The complementarity hypothesis reversed : Root trait similarity in species mixtures promotes soil organic carbon in agroecosystems

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The complementarity hypothesis reversed: Root trait similarity in species mixtures promotes soil organic carbon in agroecosystems

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ABSTRACT

Increasing species diversity in agroecosystems appears as a promising venue to restore or increase soil organic carbon (SOC). It has been hypothesized that this effect is largely driven by the greater variation of root systems in plant mixtures, which may promote complementarity. However, the magnitude of this synergistic effect and the root traits driving it are uncertain. The objective of this study is to determine which root trait composition optimizes plant mixture effects on SOC. To do so, we combined a global meta-analysis of 407 paired SOC content observations under mixed species vs. monocultures across grasslands and croplands, and root traits extracted from the GRooT database. The results show that high root mycorrhizal colonization and root tissue density for the species in the mixture have higher positive effects on SOC content. Our analysis also indicates that combining species with high similarity for these traits represents a preferable trait combination to increase SOC with plant mixtures, challenging the current paradigm around plant trait complementarity effects. We observed that the positive response of SOC content to species mixtures was tightly associated with increased root biomass and soil microbial biomass carbon, indicating an important contribution of belowground and microbial residuals to SOC. Additionally, SOC enhancements by plant species mixtures were more likely to be realized in regions with high precipitation, clay-rich soils, and when legumes are present. Our meta-analysis lays out a root-trait framework to enhance SOC with plant mixtures, which can serve as a guide for species and variety selection for field experiments and on-farm applications.

1. Introduction

Terrestrial ecosystems globally hold approximately 2100 Gt of carbon (Schulze, 2006), of which more than two-thirds are stored in soils (Amundson, 2001). However, current rapid changes such as global warming, intensive land management practices, and the loss of plant diversity, promote carbon loss and can switch soils from sinks to sources of atmospheric CO_2 (van Groenigen et al., 2014; Crowther et al., 2016; Hicks Pries et al., 2017). Therefore, increasing soil organic carbon (SOC) storage is crucial for climate change mitigation, and for the delivery of other key ecosystem services, such as reducing erosion, sustaining soil fertility, and improving agricultural productivity (Lal, 2015; Bradford et al., 2019). Over the past few years, compelling evidence from biodiversity-manipulation experiments (Lange et al., 2015; Yang et al., 2019), observations (Chen et al., 2018, 2023), and meta-analyses (Chen et al., 2019; Jian et al., 2020) have shed light on the potential of using plant mixtures instead of monocultures to increase SOC across managed ecosystems. Yet, how to design such plant mixtures to maximize SOC

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remains uncertain.

Trait-based approaches in plant ecology have allowed for a mechanistic understanding of how species diversity influences SOC, primarily in natural ecosystems (Garnier et al., 2004; De Deyn et al., 2008). Although aboveground plant traits have been commonly used due to greater data availability for a large number of species (Chen and Chen, 2021), there is now a growing recognition of the pivotal role of belowground root traits in shaping soil carbon cycling (Bardgett et al., 2014). Roots are a major source of litter input, which can represent up to 70% of total plant biomass in grassland ecosystems (Poorter et al., 2012). Moreover, for annual and herbaceous plants, root-derived carbon is usually retained in soils much more efficiently than above-ground inputs of leaves and needles (Rasse et al., 2005). Therefore, root traits can be key to predicting plant effects on SOC (Poirier et al., 2018; Freschet et al., 2021).

Root traits such as root nitrogen (N), root diameter, specific root length, and root tissue density can be categorized according to the one-dimensional root economic spectrum, depicting a trade-off between fast resource acquisition and resource conservation (Comas and Eissenstat, 2009; Weemstra et al., 2016). These traits are tightly associated with SOC dynamics by stabilization and destabilization processes (Poirier et al., 2018). For example, plants with high root N concentration can promote microbial root decomposition, leading to stable SOC formation through interactions with soil mineral surfaces (Cotrufo et al., 2019). Recent work has further broadened the root economics space by incorporating a fungal collaboration spectrum, highlighting the crucial role of mycorrhizal fungi (Bergmann et al., 2020). The capacity to establish mutualistic symbiotic relationships with mycorrhizal fungi is an important regulator for SOC turnover because such symbiosis not only increases plant productivity through the enhanced acquisition of limited resources, but also contributes to recalcitrant SOC pools via mycorrhizal fungi residues (Langley et al., 2006; Clemmensen et al., 2015). These important associations primarily established with individual species, suggest that selecting plant species based on root traits can be a pathway to guide the design of optimum plant mixtures for SOC storage in agroecosystems.

Numerous studies suggest that plant diversity generally increases SOC through complementary effects, driven by resource partitioning/niche differentiation, and biotic or abiotic facilitation among constituent species in multi-species mixtures (Fornara and Tilman, 2008; De Deyn et al., 2012; Lange et al., 2015; Prommer et al., 2020). For example, selecting species with different root depths in a mixture can promote a more efficient utilization of soil resources, thereby enhancing SOC sequestration (Homulle et al., 2021). In natural ecosystems, increasing plant species richness is often linked to maximum complementarity effects (Cardinale et al., 2007), but combining species with divergent traits seems to be more important than plant species richness *per se* (Hooper et al., 2005; Paquette and Messier, 2011). This indicates that combining plant species with high dissimilarity in trait values could be a way to promote SOC increases in managed systems through directly or indirectly regulating primary productivity, belowground carbon allocation, and carbon loss. Agroecosystems, in particular, have large potential for SOC enhancement through optimizing species combinations (Yan et al., 2022). A key challenge is to identify what traits should be diversified, as indicated by the inter-specific trait variation among mixed species. It also remains largely unknown which traits should have a high specific average value in the mixtures (represented by the community-weighted mean (CWM) trait values) in order to increase SOC. Addressing these two knowledge gaps would provide critical insights into how specific root trait combinations influence SOC levels and enhance the response of SOC to plant mixtures.

