bertrand, 2016). The positive relationship found between OF-effects on both SOC variables (estimated with Cohen's d as the difference in SOC between farming systems) and the rate of inorganic fertilization applied in CF (external N inputs, Figure 2), provides support to this hypothesized mechanism. The OF-effects on SOC increases with the higher inorganic N applied under CF, as such fertilization may also increase the chemical lability of crop residues.

Our second hypothesis stating the importance of changes in crop residue traits for SOC responses to OF was supported by the results found in the European-wide network of long-term agricultural sites. We found that the effects of ecological intensification practices (e.g. organic) on SOC stocks and on crop residue traits were related, as c. 50% of variation in $\ln\text{RR}$ SOC stocks was explained by $\ln\text{RR}$ crop residue traits (Figure 4). Importantly, increased SOC stocks in the ecological vs. conventional comparison was driven by sites (e.g. Portugal, Sweden and France Lautaret) where CF promoted higher crop leaf litter N concentration (negative $\ln\text{RR}$ leaf litter N in Figure 4), and thus larger residue decomposability and soil C losses. Intraspecific trait variation (Siefert et al., 2015), together with species replacement in sites with more than one crop (e.g. annual grasses in France, Table 1), may be driving the SOC responses found. Management-induced changes in leaf litter P concentration were not an important predictor of SOC (Table S4), which confronts with the important role for this nutrient in agroecosystems, where frequently limits crop production (Balemi & Negisho, 2012). Our results were consistent between management scenarios after accounting for differences in the quantity of crop residue inputs via NPP. $\ln\text{RR}$ NPP was not included in any of the best-fitting models (Table S5), whereas the selected crop residue quality trait, $\ln\text{RR}$ leaf litter N, still showed the greatest explanatory power ($R^2 = .33$, $p = .002$). Changes towards higher crop residue decomposability under CF is a new mechanism contributing to the higher SOC sequestration found in organic vs. CF.

Four questions remain open and are key topics for future research on land-use change effects on ecosystem services. First, root residues represent a substantial part of total crop residues (average root: shoot ratio of 0.43 in our meta-analyses) and consequently of soil C inputs (Kätterer et al., 2011). Although root traits were considered in our study, the low number of crop species with root traits data available in global databases such as TRY (Kattge et al., 2011) or FRED (Iversen et al., 2017) did not allow us to include them in our multivariate framework. Thus, we encourage future studies looking at the role of root residue traits for SOC responses to OF. Second, the link between farming systems and SOC sequestration via changes in crop residue traits is missing an important step: litter decomposition. However, the low number of studies comparing the effects of OF vs. CF on crop residue decomposition prevented us to carry out any

analysis. Instead, we used leaf and root traits as surrogates of crop residue decomposability, as they efficiently predict decomposition at the inter- (Cornwell et al., 2008) and intraspecific levels (Crutsinger, Sanders, & Classen, 2009). Therefore, studies measuring the dynamics of crop residue decomposition in farms subjected to contrasting management practices are particularly needed. Third, crop species present high intraspecific trait variability (Martin et al., 2017). Despite this, cultivar identity is not generally given in the studies comparing SOC in OF and CF, and global trait databases such as TRY or FRED do not include cultivar trait data. Functional traits of cultivars need to be included in future studies addressing the ecosystem-level implications of intraspecific trait variability in agroecosystems.

Lastly, soil decomposers are the ultimate actors in the litter decay process and may also play an important role determining the effects of farming practices on soil C storage. We found that soil respiration, a potential source of C losses, was larger in organic than in CF. Such microbial activity response may seem counterintuitive, considering increases in SOC stocks and sequestration. Nevertheless, lower soil microbial respiration per unit of microbial biomass (i.e. metabolic quotient) has been found under long-term OF in the DOK trial in Switzerland (Fließbach, Oberholzer, Gunst, & Mäder, 2007), together with shifts in soil microbial community composition towards slow growing fungi (Esperschütz, Gättinger, Mäder, Schlöter, & Fließbach, 2007). Similar changes in the physiology of the microbial community have been recently linked with increases in soil organic matter stabilization (Kallenbach, Frey, & Grandy, 2016). We hypothesize this same mechanism of altered soil microbial community composition to explain why labile litter was not related with higher SOC stabilization under CF, as predicted by the Microbial Efficiency-Matrix Stabilization framework (Cotrufo et al., 2013). Experimental tests of such framework have found that both labile and recalcitrant litter components foster soil organic matter stabilization (Cotrufo et al., 2015). In the light of our results, and those from Kallenbach et al. (2016) and Cotrufo et al. (2015), more research is needed to address whether the influence of farming practices on SOC storage is driven by changes in crop litter lability and/or in microbial carbon use efficiency and community composition.

4.1 | Synthesis and recommendations for land management

There is solid evidence that ecological intensification of agricultural lands via OF increases soil C stocks and sequestration rates, compared to CF. This occurs largely because higher external C inputs via manure are applied under OF (Kirchmann et al., 2016; Leifeld & Fuhrer, 2010). However, our study indicates that crop residue (leaves and roots) shifts in CF towards higher decomposability (higher N concentration) and soil C losses also modulate that response. Importantly, our results were found across wide geographical regions (Europe, North America and Asia) and land-use types (from cereal to vegetable and orchards), and was consistent after accounting for differences in NPP between land management scenarios. International efforts such as the 4 per 1,000 Initiative encourage SOC sequestration in

croplands to mitigate climate change and support livelihoods by enhancing long-term soil quality (Minasny et al., 2017). In this context, the choice of crop species, and more importantly their resource economics traits, should be taken into consideration (Faucon et al., 2017). Our results highlight the importance of using a trait-based framework when addressing whether the ecological intensification of agricultural systems will maintain food provision while enhancing SOC sequestration.

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AUTHORS' CONTRIBUTIONS

P.G.P., A.G. and R.M. designed the study. P.G.P., A.G., A.M., H.C., N.L., F.R., M.L. and S.S. gathered data for the global meta-analyses. All authors but P.G.P., A.M., K.H., S.L. and R.M. conducted field work in the six European agricultural sites. P.G.P. and R.M. coordinated the analysis and writing of the manuscript, and all authors contributed to writing a final version of the manuscript.

DATA ACCESSIBILITY

Data available from the Figshare Digital Repository <https://doi.org/10.6084/m9.figshare.5659048.v1> (García-Palacios, 2018).

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