A comprehensive mechanistic understanding of the links between root traits and SOC in species mixtures is missing, despite holding promise for designing species combinations strategically to progress towards climate neutrality. In this study, we addressed this knowledge gap using a meta-analysis approach by compiling data from 64 studies conducted in grasslands and croplands. We aimed to answer the following questions: (1) can we predict the effect of plant mixtures on SOC based on the root traits of the species in the mixtures? If so, (2) does maximizing root trait variation of the mixed species (i.e., the inter-specific trait variation among combined species) promote SOC? Our main hypotheses were that root traits would explain a significant proportion of the variation in SOC content induced by species mixtures, and that larger root dissimilarity between species in a mixture would increase SOC due to niche differentiation.

2. Materials and methods

2.1. Data collection

Publications prior to December 2024 that investigated the effects of plant diversity and/or plant mixtures on SOC content, SOC storage, and soil microbial biomass carbon (MBC) were acquired using the ISI Web of Science and Google Scholar with the search terms: soil carbon OR soil organic carbon OR total organic carbon OR microbial biomass carbon AND diversity OR richness OR mixture OR intercropping. Although soil MBC only constitutes approximately 1–4% of the total SOC, it plays a critical role in controlling both SOC loss and sequestration (Janssens et al., 2010; Cotrufo et al., 2015; Lange et al., 2015). Therefore, it is a well-studied parameter that serves as a proxy for the active microbial community and its contributions to soil processes, and has been used in other similar meta-analyses (e.g., Chen et al., 2019). We also searched for relevant references within these publications. The following criteria were employed to select appropriate studies: (1) they had at least one species mixture treatment and the corresponding monocultures (four studies were also included which only had one corresponding monoculture); (2) they at least reported one of SOC content, SOC storage, and soil MBC response to plant mixtures (one species response vs. multiple species response, all grown during the same period); (3) we only focused on field experiments in cropland and grassland ecosystems, excluding indoor and pot experiments. Finally, 64 studies were included in our dataset (Fig. 1a and Text S1), of which 43 studies reported SOC content, 17 studies reported SOC storage, and 34 studies reported MBC. The flowchart of preferred reporting items for systematic reviews and meta-analyses (PRISMA) can be found in the Supplementary Information (Fig. S1).

The means, number of replications, and corresponding standard deviation (SD) of SOC content, SOC storage (also calculated from SOC content and soil bulk density of each layer), and soil MBC were recorded from each study. Other plant and soil variables of importance for carbon dynamics were also included in our dataset (e.g., soil mineral N, soil available phosphorus (P), soil respiration, and above- and below-ground plant biomass). Additionally, we recorded the species richness (number of plant species), legume presence (legume vs. non-legume), soil depth, ecosystem types (i.e., grasslands and croplands), latitude, longitude, clay content, mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm) and stand age (number of years since the establishment of the experiments) from the publications. For the missing MAT and MAP, we obtained them from the WorldClim 2 database (Fick and Hijmans, 2017). Missing information on soil texture was extracted from the SoilGrids (Hengl et al., 2017).

2.2. Meta-analysis

We assessed the effect of plant mixtures on the individual variables by calculating the natural logarithmic response ratio (RR) of the mixture treatment relative to each monoculture treatment: $RR = \ln (X_t/X_c)$, where X_c is the control mean (i.e., data from each monoculture) and X_t is the treatment mean (i.e., data from species mixtures plots) (Hedges et al., 1999). Effect sizes and variances were calculated using the *escalc* function from the R package *metafor* (Viechtbauer, 2010). For those studies which did not report SD, we estimated them using the average

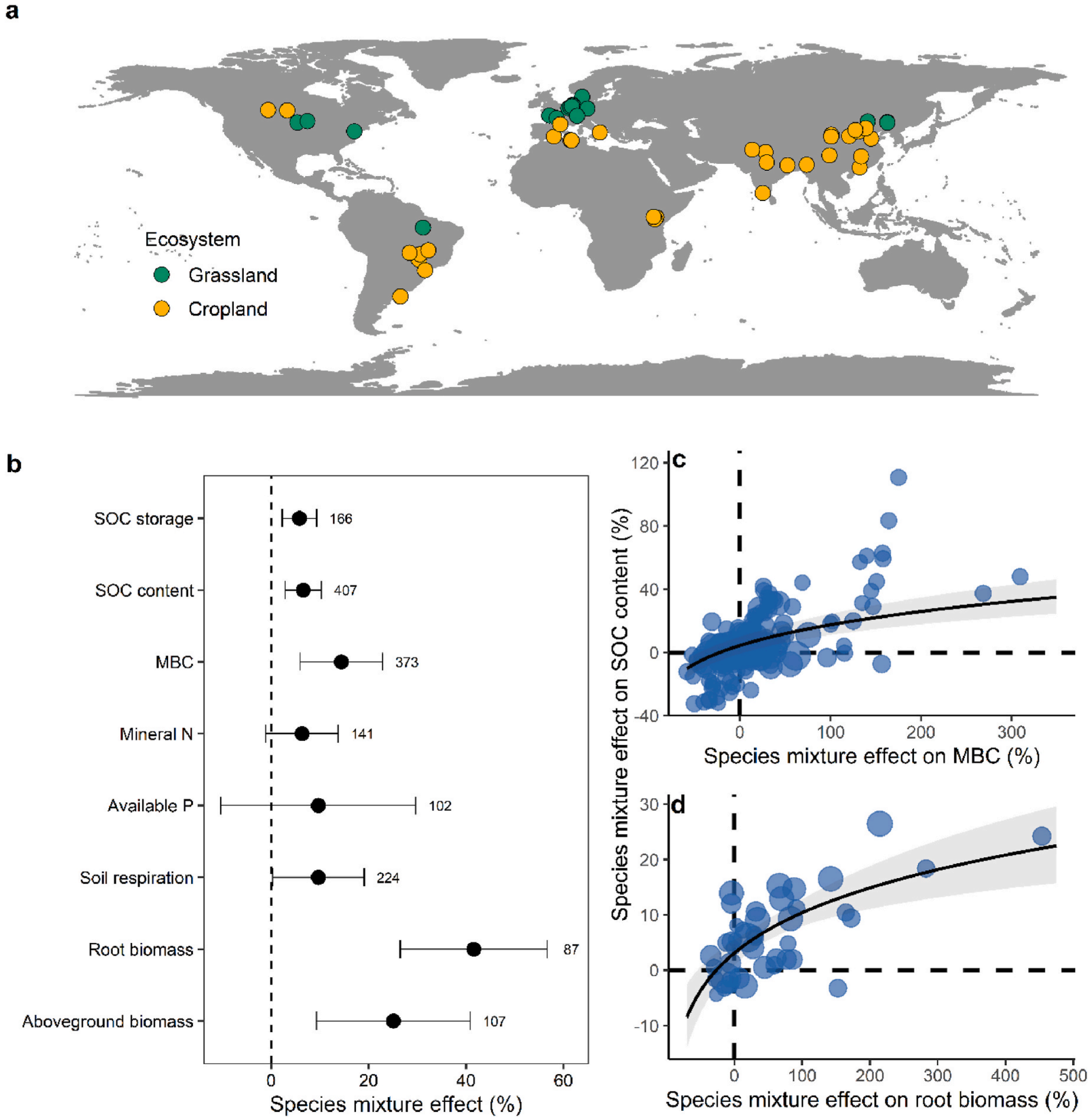

Fig. 1. Global distribution of the studies used in this meta-analysis (a), overall effect of species mixtures on multiple soil and plant variables of importance for carbon dynamics (b), and relationship between species mixtures effects on SOC content and on MBC (c), as well as on root biomass (d). The points in (b) are the mean value of response ratios (RR) expressed as percentage changes, and error bars represent 95% confidence intervals. The numbers at the right side of the error bars represent the number of observations. The regression line in (c) and (d) is based on mixed-effects meta-regression models and 95% confidence intervals ($R^2 = 0.39$, $P < 0.001$, n = 189 for (c); $R^2 = 0.57$, $P < 0.001$, n = 42 for (d)). Points in (c) and (d) represent the individual observations in the meta-analysis, with point sizes proportional to model weights.

coefficient of variation (CV) across the dataset (SD = CV × mean; van Groenigen et al., 2017). The final dataset included 407 observations for SOC content, 166 observations for SOC storage, and 373 observations for MBC. The mean effect sizes were estimated in a weighted, mixed-effects model using the *rma.mv* function in the *metafor* package (Viechtbauer, 2010), where RR was weighted by the inverse of its variance. If the 95% confidence intervals for the RR of one variable overlapped with zero, then it was considered as non-significant response to plant mixtures. For most studies, there was one mixture treatment and multiple control treatments (i.e., one from each monoculture of the mixed species). For several studies, there was only one control (i.e., one monoculture), but multiple mixture treatments due to multiple levels of species richness levels (e.g., 3, 6, 9 species). This means we calculated multiple RRs from one complete mixture combination; we accounted for this non-independence of observations using “study” and “observation” as random factor (van Groenigen et al., 2017). The mean effect size was transformed into percentage change calculated as ($e^{RR} - 1$) × 100% for the sake of interpretation.

2.3. Root traits extraction, imputation, and analysis

For each plant species in our dataset, we extracted several primary mean fine-root traits from the Global Root Trait (GRooT) database (Guerrero-Ramírez et al., 2020), focusing on root diameter, specific root length, root tissue density, root N concentration, and root arbuscular mycorrhizal fungi colonization (there were no woody plant species with ectomycorrhiza included amongst the crops), which are central components of the root economics spectrum and of plant effects on SOC (Poirier et al., 2018; Kong et al., 2019; Bergmann et al., 2020). There were 17 studies excluded from the root traits extraction process because these studies only reported the species richness without providing detailed species identity or composition information. For the species of our dataset, missing values of root diameter, root tissue density, root N concentration, specific root length, and root mycorrhizal colonization from the GRooT database accounted for 13.0%, 15.3%, 26.6%, 14.3% and 7.3%, respectively. To ensure there were no missing trait values, we conducted missing trait imputation following Carmona et al. (2021). We first retained the species which at least had one root trait value, and then imputed other trait values by using the *missForest* package. Our imputation process integrated the evolutionary relationships among species by introducing the initial five phylogenetic eigenvectors into the imputation matrix. The phylogenetic tree was constructed using the R package *V.Phylomaker*, utilizing the GBOTB phylogeny as the foundation (Carmona et al., 2021). Subsequently, for each trait we calculated the inter-specific root trait variation in each mixture (as well as the CWM), based on the trait value of each species in the mixtures and its proportional abundance (Kraft et al., 2014; Roscher et al., 2018), to explore to what extent maximizing root trait diversity drives the potential changes in SOC. For mixtures composed of three or more species, inter-species variation in root traits was calculated as the mean pairwise absolute trait variation among species.

2.4. *Variable importance*

We used a random-meta-forest approach with the *metaForest* package to identify potentially relevant moderators predicting the effects of plant mixtures on SOC content. We primarily focused our analysis on the SOC content instead of SOC storage due to the larger data availability (407 observations vs. 166 observations in total, and for the random forest analysis which requires simultaneously matching the data with root traits, the available observations were 238 vs. 103). This approach is based on machine learning random forest algorithms and incorporates the variance and weight of each study as in classic meta-analysis, which is robust to overfitting, allows for numerous predictors, and accounts for nonlinear relationships (Terrer et al., 2021). Accordingly, the shape of the relationship does not constrain the predictive capacity of a given variable. We first run the meta-forest model incorporating the five CWMs for the root traits and the inter-specific root trait variation by using the R package *metaForest* (van Lissa, 2020). We found that root trait variation was more important than CWMs for all the root traits, and therefore, our final model only included root trait variation. Then, 13 potential predictors were included in the meta-forest model where nine predictors were related to plant traits and plant management (root diameter variation, root tissue density variation, root N concentration variation, root mycorrhizal colonization variation, specific root length variation, stand age, species richness, ecosystem types, and legume presence), and four predictors were related to soil and environmental factors (MAT, MAP, clay content, and absolute latitude). A full model with all 13 predictors incorporated was ran initially, followed by two separate models: one focusing on plant traits and management predictors, and the other on soil and climatic predictors. We performed variable pre-selection with 10,000 iterations and 100 replications, using a recursive algorithm in the preselect function from *metafor*. Predictors with negative variable importance were dropped using the *preselect_vars* function, while predictors with positive predictive performance were maintained. Parameters of the meta-forest model were further optimized using the *train* function from the *caret* package (Kuhn, 2008), and calculated 10-fold cross validated R^2 by using 75% of the data as training data and 25% as validation data. The relative importance of each predictor was derived from the optimized model. Partial dependence plots were produced that visualize the association of important moderators with the effect size, while accounting for the average effect of all other moderators.

To further clarify the significance of each predictor's effect, we used the *rma.mv* function to run another mixed-effects meta-regression model selection procedure for each of the most important predictors identified by random forest analysis. We fitted linear, unimodal, and logarithmic meta-regressions to identify the best model describing the relationships between the most important predictors and LnRR, based on the Akaike information criterion (AIC); the model with lower AIC was retained. The *P* value for the individual relationship between root traits variation and SOC content response to plant mixtures was obtained by the *ANOVA* function.

3. Results

3.1. *The effects of plant mixtures on plant and soil variables*

Averaged across all studies, plant species mixtures significantly increased SOC storage by 5.8% (95% confidence interval (CI), 2.2%–9.6%), SOC content by 6.6% (CI: 2.7–10.6%), and soil MBC by 14.8% (CI: 5.3–24.3%) (Fig. 1b). Moreover, soil respiration (mean = 9.7%; CI: 0.3–19.1%), root biomass (41.6%; CI: 26.5–56.6%), and aboveground biomass (25.1%; CI: 9.3–40.8%) also showed a significantly positive response to species mixtures, while soil mineral N (6.3%; CI: 1.2–13.7%) and soil available P (9.7%; CI: 10.3–29.7%) showed a positive trend (Fig. 1b). Meta-regression analysis revealed that the response of SOC content to species mixtures was positively correlated with the response of soil MBC ($P < 0.001$, $R^2 = 0.39$, Fig. 1c) and the response of root biomass ($P < 0.001$, $R^2 = 0.57$, Fig. 1d). Additionally, the effect of species mixtures on SOC content was more pronounced in the topsoil (<20 cm) compared to the subsoil (>20 cm) ($P = 0.036$, Fig. S2).

3.2. *Key predictors of SOC content response to plant mixtures*

Our random meta-forest model revealed that inter-specific variations in root traits were more important predictors of the response of SOC content to species mixtures compared to stand age, presence of legumes, ecosystem types, and species richness (Fig. 2a). Among the root traits assessed in species mixtures, root mycorrhizal colonization variation and root tissue density variation were the two most powerful predictors (Fig. 2a). Root N concentration variation was also a good predictor, although explaining a lower proportion of the variation. Furthermore, meta-regression analysis and partial dependence plots showed that the responses of SOC content to plant species mixtures shifted from positive to negative with increasing root tissue density variation (i.e., when the root tissue density of the species in the mixtures differed largely) ($P = 0.139$, Fig. 3a and Fig. S3), root mycorrhizal colonization variation ($P = 0.110$, Fig. 3b and Fig. S3), and root N concentration variation ($P = 0.030$, Fig. 3c and Fig. S3), whereas intermediate specific root length variation was associated with the lowest LnRR ($P = 0.030$, Fig. S4a). Generally, the cross-validated R^2 of our random forest models was relatively high ($R^2 = 0.35$–0.41), while the *P*-values of individual moderators were sometimes high. Across monocultures and species mixtures, the observed SOC content increased with increasing CWM of root tissue density ($P < 0.001$); the associations with CWM of root mycorrhizal colonization ($P = 0.239$) and root N concentration ($P = 0.434$) were less clear (Fig. S5). Among the climatic, soil and geographic moderators tested, MAP and soil texture (clay content) had the greatest influence on SOC content response to species mixtures (Fig. 2b and Fig. S6). When combining all 13 predictors into one model, the most important predictors were largely similar (i.e., root mycorrhizal colonization variation, root tissue density variation, and clay content, Fig. S7) but the model performance was lower (cross-validated R^2 was 0.348 for plant traits and management predictors, and 0.411 for soil and climatic predictors vs. 0.311 for the full model).

The positive species mixture effects on the tested variables differed among ecosystem types and plant functional groups (Fig. 4). Specifically, we found that SOC storage, MBC, mineral N, soil respiration, and aboveground biomass, generally had a greater response to species mixtures in grasslands than in croplands (Fig. 4a). Legume-based species mixtures also showed a larger response relative to non-legume mixtures

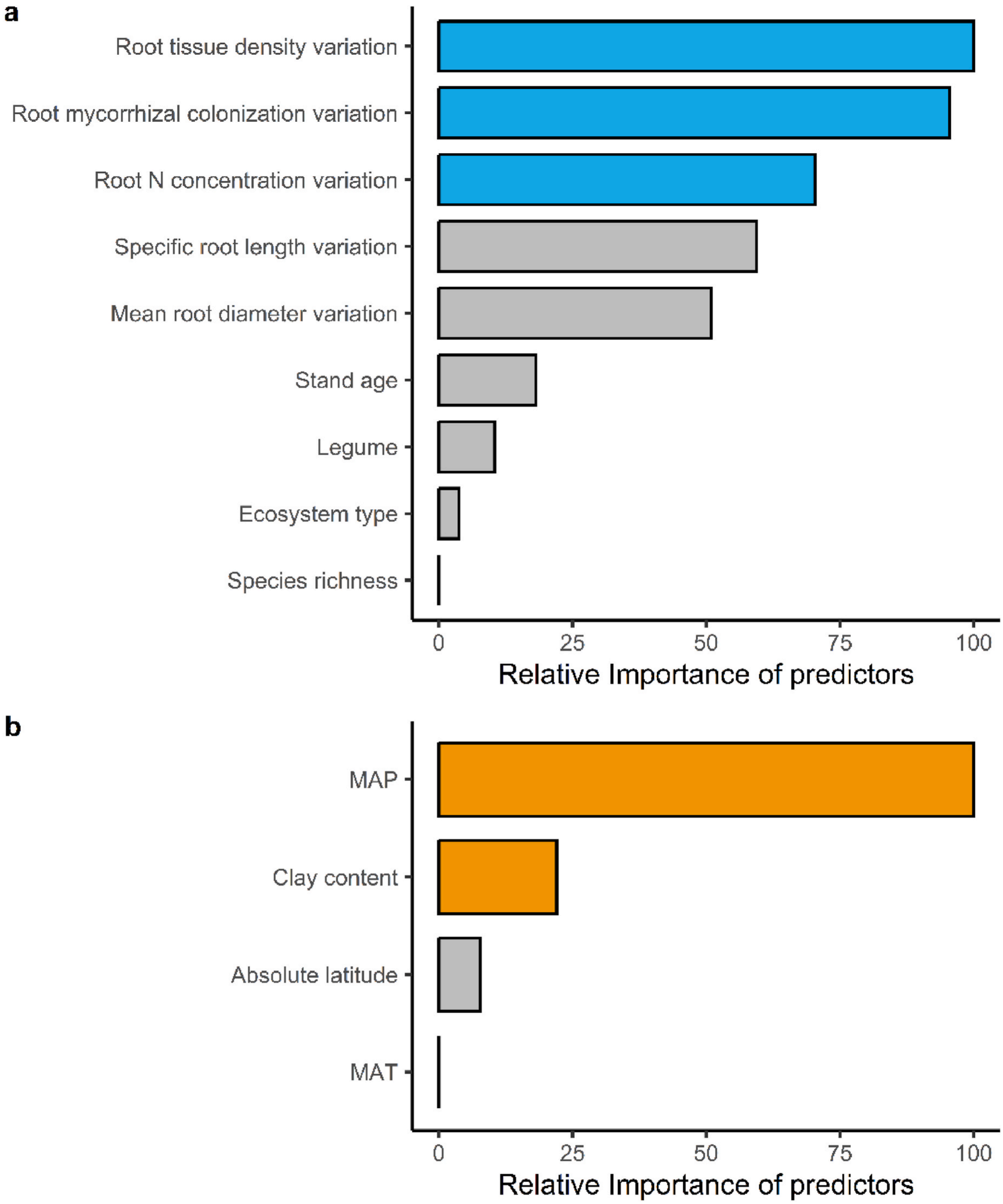

Fig. 2. The most important predictors for the effects of species mixtures on SOC content (LnRR). (a) Relative importance of nine predictors within inter-specific root traits variation and management factors (n = 238, cross-validated $R^2 = 0.348$), and (b) relative importance of four predictors within climatic, soil and geographic factors (n = 399, cross-validated $R^2 = 0.413$). The colored bars represent the most important predictors.

for SOC storage, MBC, mineral N, available P, root biomass, and aboveground biomass (Fig. 4b).

4. Discussion

4.1. Root traits and SOC content in species mixtures

Our meta-analysis shows that implementing species mixtures can increase SOC content in agroecosystems. The observed increase in SOC was tightly associated with increases in MBC and root biomass (Fig. 1c and d). Species mixtures can promote SOC directly through higher plant carbon inputs, as indicated by the strong increases observed in above- and below-ground biomass in species mixtures compared to single species (Fig. 1b and d), and indirectly through stimulating microbial growth, turnover, biomass, and necromass stabilization on soil minerals (Lange et al., 2015; Liang et al., 2017; Prommer et al., 2020). Microbial residuals are a critical component of SOC, regulating the formation of mineral-associated carbon and thereby contributing to long-term carbon stabilization (Cotrufo et al., 2019; Liang et al., 2019). We also observed that plant species mixtures can accelerate SOC losses by stimulating soil

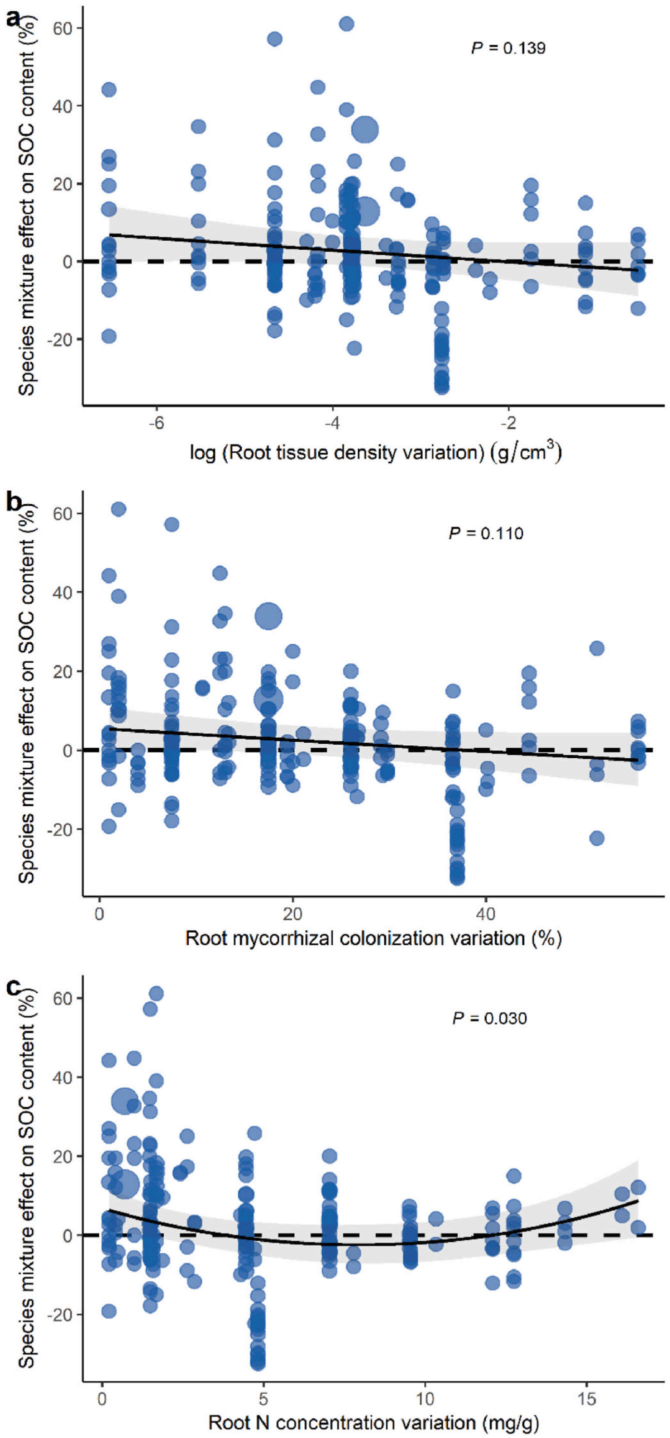

Fig. 3. Meta-analytic scatterplots of the most important factors controlling the effect of species mixtures on SOC content (identified by the random-meta-forest approach). (a) Inter-specific variation in root tissue density (g/cm^3), (b) inter-specific variation in root mycorrhizal colonization (%), and (c) inter-specific variation in root N concentration (mg/g).

respiration (Fig. 1b), which could partially offset increases in SOC. However, this effect seems to be weaker than that on carbon inputs and microbial growth, or driven by autotrophic root respiration, as species mixtures induced more abundant root systems, thus resulting in an overall increase in SOC content.

In agreement with our first hypothesis, our results demonstrate that root traits account for a significant proportion of the variation in the response of SOC content to species mixtures. We identified possible root trait combinations that optimize SOC content benefits of species mixtures (Figs. 2 and 3, S5). In contrast to our second hypothesis, and challenging current paradigms around plant diversity, wherein high diversity promotes SOC through niche differentiation (Barry et al., 2019), we found that low variation of certain traits in plant mixtures may be beneficial for promoting SOC content. In particular, similar levels of root mycorrhizal colonization and root tissue density represent preferable trait combinations to increase SOC with plant mixtures (Fig. 3). High values of root mycorrhizal colonization and root tissue density were also associated with higher SOC content both in monocultures and mixtures (Fig. S5). We propose several hypotheses to explain this unexpected effect of trait diversity on SOC. First, species with similar and higher colonization could increase the inoculum (both hyphae and spores) for their coexisting species (Chen et al., 2005), and such positive species interactions could improve nutrient acquisition, belowground carbon allocation (De Deyn et al., 2012), and plant growth (Chen et al., 2022). Second, symbiosis with mycorrhizae is positively related with the physical protection of soil organic matter (Poirier et al., 2018), because the physical enmeshment of soil particles by extensive networks of hyphae facilitates the formation of stable aggregates, promoting soil organic matter stabilization (Hallett et al., 2009). In parallel, large networks of hyphae with similar and high root mycorrhizal colonization in mixed species can reduce soil carbon loss by immobilizing carbon in their mycelium and by extending root lifespan (Langley et al., 2006; Rillig and Mummey, 2006). Third, high mycorrhizal colonization can increase the net rhizodeposition of the colonized root (Zhou et al., 2020), and colonized roots are more recalcitrant than non-colonized roots (Fogel, 1980), facilitating SOC accumulation. Overall, our results highlight the critical role of fungi in plant mixtures.

Augmented SOC can also be achieved when combining species with similar and high root tissue density values. High root tissue density can increase SOC by decreasing decomposition rates, and this applies to both monocultures and species mixtures. This is because root tissue density determines the toughness and tensile strength of the litter, and consequently, high root tissue density extends the time required for microbial penetration (Makita et al., 2015). Furthermore, given the differences in decomposition rates between roots of high and low tissue density, the rapid decomposition of low root tissue density roots releases labile carbon that stimulates microbial activity and accelerates the breakdown of more recalcitrant high root tissue density root material, which ultimately enhances SOC loss. In contrast, when species have similar root tissue density values, this priming effect could be significantly reduced, thereby minimizing SOC depletion.

The two main root traits identified in our study as predictors of SOC content in plant mixtures, root tissue density and root mycorrhizal colonization, capture the two dominant dimensions of the recently developed root economics space, proposing "conservation" and "collaboration" gradients (Bergmann et al., 2020). Although our model including multiple root traits explained a relatively high proportion of the total variation in the effects of species mixtures on SOC content, individual root traits accounted for only a limited portion of this variation, and the individual relationships between root traits and SOC content were mostly not significant. This indicates that the two dominant dimensions of root traits should be simultaneously considered when selecting species mixtures for SOC accrual, highlighting the importance of considering a range of root functional traits rather than relying on single-trait species selections. Such an integrative approach may allow to maximize both the quantity and quality of root-derived carbon inputs, as well as optimize microbial interactions and nutrient cycling.

4.2. *Contextualising the importance of mixtures for SOC content*

We found that the response of SOC content and MBC to species mixtures tended to be greater in grasslands than in croplands (Fig. 4a), which is consistent with the results of Chen et al. (2019). This could be

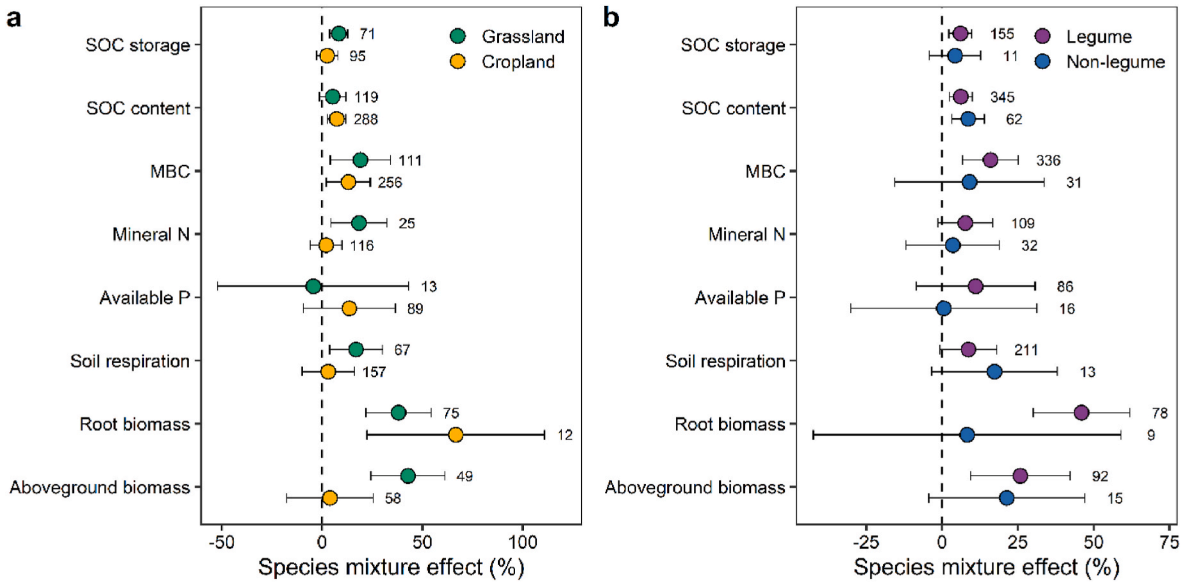

Fig. 4. Species mixture effects on multiple soil and plant variables of importance for carbon dynamics among ecosystem types (a), and in the presence/absence of legumes (b). The points are the mean value of response ratios (RR) which were quantified as percent changes, and error bars represent 95% confidence intervals. The numbers at the right side of the error bars represent the number of observations.

due to a difference in experimental duration between the two types of agroecosystems. The average experimental duration of grasslands and croplands is 5.8 and 2.4 years in our dataset, respectively. The longer experimental duration would lead to a stronger mixture effect, as biodiversity impacts on SOC strengthen over time (Fornara and Tilman, 2008; Lange et al., 2015). Additionally, perennial plants in grasslands have higher root biomass and net rhizodeposition than annual crops, making it easier for mixtures to elicit an effect on SOC (Pausch and Kuzyakov, 2018). Another explanation is that grassland studies typically had a higher species richness compared to croplands, which could further increase SOC (Cong et al., 2014; Xu et al., 2020), although we found that species richness was not as important in agroecosystems for SOC compared to other predictors. For example, the most studied grassland sites, i.e., the Jena and Minnesota biodiversity-grassland experiments, included communities with up to 60 species, whereas the richness level for the cropland dataset generally consisted of 2 or 3 species.

Legumes are generally believed to increase SOC in species mixtures (Duchene et al., 2017; Fornara and Tilman, 2008), which was partially supported by our results. The positive effects of legumes could be associated with their high root N concentration due to the symbiotic association between legume roots and N_2-fixing bacteria (Freschet et al., 2017). The N-rich roots of legumes allow for rapid decomposition, which can promote fast and efficient MBC buildup (Fig. 4b) (Martins and Angers, 2015; Liang et al., 2017). Our study also showed that legume-based communities increase plant productivity and soil mineral N availability (Fig. 4b), which can contribute to soil carbon inputs and decrease nutrient limitations for soil carbon storage. However, although the presence of legumes significantly increased SOC storage, SOC content, and MBC, and mixtures without legumes did not increase significantly these carbon pools, the overall effect of legumes was within the range of that seen by non-legume systems (Fig. 4b). A possible explanation could be that the number of comparisons between with legumes and without was strongly biased towards with legumes, giving stronger statistical power to the mixtures with legumes and therefore a higher likeliness of detecting a significant effect. This potential bias induced by the large variation in number of observations for this comparison precludes us from drawing strong conclusions regarding differences between mixtures with or without legumes. Future research leveraging larger datasets and long-term experiments is crucial to refine our understanding of the role legumes play in SOC dynamics.

Our analyses indicate the climatic and soil conditions in which plant mixture induced increases in SOC are more likely to occur. Indeed, the larger increases in SOC content by species mixtures were found in regions with high precipitation and clay content (Fig. S6). This is probably because high precipitation can reduce the competition for water among the species, allowing for more effective resource partitioning and facilitating increased SOC accumulation (Yang et al., 2011). Soils rich in clay content offer a unique environment for SOC accrual, because organic molecules get stabilized on clay fractions, potentially safeguarding the additional soil carbon inputs in mixtures from rapid microbial decomposition (Singh et al., 2018).

Interestingly, we observed a significantly higher increase in SOC content induced by mixtures in the topsoil (<20 cm) compared to the subsoil (>20 cm) (Fig. S2). This trend may be attributed to the predominant presence of root systems within the topsoil in grasslands and croplands (Jackson et al., 1996), where higher plant and microbial turnover could lead to larger mixture effects. Such effect has the potential to extend into the subsoil over time through processes such as the transport of already stored SOC by bioturbation enabled by deep-burrowing earthworms, and via leaching of dissolved organic carbon from topsoil to subsoil (Lange et al., 2023). Using deep rooting plants in mixtures might also leverage their potential for SOC in subsoil.

4.3. *Implications and limitations*

Contrary to the dominant paradigm stating that high diversity promotes ecosystem functions through complementarity effects (Cardinale et al., 2007; Barry et al., 2019), our results show that plant mixtures with similar and high root mycorrhizal colonization and root tissue density may have greater potential to increase SOC content. The complementarity paradigm was mainly developed from biodiversity–ecosystem functioning studies focusing on plant productivity and high diversity in natural systems. Our analysis focuses on agricultural grasslands and croplands where constraints on water and nutrient availability are typically less pronounced than in natural ecosystems. As a result, competition may be lower within these comparatively more stable and productive environments (Warren et al., 2009; Paquette and Messier, 2011), thereby diminishing the importance of complementarity. Moreover, plant mixture effects on SOC is not only driven by changes in plant productivity, but also depend on plant effects on microbially-driven SOC stabilization and destabilization processes. However, our results also indicate that plant species selection may have limited potential to increase SOC targets on its own (Figs. 2 and 4, and Fig. S6), and therefore species selection should be complemented with other proven strategies to promote SOC accrual (Bossio et al., 2020; Beillouin et al., 2023).

Our study revealed research gaps to be addressed in future studies. First, we primarily focused on SOC content instead of SOC storage due to the availability of the number of observations. While SOC content provides valuable insights, evaluating changes in SOC storage is crucial for understanding the full sequestration potential, as it accounts for bulk density—a key factor in quantifying carbon stocks. However, it is important to note that our database is unlikely to be strongly affected by variations in bulk density. This is because our comparisons were conducted within the same study and focused on differences between monocultures and species mixtures, minimizing the influence of strong bulk density changes typically induced by tillage or other soil management practices. Nonetheless, evaluating changes in SOC storage in future studies will provide a better understanding of the traits in mixtures required to stimulate SOC sequestration. Second, we found that augmented SOC content in species mixtures is associated to MBC, indicating that microbial residuals contribute to SOC. Including data on microbial necromass carbon, which is crucial for SOC storage and has been shown to increase with plant mixtures (Liu et al., 2024; Mou et al., 2024; Zhu et al., 2024), could improve further our mechanistic understanding of how plant mixtures modify SOC though changes in soil microbial communities. This was not an option in our study due the current limited data availability linking plant mixtures and microbial necromass. Third, the data availability for high levels of species richness (>4) was limited, because these higher levels of plant diversity are common in natural systems but not in agroecosystems. Accordingly, our results and recommendations primarily apply for species mixtures of relatively low diversity. Once the number of studies investigating higher species richness levels in agroecosystems increases, it will be crucial to test if the proposed root-trait framework applies to species-rich mixtures. Finally, species trait values extracted from the GRooT database were calculated by aggregating multiple studies. In regional-to-global scale trait-based ecology, this approach of using species average trait values is commonly used (McGill et al., 2006; Shipley et al., 2006; Ackerly and Cornwell, 2007). However, this approach does not capture the potential role played by trait variation within species. Although intra-species variation is generally smaller than inter-species variation (Albert et al., 2010), trait variation within species can be substantial (Bolnick et al., 2011; Umana and Swenson, 2019), and therefore including this perspective could be beneficial for future research.

5. Conclusions

Our results indicate that combining plant species with high similarity (and not high variation) for mycorrhizal colonization and root tissue density may have potential to increase SOC. This suggests that the complementarity paradigm that often promotes positive biodiversity effects should be revised and reversed for the control of SOC with plant mixtures in agroecosystems. The increases in SOC with plant mixtures were tightly associated with higher root biomass and soil microbial biomass carbon. Overall, our study lays out a new root-trait framework for the design of plant mixtures to enhance SOC sequestration in agroecosystems.

CRediT authorship contribution statement

Shuang Yin: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Xinli Chen:** Writing – review & editing, Methodology, Data curation. **Gabin Piton:** Writing – review & editing, Methodology. **César Terrer:** Writing – review & editing, Methodology. **Zhenghu Zhou:** Writing – review & editing. **Gerlinde B. De Deyn:** Writing – review & editing. **Isabelle Bertrand:** Writing – review & editing. **Daniel Rasse:** Writing – review & editing. **Ji Chen:** Writing – review & editing. **Jose Antonio Navarro-Cano:** Writing – review & editing, Methodology. **Diego Abalos:** Writing – review & editing, Writing – original draft, Visualization, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2025.109736.

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